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Dietary Segregation of Pelagic and Littoral Fish Assemblages in a Highly Modified Tidal Freshwater Estuary

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Abstract.—Estuarine food webs are highly variable and complex, making identification of their trophic pathways difficult. Energy for the food web of the San Francisco Estuary is thought to be based largely on in situ phytoplankton production, but little attention has been paid to littoral habitats, where other energy sources may be important. We analyzed the stomach contents of over 960 juvenile fishes and the stable carbon and nitrogen isotope ratios of these fishes and their potential food resources in pelagic and littoral habitats from the tidal freshwater area of the estuary. The mixing model IsoSource was used to examine energy sources important to consumers. Our results show evidence of two predominant food web pathways. Pelagic fishes and some littoral fishes showed strong dependence on a zooplankton–phytoplankton trophic pathway. However, the majority of fishes in littoral habitats had diets and carbon isotope ratios consistent with energy arising from submerged aquatic vegetation and epiphytic macroalgae. IsoSource revealed that the overall majority of nutrition of littoral fishes originated from consumption of grazer amphipods. Examining both stable isotopes and stomach contents allowed us to identify a food web with contributions to resident fishes that had been previously underestimated in the estuary. This study provides insight to how estuarine food webs have changed over the last few decades and highlights why the functions of habitats must be understood for effective restoration planning.

The tidal freshwater reach of an estuary is a physically complex environment with habitat characteristics varying over all spatial scales. Habitat edges abound, and tidal and river flows connect habitats, providing foraging opportunities for a variety of estuarine species. This complexity makes investigation of feeding relationships difficult; organisms collected in a particular habitat may have fed elsewhere (Hoffman et al. 2007) or relied on trophic pathways initiated in upriver (Howarth et al. 1996) or seaward environments (Garman and Macko 1998; Stewart et al. 2004). Thus, energy sources and pathways for tidal freshwater food webs remain poorly understood.

Support for the idea that estuarine food webs are primarily supported by the export of marsh detritus (Teal 1962; Odum and Heald 1975) has diminished

over the last few decades (Chanton and Lewis 2002; Sobczak et al. 2002). A variety of organic carbon sources may support coastal and estuarine consumers, including phytoplankton (Canuel et al. 1995; Deegan and Garritt 1997; Sobczak et al. 2002; Howe and Simenstad 2007), submerged aquatic vegetation (SAV; Fry 1981; Kitting et al. 1984), benthic algae (Hecky and Hesslein 1995; Deegan and Garritt 1997; Kwak and Zedler 1997; Page 1997), epiphytic macroalgae (Kitting et al. 1984; Moncrieff and Sullivan 2001; Vizzini et al. 2002), and terrestrial vegetation (Chanton and Lewis 2002).

Recent work in the San Francisco Estuary not only counters the in situ detrital hypothesis as the primary source of food web production but also the "pulse" paradigm, which holds that tidal freshwater food webs are driven by episodic energetic inputs (Odum et al. 1995). These studies have demonstrated the importance of in situ phytoplankton production as the primary source of available organic carbon for pelagic consumers in the tidal freshwater region of the estuary (Canuel et al. 1995; Jassby and Cloern 2000; Mueller-
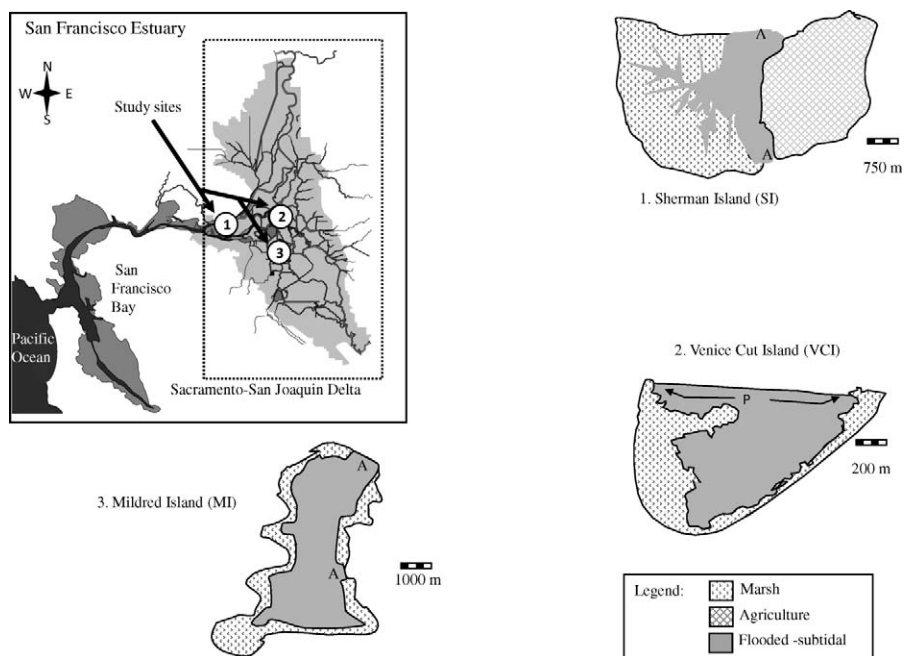
FIGURE 1.—Map of the San Francisco Estuary and Sacramento–San Joaquin Delta, California. The study sites are Sherman, Mildred, and Venice Cut islands. Breach locations were either planned (P) for channel modification or accidentally (A) opened during a levee failure.

Solger et al. 2002; Sobczak et al. 2002, 2005). However, the relative importance of phytoplankton as an energy source for consumers in other habitats is unclear. In addition, long-term declines in phytoplankton production may be increasing the relative importance of other energy sources (Jassby et al. 2002). The answers to these questions remain outstanding because long-term monitoring and special studies have focused on pelagic habitats (Orsi and Mecum 1996; Kimmerer 2002a, 2006; Mueller-Solger et al. 2002; Sobczak et al. 2002).

We used gut content analysis and stable isotopes (carbon and nitrogen) to determine what food sources were important for fishes in pelagic and littoral habitats in the tidal freshwater region of the San Francisco Estuary, known as the Sacramento–San Joaquin Delta (hereafter, Delta). We focused on comparisons between pelagic sources (i.e., phytoplankton) versus energy sources distinguishable by C and N isotopes (Cloern et al. 2002). The questions of this study were (1) do fishes in the Delta mainly rely on phytoplankton–zooplankton trophic pathways, or is their consumption supported by other organic matter sources; and (2) do the diets and food webs of fishes differ by habitat where they reside? The answer to the first question will provide insights into the mechanisms of food web variability that can explain why certain fishes in the estuary have

flourished while others have declined (Brown and Michniuk 2007; Sommer et al. 2007). Answers to the second question can shed light on mechanisms underlying the coupling of fish with their physical habitats, providing necessary information for ongoing restoration efforts.

Study Area

The study area is located at the eastern boundary of the San Francisco Estuary in the Delta (Figure 1). The Delta is a highly complex and modified tidal freshwater ecosystem (Atwater et al. 1979; Nichols et al. 1986). The Delta receives the majority of its flow from the Sacramento and San Joaquin rivers, which drain about 100,000 km^2 of the surface area of California. In the southern Delta are two massive water diversions that have greatly altered flow patterns throughout the tidal reaches of the watershed. Natural sloughs have been dredged and deepened to accommodate shipping traffic or movement of water towards the export facilities, especially in the south Delta. Much of the marsh habitat in the Delta was drained and converted to agricultural tracts in the late 1800s (Atwater et al. 1979). Many of these agricultural tracts have been armored with rip-rap. The estuary is considered one of the most highly invaded ecosystems in North America (Cohen and Carlton 1998). Of note, the fish community

in the Delta is now dominated by introduced species, many of which are associated with introduced species of SAV (Grimaldo et al. 2004; Nobriga et al. 2005; Brown and Michniuk 2007).

Much of the available shallow-water habitat for fishes in the Delta is located in flooded islands. Flooded islands are former tidal wetlands that were leveed in the past but have since been reintroduced to tidal flow by accident (i.e., levee failure) or through intentional purposes for restoration. The interiors of many of flooded islands are between 2 and 5 m below sea level, a result of subsidence that occurred from aerobic decomposition of peat soils during agricultural periods (Reed 2002; Mount and Twiss 2005). Tidal exchange between adjacent channels and flooded islands varies by site, depending on the breach size and depth (Lucas et al. 2002).

Methods

Study sites.—Three flooded islands from the central and western Delta were selected as study sites: Sherman Island (SI), Mildred Island (MI), and Venice Cut Island (VCI). All study sites have partially intact levees and have remained mostly at subtidal elevations since they were re-connected to tidal flow (SI = 80 years, MI = 25 years, and VCI = 74 years). Mildred Island is just over 5 m below sea level and is approximately 4.1 km^2 in surface area. In contrast, SI and VCI are on average less than 3 m deep and are approximately 4.0 and 0.6 km^2 in surface area, respectively. The subtidal interiors of SI and VCI are colonized by extensive beds of Brazilian waterweed *Egeria densa*, an introduced SAV. In contrast, MI is characterized as a large open-water embayment with SAV (mostly Brazilian waterweed) confined to the littoral margins. Additionally, open-water shoals were found at all sites and generally occurred in narrow strips between subtidal SAV and adjoining marsh or levees.

