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**Food web analysis of southern California coastal wetlands
using multiple stable isotopes**

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Abstract Carbon, nitrogen, and sulfur stable isotopes were used to characterize the food webs (i.e., sources of carbon and trophic status of consumers) in Tijuana Estuary and San Dieguito Lagoon. Producer groups were most clearly differentiated by carbon, then by sulfur, and least clearly by nitrogen isotope measurements. Consumer ^{15}N isotopic enrichment suggested that there are four trophic levels in the Tijuana Estuary food web and three in San Dieguito Lagoon. A significant difference in multiple isotope ratio distributions of fishes between wetlands suggested that the food web of San Dieguito Lagoon is less complex than that of Tijuana Estuary. Associations among sources and consumers indicated that inputs from intertidal macroalgae, marsh microalgae, and *Spartina foliosa* provide the organic matter that supports invertebrates, fishes, and the light-footed clapper rail (*Rallus longirostris levipes*). These three producers occupy tidal channels, low salt marsh, and mid salt marsh habitats. The only consumer sampled that appears dependent upon primary productivity from high salt marsh habitat is the sora (*Porzana carolina*). Two- and three-source mixing models identified *Spartina* as the major organic matter source for fishes, and macroalgae for invertebrates and the light-footed clapper rail in Tijuana Estuary. In San Dieguito Lagoon, a system lacking *Spartina*, inputs of macroalgae and microalgae support fishes. *Salicornia virginica*, *S. subterminalis*, *Monanthochloe littoralis*, sewage-

derived organic matter, and suspended particulate organic matter were deductively excluded as dominant, direct influences on the food web. The demonstration of a salt marsh-channel linkage in these systems affirms that these habitats should be managed as a single ecosystem and that the restoration of intertidal marshes for endangered birds and other biota is compatible with enhancement of coastal fish populations; heretofore, these have been considered to be competing objectives.

Key words Food web · Restoration · Salt marsh · Stable isotopes · Wetland

Introduction

A strong food web linkage between salt marsh vascular plants and nearshore fish consumers (via detritus production and consumption) has been argued for many North American coastal ecosystems, including the Atlantic (Teal 1962; Odum and de la Cruz 1967; Odum and Heald 1975; Haines and Montague 1979), the Gulf of Mexico (Darnell 1961; Turner 1977), and the Pacific Northwest (Naiman and Sibert 1979; Kistritz and Yesaki 1979). The Atlantic Coast argument is strengthened by evidence that the highly productive Atlantic menhaden (*Brevoortia tyrannus*) makes direct use of cellulose (Peters and Schaaf 1981; Lewis and Peters 1984), and not just the bacteria and associated microfauna that help decay vascular plant matter. Yet other researchers report that coastal food webs are fueled by algal producers, either phytoplankton (Nixon et al. 1976; Haines 1977; Gleason and Wellington 1988), "eelgrass, epiphytes, and macroalgae" (Simenstad and Wissmar 1985), or epibenthic microalgae (Sullivan and Moncreiff 1990). The issue is further complicated by documentation that mussels in different areas feed opportunistically on what is most available (Peterson and Howarth 1987). Thus, the base of an estuarine food web may include salt marsh vascular plants, salt marsh algae, algae in the water column, and upstream sources; there is no para-

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digm stating which source dominates, and dominance may shift spatially or temporally.

In southern California, information on producer-consumer relationships is insufficient to predict the relative roles of marsh producers, phytoplankton, or allochthonous detritus in coastal wetland food webs (Onuf 1987; Horn and Allen 1985). The small sizes of the region's tidal wetlands (Zedler 1982) and low rates of vascular plant productivity (Onuf et al. 1979; Zedler et al. 1980) might indicate minimal salt marsh contributions, but the highly productive epibenthic algae (Zedler 1980; Onuf 1987) and their potentially high digestibility suggest that at least the algae of the salt marshes would be important to the food base.

In their review of stable isotope techniques, Peterson and Fry (1987) concluded that "Determining the importance of marsh grass production for secondary production in estuaries is critical because of the intense development pressures on coastal ecosystems...". The pressure to develop coastal habitats in southern California is immense (Zedler 1991), but the ecological setting is very complex, because these marshes are not dominated by a single vascular plant. The broad marsh plain supports *Salicornia virginica* and other succulents, and it occurs between a narrow strip of *Spartina foliosa* at the tidal creek edge and a band of *Salicornia subterminalis* and *Monanthochloe littoralis* at the upland boundary (Zedler 1982). Also, each wetland has many unique features, due to the variety of hydrologic settings (Ferren et al. 1996).

This study was designed to identify organic matter sources that support consumers in different wetland habitats and to seek trophic linkages between salt marsh and channel habitats. Such knowledge is critical to define food web support functions that may be required for effective restoration and mitigation projects. If salt marsh habitat for resident marsh birds is being planned, e.g., for the endangered light-footed clapper rail (*Rallus longirostris levipes*) and Belding's Savannah sparrow (*Passerculus sandwichensis beldingi*), their dependency on shallow waters must be known. Similarly, for projects designed to provide fish habitat, we need to know if it is sufficient to excavate a channel or basin, or whether vegetated marsh habitat should also be included.

As a first step in elucidating food webs, we used multiple stable isotope analyses to determine if animals utilize the plant foods produced in the salt marshes of two very different systems: an estuary with a long history of good tidal flushing and *Spartina foliosa* in the salt marsh (Tijuana Estuary) and a lagoon with frequent, prolonged closure to tidal action, fewer vascular plant species, and only an experimental planting of *Spartina foliosa* (San Dieguito Lagoon). We expected to distinguish salt marsh plants from one another, because species with C_3 (*Salicornia*) and C_4 (*Spartina*, *Monanthochloe*) photosynthetic pathways are present and have distinct carbon isotopic composition (Farquhar et al. 1989), and we expected to distinguish vascular plants

from epibenthic algae as in other studies (e.g., Peterson et al. 1986; Sullivan and Moncreiff 1990). Because Tijuana Estuary has large inputs of raw sewage, we asked if sewage enters the estuarine food web. We also anticipated differences between the isotopic distributions of consumers from the estuary and the lagoon, because of differences in vegetation type, marsh area, watershed area, and inflowing wastewaters. Finally, we discussed the implications of our results to wetland management, restoration, and mitigation.

Methods

Study sites

Two coastal wetlands located in San Diego County, California, were selected for study to represent differing physical and biotic environments within the region (Fig. 1). The primary study area was the northern arm of Tijuana Estuary, the largest intact coastal wetland in San Diego County (c. 382 ha wetland habitat). The northern arm is composed of a network of fully tidal channels, small embayments, and an intertidal area that supports mostly salt marsh vegetation, including *Spartina foliosa* (Zedler et al. 1992). A subset of data was collected from San Dieguito Lagoon, a smaller coastal wetland north of San Diego (c. 91 ha wetland habitat). It is intermittently open to tidal flushing, and much of the salt marsh there has been converted to upland habitat. *S. foliosa* does not occur in San Dieguito Lagoon, except for rare experimental plantings, but other salt marsh vegetation is present (primarily *Salicornia virginica*).

The history, physical setting, ecology, and management have been described in detail for Tijuana Estuary by Zedler et al. (1992) and for San Dieguito Lagoon by MEC (1993). The wetlands are formed by the terminus of the Tijuana River (4,483-km² watershed) and that of the San Dieguito River (896-km² watershed) with the Pacific Ocean. Three-fourths of the Tijuana River watershed lies in Mexico, but the entire estuary is located within the United States. While both salt marsh ecosystems have been altered and degraded by human activities and are considered highly variable environments, the northern arm of Tijuana Estuary remains less disturbed and more ecologically functional than its southern arm or San Dieguito Lagoon. Accordingly, large-scale restoration projects are planned for the southern arm of Tijuana Estuary (Entrix et al. 1991; Zedler et al. 1992) and for San Dieguito Lagoon (MEC 1993).

Field collections

Organic materials (producers and consumers) were collected during March–April and August–September 1994 from four sites within the northern arm of Tijuana Estuary and from two sites in San Dieguito Lagoon (Fig. 1). Because seasonal changes in *Spartina* isotopic composition have been measured (Peterson et al. 1986), we collected *S. foliosa* from all four sites in Tijuana Estuary during March and September. In addition, sewage-derived organic matter (SDOM) was collected during February 1994 from Smuggler's Gulch, a canyon on the southern edge of Tijuana Estuary that regularly receives raw sewage effluent from the city of Tijuana, Mexico. Sewage sludge was also collected during March 1994 directly from Pump Station Number 3, a sewage collection facility in the city of Tijuana and the source of outflows to Smuggler's Gulch.