Analysis of trophic interactions.—Our study questions were approached by analyzing trophic interactions by using two techniques that reflect different time scales. Stomach content analysis provides information on the diets of fishes over a short time scale (i.e., hours), but its utility as a tool for investigating food webs is limited in that it offers a snapshot of the fishes' recent diets. Stable isotope (δ^{13}C and δ^{15}N) ratios can reveal information about how the fishes' diets are integrated over a much longer time scale (e.g., days and weeks), although interpretation requires sufficient knowledge of isotopic variability in lower trophic levels, which can reflect assimilation of multiple end members (Phillips and Gregg 2001; Cloern et al. 2002). Therefore, food webs were determined by using δ^{13}C–δ^{15}N biplots, where trophic connections are inferred through similarity of signatures assuming trophic fractionation and mixing models by using IsoSource software (Phillips and Gregg 2003). IsoSource can help improve resolution of multiple end member contributions as it calculates ranges of source proportional contributions to a mixture based on stable isotope signatures when the number of sources is too large to permit a unique solution. Note the time scale for equilibrium between ingestion and incorporation into the tissue of the animal is needed for unequivocal use of stable isotope data or mixing models to infer diets (Vander Zanden and Rasmussen 2001). Since we do not know the time to equilibrium for each fish and its prey, our inferences about diet are based on consistent patterns of variability between stable isotope approaches and the stomach contents.

Animal and plant collections.—Our study focused on summer and fall periods when fishes are at their highest abundances (Feyrer and Healey 2003; Grimaldo et al. 2004). The food webs of fishes were examined from pelagic and littoral habitats at all study sites, but only MI was sampled in the fall of 1999 (Table 1). Food webs of littoral habitats comprised samples from SAV and open-water shoals, which were treated independently in the data analyses. Fishes in pelagic areas were collected by using purse seines. Fishes from littoral habitats were collected by using either beach seines in open shoals or block-net enclosures with repeated hauling. We sampled repeatedly until at least eight individuals of selected species were collected from each site. Fishes were transferred on ice to the laboratory, where they were sorted by species, measured to the nearest millimeter fork length (FL), and weighed to the nearest 0.01 g wet weight.

Primary producers except phytoplankton and invertebrates from each site and habitat were collected concurrently with fish for isotopic analysis. The upper stem and leaves were removed from Tule *Scirpus acutus* and Brazilian waterweed (SAV), and epiphytic macroalgae were scraped from the blades and stems of SAV at each study site. Stable isotope information for phytoplankton was obtained from another source (discussed below). The most common invertebrates were sampled from one or several areas within each habitat to obtain sufficient biomass of individual species. Invertebrates in SAV were collected by vigorously shaking uprooted plants into buckets and then using sieves to sort plant and animal components. Crustaceans (amphipods), chironomid pupae (family Chironomidae), damselfly larvae (suborder Zygoptera), and snails (family Physidae) were hand-picked from sieves, sorted into individual vials with distilled water, and allowed to depurate for several hours before they were placed on ice for transfer to a freezer. Asiatic

TABLE 1.—Summary of consumers collected in the Sacramento–San Joaquin Delta for food web analysis. Samples were collected at one study site in fall 1999 and at three study sites in summer 2000. Consumer origin is indicated: native (N), introduced (I), or unknown (U). Organisms were collected in pelagic (P) and littoral areas, including open-water shoals (OWS) or submerged aquatic vegetation (SAV). The feeding mode of invertebrates are provided in parentheses (SF = suspension feeding, G = grazing, and P = predatory). The total number of samples (N_S) pooled across sites and total number of individuals (N_I) collected are provided.

Consumer	Origin	Habitat	N_S	N_I
Invertebrates				
Zooplankton	U	P (SF)	6	> 10,000
Asiatic clam *Corbicula fluminea*	I	OWS (SF)	5	129
Gammarus diberi	I	SAV (G)	16	514
Hyalella azteca	N	SAV (G)	2	45
Corophium spp.	U	SAV (SF)	18	512
Chironomid pupae	U	SAV (SF)	7	770
Family Physidae (snails)	U	SAV (G)	8	303
Zygoptera (damselflies)	U	SAV (G/P)	11	155
Fishes				
American shad *Alosa sapidissima*	I	P	11	50
Threadfin shad *Dorosoma petenense*	I	P	13	80
Rainwater killifish *Lucania parva*	I	OWS	11	43
Mississippi silverside *Menidia audens*	I	OWS	20	193
Yellowfin goby *Acanthogobius flavimanus*	I	OWS	11	27
Striped bass *Morone saxatilis*	I	OWS	6	8
Hitch *Lavinia exilicauda*	N	OWS	11	64
Chinook salmon *Oncorhynchus tshawytscha*	N	OWS	6	61
Splittail *Pogonichthys macrolepidotus*	N	OWS	5	9
Bluegill *Lepomis macrochirus*	I	SAV	11	63
Redear sunfish *Lepomis microlophus*	I	SAV	21	101
Prickly sculpin *Cottus asper*	N	SAV	11	15
Black crappie *Pomoxis nigromaculatus*	I	SAV	16	76
Largemouth bass *Micropterus salmoides*	I	SAV	21	130
Golden shiner *Notemigonus crysoleucas*	I	OWS	11	25
Shimofuri goby *Tridentiger bifasciatus*	I	SAV	5	14

clams *Corbicula fluminea* were excavated from below the sediment surface (≤15 cm deep) of open-water shoals by using shovels, allowed to depurate for 12 h, and then frozen. No other invertebrates were abundant in open-water shoals. Zooplankton were collected from open-water pelagic areas by using a 110-μm mesh net towed for 10 min below the surface. Samples of zooplankton at VCI were inadvertently destroyed, so samples collected at MI in 2000 were used as their replacement for food web interpretation.

Stable isotope preparation.—Invertebrates were rinsed, and whole bodies of at least 10 individuals were pooled for isotope analysis. The digestive tracts of clams and snails were removed, and the muscle tissue was saved for analysis. White muscle tissue was dissected from above the mid-dorsal region of fishes longer than 50 mm FL. A whole-side muscle fillet was obtained from fishes less than 50 mm FL. Plant and animal tissue samples were dried (60°C for 24 h) and ground into powder by using either a mortar and pestle or Wiley mill. Aliquots (10–20 mg) of this powder were placed into tin capsules for analysis. The $\delta^{13}C$ and $\delta^{15}N$ ratios of samples were determined at the Stable Isotope Facility, University of California–Davis, by using a Europa Scientific Hydra 20/20 continuous-flow mass spectrometer and a Europa ANCA-SL elemental analyzer.

The ratio of heavy and light isotopes is expressed as:

$$\delta X = 10^3[(R_{sample}/R_{standard}) - 1], \qquad (1)$$

where $X = {}^{13}C$ or ${}^{15}N$ and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ (Lajtha and Michener 1994). The standards were Peedee Belemnite for C and atmospheric nitrogen for N (Lajtha and Michener 1994). Carbon and nitrogen isotopes fractionate approximately 0.8‰ (DeNiro and Epstein 1978) and 3.4‰ (Minagawa and Wada 1984), respectively, between consumer levels.

Additional sources of primary producer data.—To supplement the data on primary producers, we calculated the mean (±SD) C and N isotopes of tidal freshwater primary producers from Cloern et al. (2002). This data set overlapped with our study period and included samples of seston characterized by high chlorophyll-*a* content (10 μg of chlorophyll *a*/L) and low C:N ratios (<9 g of C/ g of N) as surrogates for phytoplankton signature (see Methods in Cloern et al. 2002). It also included samples on terrestrial vegetation and floating aquatic vegetation, which were not measured in our study. Because the samples in Cloern et al. (2002) represent a broader spatial and temporal

data set, we believe they capture the variability in isotopic signatures better than our study; therefore, those samples were used as the benchmark for examining the basal sources of energy in this study.

Stomach content analysis.—The stomachs from a subset of fishes collected at study sites in 2000 were removed and analyzed for dietary composition. Prey items from each stomach were identified to the lowest taxonomic resolution and counted. The taxonomic categories used for diet analyses were zooplankton (copepods, cladocerans, and crab zoea), chironomid pupae, amphipods (*Gammarus daiberi*, *Hyalella azteca*, and *Corophium* spp.), snails, clams, damselfly larvae, aquatic and terrestrial macroinvertebrates, and fish or fish eggs.

Identification of energy sources fuelling food webs.—Because Cloern et al. (2002) found that some primary producers were indistinguishable by $\delta^{13}C$ and $\delta^{15}N$ signatures, we selected a priori primary producers with relatively enriched $\delta^{13}C$ signatures (SAV and epiphytic macroalgae) versus those with relatively depleted $\delta^{13}C$ signatures (phytoplankton, terrestrial vegetation, emergent vegetation, and floating aquatic vegetation) as the base levels of discrimination. Differences between $\delta^{13}C$ and $\delta^{15}N$ of these two groups were explicitly tested by using analysis of variance (ANOVA). The mean ($\pm SD$) $\delta^{13}C$ and $\delta^{15}N$ signatures of primary producers measured in this study were pooled and plotted versus those measured in Cloern et al. (2002) to visually examine consistency between data sets. Differences between the data sets were not analyzed statistically since we did not measure seston, terrestrial vegetation, or floating aquatic vegetation. However, good agreement between measured data would serve to strengthen the conclusions drawn on dominant food web pathways.

The IsoSource mixing model was used to determine the contribution of primary producers to invertebrates and the contribution of prey to fishes (Phillips and Gregg 2003). For invertebrates, source contributions at 1% increments were determined by using $\delta^{13}C$ only because initial attempts using $\delta^{15}N$ signatures could not resolve feasible solutions (up to 0.1 tolerance) in most cases. Solutions could not be determined because the $\delta^{15}N$ signatures of invertebrates were enriched higher than the 3.4‰ fractionation level assumed between trophic levels. The discrepancy could arise from variation in the fractionation of the consumer (Vander Zanden and Rasmussen 2001) or because of variability in the primary producers' $\delta^{15}N$ signatures (Cloern et al. 2002). Because fractionation in $\delta^{15}C$ is relatively minor (0.8‰; DeNiro and Epstein 1978), it has a smaller effect on the modeled results and therefore is a reasonable estimator of energy sources

when used alone (Melville and Connolly 2005). The sources used for invertebrates included all the primary producers measured by Cloern et al. (2002), but for meaningful biological interpretation, reported contributions are those summed by the two distinguishable groups based on their $\delta^{13}C$ signatures (i.e., enriched versus depleted sources).

What are the dominant food sources used by fishes?—The identification of food webs using stomach content data were examined by using a modified index of relative importance (IRI) metric (Pinkas et al. 1971; see Liao et al. 2001):

$$IRI = \%O(\%N + \%W), \qquad (2)$$

where %O is percent frequency of occurrence, %N is percent of diet by numbers, and %W is percent of diet by weight. The IRI values of prey were summed to yield a grand total IRI value from which the relative importance of each prey category was then expressed as a percentage. The IRI percentages were calculated for early juvenile (19–49 mm FL), late juvenile (50–99 mm FL), and subadult or adult (>100 mm FL) stages to examine potential influences diet selection with size. Individual weights for invertebrates were obtained from Toft et al. (2003).

Trophic connections between fishes and invertebrates were inferred by comparing their relative $\delta^{13}C$ and $\delta^{15}N$ signatures in consumer biplots for each site while accounting for fractionation. The functional feeding groups of invertebrates (Thorp and Covich 2001) and the habitats where fishes were collected were pooled for the biplots graphs. For fishes in SAV, early juveniles were discriminated from late juveniles to tease out possible size-related feeding changes given that there were multiple species represented by different sizes.

IsoSource was used to determine the sources of food important to the nutrition of fishes. The mean $\delta^{13}C$ and $\delta^{15}N$ signatures of fishes and invertebrates were used unless the model failed to converge to solution, in which case standard deviations of isotopic signatures were applied to find a solution. Sources were selected a priori from the stomach content results (Phillips et al. 2005), and early and late juvenile fishes were assumed to have the same prey field. Because threadfin shad had empty stomachs, we assumed their diet composition to be similar to that of American shad; this assumption is reasonable based on previous diet work in the estuary (Turner 1966b; Feyrer et al. 2003). Omnivorous species, such as the golden shiner and hitch, were ignored given that we did not analyze their stomachs for prey contents. In a few cases, the isotopic signatures of prey (e.g., fish eggs) were not available; therefore, the sources were limited to those with measured

isotopic values. To provide a biological realism to the IsoSource output, contributions of prey that accounted for less than 5% of total IRI in the stomachs were constrained to the most dominant prey in the stomachs (Phillips et al. 2005).

Did diets differ among habitats?—To determine if the stomach contents of fishes differed by habitat, we applied the nonparametric analysis of similarity (ANOSIM) to the IRI percentages by using Primer statistical software (version 6.1.11; Clarke 1993). Early and juvenile fishes from SAV were tested independently to determine if size influenced differences in diets among habitats. A similarity matrix was generated on the diet data by using the Bray–Curtis similarity measure prior to ANOSIM tests (9,999 permutations). The ANOSIM generates a value of R that is scaled to lie between -1 and $+1$, with a value of zero representing the null hypothesis—in this case, that there was no difference in diet selection. Similarity percentage (SIMPER) analysis was used to reveal prey responsible for ANOSIM differences.

A nested analysis of covariance (ANCOVA) was used to test the hypothesis that $\delta^{13}C$ and $\delta^{15}N$ signatures of fish species differed among the three sites (MI, VCI, and SI) and habitats nested within sites (SAV, open-water shoals, and pelagic areas). Length was included in the model as a covariate to account for ontogenetic shifts in diet. Data from MI (1999) were not used in the model to eliminate effects due to interannual variability.

Results

Fish Collections

Nine-hundred fifty-nine fish (9 families, 16 species) were collected for diet and isotope analysis. The species composition of fish generally reflected relative abundance in their environment (Feyrer and Healey 2003; Grimaldo et al. 2004; Nobriga et al. 2005; Brown and Michniuk 2007). The dominant species collected were introduced species (Table 1). The most numerous native fish collected were splittail, Chinook salmon, and hitch, all in open-water shoals. Chinook salmon included fish with and without coded-wire tags applied in hatcheries. Since not all hatchery fish are routinely tagged, the untagged fish were an unknown combination of fish potentially reared in hatcheries or fish that were spawned in the wild.

Identification of Energy Sources Fuelling Food Webs

Seston, terrestrial, emergent, and floating aquatic vegetation types were significantly different than SAV and epiphytic macroalgae with respect to $\delta^{15}N$ (ANOVA: $F = 71.29$; df $= 1$, 160; $P < 0.001$) and $\delta^{13}C$ ($F = 129.95$; df $= 1$, 160; $P < 0.001$). Overall, the mean ($\pm SD$) $\delta^{13}C$ signatures of seston, terrestrial, emergent, and floating aquatic vegetation were between $-31‰$ and $-25.9‰$, whereas the mean and standard deviation of $\delta^{13}C$ signatures of SAV and epiphytic macroalgae were between $-27‰$ and $-12‰$ (Figure 2a). The $\delta^{13}C$ signatures of primary producers measured in this study were similar to those in the Cloern et al. (2002) data set (Figure 2). Our limited primary producer data set shows some distinction in the $\delta^{13}C$ signatures of SAV and epiphytic macroalgae, but as previously mentioned, it probably does not capture the variability in primary producer isotopes as well as the more robust data set of Cloern et al. (2002). Therefore, we are assuming the more conservative assignment of a SAV–epiphytic macroalgae food web rather than attempting to distinguish between SAV and epiphytic macroalgae. Filamentous algae measured at SI and VCI had enriched $\delta^{13}C$ signatures.

Grazing and predatory invertebrates collected from SAV generally had enriched $\delta^{13}C$ signatures between $-21‰$ and $-17‰$, except for *Gammarus daiberi* from VCI, which had relatively depleted $\delta^{13}C$ signatures (Table 2). Suspension feeders had depleted $\delta^{13}C$ signatures relative to grazing invertebrates across sites, except for chironomid pupae at MI (2000), VCI, and SI.

Primary producers with depleted $\delta^{13}C$ signatures were modeled by IsoSource to be the dominant food source to zooplankton (Table 3), except at MI (1999), where a solution could not be resolved. Primary producers with enriched $\delta^{13}C$ signatures were modeled to be the primary food of chironomid pupae. For clams and *Corophium* spp., depleted primary producers were modeled to be their primary food at MI (both years) but not at VCI or SI. Except for *Gammarus daiberi* at VCI, primary producers with enriched $\delta^{13}C$ signatures were modeled to be the primary food sources of grazing and predatory invertebrates.

Identification of Food Sources Important to Fishes

The IRI values were calculated for 675 fishes, excluding fish with empty stomachs and herbivorous individuals. Zooplankton, chironomid pupae, and amphipods were the dominant prey consumed for all species examined, except for subadult–adult largemouth bass (Figure 3). Based on IRI, zooplankton was the primary prey of American shad, Chinook salmon (hatchery and untagged), Mississippi silversides, splittails, shimofuri goby, rainwater killifish, and most early juvenile centrarchid fishes. Grazer amphipods dominated the diets of all other early juvenile and late juvenile fishes.