Detritus suspended in the water column was collected and analyzed as a potentially critical link in the food web. Water samples were collected from each of the six sampling sites for subsequent analysis of suspended particulate matter. Suspended particulate

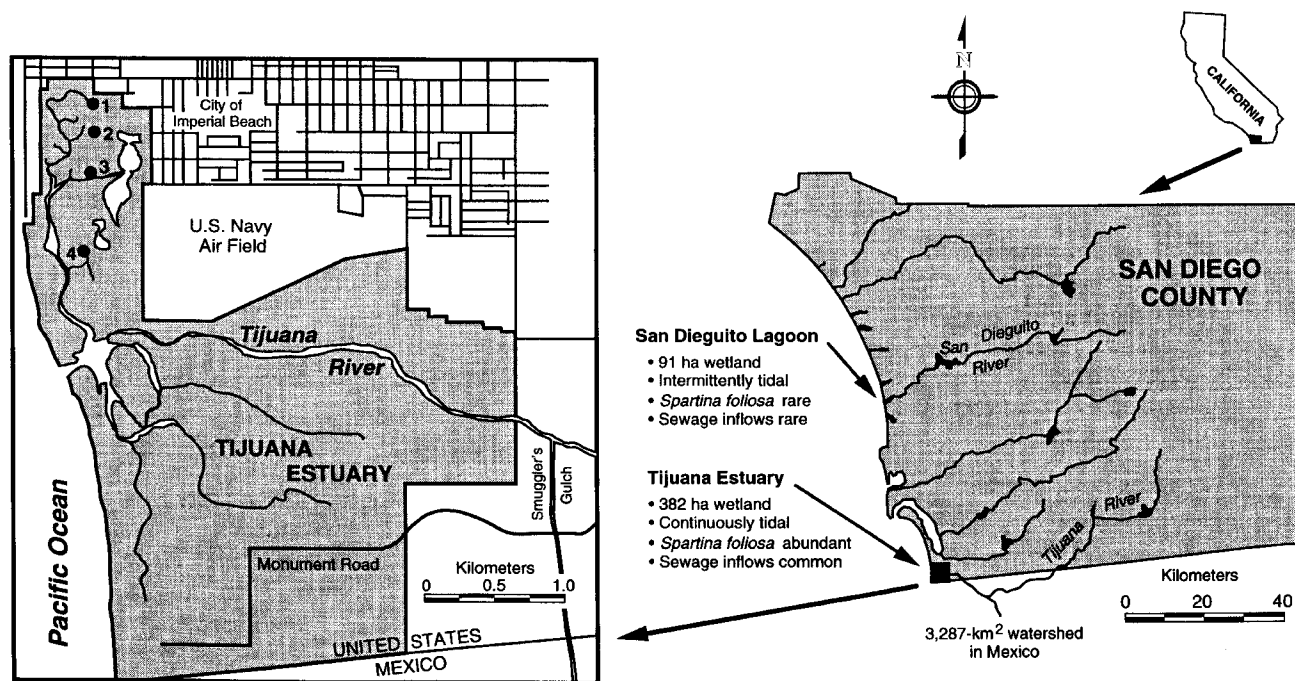


Fig. 1 Map of San Diego County (California, USA) showing locations of San Dieguito Lagoon, Tijuana Estuary, and primary sampling sites in the northern arm of Tijuana Estuary

organic matter (POM) for stable isotope analyses was collected by filtering 400 l of water from each site through a 30- μ m mesh plankton net and included living (plankton) and nonliving (detritus) components. SDOM was collected from Smuggler's Gulch by scraping the fine, oily surface sediment from the underlying substrate during a period immediately following a known raw sewage inflow.

Two types of conspicuous marsh microalgae were collected, and both were composed primarily of cyanobacteria (epibenthic cyanobacterial mats and colonial cyanobacteria in pools), but included other algal taxa. Epibenthic microalgal mats (*Schizothrix* sp.) were separated from the underlying salt marsh substrate and then rinsed. Colonial microalgae (*Microcystis* sp.) were collected from salt marsh pools by pipetting water containing high densities of globular colonies. Macroalgae were gathered by hand from subtidal and intertidal zones. Salt marsh vascular plant tissue was collected by trimming live portions of plants. All plant samples were stored in plastic bags on ice in the field and later refrigerated until laboratory processing.

Invertebrates were collected by hand, sieving sediment cores, and using a Yaby pump (specifically for burrowing shrimp). Invertebrates were stored on ice, then frozen until laboratory processing. A 15-m bag seine constructed of 3-mm mesh netting was used to collect most fish species from channel habitats. Striped mullet (*Mugil cephalus*) actively avoided collection by seine, but were successfully captured by gill net. Juvenile California killifish (*Fundulus parvipinnis*) were captured in intertidal, salt marsh habitat during high-tide periods with a dip net. Fish were stored on ice in the field and later transferred to a freezer for subsequent laboratory processing. Frozen bird specimens were provided by U.S. Fish and Wildlife Service personnel at the Tijuana Slough National Wildlife Refuge.

We stratified habitats where organic materials were collected into five broad categories according to intertidal elevational range and patterns of vegetation occurrence (Zedler 1984): channel, marsh pool, low marsh [c. 0.2–0.4 m National Geodetic Vertical Datum (NGVD)], mid marsh (c. 0.3–0.9 m NGVD), and high marsh (c. 0.8–1.6 m NGVD).

Laboratory processing and analysis

The weight of particulate matter in water samples was determined by filtering measured volumes of water and following procedures detailed by Strickland and Parsons (1972). Particulate matter was quantified as dry weight per volume and ashed dry weight per volume, and percent organic matter was computed as the difference between dried and ashed weights, expressed as a proportion of the dried weight. Salinity of water samples used to quantify particulate matter was measured, and chlorophyll *a* concentration was determined by extraction and the spectrophotometric method (PERL 1990; APHA 1992).

Particulate matter derived from the 400-l filtrate was concentrated on a glass fiber filter and was rinsed with 10% hydrochloric acid (HCl) under gentle vacuum filtration to dissolve any calcium carbonate (CaCO_3) that may have been present, followed by a distilled water rinse. The filter and detritus were dried at 60°C to a constant weight and were then sealed in a glass vial for later isotope analysis. SDOM was dried at 60°C to a constant weight, ground to fine powder, stirred to homogenize the sample, and stored in a glass vial.

The uppermost layer of microalgal mats was carefully excised using a scalpel to attain a sample of living material and to exclude the sulfur bacteria found beneath the epibenthic mat. Water samples containing colonial microalgae were filtered, and the filtrate was sorted to obtain a pure sample. Macroalgae were sorted in the laboratory to attain samples containing only one genus. The sorted algae samples were rinsed with 10% HCl under a gentle vacuum, followed by a distilled water rinse, and dried to a constant weight. Dried matter was then ground using a mortar and pestle or a Wiley mill equipped with a number-40 mesh delivery tube. This dry powder was used directly for carbon and nitrogen isotope analyses. For sulfur analysis, the powder was additionally rinsed twice with distilled water to leach inorganic sulfate and then redried, ground, and stored. Vascular plants were rinsed with distilled water, dried, and ground using a Wiley mill. The powder was stored for carbon and nitrogen analyses, and a subsample was rinsed to leach inorganic sulfates.

Thawed whole organisms were used as tissue samples of small invertebrates, such as amphipods and isopods. Shells were removed from mollusks before processing, and muscle tissue was dissected from crabs and shrimp and retained. Only muscle tissue was pro-

cessed for *Aplysia californica*. Because of low individual weight, a composite tissue sample from more than one individual was used for all invertebrates except *A. californica*. Invertebrate tissue was rinsed with 10% HCl, followed by distilled water, and then dried. The dry tissue was ground using a mortar and pestle or a Wiley mill. A subsample of the dry powder was rinsed to remove inorganic sulfate if a sufficient quantity of sample was available.

A composite tissue sample from more than one individual was used for most fish species, except for striped mullet, large topmelt (*Atherinops affinis*), and diamond turbot (*Hypsopsetta guttulata*), for which samples from individuals provided a sufficient quantity of tissue. White muscle tissue was dissected from thawed large fish for stable isotope analyses. For small fish, the head and viscera were removed, and the remainder of the body, consisting primarily of white muscle, was retained for isotope analyses. Final preparation of fish tissue was similar to that for invertebrates, including an acid rinse, drying, grinding, and removing inorganic sulfates if sufficient material was available.

Breast and wing muscle was dissected from two species of wetland birds collected from Tijuana Estuary. Bird muscle tissue was processed separately for each individual using the same techniques described above for fish tissue.

Stable isotope measurement

The measurement of carbon, nitrogen, and sulfur stable isotope ratios of organic matter was performed by Coastal Science Laboratories of Austin, Texas. The measurement process involved complete conversion of the sample to a gas by combustion and separation of pure gases (CO₂, N₂, and SO₂; Fry and Sherr 1984; Peterson and Fry 1987). A pure gas was then introduced into an isotope ratio mass spectrometer, and the isotopic composition was quantified relative to a standard reference material. Standards were carbon in the PeeDee limestone, nitrogen gas in air, and sulfur from the Cañyon Diablo meteorite. Results for each element were expressed as parts per thousand (‰) differences from the corresponding standard (δ):

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

where X is ¹³C, ¹⁵N, or ³⁴S, and R is the corresponding ratio of ¹³C/¹²C, ¹⁵N/¹⁴N, or ³⁴S/³²S. The δ values include a measure of both heavy and light isotopes, whereby higher δ values denote a greater proportion of the heavy isotope. Standard deviations of δ¹³C, δ¹⁵N, δ³⁴S replicate analyses were 0.2‰, 0.2‰, and 0.5‰, respectively.