The mean $\delta^{13}C$ signatures of pelagic fishes, early juvenile centrarchids, and Mississippi silversides from

TABLE 2.—Mean (±SD) stable isotope (δ^{13}C and δ^{15}N) signatures of invertebrates and fishes by study site in the Sacramento–San Joaquin Delta. Life stage is designated as early juvenile (EJ; fork length [FL] < 50 mm), late juvenile (LJ; FL = 50–99 mm), and subadult/adult (SA/A; FL > 100 mm). Chinook salmon were either hatchery (H) or untagged (UT). Zooplankton samples from Mildred Island (MI; 2000) were used for Venice Cut Island (VCI).

Consumer	MI (1999)		MI (2000)		VCI	
	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
Invertebrates						
Zooplankton	−34.94	11.43	−31.47 (1.17)	9.29 (2.48)	−31.47 (1.17)	9.29 (2.48)
Asiatic clams	−29.79 (1.67)	12.75 (0.34)	−28.61 (0.77)	12.79 (1.22)	−24.68 (0.27)	14.31 (0.25)
Gammarus daiberi	−21.41 (3.18)	13.23 (2.30)	−20.25 (1.46)	12.17 (2.27)	−25.35 (0.15)	11.15 (0.42)
Hyalella azteca					−20.58 (0.47)	11.36 (0.55)
Corophium spp.	−30.81 (0.37)	14.01 (0.86)	−29.43 (0.96)	13.34 (2.91)	−25.64 (0.30)	11.07 (0.44)
Chironomid pupae	−24.30 (2.12)	12.30 (0.89)	−19.54 (1.32)	11.08 (0.80)	−17.12	10.22
Snails	−22.51 (0.82)	15.05 (1.43)	−22.51 (1.43)	15.05 (0.82)	−20.76 (0.11)	13.36 (0.49)
Damselfly larvae	−24.19 (3.24)	15.25 (0.71)	−22.67 (0.54)	15.21 (3.43)	−21.28 (0.62)	15.03 (0.72)
Fishes						
American shad LJ					−25.93 (1.54)	15.45 (0.41)
Black crappie EJ			−30.21 (0.32)	15.09 (0.13)	−22.93 (1.85)	16.12 (0.38)
Black crappie LJ			−23.97 (4.74)	15.43 (0.34)	−21.37 (0.90)	16.07 (0.48)
Bluegill EJ					−20.11 (0.91)	17.16 (0.57)
Bluegill LJ			−24.81 (1.32)	17.06 (0.63)	−20.30 (0.99)	16.44 (1.02)
Bluegill A			−22.76 (2.30)	17.18 (1.59)		
Chinook salmon LJ/UT					−19.53 (2.32)	15.18 (0.38)
Chinook salmon LJ/H					−23.73 (3.18)	12.39 (1.74)
Golden shiner LJ					−19.86 (0.48)	16.75 (0.76)
Hitch LJ					−20.30 (1.36)	16.04 (0.46)
Hitch A						
Mississippi silversides EJ			−30.41 (0.32)	15.78 (0.35)	−23.77 (2.15)	16.31 (0.36)
Mississippi silversides LJ	−27.15 (1.85)	15.68 (1.29)	−28.56 (0.90)	16.61 (0.23)	−23.63 (2.38)	16.50 (0.76)
Largemouth bass LJ	−22.47 (2.99)	18.04 (1.03)	−25.56 (4.05)	16.67 (0.56)	−19.45 (1.06)	17.38 (0.75)
Largemouth bass EJ			−27.70 (1.62)	15.87 (0.31)		
Largemouth bass SA/A			−25.39 (1.13)	17.98 (0.75)		
Prickly sculpin EJ					−21.13 (1.82)	16.82 (0.73)
Prickly sculpin LJ					−20.80 (1.42)	17.35 (0.47)
Rainwater killifish EJ					−20.71 (1.24)	16.32 (0.51)
Redear sunfish EJ	−21.31 (1.60)	16.07 (1.22)	−22.19 (1.36)	17.73 (0.16)	−20.33 (1.20)	16.37 (0.73)
Redear sunfish LJ	−22.08 (2.69)	17.14 (0.83)	−22.07 (1.63)	16.96 (0.97)	−20.71 (1.75)	16.73 (0.46)
Redear sunfish A					−20.91 (0.76)	16.46 (0.55)
Shimofuri goby EJ						
Shimofuri goby LJ						
Splittail LJ						
Striped bass LJ					−22.20 (1.18)	17.15 (0.64)
Threadfin shad LJ	−30.83 (0.68)	16.00 (1.19)	−28.52 (0.50)	14.80 (0.61)		
Yellowfin goby LJ					−20.75 (0.87)	17.07 (0.36)

TABLE 3.—Mean contribution (%) of enriched (>−27‰ δ^{13}C) and depleted (<−27‰ δ^{13}C) primary producers to the carbon assimilated by invertebrates as determined by IsoSource for three sites in the Sacramento–San Joaquin Delta (MI = Mildred Island; VCI = Venice Cut Island; SI = Sherman Island). Values in parentheses are the ranges of possible solutions. Feeding modes (FM) are defined in Table 1. The mean δ^{13}C signatures of invertebrates and primary producers were used except in cases where standard deviations were applied to allow feasible solutions. Empty cells indicate where invertebrates were absent from field collections. In one case, no solution (ns) could be found.

Organism	FM	MI (1999)		MI (2000)		VCI	
		Depleted	Enriched	Depleted	Enriched	Depleted	Enriched
Zooplankton	SF	ns	ns	92 (77–100)	8 (0–23)	83 (61–1)	17 (0–39)
Asiatic clams	SF	86 (68–96)	13 (4–32)	93 (78–100)	7 (0–22)	33 (0–46)	54 (69–100)
Corophium spp.	SF	92 (76–100)	7 (0–24)	98 (96–100)	2 (0–4)	50 (15–69)	50 (31–85)
Chironomid pupae	SF	38 (0–54)	62 (46–100)	5 (0–8)	95 (92–100)	21 (0–28)	80 (72–100)
Snails	G	24 (0–33)	76 (67–100)	24 (0–33)	76 (67–100)	10 (0–14)	90 (86–100)
Gammarus daiberi	G	15 (0–21)	85 (79–100)	6 (0–8)	94 (92–100)	47 (9–65)	52 (35–91)
Hyalella azteca	G					8 (0–12)	92 (88–100)
Damselfly larvae	G/P	37 (0–52)	63 (48–100)	25 (0–35)	75 (65–100)	14 (0–20)	86 (80–100)

TABLE 2.—Extended.

Consumer	SI	
	$\delta^{13}C$	$\delta^{15}N$
Invertebrates		
Zooplankton	−29.87 (0.69)	12.88 (0.72)
Asiatic clams	−23.04 (0.08)	13.52 (0.39)
Gammarus daiberi	−19.53 (0.11)	12.05 (0.04)
Hyalella azteca	−19.40 (0.20)	10.81 (0.23)
Corophium spp.	−22.77 (0.24)	11.20 (0.76)
Chironomid pupae	−18.78 (0.16)	10.08 (0.16)
Snails	−19.05 (0.44)	11.90 (0.13)
Damselfly larvae	−19.93 (0.26)	12.80 (0.09)
Fishes		
American shad LJ	−23.57 (2.52)	15.67 (0.69)
Black crappie EJ		
Blackcrappie LJ	−21.58 (0.85)	15.35 (0.31)
Bluegill EJ		
Bluegill LJ		
Bluegill A		
Chinook salmon LJ/UT		
Chinook salmon LJ/H		
Golden shiner LJ	−20.09 (1.51)	15.41 (0.77)
Hitch LJ	−19.30 (1.34)	14.80 (0.54)
Hitch A	−19.27 (1.26)	15.23 (0.64)
Mississippi silversides EJ	−21.92 (0.94)	16.20 (0.33)
Mississippi silversides LJ	−20.18 (1.44)	16.21 (0.34)
Largemouth bass LJ	−19.29 (1.70)	16.80 (0.46)
Largemouth bass EJ		
Largemouth bass SA/A		
Prickly sculpin EJ		
Prickly sculpin LJ		
Rainwater killifish EJ	−19.22 (0.94)	16.04 (0.41)
Redear sunfish EJ	−20.31 (2.03)	15.53 (0.10)
Redear sunfish LJ	−21.23 (0.22)	15.91 (0.51)
Redear sunfish A	−20.85 (1.04)	16.36 (0.94)
Shimofuri goby EJ	−21.27 (1.61)	15.62 (0.62)
Shimofuri goby LJ	−21.43 (1.81)	15.20 (1.81)
Splittail LJ	−19.95 (2.53)	15.45 (0.68)
Striped bass LJ		
Threadfin shad LJ	−24.44 (1.88)	14.46 (1.06)
Yellowfin goby LJ	−24.35 (3.05)	14.71 (1.07)

TABLE 3.—Extended.

Organism	SI	
	Depleted	Enriched
Zooplankton	97 (91–100)	3 (0–9)
Asiatic clams	24 (0–33)	76 (67–100)
Corophium spp.	26 (0–36)	74 (64–100)
Chironomid pupae	25 (0–35)	75 (65–100)
Snails	2 (0–4)	98 (96–100)
Gammarus daiberi	3 (0–4)	97 (96–100)
Hyalella azteca	5 (0–8)	95 (92–100)
Damselfly larvae	3 (0–5)	97 (95–100)

MI (both years) had $\delta^{13}C$ ratios less than −23‰ (Table 2). All other fishes from SAV and open-water shoals had $\delta^{13}C$ signatures between −23‰ and −17‰. The biplots show that the $\delta^{13}C$ signatures of fishes from SAV were enriched relative to grazing and predatory invertebrates, except for early juvenile fishes from MI (2000) and SI (Figure 4). The $\delta^{13}C$ signatures of pelagic fishes were enriched relative to suspension feeders at MI (1999 and 2000) and VCI. As a group, open-water fishes had $\delta^{13}C$ signatures similar to those of grazing and predatory invertebrates at SI.

The contributions of invertebrates to the nutrition of fishes were determined for most species in IsoSource (Table 4). However, in many cases the standard deviation was applied to the mean isotopic signatures to allow feasible solutions (0.1 tolerance), which we determined resulted in an approximate 15% difference in modeled ranges of sources for standard deviations over 1.0. Therefore, emphasis on IsoSource results is placed on dominant contributors between enriched and depleted invertebrate groups rather than on the mean values or small contributors within groups (Phillips and Gregg 2003).

Diet Patterns by Habitat

The ANOSIM revealed that the diets of fishes were overall significantly different among habitats ($P < 0.05$; global $R = 0.23$). Subsequent pairwise comparisons in ANOSIM revealed that pelagic fishes had diets that were significantly different from those of late juvenile fishes collected in SAV ($P < 0.05$; $R = 0.92$) but not significantly different from those of early juvenile fishes in SAV ($P = 0.20$; $R = 0.32$). The SIMPER analysis revealed that the percentage in diet differences between pelagic and late juvenile fishes from SAV was most attributable to amphipods (44%) and zooplankton (33%). Similarly, fishes from open-water shoals and late juvenile SAV fishes had significantly different diets ($P < 0.01$; $R = 0.42$), where chironomid pupae contributed to 38% of the attributable difference between diet selection. No other pairwise differences in diets were significantly demonstrated in ANOSIM.

The $\delta^{13}C$ signatures of fishes differed among habitats ($F = 59.61$; df = 6, 940; $P < 0.001$) nested within sites (ANCOVA: $F = 377$; df = 2, 942; $P < 0.001$). The $\delta^{15}N$ signatures of fishes differed by habitat ($F = 30.8$; df = 6, 940; $P < 0.001$) but not sites ($F = 2.11$; df = 2, 942; $P = 0.12$). Fish length did not have a significant effect on $\delta^{13}C$ ($F = 0.1$; df = 1, 945; $P = 0.10$) or $\delta^{15}N$ ($F = 0.26$, df = 1, 945; $P = 0.61$) signatures.
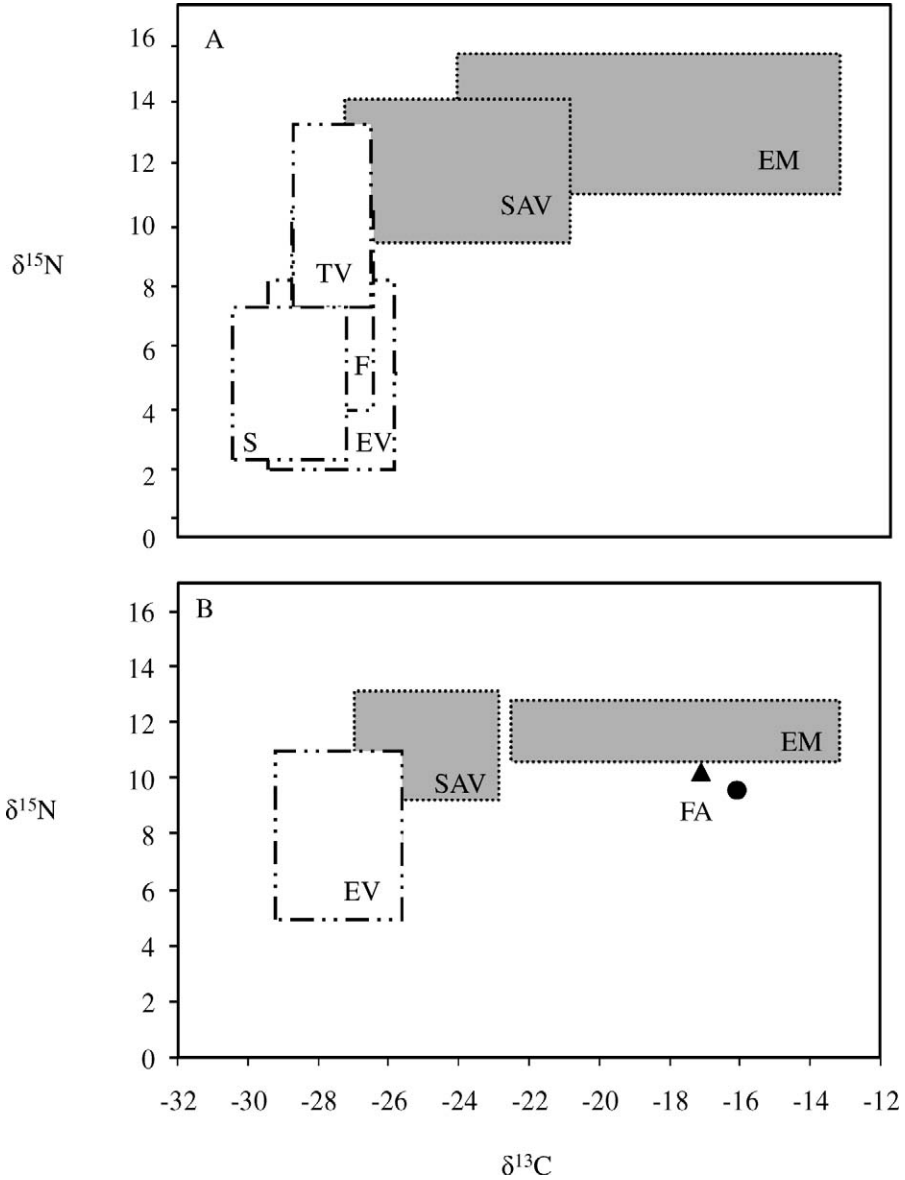
FIGURE 2.—Upper and lower standard deviations (dashed lines) of primary producer stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in the Sacramento–San Joaquin Delta. Data represent **(A)** those calculated from a subset of freshwater primary producers measured by Cloern et al. (2002) and **(B)** those measured in this study (EM = epiphytic macroalgae; SAV = submerged aquatic vegetation; EV = emergent vegetation; F = floating aquatic vegetation; TV = terrestrial vegetation; FA = filamentous algae, for which black circles = Sherman Island and black triangles = Venice Cut Island; S = phytoplankton-rich seston). Shading represents significantly different groups (see text for details).