Statistical comparisons and models

Analysis of variance (ANOVA) was used to compare isotope ratios for each element among producer groups within Tijuana Estuary and between fish consumers from each wetland (Zar 1984). We performed a nested ANOVA on producer isotope ratios of each element within Tijuana Estuary, with individual taxa (or types) of producers nested within six broader producer groups (SDOM, POM, microalgae, macroalgae, C₃ succulents, and C₄ grasses). If that ANOVA detected a significant producer group main effect, then significant pairwise differences among producer group means were detected using a Tukey multiple comparison procedure. We used one-way ANOVA, quantifying variance within and among fish species, to detect differences in isotope ratios between wetlands, using the among-species mean square as the error term in F tests. Dispersion of fish isotope ratios between wetlands was compared by testing equality of covariance matrices, formed by incorporating data from all three elements (C, N, and S), using Bartlett's modification of the likelihood ratio test of homogeneity of the within-group matrices (Morrison 1976; SAS 1988).

We examined associations among producer and consumer isotopic distributions to identify the most important organic matter

sources and then developed a series of simple, two- and three-source mixing models (Fry and Sherr 1984) to approximate relative inputs of each source to each wetland food web. The generalized mixing models used were:

$$\delta X_{\text{consumer}} = p\delta X_{\text{producer1}} + (1-p)\delta X_{\text{producer2}}, \text{ and}$$

$$\delta X_{\text{consumer}} = p\delta X_{\text{producer1}} + (1-p-q)\delta X_{\text{producer2}} + q\delta X_{\text{producer3}};$$

where δ X is the mean ¹³C or ³⁴S δ value for a consumer or producer group, and p and q are the proportional inputs of producers. Both δ¹³C and δ³⁴S models were required to solve three-source models, and ranges of possible input combinations were estimated using two-source models. End member values incorporated into mixing models were wetland-specific mean values for consumer and producer groups, except that microalgae mean δ values measured from Tijuana Estuary were used in San Dieguito Lagoon models. Similar two-source models have been used by other investigators for related objectives (Haines 1976a; Hughes and Sherr 1983; Van Dover et al. 1992).

Results

Particulate matter and sewage isotopic composition

Although both wetlands were fully tidal on collection dates (March 1994), water samples collected from each were brackish, with salinities averaging 22‰ in Tijuana Estuary and 25‰ in San Dieguito Lagoon (Table 1). The mean dry weight of particulate matter in Tijuana Estuary water was 33.2 mg l⁻¹ and was composed of an average of 25.9% organic matter containing 0.65 μg l⁻¹ chlorophyll a . Compared to Tijuana Estuary, San Dieguito Lagoon had a higher mean dry weight of particulate matter (42.2 mg l⁻¹) with a similar proportion of organic matter (26.0%) and a much higher chlorophyll a concentration (5.77 μg l⁻¹).

Stable isotope ratios of POM samples were similar within and between wetlands (Table 2). Variation in δ¹³C and δ¹⁵N values was low among sampling sites in Tijuana Estuary (SE < 0.6‰) and was slightly higher for δ³⁴S (SE = 1.1‰). Absolute differences in mean POM isotope ratios between wetlands were 1.6‰, 1.5‰, and 2.3‰ for δ¹³C, δ¹⁵N, and δ³⁴S, respectively. POM mean δ values at Tijuana Estuary were higher for all three elements, relative to those of San Dieguito Lagoon.

SDOM stable isotope ratios also varied little among samples (Table 2). δ¹³C and δ¹⁵N values were equivalent among SDOM samples (SE = 0.1‰), and δ³⁴S values showed greater variation (SE = 1.1). Much of the δ³⁴S variation among samples was due to a 4.0‰ mean enrichment of the two samples collected from the City of Tijuana sewage pump station, relative to those from Tijuana Estuary. Differences in mean isotope ratios between collection sites were negligible for δ¹³C (0.1‰) and δ¹⁵N (0.3‰). The similarity in isotopic composition of SDOM samples collected from two sources (municipal collector and canyon) confirmed the assumption that the organic material collected from Smuggler's Gulch in Tijuana Estuary was derived from domestic sewage.

Table 1 Salinity and concentrations of suspended particulate matter and chlorophyll in water samples from Tijuana Estuary (30 March 1994) and San Dieguito Lagoon (31 March 1994) collected

Site number	Salinity (‰)	Particulate matter			Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)
		Dry weight (mg l^{-1})	Ashed weight (mg l^{-1})	% Organic matter	
Tijuana Estuary					
1	24.0	37.8	31.3	17.2	0.78
2	22.0	31.7	21.8	31.4	0.83
3	19.5	30.3	21.8	28.0	0.24
4	23.0	33.1	24.1	27.1	0.76
Mean (\pm SD)	22.1 (\pm 1.9)	33.2 (\pm 3.3)	24.8 (\pm 4.5)	25.9 (\pm 6.1)	0.65 (\pm 0.27)
San Dieguito Lagoon					
1	25.5	35.0	24.3	30.6	2.31
2	25.0	49.4	38.8	21.4	9.22
Mean (\pm SD)	25.2 (\pm 0.4)	42.2 (\pm 10.2)	31.5 (\pm 10.3)	26.0 (\pm 6.5)	5.77 (\pm 4.89)

Primary producer isotopic composition

Among-taxa variation in isotope ratios of primary producers was substantial, but δ values within taxa were similar (Table 2). Although sample sizes varied among taxa, most standard errors of mean δ values were less than 1.0‰, and only one exceeded 2.0‰. The two

in association with suspended particulate organic matter samples analyzed for stable isotope ratios

Salicornia species were the most depleted producers in ^{13}C , and *Schizothrix* (marsh microalgal mats) and *Spartina* were most enriched. $\delta^{15}\text{N}$ values were lowest for *Monanthochloe* and highest for *Salicornia virginica* (from San Dieguito Lagoon), and extremes in $\delta^{34}\text{S}$ were both forms of marsh microalgae (low) and *Enteromorpha* (high).

Table 2 Stable isotope ratios (‰) of suspended particulate organic matter (POM), sewage-derived organic matter (SDOM), and primary producers (including habitat type where collected) collected

from Tijuana Estuary and San Dieguito Lagoon. Data are sample size (*n*) and mean δ values (\pm SE)

Material	Habitat type	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Tijuana Estuary					
POM	–	4	-20.8 ± 0.4	10.9 ± 0.6	8.6 ± 1.1
SDOM	–	4	-23.7 ± 0.1	5.6 ± 0.1	4.6 ± 1.1
Marsh microalgae					
<i>Microcystis</i> sp.	Marsh pool	1	-17.7	5.0	9.5
<i>Schizothrix</i> sp.	Mid marsh	1	-15.3	3.0	4.8
Macroalgae					
<i>Enteromorpha</i> sp.	Channel	4	-19.2 ± 1.0	11.9 ± 2.0	19.6 ± 0.8
<i>Gracilaria</i> sp.	Channel	2	-20.2 ± 0.1	11.4 ± 0.1	18.6 ± 0.2
<i>Rhizoclonium</i> sp.	Mid marsh	1	-20.2	9.6	17.5
<i>Ulva</i> sp.	Channel	4	-19.1 ± 0.7	13.4 ± 0.5	18.6 ± 1.3
Vascular salt marsh plants					
<i>Monanthochloe littoralis</i>	High marsh	4	-16.2 ± 0.1	2.5 ± 0.2	13.7 ± 1.2
<i>Salicornia subterminalis</i>	High marsh	4	-27.0 ± 0.2	9.0 ± 2.0	14.3 ± 1.2
<i>Salicornia virginica</i>	Mid marsh	4	-26.7 ± 0.2	11.0 ± 1.2	12.3 ± 2.2
<i>Spartina foliosa</i>	Low marsh	8	-15.1 ± 0.2	10.3 ± 0.3	11.5 ± 0.5
San Dieguito Lagoon					
POM	–	2	-22.4 ± 0.8	9.4 ± 0.8	6.3 ^a
Macroalgae					
<i>Enteromorpha</i> sp.	Channel	2	-18.6 ± 1.6	11.4 ± 0.1	17.9 ± 0.9
<i>Gracilaria</i> sp.	Channel	2	-21.4 ± 0.4	11.3 ± 0.3	16.9 ± 0.5
<i>Ulva</i> sp.	Channel	1	-15.4	10.3	17.3
Vascular salt marsh plants					
<i>Salicornia virginica</i>	Mid marsh	2	-27.6 ± 0.2	14.2 ± 0.6	16.0 ± 1.0

^a *n* = 1

Isotope ratios of primary producers appeared to differentiate according to organismal characteristics (physiology, morphology, and phylogeny) rather than by habitat. Broader producer taxonomic groups were easily distinguished by isotopic composition with little overlap in ranges; these included microalgae, macroalgae, C₃ succulents (*Salicornia* spp.), and C₄ grasses (*Monanthochloe* and *Spartina*). Isotope ratio means of these producer groups, POM, and SDOM were statistically differentiated most clearly by the carbon isotope, then by sulfur, and least clearly by nitrogen (Fig. 2). Considering multiple isotopes collectively further distinguished producers, because the rankings of producer means were distinct for each isotope (Fig. 2).