Discussion

Major Food Web Pathways

The stable isotope analysis broadly supported the diet analysis in providing evidence of pelagic and littoral food webs in the tidal freshwaters of the estuary. Although other studies have reported diet information for fishes in the Delta (Turner 1966a, 1966b; Toft et al. 2003; Nobriga and Feyrer 2007), this is the first study we know of that shows the importance of littoral-based carbon (SAV–epiphytic macroalgae) to the nutrition of fishes in the Delta. The results presented here suggest that trophic connections between prey and fishes were
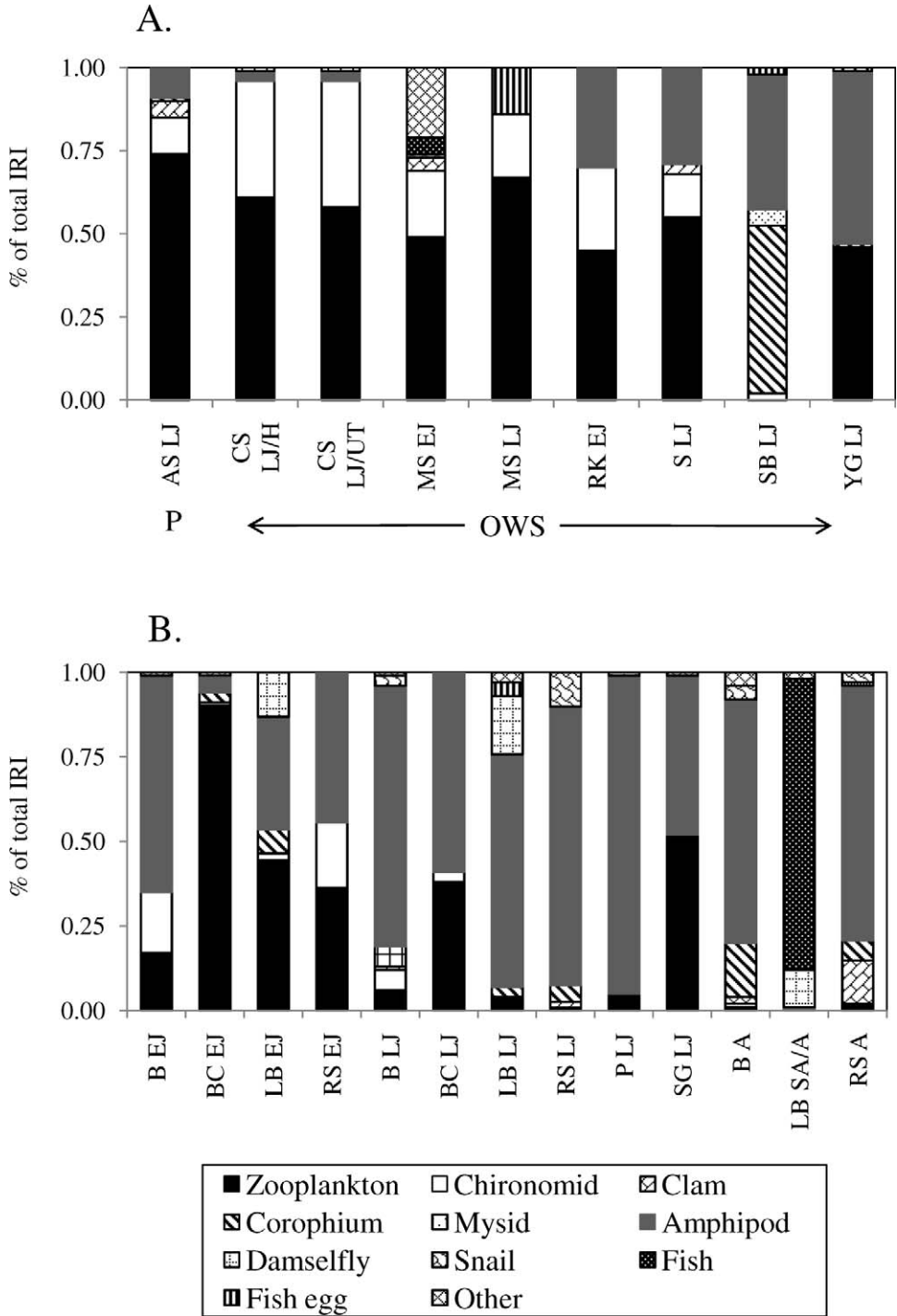
FIGURE 3.—Percent index of relative importance (% IRI) of diet items identified in the stomach contents of fishes collected from three habitats in the Sacramento–San Joaquin Delta: **(A)** fishes collected in pelagic (P) and open-water shoals (OWS); and **(B)** fishes collected in submerged aquatic vegetation. Data were pooled across study sites from 2,000 collections (AS = American shad; B = bluegill; BC = black crappie; CS = Chinook salmon; LB = largemouth bass; MS = Mississippi silverside; P = prickly sculpin; RK = rainwater killifish; RS = redear sunfish; S = splittail; SB = striped bass; SG = shimofuri goby; YG = yellowfin goby). Life stage codes (EJ, LJ, SA, A) and status codes (H, UT) are defined in Table 2.
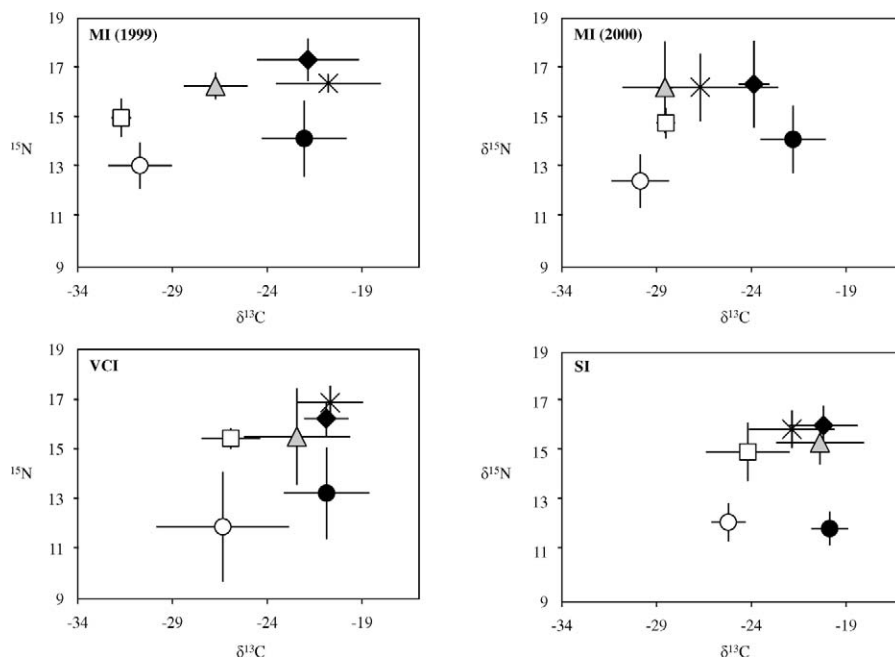
FIGURE 4.—Mean stable isotope (δ^{13}C and δ^{15}N) ratios ($\pm$SD) of consumers distinguished by functional groups for each study site in the Sacramento–San Joaquin Delta (SI = Sherman Island; MI = Mildred Island; VCI = Venice Cut Island). Invertebrates were grouped by their general feeding modes (open circles = suspension feeders; black circles = grazers/predators). Fishes were grouped by habitat and life stage (submerged aquatic vegetation [SAV] only; open squares = pelagic; gray triangles = open-water shoal; X-symbols = early juvenile SAV; black diamonds = late juvenile SAV).

generally linked to their physical habitat (Deegan and Garritt 1997; Paterson and Whitfield 1997; Toft et al. 2003), but small to modest energy contributions crossed between habitats, especially in open-water shoals. The influence of seasonal variability in food webs cannot be addressed (Chanton and Lewis 2002; Howe and Simenstad 2007) since we only analyzed samples from two seasons in different years. Nonetheless, our study has broad implications about the functions of tidal freshwater habitats for fishes during their critical juvenile rearing periods, providing information that helps interpret potential historic shifts in the food web as well information to guide for restoration projects.

Pelagic Food Webs

Before the importance of phytoplankton-based food web can be discussed, we must first revisit the data collected here and from others that demonstrate its importance to pelagic consumers. As Cloern et al. (2002) found in their estuarywide data set, we show that the δ^{13}C signatures of phytoplankton-rich seston were distinct from those of SAV and epiphytic macroalgae but indistinguishable from those of terrestrial, emergent, and floating aquatic vegetation. This

suggests that assignment of energy sources fuelling pelagic food webs is equivocal when using C and N stable isotopes. However, in order for emergent, terrestrial, or floating aquatic vegetation to be incorporated by zooplankton and other suspension feeders, it would have to be routed through a detrital microbial loop. However, experimental work shows that the detrital-derived energy is of minor significance to pelagic pathways compared to phytoplankton, which is far more bioavailable (Sobczak et al. 2002, 2005) and nutritious for zooplankton (Mueller-Solger et al. 2002). This study and others in the estuary have demonstrated, using different approaches, that phytoplankton is the dominant energy source for pelagic consumers (Canuel et al. 1995; Jassby and Cloern 2000; Mueller-Solger et al. 2002; Sobczak et al. 2002, 2005). Contributions of detrital material to pelagic consumers cannot be ruled out entirely, but for the purposes of our study phytoplankton is assigned as the basal source of food for pelagic food webs (i.e., consumers with depleted δ^{13}C signatures) based on its likely dominance in assimilation to upper trophic levels.