No substantial seasonal difference was found in *Spartina foliosa* isotopic composition. Mean values (\pm SE) from March samples were -15.7‰ ($\pm 0.1\text{‰}$) for $\delta^{13}\text{C}$, 10.6‰ (± 0.6) for $\delta^{15}\text{N}$, and 12.3‰ ($\pm 0.9\text{‰}$) for $\delta^{34}\text{S}$, compared to corresponding values of -14.4‰ ($\pm 0.1\text{‰}$), 10.3‰ ($\pm 0.3\text{‰}$), and 10.8‰ (± 0.4) from September samples from the same sites. Macroalgae samples of corresponding genera from the two wetlands were generally similar in isotopic composition, with the exception of *Ulva*, which was over 3‰ depleted in ^{13}C and enriched in ^{15}N at Tijuana Estuary (Table 2). *Salicornia virginica* mean $\delta^{13}\text{C}$ values were equivalent between wetlands, but $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values were both over 3‰ depleted in Tijuana Estuary samples.

Consumer isotopic composition

Invertebrate isotope ratios were variable among species, but encompassed narrow ranges overall, relative to those of producers (Table 3). Mean invertebrate values (\pm SE) were -18.6‰ ($\pm 0.6\text{‰}$) for $\delta^{13}\text{C}$, 11.8‰ ($\pm 0.5\text{‰}$) for $\delta^{15}\text{N}$, and 14.5‰ ($\pm 0.4\text{‰}$) for $\delta^{34}\text{S}$. Extremes in invertebrate δ values were found in *Melampus olivaceus*

and *Cerithidia californica* for $\delta^{13}\text{C}$, in *Trichocorixa reticulata* and *Bulla gouldiana* for $\delta^{15}\text{N}$, and in *T. reticulata* and *Ligia occidentalis* for $\delta^{34}\text{S}$.

Variation in fish isotope ratios was relatively low, spanning ranges that were narrow overall and similar in width to those of invertebrates (Table 3). Considering each species and size class as a single datum, mean δ values (\pm SE) of Tijuana Estuary fishes were -16.0‰ ($\pm 0.4\text{‰}$) for $\delta^{13}\text{C}$, 15.6‰ ($\pm 0.4\text{‰}$) for $\delta^{15}\text{N}$, 10.4‰ ($\pm 0.5\text{‰}$) for $\delta^{34}\text{S}$. Corresponding values for San Dieguito Lagoon were -18.1‰ ($\pm 0.4\text{‰}$) for $\delta^{13}\text{C}$, 15.3‰ ($\pm 0.1\text{‰}$) for $\delta^{15}\text{N}$, 11.9‰ ($\pm 0.3\text{‰}$) for $\delta^{34}\text{S}$. Isotope ratios of fishes from Tijuana Estuary appeared to be related to fish size for individual species. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values both increased with fish size for California killifish and topmelt. Among San Dieguito Lagoon fishes, a similar trend was observed for $\delta^{13}\text{C}$ values of topmelt, but no size-related trend was observed for $\delta^{15}\text{N}$ values. Differences in fish isotopic composition between wetlands were statistically significant for $\delta^{13}\text{C}$ ($P = 0.015$), but not for $\delta^{15}\text{N}$ or $\delta^{34}\text{S}$ ($P > 0.05$). A significant difference was detected between the three-isotope, covariance matrices of fish δ values of the two wetlands ($\chi^2 = 12.7$, $P = 0.048$), indicating that the distribution of isotope ratios of San Dieguito Lagoon fishes was significantly more restricted than that of Tijuana Estuary fishes.

There was little overlap in the ranges of isotope ratios spanned by invertebrates compared to those of fishes (Table 3). In general, fishes were enriched in ^{13}C and ^{15}N , and depleted in ^{34}S , relative to invertebrates. Absolute differences in mean δ values of invertebrates and fishes from Tijuana Estuary were 2.6‰ for $\delta^{13}\text{C}$, 3.8‰ for $\delta^{15}\text{N}$, and 4.1‰ for $\delta^{34}\text{S}$.

Isotope ratios of the two bird species sampled from Tijuana Estuary were distinct from one another (Table 3). Absolute differences in their mean δ values were 6.0‰ for $\delta^{13}\text{C}$, 5.8‰ for $\delta^{15}\text{N}$, and 4.6‰ for $\delta^{34}\text{S}$. Variation in isotope ratios between the two sora (*Porz-*

Fig. 2a-c Results of Tukey multiple comparison procedure to detect significant differences ($P < 0.05$) among isotope ratio means ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) of primary producer groups, sewage-derived organic matter (SDOM), and suspended particulate organic matter (POM) from Tijuana Estuary. A common solid line above organic matter groups indicates no significant difference detected among the included means

(a) $\delta^{13}\text{C}$						
Material	C ₃ succulents	SDOM	POM	Macroalgae	Microalgae	C ₄ grasses
Mean (‰)	-26.8	-23.7	-20.8	-19.4	-16.5	-15.5
\pm SE	± 0.1	± 0.1	± 0.4	± 0.4	± 1.2	± 0.2
N	8	4	4	11	2	12

(b) $\delta^{15}\text{N}$						
Material	Microalgae	SDOM	C ₄ grasses	C ₃ succulents	POM	Macroalgae
Mean (‰)	4.0	5.6	7.8	10.0	10.9	12.1
\pm SE	± 1.0	± 0.1	± 1.2	± 1.1	± 0.6	± 0.8

(c) $\delta^{34}\text{S}$						
Material	SDOM	Microalgae	POM	C ₄ grasses	C ₃ succulents	Macroalgae
Mean (‰)	4.6	7.2	8.6	12.3	13.3	18.9
\pm SE	± 1.2	± 2.4	± 0.9	± 0.6	± 1.2	± 0.5

Table 3 Stable isotope ratios (‰) of invertebrate, fish, and avian consumers (including habitat type where collected) collected from Tijuana Estuary and San Dieguito Lagoon. Data are sample size (*n*) and mean δ values (\pm SE); mean total length and wet weight (\pm SD) are given for fish size groups