Pelagic fishes exhibited the most dependence on a phytoplankton-based food web. The stomach content analysis revealed that American shad had 74% IRI for

TABLE 4.—Mean contribution (%) of invertebrates to the muscle tissues of fishes as determined by IsoSource for three sites in the Sacramento–San Joaquin Delta (MI = Mildred Island; VCI = Venice Cut Island; SI = Sherman Island). Invertebrates are distinguished by their relative δ^{13}C signatures from each site. Values in parentheses are the ranges of possible solutions. The mean δ^{13}C and δ^{15}N signatures of fishes and invertebrates were used except in cases where standard deviations were applied to find feasible solutions. Sources were selected a priori from the stomach content analysis: zooplankton (Z); chironomid pupae (CP); Asiatic clams (C); *Corophium* spp. (CO); grazer amphipods (GA, *Gammarus daiberi* and/or *Hyallella azteca*); Zygoptera (ZY), and snails (S). Based on the stomach content analysis, contributions of rare prey ($\leq 5\%$ index of relative importance) were constrained to the most dominant prey item to reflect realistic feeding patterns. Habitat codes are defined in Table 1. Life stage codes are defined in Table 2.

Site	Habitat	Species	Depleted δ^{13}C signatures			Enriched δ^{13}C signatures			
			Z	C	CO	GA	CP	ZY	S
MI 1999	P	Threadfin shad LJ	40 (34–47)		30 (24–34)	15 (0–29)	15 (0–34)		
	OWS	Mississippi silverside LJ	26 (18–33)	5 (0–17)		6 (0–22)	61 (45–70)		1 (0–5)
	SAV	Redear sunfish EJ	2 (0–8)		3 (0–12)	86 (68–98)	9 (0–29)		
	SAV	Redear sunfish LJ	1 (0–2)	1 (0–7)	2 (0–7)	62 (46–72)	5 (0–19)		29 (21–37)
	SAV	Largemouth bass LJ	1 (0–4)		3 (0–9)	72 (60–82)	5 (0–16)	20 (9–26)	
MI 2000	P	Threadfin shad LJ	62 (55–69)	5 (0–13)	3 (0–13)	2 (0–8)	28 (23–31)		
	OWS	Mississippi silverside LJ	80 (65–90)	14 (0–35)			2 (0–4)		4 (0–11)
	SAV	Black crappie EJ	58 (52–63)		38 (32–44)	2 (0–5)	2 (0–5)		
	SAV	Black crappie LJ	10 (5–16)		27 (21–33)	47 (32–63)	15 (0–31)		
	SAV	Bluegill LJ	6 (0–22)	15 (0–47)	22 (0–49)	35 (0–49)	7 (0–28)		14 (0–33)
	SAV	Bluegill A	1 (0–7)	7 (0–21)	9 (0–21)	44 (38–54)	2 (0–9)		37 (26–43)
	SAV	Redear sunfish EJ	3 (0–15)	6 (0–25)	7 (0–25)	58 (38–77)	4 (0–14)		21 (0–42)
	SAV	Redear sunfish LJ	5 (0–20)	6 (0–25)	5 (0–23)	50 (0–76)	19 (4–39)		16 (0–62)
	SAV	Largemouth bass EJ	45 (23–64)		17 (0–48)	12 (0–36)	14 (0–26)	10 (0–31)	
	SAV	Largemouth bass LJ	26 (13–42)		20 (0–40)	37 (22–51)	5 (0–14)	10 (0–26)	
VCI	P	American shad LJ	51 (35–75)	7 (0–29)	25 (0–43)	7 (0–29)	9 (0–27)		
	OWS	Mississippi silverside EJ	38 (23–45)	16 (0–41)		10 (0–45)	5 (0–19)		17 (0–42)
	OWS	Chinook salmon LJ/UT	5 (0–15)			37 (11–61)	58 (39–74)		
	SAV	Black crappie EJ	14 (12–17)	10 (5–14)	1 (0–8)	73 (67–78)	1 (0–4)		
	SAV	Black crappie LJ	0.5 (0–1)	6 (3–9)	0	93 (88–96)	1 (0–3)		
	SAV	Bluegilll LJ	1 (0–2)	1 (0–8)	1 (0–3)	36 (29–49)	31 (27–35)		31 (24–35)
	SAV	Largemouth bass LJ	2 (0–7)		9 (0–32)	73 (63–82)	15 (5–24)		
	SAV	Redear sunfish EJ	14 (1–25)			44 (32–52)	3 (0–13)		38 (29–49)
	SAV	Redear sunfish LJ	1 (0–7)		2 (0–11)	13 (1–42)	8 (0–16)		74 (53–93)
	SAV	Prickly sculpin LJ	24 (13–36)			51 (33–87)	14 (0–33)		
SI	P	American shad LJ	59 (53–65)	15 (0–34)		15 (0–39)	10 (0–25)		
	P	Threadfin shad LJ	50 (41–58)	6 (0–14)	19 (0–42)	9 (0–21)	16 (0–33)		
	OWS	Mississippi silverside LJ	16 (14–19)	6 (0–14)		27 (0–27)	22 (13–31)		28 (0–68)
	OWS	Yellowfin goby LJ	6 (0–13)		13 (0–31)	61 (35–92)			19 (0–44)
	OWS	Splittail LJ	8 (1–8)	3 (0–7)		81 (74–88)	6 (2–11)		
	SAV	Black crappie LJ	12 (9–16)		4 (0–11)	78 (66–89)	6 (0–15)		
	SAV	Largemouth bass LJ	2 (0–5)		3 (0–14)	92 (82–100)	3 (0–12)	8 (4–13)	
	SAV	Redear sunfish EJ	8 (2–12)		4 (0–18)	81 (75–92)	3 (0–13)		
	SAV	Redear sunfish LJ	0.5 (0–1)	22 (17–27)	1 (0–3)	44 (23–83)	2 (0–9)		30 (0–55)
	SAV	Redear sunfish A	1 (0–2)	14 (0–39)	8 (0–27)	32 (0–93)	29 (0–81)		8 (0–27)
	SAV	Shimofuri goby LJ	2 (0–9)	14 (0–37)	4 (0–18)	53 (8–96)	9 (0–49)		17 (0–45)

zooplankton, and IsoSource modeled zooplankton to be the dominant nutrition for both American shad and threadfin shad at all sites. These results are not unexpected for these species since they are largely zooplanktivorous (Turner 1966b; Feyrer et al. 2003). However, we were surprised that contributions of amphipods were modeled to account for up to a third of the nutrition in these species despite only having 9% of the total IRI for American shad. This suggests that American shad and threadfin shad diets can be modestly coupled with food from SAV, which appeared to be important for these fishes at SI based on their trophic position in the biplot graph (Figure 4).

The stable isotope analyses revealed that energetic contributions of pelagic prey to fishes in littoral habitats were of minor importance despite the stomach content analysis that indicated otherwise. For example, ANOSIM demonstrated that there were no statistical differences in diet selection between pelagic fish and early juvenile fish from SAV or fishes from open-water shoals. In most cases, zooplankton accounted for the highest IRI of the fishes in these groups, yet IsoSource modeled zooplankton to be of primary nutrition to only early juvenile largemouth bass and black crappies at MI (2000) and Mississippi silversides at VCI and MI (2000). The discrepancy between the two approaches underscores how stomach contents can be poor

estimators of longer-term feeding patterns, especially for age-0 fishes that can undertake dramatic shifts in their $\delta^{13}C$ signatures when switching from zooplankton to littoral or benthic prey (Vander Zanden et al. 1998).

Littoral Food Webs

As previously noted, the stable isotope signatures of SAV and epiphytic macroalgae were not unique from each other in the Cloern et al. (2002) data, but they were distinct from phytoplankton-rich seston and other primary producers (e.g., emergent and terrestrial vegetation), allowing for discrimination of an alternative energy source for consumers. Many studies show that invertebrates actually graze on the epiphytic macroalgae of SAV rather than on the SAV itself (Kitting et al. 1984; Duffy and Harvilicz 2001; Moncrieff and Sullivan 2001), but discrimination to this level of detail was beyond the scope of this study. Note that the filamentous algae measured in our study had enriched $\delta^{13}C$ signatures (mean = $-17.09‰$ at VCI; mean = $-16.58‰$ at SI), suggesting it as a possible energy source for consumers in littoral habitats. However, we deemphasize its importance since it was only present in small quantities and likely represented a small fraction of the primary producer biomass available for energy conversion.

Fishes in SAV

The importance of algal-grazer food webs is well documented in littoral systems (Fry 1981; Kitting et al. 1984; Duffy and Harvilicz 2001); however, only a few estuarine studies have linked SAV or epiphytic macroalgae as the major energy source for such a large contingency of fishes as we did here (Paterson and Whitfield 1997). The grazer amphipods *Gammarus daiberi* and *Hyalella azteca* were the primary intermediaries between SAV–epiphytic macroalgae derived energy and fish diets in SAV. For late juvenile fishes, grazer amphipods were dominant in their stomachs and modeled to be their primary source of nutrition, indicating they were at dietary equilibrium (i.e., consumption to absorption). As previously noted, some early juvenile fishes from SAV had high IRIs for zooplankton (Figure 3), but overall their modeled sources of nutrition were dominantly influenced by grazer amphipods or snails (redear sunfish from VCI). This suggests that either grazer amphipods or snails were consumed at higher rates than reflected by the fishes' diets or that small contributions of these prey, which are heavier than zooplankton, can overwhelm the $\delta^{13}C$ signature in the muscle tissue of the fishes. Additional work could be done to address such isotopic variability issues (Vander Zanden and Rasmussen 2001) or the variability in diets resulting from seasonal changes in food composition (Howe and Simenstad 2007), but we suspect that fishes in SAV would show little deviance from diet patterns observed here given that their habitat is highly structured and probably receives little food subsidies from adjacent habitats.