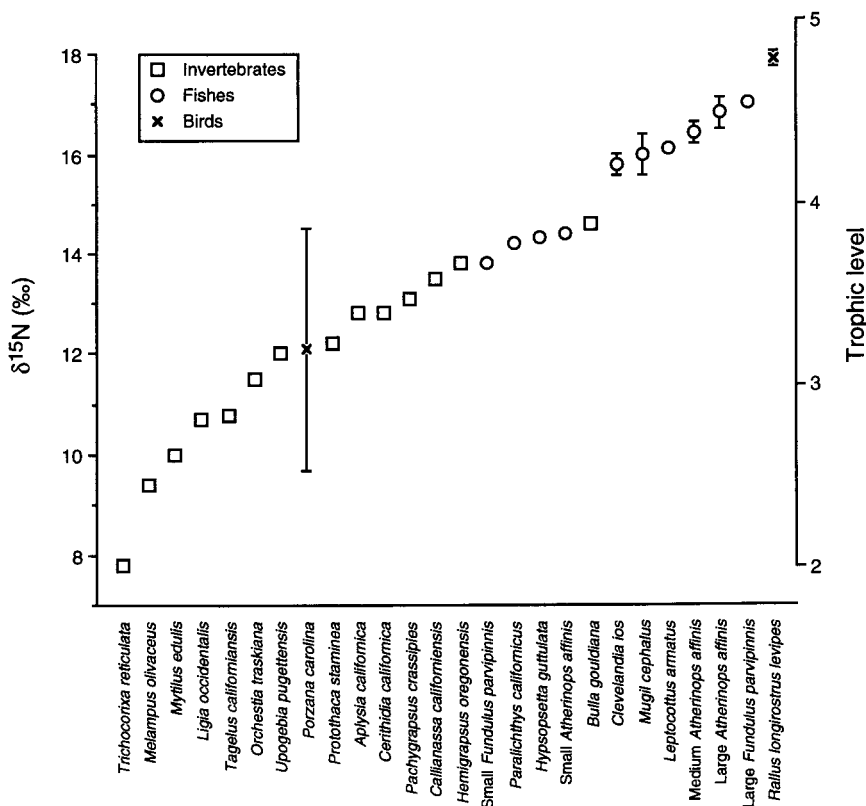
Species	Habitat type	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Tijuana Estuary					
Invertebrates					
<i>Ligia occidentalis</i> (Isopod)	Low marsh	1	-21.7	10.7	16.6
<i>Orchestia traskiana</i> (Amphipod)	Low marsh	1	-21.8	11.5	14.1
<i>Callinassa californiensis</i> (Bay ghost shrimp)	Channel	1	-17.4	13.5	14.8
<i>Upogebia pugettensis</i> (Blue mud shrimp)	Channel	1	-18.6	12.0	16.2
<i>Hemigrapsus oregonensis</i> (Yellow shore crab)	Channel	1	-17.4	13.8	14.3
<i>Pachygrapsus crassipies</i> (Striped shore crab)	Channel	1	-17.8	13.1	16.1
<i>Trichocorixa reticulata</i> (Water boatman)	Marsh pool	1	-18.4	7.8	10.9
<i>Aplysia californica</i> (California brown sea hare)	Channel	1	-19.9	12.8	16.0
<i>Bulla gouldiana</i> (Cloudy bubble snail)	Channel	1	-16.1	14.6	15.3
<i>Cerithidia californica</i> (California horn snail)	Channel	1	-15.8	12.8	13.7
<i>Melampus olivaceus</i> (Olive ear snail)	Channel	1	-22.5	9.4	15.4
<i>Mytilus edulis</i> (Bay mussel)	Channel	1	-18.0	10.0	13.7
<i>Protothaca staminea</i> (Common littleneck clam)	Channel	1	-18.0	12.2	14.0
<i>Tagelus californianus</i> (California jackknife clam)	Channel	1	-17.7	10.8	12.2
Fishes					
<i>Fundulus parvipinnis</i> (California killifish)					
Small (22 \pm 7 mm; 0.13 \pm 0.15 g)	Marsh pool	1	-18.2	13.8	10.3
Large (59 \pm 3 mm; 2.49 \pm 0.50 g)	Channel	1	-17.0	17.0	9.2
<i>Atherinops affinis</i> (Topsmelt)					
Small (37 \pm 5 mm; 0.31 \pm 0.11 g)	Channel	1	-16.3	14.4	11.2
Medium (109 \pm 8 mm; 8.62 \pm 2.31 g)	Channel	2	-16.6 \pm 0.4	16.4 \pm 0.2	11.4 \pm 0.6
Large (212 \pm 14 mm; 73.6 \pm 20.4 g)	Channel	2	-15.4 \pm 0.5	16.8 \pm 0.3	10.7 \pm 0.4
<i>Leptocottus armatus</i> (Staghorn sculpin)	Channel	1	-14.6	16.1	12.1
<i>Mugil cephalus</i> (Striped mullet)	Channel	4	-16.1 \pm 0.2	16.0 \pm 0.4	7.4 \pm 0.2
<i>Clevelandia ios</i> (Arrow goby)	Channel	2	-14.3 \pm 0.1	15.8 \pm 0.2	9.0 \pm 0
<i>Hypsopsetta guttulata</i> (Diamond turbot)	Channel	1	-15.4	14.3	10.5
<i>Paralichthys californicus</i> (California halibut)	Channel	1	-16.1	14.2	11.9
Birds					
<i>Rallus longirostris levipes</i> (Light-footed clapper rail)	Unknown	2	-18.4 \pm 0.2	17.9 \pm 0.1	14.6 \pm 1.2
<i>Porzana carolina</i> (Sora)	Unknown	2	-24.4 \pm 3.8	12.1 \pm 2.4	10.0 \pm 4.0
San Dieguito Lagoon					
Fishes					
<i>Atherinops affinis</i> (Topsmelt)					
Small (41 \pm 7 mm; 0.32 \pm 0.19 g)	Channel	1	-19.9	15.4	11.5
Medium (109 \pm 4 mm; 8.14 \pm 1.19 g)	Channel	2	-18.5 \pm 0.1	15.5 \pm 0.6	13.2 \pm 1.4
Large (130 \pm 13 mm; 14.0 \pm 4.7 g)	Channel	1	-17.7	15.4	11.9
<i>Clevelandia ios</i> (Arrow goby)					
Small (35 \pm 4 mm; 0.37 \pm 0.13 g)	Channel	2	-17.6 \pm 0	15.2 \pm 0.2	11.6 \pm 0.2
Large (47 \pm 4 mm; 0.91 \pm 0.27 g)	Channel	2	-17.6 \pm 0.1	15.3 \pm 0.1	11.8 \pm 0.6
<i>Hypsopsetta guttulata</i> (Diamond turbot)	Channel	1	-17.5	14.8	11.4

ana carolina) specimens sampled (mean SE = 3.4‰) was much greater than that of the two light-footed clapper rails (mean SE = 0.5‰). Isotopic composition of the light-footed clapper rail was most closely associated with that of invertebrates for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, but distinct from that of other consumers for $\delta^{15}\text{N}$; while δ values of the sora were distinct for $\delta^{13}\text{C}$, but similar to invertebrate $\delta^{15}\text{N}$ and fish $\delta^{34}\text{S}$ values.

Nitrogen isotopic distributions have been shown to be robust indicators of trophic position in marine ecosystems, where ^{15}N enrichment increases predictably with trophic level of consumers (Peterson and Fry 1987; Fry 1988, 1991). Thus, the univariate plot of $\delta^{15}\text{N}$ values of consumers from Tijuana Estuary provided a progressive ranking of trophic position, and by incorpo-

rating a generalized trophic enrichment factor of 3.6‰ (Fry 1988), the number of trophic levels (food chain length) and consumer trophic positions were approximated. This analysis indicated a total of four trophic levels estimated for the Tijuana Estuary food web (Fig. 3). Five invertebrate species represented the primary consumer trophic level (TL 2), and the secondary consumer level (TL 3) included nine invertebrates, four fish species, and the sora. Tertiary consumers (TL 4) included six fishes and the light-footed clapper rail, which held the top trophic position of consumers that we sampled. The maximum $\delta^{15}\text{N}$ value of 15.5‰ of fishes collected from San Dieguito Lagoon lies near the margin of trophic levels 3 and 4 (15.0‰), suggesting that one less trophic level may exist in that aquatic food web.

Fig. 3 Trophic level estimation for invertebrates, fishes, and birds of Tijuana Estuary based on mean (\pm SE) ranked nitrogen isotopic distributions ($\delta^{15}\text{N}$). Sample sizes are given in Table 3



Associations among producer and consumer isotope ratios

Dual isotope biplots revealed associations among isotopic distributions of producers and consumers, suggesting linkages in food web structure (Fig. 4). The biplots of δ values from Tijuana Estuary and San Dieguito Lagoon producers and consumers showed generally similar configurations between wetlands for corresponding end members (Fig. 4). Among dual isotope biplots, the $\delta^{13}\text{C}$ versus $\delta^{34}\text{S}$ is considered the most informative in resolving food web structure, because of a high ratio of among- to within-producer isotope ratio variation and minimal isotopic fractionation associated with trophic transfers (Peterson et al. 1985, 1986; Peterson and Fry 1987). The $\delta^{13}\text{C}$ versus $\delta^{34}\text{S}$ plot from Tijuana Estuary showed invertebrate isotope ratios primarily distributed intermediate between those of macroalgae and C_4 grasses, and fish values were placed between those of microalgae and C_4 grasses (Fig. 4a). $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ isotopic composition of both invertebrates and fishes was intermediate to those of macroalgae and microalgae. Overall, the distribution and ranges of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values strongly suggest macroalgae, microalgae, and C_4 grasses as the most substantial inputs to the base of the food web in Tijuana Estuary. The relative depletion of *Salicornia* species (C_3 succulents) in ^{13}C and of SDOM in ^{13}C and ^{34}S , suggests minimal invertebrate and fish support from these sources. The relative depletion of POM in these two isotopes suggests that the food web is not directly dependent on sus-

pended particulate matter in the water column and that POM is composed of a mixture of sources.

The disparate $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of the two bird species suggest differing diets and ultimate sources of foods (Fig. 4a). Values for the light-footed clapper rail were among those of invertebrates, while those of the sora fell well out of the range of other animal $\delta^{13}\text{C}$ values. Sora $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ isotopic composition was intermediate to those of *Salicornia* and microalgae. The arrangement of these isotope ratios suggests that the light-footed clapper rail and sora utilize different foods within the salt marsh ecosystem and that the sora may feed upon organisms found outside the marsh or items not sampled in this study.

The biplots including $\delta^{15}\text{N}$ values confirm results from the $\delta^{13}\text{C}$ versus $\delta^{34}\text{S}$ plot (Fig. 4). The relative depletion of *Monanthochloe* in ^{15}N resulted in an outlying placement in the $\delta^{15}\text{N}$ versus $\delta^{34}\text{S}$ plot that excludes this genus as a likely contributor to fish and invertebrate support. Thus, *Spartina* was the primary C_4 contributor to the food web of Tijuana Estuary. The significant depletion (2.1‰ difference in mean values) of ^{13}C in San Dieguito Lagoon fishes (where *Spartina* is rare) relative to those of Tijuana Estuary fishes (where *Spartina* is abundant) adds supplementary evidence that *Spartina* contributes substantial organic matter to the base of the Tijuana Estuary food web.

The collective examination of isotopic distributions to elucidate associations among isotope ratios of producers and consumers suggests that a mixture of inputs from macroalgae, microalgae, and *Spartina* provides the

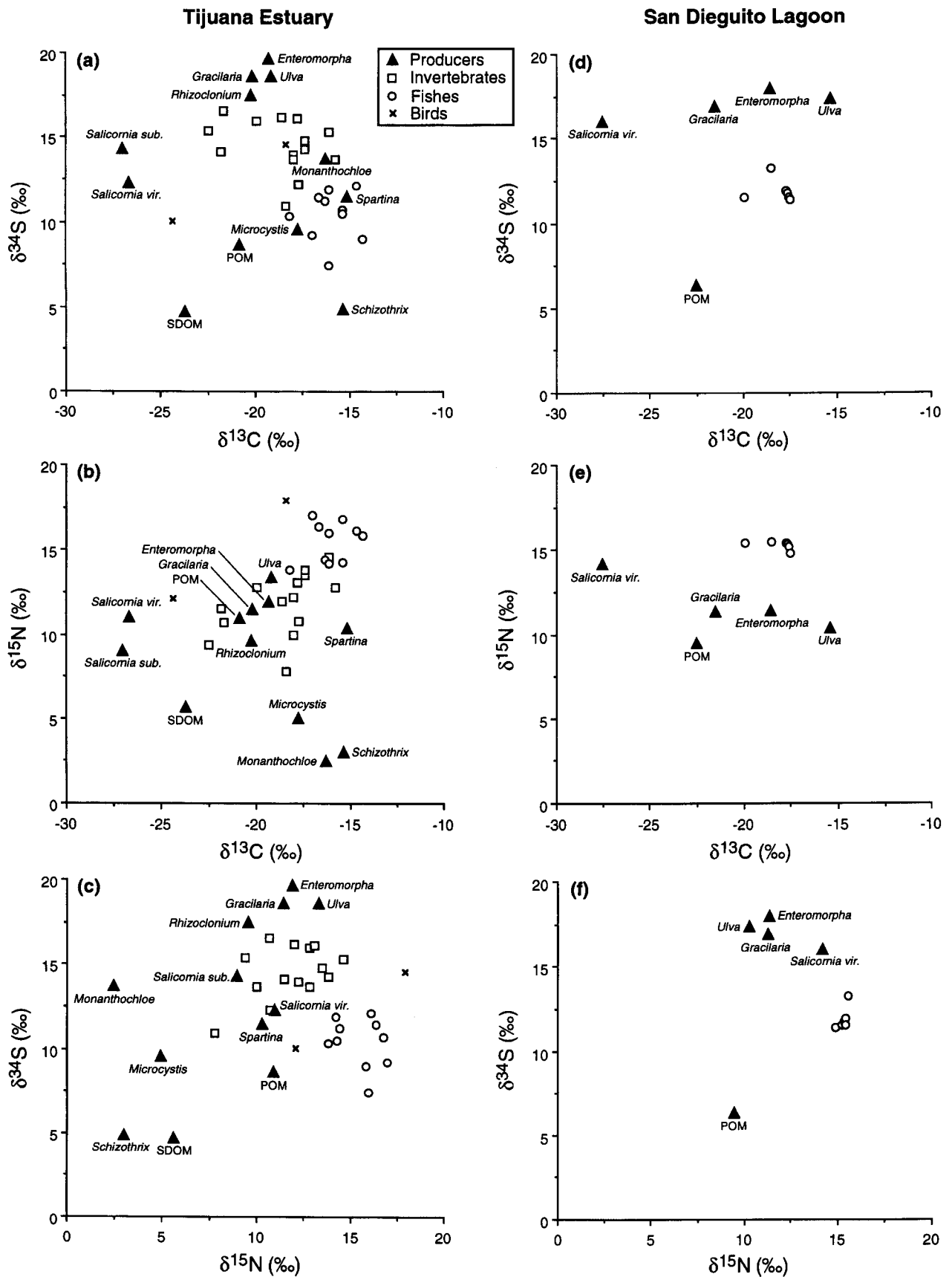


Fig. 4a-f Dual isotope plots of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ mean values for primary producers, sewage-derived organic matter (SDOM), suspended particulate organic matter (POM), and consumers of Tijuana Estuary (a-c) and San Dieguito Lagoon (d-f)

organic matter that forms the base of the food web that supports invertebrates, fishes, and the light-footed clapper rail. These producers together occupy three habitat types: tidal channels, low salt marsh, and mid salt marsh, a finding that indicates connectivity among these habitats. The only consumer sampled that appears dependent upon primary productivity from high salt marsh habitat is the sora.

Approximations using simple, two- and three-source mixing models suggested variations in relative contributions of organic matter sources among wetland food webs and consumers (Table 4). Two- and three-source mixing models solved for Tijuana Estuary produced ranges of relative inputs of *Spartina*, microalgae, and macroalgae (two-source models) that were consistent with either $\delta^{13}\text{C}$ or $\delta^{34}\text{S}$ distributions and precise estimates of relative inputs (three-source models) consistent with both $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ distributions. The solution of two- and three-source models indicated that *Spartina* provides the majority of organic matter that supports the fishes of Tijuana Estuary, supplemented with a substantial input of microalgae and a minimal macroalgae input. Model estimates suggested that macroalgae are the major producers supporting Tijuana Estuary invertebrates and the light-footed clapper rail with substantial input from microalgae and minimal input from *Spartina*. The marginally negative estimate for *Spartina* importance to Tijuana Estuary invertebrates indicated a minimal or no trophic linkage between those groups. Macroalgae and microalgae were the only sources incorporated into models for San Dieguito Lagoon, because *Spartina* is rare in that wetland. Estimates from those models suggest that inputs of macroalgae and microalgae support San Dieguito Lagoon fishes with that of macroalgae likely more important.

Discussion

Evidence discerning the food web base

Our primary objective in this research was to identify autotrophic producers that form the base of the food

web in southern California coastal wetlands. Our collective results indicate that macroalgae, marsh microalgae, and *Spartina* all support consumers in these ecosystems. Mixing model coefficients and a similarity between wetlands in isotopic compositions of producers and consumers indicate that when *Spartina* is absent from a salt marsh, organic inputs of macroalgae and microalgae form the base of the food web. The exception to the isotopic similarity is a significant difference in carbon isotopic composition of fishes that likely resulted from differential inputs of *Spartina*. In wetlands where *Spartina* does not occur, macroalgae become a more important source of organic matter for fishes. Furthermore, the relative contribution of these producers appears highly variable among consumers within a wetland, and our results may describe two complementary food web components – one of fishes supported primarily by *Spartina* and another of invertebrates and the light-footed clapper rail utilizing macroalgae as a primary source. However, each of the three producer sources plays a substantial role in supporting at least one consumer group (invertebrates, fishes, or birds). Our findings deductively exclude *Salicornia*, *Monanthochloe*, SDOM, and suspended POM as dominant, direct influences on the food web.

While stable isotope evidence has suggested that matter from sewage-derived outfalls enters offshore marine food webs (Spies et al. 1989; Van Dover et al. 1992), we found no compelling evidence to suggest a direct influence of SDOM on consumers in Tijuana Estuary. SDOM may, however, contribute indirectly to consumers of the estuarine food web by providing a source of inorganic nitrogen to marsh microalgae or other producers. SDOM and both types of microalgae have similar $\delta^{15}\text{N}$ values (Figs. 4b, c, Table 2), suggesting that these producers may have utilized nitrate or ammonium from sewage inflows. It is also plausible, however, considering the low $\delta^{15}\text{N}$ values measured (near zero), that microalgae are fixing nitrogen from the atmosphere, and that the sewage influence is minimal. The conversion of sewage urea to nitrate through hydrolysis and volatilization may increase resulting $\delta^{15}\text{N}$ values by 5–15‰ (Heaton 1986), which further limits

Table 4 Ranges of relative importance of inputs by primary producers in supporting invertebrate, fish, and bird consumers in Tijuana Estuary and San Dieguito Lagoon, based on two- and three-source mixing models

Consumer	Model	Producer relative importance (%)		
		Macroalgae	Marsh microalgae	<i>Spartina foliosa</i>
Invertebrates	Tijuana Estuary 2-source	42.3–76.1	0–36.0	0–57.7
	3-source	64.7	37.1	–1.8
Fishes	2-source	0–28.1	0–71.9	0–80.4
	3-source	7.8	38.5	53.7
Light-footed clapper rail	2-source	43.7–71.7	0–40.6	0–56.3
	3-source	62.3	30.8	6.9
Fishes	San Dieguito Lagoon 2-source	46.1–80.0	20.0–53.9	0

our ability to determine the ultimate fate of sewage derived nitrogen. Additional fine scale studies would be required to resolve the dilemma in southern California wetlands.

Our identification of food web organic matter sources and the lack of association between suspended POM and consumer isotopic compositions in these ecosystems challenges the dogma of a vascular-plant-based system that supports consumers through a detrital pathway (Mitsch and Gosselink 1993). Furthermore, we were unable to discern the sources of suspended POM in these systems. While *Spartina* presumably enters the Tijuana Estuary food web as detritus, our results suggest the possibility that a primary linkage between producers and consumers may be grazer-based or through benthic detritus. It appears that at least one component of the primary consumers we sampled feeds directly on macroalgae and microalgae – possibly in a state of decomposition with associated microfauna – with additional inputs from *Spartina* via a detrital pathway. Meiofaunal grazers, which we did not sample, may be an additional link in the food web (e.g., Sherr and Sherr 1988; Sullivan and Moncreiff 1990).