Fishes in Open-Water Shoals

Several studies have shown that fishes in intertidal habitats typically time their feeding coincident with tides that promote access to prey in adjacent habitats (Weisberg et al. 1981; Kneib 1984, 1987; Madon et al. 2001). Such tide-dependent foraging could lead to great variability in the daily composition of food consumed by open-water fishes. Therefore, we are not surprised to see a divergence between diets inferred by stomach contents and stable isotopes for fishes in open-water shoals. For example, splittails and rainwater killifish had high IRIs for pelagic prey, but their mean $\delta^{13}C$ signatures were less than $-20‰$ and IsoSource modeled amphipods with enriched $\delta^{13}C$ signatures to be their dominant prey. Food resources from SAV could also be inferred for omnivorous species, such as the golden shiner and hitch, which had mean $\delta^{13}C$ signatures less than $-21‰$. Based on the enriched $\delta^{13}C$ signatures of most consumers in open-water shoals, a terrestrial- or marsh-derived food web pathway is not substantiated (Kwak and Zedler 1997; Howe and Simenstad 2007). Rather, our findings highlight the importance of energy imports from adjacent SAV as the primary subsidy to consumers in open-water shoals (Hyndes and Lavery 2005; Melville and Connolly 2005; Cardona et al. 2007).

As demonstrated by the ANOSIM and SIMPER analysis, fishes in open-water shoals consumed more chironomid pupae than did late juvenile fishes in SAV. The importance of chironomid pupae to the stomachs and muscle tissues of open-water fishes was most apparent for Mississippi silversides and Chinook salmon. For example, chironomid pupae accounted for the second-highest IRI in the stomachs of these species and were modeled by IsoSource to be the primary food source of untagged Chinook salmon (VCI) and Mississippi silversides at MI (1999). Sommer et al. (2001) found that chironomid pupae were the dominant prey of Chinook salmon in the Yolo Bypass floodplain upstream of the Delta, suggesting that there is a continuum in this prey selection between upstream and estuarine habitats. Interestingly, chironomid pupae are typically suspension feeders (Thorp and Covich 2001), but IsoSource modeled their energy as mostly arising from primary producers with enriched $\delta^{13}C$ signatures at VCI. Because chironomid pupae

were represented in many of the fish diets, resolving the importance of detrital energy in its assimilated energy could be helpful for understanding the role of the microbial loop to upper consumers in the food web (Sobczak et al. 2002; Howe and Simenstad 2007).

Hatchery Chinook salmon were on average 3‰ more depleted in $\delta^{13}C$ and $\delta^{15}N$ than untagged Chinook salmon, but their stomach contents were nearly identical. The isotopic differences between untagged and hatchery fish are probably best explained by the influence of the hatchery feed in the muscle tissues of hatchery fish, which were released in the Delta just 4 weeks prior to their capture (P. Cadrett, U.S. Fish and Wildlife Service, personal communication).

Historic Shifts in the Food Web

During the 1960s, mysid shrimp *Neomysis mercedis* and *Corophium* spp. were the dominant prey consumed by centrarchids in the Delta (Turner 1966a). We did not find any mysid shrimp in the stomachs of centrarchids, and only black crappies consumed *Corophium* spp. more frequently than *Gammarus daiberi* and *Hyalella azteca*. *Gammarus daiberi* was first detected in the Delta in 1983 and is now one of the most dominant amphipods in the Delta (California Department of Water Resources 2008). In contrast, mysid shrimp abundance has diminished to scant levels in the Delta since the overbite clam *Corbula amurensis* invaded the lower estuary and effectively wiped out pelagic phytoplankton, the major food resource for mysids (Orsi and Mecum 1996). The food sources used by centrarchids in this study (grazer amphipods) versus those sources consumed in the 1960s (i.e., mysids and *Corophium*; Turner 1966a) suggest that there has been a dramatic shift in energy flow in these species and perhaps other nearshore consumers. Feyrer et al. (2003) documented a dietary shift from mysids to amphipods for many fishes in the lower estuary between the 1980s and 2000s. This apparent shift to grazer amphipods may partially explain why centrarchids in the Delta have increased in abundance over the last two decades (Brown and Michniuk 2007), whereas declines in pelagic production have apparently had adverse consequences for pelagic fish populations in the estuary (Sommer et al. 2007).

Consequences for Restoration

Restoration planning for the Delta has emphasized creation of shallow habitat in the belief that such areas would support native fishes (Brown 2003; CALFED Bay–Delta Authority 2004). Our study and others (Feyrer and Healey 2003; Toft et al. 2003; Grimaldo et al. 2004; Nobriga et al. 2005; Nobriga and Feyrer 2007) show that native and introduced fishes in the Delta use a variety of habitats and that their trophic pathways vary with their body size and prey selection. Others have shown that physical habitat for native fishes can also be defined by water quality conditions (Feyrer et al. 2007) or some measure of freshwater inflow (Kimmerer 2002a, 2002b). Thus, no single habitat template or food source can be expected to benefit all native fishes.

Restoration efforts should focus on processes that govern predation, bioenergetics (i.e., growth, feeding, etc), and trophic relationships (Zedler et al. 1997; Madon et al. 2001; Madon 2008). For example, we found that open-water shoals supported the most native species (three), but the mechanisms that would explain their importance for native fishes are not clear. In other estuaries, intertidal shoals are key habitats where fishes reside to gain access to marsh plains during flood tides (Weisberg et al. 1981; Kneib 1984; Madon et al. 2001) or to escape predators from deep subtidal waters (Kneib 1987) or adjacent SAV habitats (Rozas and Odum 1988). We believe that creation of open-water shoals would promote native fish use in littoral areas; however, companion research on the functions of this habitat are needed to address uncertainty associated with long-term sustainability of this habitat and native fish populations in the estuary (Kwak and Zedler 1997; Madon 2008).

In the southeastern U.S. estuaries, SAV restoration is studied and promoted in regional management plans because it provides valuable habitat for many native invertebrates and fishes in those ecosystems (Orth et al. 1984; Rozas and Odum 1987; Rozas et al. 2005; Baldizar and Rybicki 2007). However, in the San Francisco Estuary, Brazilian waterweed and other introduced species of SAV are considered a nuisance because they impede recreational boat traffic, clog water diversions, and provide little or no economic value (California Department of Boating and Waterways 2000). Biologically, the Brazilian waterweed may be considered an ecosystem engineer (Jones et al. 1994) because it has altered the physical environment of the estuary, which in turn has had direct and indirect consequences for native fish populations in the estuary (Brown 2003; Nobriga et al. 2005; Brown and Michniuk 2007; Feyrer et al. 2007). Here, we show that Brazilian waterweed supports invertebrates that are important energy sources for fishes in the Delta. It also supports an abundance of habitat (i.e., leaves and stems) for epiphytic macroalgae, which along with the plant itself, play an important role in the basal source of energy supporting littoral food webs. By all accounts, Brazilian waterweed is well established and unlikely to be eradicated from the Delta. Thus, restoration projects

may want to consider conditions that promote it in smaller patch sizes that provide the greatest enhancement to native species dependent on edge or openwater habitats. In many ecosystems, relationships between SAV patch size and fish or invertebrate communities are well understood (Werner et al. 1983; Rozas and Odum 1988; Thorp et al. 1997); such relationships have yet to be revealed in the Delta, where mixes of native and introduced species dominate (Brown 2003).

Finally, there is very little evidence that flooded islands support native pelagic fishes (delta smelt *Hypomesus transpacificus* and longfin smelt *Spirinchus thaleichthys*; Grimaldo et al. 2004; Nobriga et al. 2005). Much of the justification for restoring flooded islands hinged on the premise that such areas would provide beneficial habitat for imperiled smelts, but these species are often found in the tidally dominated open waters and channels of the Delta (Grimaldo et al. 2004; Rockriver 2004). Deep, flooded islands such as MI are productive areas (Lucas et al. 2002; Mueller-Solger et al. 2002; Lopez et al. 2006) that support large numbers of zooplankton and pelagic fishes (Grimaldo et al. 2004). Therefore, viable restoration alternatives for pelagic fishes could involve altering flooded island breach designs to allow maximum export of lower trophic production to larger channels in the Delta, where it can be incorporated into the pelagic food web.

Acknowledgments

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