Trophic structure and interactions

We estimated a total of four trophic levels for the Tijuana Estuary food web by examining the ^{15}N isotopic distributions of consumers in that system (Fig. 3), and possibly one fewer trophic level in San Dieguito Lagoon. These trophic level estimates and precise trophic position of consumers should be interpreted with caution, as ^{15}N distributions of consumers are a function of source mixing as well as trophic enrichment. Furthermore, an additional trophic level presumably exists at each wetland that we studied (five total at Tijuana Estuary), composed of terrestrial top carnivores such as raptorial birds (e.g., northern harrier, *Circus cyaneus*), canids (e.g., coyote, *Canis latrans*), and feral animals (e.g., domestic cat, *Felis catus*) that are known from these wetlands (Zedler 1982).

In general, invertebrates occupied lower trophic positions than fishes, and smaller fishes were lower than larger individuals of the same species. The consumer in the lowest trophic position was *Trichocorixa reticulata*, which almost certainly feeds on the cyanobacteria *Microcystis*, based on their co-occurrence in shallow intertidal marsh pools and similar isotopic distributions. Juvenile California killifish were collected in the same marsh pools and had similar $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values as *Microcystis* and *T. reticulata* and an enriched $\delta^{15}\text{N}$ value, suggesting that the killifish were feeding on *T. reticulata* and that a three-level food chain exists in this microhabitat. The placement of the light-footed clapper rail at the highest trophic position is in accord with descriptions of its diet consisting of intertidal invertebrates and fishes (Eddleman and Conway 1994).

Comparison of Tijuana Estuary and San Dieguito Lagoon

Several ecological implications can be drawn by comparing isotopic compositions of producers and consumers between these two wetlands. The minor differences that we noted in producer isotope ratios were likely related to differences in tidal influence between the wetlands. The finding that the distribution of isotope ratios of San Dieguito Lagoon fishes was significantly more restricted than that of Tijuana Estuary fishes suggests that the food web of San Dieguito Lagoon is less complex and supports fewer trophic links than that of Tijuana Estuary. This difference may be related to both the number of species and connectance in each food web (Pimm 1982; Cohen and Newman 1988).

In this study, we compared isotope ratios of fishes from a wetland where *Spartina* is abundant (Tijuana Estuary) to those from a wetland where it is rare (San Dieguito Lagoon), to assess if *Spartina* ultimately supports consumers. We found differences in δ values of fishes between the two wetlands that were significant for ^{13}C , but not for ^{15}N or ^{34}S . $\delta^{13}\text{C}$ values of San Dieguito Lagoon fishes were 2.1‰ depleted, relative to those of Tijuana Estuary. This relative depletion represents a shift in $\delta^{13}\text{C}$ of San Dieguito Lagoon fishes away from that of *Spartina* and toward those of other producers identified as contributing sources to the Tijuana Estuary food web (macroalgae and microalgae). This comparison of consumers found in differing ecosystems provides supporting evidence that *Spartina* provides organic matter to the food web in wetlands where it occurs. Other examples of this comparative approach include isotopic analyses of consumers in marshes dominated by C_3 versus C_4 plants (Hackney and Haines 1980; Hughes and Sherr 1983), offshore consumers versus those found in seagrass meadows and salt marshes (Fry 1983), and consumers upstream versus downstream of a coastal deepwater sewage outflow (Van Dover et al. 1992).

Organic matter, producer, and consumer isotopic composition

The mean stable isotope ratios that we measured for SDOM originating from Tijuana, Mexico (Table 2), fell within the range of those reported from analyses of sewage from United States coastal populations, including samples originating from southern California municipalities (Van Dover et al. 1992 and references cited therein). Mean SDOM δ values from our analyses were slightly depleted in ^{13}C (−23.7‰ versus −22.8‰) and enriched in ^{15}N (5.6‰ versus 3.3‰) and ^{34}S (4.6‰ versus 2.5‰), relative to the mean of nine measurements of SDOM from United States sources (Van Dover et al. 1992).

The isotopic composition of detritus in salt marsh estuaries varies widely depending upon that of the autotrophic originating sources. Data on multiple stable

isotope ratios of POM from salt marshes are rare in the literature. Mean δ values of several POM size fractions from a Mississippi salt marsh (Sullivan and Moncreiff 1988a) were similar to those from Tijuana Estuary and San Dieguito Lagoon (Table 2), but Mississippi POM was depleted in ^{15}N , compared to that from southern California (5.2‰ versus 10.4‰). Detrital production dynamics in Tijuana Estuary have been shown to vary seasonally (Winfield 1980), and additional measurements may be required to describe the mean isotopic composition of detritus over an annual cycle.

We analyzed isotopic composition of two marsh microalgal communities, each dominated by different cyanobacterial genera (*Microcystis* and *Schizothrix*), and four genera of macroalgae that may be compared to results of other studies. The δ values for all three isotopes that we measured for both microalgal communities (Table 2) fell within ranges reported for epibenthic microalgae and cyanobacteria in other studies (-21‰ to -13‰ $\delta^{13}\text{C}$, -1‰ to 6‰ $\delta^{15}\text{N}$, $4\text{--}18\text{‰}$ $\delta^{34}\text{S}$; Haines 1976b; Peterson et al. 1986; Peterson and Howarth 1987; Craft et al. 1988; Sullivan and Moncreiff 1990; Currin et al. 1995). The δ values for macroalgae that we measured (Table 2) were more similar to mean values compiled for plankton (-21‰ $\delta^{13}\text{C}$, 9‰ $\delta^{15}\text{N}$, 19‰ $\delta^{34}\text{S}$; Peterson et al. 1985) than to those for macroalgae (-17‰ $\delta^{13}\text{C}$, 7‰ $\delta^{15}\text{N}$, 16‰ $\delta^{34}\text{S}$; Currin et al. 1995).

The isotopic composition of *Spartina foliosa* from Tijuana Estuary differed from that of *S. alterniflora* from eastern salt marshes. *S. foliosa* δ values (Table 2) were ^{13}C -depleted and enriched in ^{15}N and ^{34}S , relative to the corresponding ranges reported for *S. alterniflora* (-12‰ to -13‰ $\delta^{13}\text{C}$, 2‰ to 6‰ $\delta^{15}\text{N}$, -10‰ to 1‰ $\delta^{34}\text{S}$; Peterson et al. 1985; Peterson and Howarth 1987; Craft et al. 1988; Sullivan and Moncreiff 1990; Currin et al. 1995). The isotopic difference was especially prominent in $\delta^{34}\text{S}$ values, which differed by over 10‰ between species. The difference in carbon isotopic composition likely reflects differences in isotopic fractionation during uptake, while the large disparity in sulfur composition indicates that *S. foliosa* uses seawater sulfate at a substantially greater proportion than sulfides produced in anoxic marsh sediments (Peterson and Fry 1987). The differences in isotopic compositions of *S. foliosa* and *S. alterniflora* that we demonstrated reflect differences in physiological ecology between the species and affirm that caution should be exercised in substituting isotope ratios of *S. alterniflora* from Atlantic marshes as generalized values for other species of *Spartina*, particularly in Pacific Coast ecosystems (e.g., Spiker and Schemel 1979).

Other investigators in some cases have reported substantial variation in *S. alterniflora* isotope ratios associated with season or location within a marsh (Peterson et al. 1986; Sullivan and Moncreiff 1990). However, we found only minor variation in *S. foliosa* isotopic composition in Tijuana Estuary among four sites and between two seasons. The isotopic composition of the two *Salicornia* species that we analyzed from two wet-

lands was depleted in ^{13}C (Table 2), characteristic of upland and marsh C_3 vascular plants studied by others (Peterson et al. 1986; Peterson and Howarth 1987; Craft et al. 1988; Sullivan and Moncreiff 1990). Our *Salicornia* $\delta^{34}\text{S}$ values exceeded those reported for C_3 plants associated with eastern salt marshes by over 7‰, indicating a greater reliance on seawater sulfate for C_3 high marsh plants in southern California systems.

The isotopic composition of consumers varies widely within and among ecosystems and reflects that of their diet and the ultimate sources of organic matter to the corresponding food web (Peterson and Fry 1987). The isotopic composition of consumers in Tijuana Estuary appears to describe a single interconnected food web, which may contain two subcomponents, supporting invertebrate and fish consumers and the light-footed clapper rail. The light-footed clapper rail is nonmigratory and is found in low tidal marsh habitat dominated by *Spartina foliosa* and *Salicornia virginica* where it feeds on intertidal invertebrates and fishes (Eddleman and Conway 1994). Sora isotopic composition was distinct from all other consumers sampled, and δ values of the two specimens sampled varied widely. The sora is migratory and is found in freshwater, brackish, or salt marshes associated with emergent vegetation, including *Spartina* (Melvin and Gibbs 1994). Also, its food habits are much more varied than those of the light-footed clapper rail; soras feed on a variety of plant material and terrestrial and aerial invertebrates, which would explain the observed variance and similarity in isotopic composition of the sora and *Salicornia* and other upland C_3 plants.

The minimum $\delta^{15}\text{N}$ value of consumers collected in our study (7.8‰ for *Trichocorixa reticulata*; Table 3) is higher than corresponding minima from Atlantic and Gulf salt marshes (2.2‰ to 6.2‰; Peterson et al. 1985; Peterson and Howarth 1987; Fry 1988; Sullivan and Moncreiff 1990; Currin et al. 1995). This ^{15}N enrichment in consumers reflects a similar enrichment, relative to Atlantic and Gulf systems, of macroalgae and *Spartina foliosa*, two of the three sources of food web organic matter that we identified. This finding suggests that a source of ^{15}N -enriched dissolved inorganic nitrogen is available in southern California marshes, but its origin has not been identified. Previous studies suggest that possible sources of ^{15}N -enriched inorganic nitrogen in these systems may include volatilized sewage (Heaton 1986), watershed runoff or groundwater inputs (Winfield 1980; Page 1995; Page et al. 1995), or tidal import from seawater (Winfield 1980; Liu and Kaplan 1989).

Regional comparisons

Numerous studies of Atlantic and Gulf of Mexico salt marshes employing only a single stable isotope reported varying relative influences of vascular plants and algae as organic matter sources supporting the salt marsh food

web (Haines 1976a, b, 1977; Haines and Montague 1979; Hackney and Haines 1980; Kneib et al. 1980; Hughes and Sherr 1983; Schwinghamer et al. 1983). In general, these studies suggest that *Spartina* detrital inputs to the food web are dominant in supporting consumers in Atlantic Coast salt marshes, but phytoplankton or benthic algae may be equally or more important sources in Gulf systems. The role of terrestrial import and C_3 plant contributions to these food webs could not be resolved by single isotope approaches, but may be important in some marshes (e.g., Hackney and Haines 1980).

Application of multiple stable isotopes (^{13}C , ^{15}N , and ^{34}S) to identify sources of organic matter in salt marsh food webs has provided more conclusive results and allowed the consideration of more producers relative to those studies applying a single isotope. Multiple stable isotope research in salt marshes of Massachusetts and Georgia (Atlantic Coast) indicated that *Spartina* and algae may be nearly equally important contributors to those food webs, with the balance shifting depending on location in the marsh, feeding mode, size, and trophic position of consumers (Peterson et al. 1985, 1986; Peterson and Howarth 1987). Conversely, multiple isotope evidence from Louisiana and Mississippi (Gulf Coast) salt marshes suggested that *Spartina* is not an important source of organic matter in those systems, and that the food webs are primarily supported by benthic and planktonic algae (Fry 1983; Sullivan and Moncreiff 1990).

The food webs of the southern California wetlands that we studied do not readily conform to generalizations that may be developed for Atlantic and Gulf coast wetlands. The substantial relative contribution of algae to the salt marsh food webs of southern California and Gulf systems may reflect high rates of algal primary production, relative to those of vascular plants. In Atlantic salt marshes, the ratio of annual epibenthic algae production to vascular plant aerial production typically ranges from 0.25–0.43 (Sullivan and Moncreiff 1988b; Pinckney and Zingmark 1993; and references cited therein), but has ranged up to 0.61 in a Mississippi Gulf Coast salt marsh (Sullivan and Moncreiff 1988b) and from a minimum of 0.76 to as high as 1.40 in Tijuana Estuary (Zedler 1980). Furthermore, production estimates of vascular plants in Tijuana Estuary and Mugu Lagoon suggest that vascular plant productivity is lower in southern California salt marshes than in corresponding eastern U.S. systems (Onuf et al. 1979; Winfield 1980). Total primary productivity may be similar between East and West coast salt marshes, however, with the difference in vascular plant production compensated for by that of algae.

Our results suggest that *Spartina foliosa* is an important source of organic matter for the food web of Tijuana Estuary – a finding that may be contrary to expectations. In San Francisco Bay, $\delta^{13}C$ analyses revealed that *Spartina* was not an important source of detritus in that large estuarine system (Spiker and

Schemel 1979). A minimal influence may also have been expected in our study considering the restricted range in which *Spartina* is distributed within salt marshes where it occurs in southern California. A lower photosynthetic potential of *Spartina foliosa*, compared to its eastern congener, *S. alterniflora* (Seneca and Blum 1984), would also reduce its potential input to the food web. Nonetheless, the spatial proximity of *Spartina foliosa* in low salt marsh habitats to aquatic consumers likely facilitates organic matter inputs through a detrital pathway.

Success in identifying ultimate sources (primary producers) of organic matter in a food web is dependent upon the ability to differentiate potential sources isotopically. This differentiating ability diminishes as additional sources are considered and isotopic distributions overlap. Southern California coastal wetlands are distinct in their topography, hydrology, and vegetation (Zedler 1982). They are small and discrete, usually confined to narrow river valleys that are separated by hills or mountains. In the wetlands we sampled, high salt marsh habitat (c. 0.8–1.6 m NGVD) lies within meters of intertidal channels or bays. Thus, producers associated with all marsh habitats must be considered as potential sources of organic matter for the aquatic food web. In contrast, Atlantic or Gulf coastal wetlands typically support vast stands of monotypic vegetation that may span kilometers, and fewer producers require consideration. Untreated wastewater inflows in southern California wetlands constitute an additional anthropogenic source of organic matter to include in food web analysis, which is generally less applicable to eastern coastal wetlands. Because more sources warrant examination in southern California coastal wetlands, it may be more difficult to resolve food webs using stable isotope techniques in these systems.

Management implications

In order to manage coastal wetland fishes, it is critical to understand how the different habitats that provide foods are coupled with habitats that support spawning and nursery functions and provide resting and refuge areas. Tidal systems have great potential for significant linkages between marshes and channels, with two-way exchanges of consumers and foods being possible. That is, fishes may move into the marsh to feed, and foods may move into the channels to be consumed. Our finding that macroalgae, marsh microalgae, and *Spartina* all contribute to the wetland food web supports this linkage and affirms that these habitats should be managed as a single ecosystem. Knowing that this link exists is important for planning habitat enhancement and restoration projects. There are even greater implications for restoration projects that take place within a mitigation context.

There are few suitable mitigation sites in southern California, and choices are often made between creating channel habitat designed primarily for fishes versus

marsh habitat for endangered birds. While there is good understanding that channel fishes and invertebrates support birds that reside in salt marshes, the importance of the marshes to fish production has not been clarified, and the tradeoffs are unclear. Recently, the Port of Los Angeles constructed > 40 ha of fish habitat basins at Anaheim Bay, mostly without basin-salt marsh linkages or watershed-basin linkages (MEC 1991). Similarly, the Port of Long Beach was required to provide fish habitat at Batiquitos Lagoon to compensate for filling and expansion of port facilities (City of Carlsbad 1989); initial plans showed very little marsh area. Fishes are present in these basins, but it is not clear if the habitats function as effective feeding sites. Although mitigators receive full credit for creating channel or basin habitat, a rationale for giving fish mitigation credits for marsh restoration has been lacking. The plans for Anaheim Bay and Batiquitos Lagoon may well have been different, had there been clear evidence that fish depend on marshes for a significant portion of their food supply.

Our information comes in time to influence future restoration projects, including two that are large and involve tradeoffs between fish and endangered bird habitat.

1. The State Coastal Conservancy and California Department of Parks and Recreation (Entrix et al. 1991) propose to restore 200 ha of salt marsh and tidal channels at Tijuana Estuary, effectively doubling the area of tidal wetland in that system. Funding to implement the project may need to come from mitigation projects, many of which are designed to compensate for damage to fish habitat. Without evidence that salt marsh producers are useful to fishes, port authorities will be uninterested in the Tijuana Estuary restoration project, which is large (200 ha) and one of the few that focuses on lost salt marsh habitat.

2. California Edison must substantially restore 60.7 ha of coastal wetland (habitat types not specified) to mitigate damages caused to fish populations that are entrained in the cooling water intake of their San Onofre Nuclear Generating Station (CCC 1991). The California Coastal Commission also recognized the value of supporting biodiversity and food web support functions, and they included a requirement for habitat that would support rare species. Our information on the salt marsh-channel linkage shows that these goals are not incompatible, and that construction of tidal marshes contributes to both objectives.

Our study demonstrates a channel-marsh interaction, but an important ecological question remains: to what degree do fishes actually depend on marsh producers? If marsh plants are critical to the food web, then fish-mitigation credit should be given for restoring or creating tidal marsh habitat. Negotiations surrounding mitigation agreements are complex, with ratios of 1:1 to 4:1 commonly used by the California Coastal Commission. That is, a mitigator who damages 1 ha of wetland may be asked to replace it with 4 ha of restored land. We look to future studies to quantify these spatial rela-

tionships and to make more specific recommendations for wetland restoration and mitigation.

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