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ARTICLE

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Does tidal marsh restoration lead to the recovery of trophic pathways that support estuarine fishes?

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Abstract

Evaluation of tidal marsh restoration success is typically based on the recovery of habitat size and target species. However, food-web structure may provide valuable insight into ecosystem functioning trajectories. Here, we studied restored tidal marshes of different ages (*new*, *young*, *old*; spanning 1–150 years) in comparison with nearby reference sites along the San Francisco Estuary. We asked: (1) How does restoration help recover energy pathways that support fishes? (2) Do fishes rely more on algal versus detrital pathways in restored sites?; and (3) How does food-web structure vary as a function of species origin and life history? To answer these questions, we sampled fish ($n = 806$) and basal resources (emergent vegetation and phytoplankton; $n = 109$) seasonally over two hydrologically contrasting years. Using stable isotopes (δ^{13}C, δ^{15}N, and δ^{34}S), we calculated fish isotopic niche volumes, food chain lengths, and the relative importance of algal versus detrital energy pathways. We found that food chains in restored sites were 8% shorter than in their paired reference sites. Additionally, the *young* and *old* restored sites had 37% smaller niche volumes than their references, but the opposite was true for the *new* restored site (11% larger), illustrating the characteristic trophic surge of early succession. Fishes found in restored sites relied significantly less on detrital energy (7% less) than fishes found in reference sites, and resident fishes showed 12% higher reliance on the detrital pathway than transient species. Finally, most of the native niche volume overlapped with that of introduced fish, which was in turn 38% larger, and a similar pattern was observed when comparing resident to transient fish. Our findings demonstrate that food-web structure does not immediately recover with tidal marsh restoration, even if fish assemblages are species-rich; and show that transient trophic surges may complicate restoration success assessments of newly restored marshes. We contend that incorporating recovery of energy pathways as an indicator of performance may help strengthen monitoring and design of wetland ecosystem restoration projects.

KEYWORDS
allochthony, ecosystem restoration, food-web ecology, niche volume, stable isotopes, wetlands

INTRODUCTION

Wetlands are critically important habitats that provide nearly 40% of the Earth's annual ecosystem services while covering less than 2% of its surface (Junk et al., 2013). These services include protection from sea-level rise and flooding, water quality enhancement, carbon sequestration, and fisheries production (Gilby et al., 2021; Vitousek et al., 1997; Zedler & Kercher, 2005). Despite their importance, more than half of the wetlands that existed in the early 1900s have been lost to human activity (Mitch & Gosselink, 2007). The passing of the Clean Water Act in 1977 marked a historical inflection point in wetland conservation in the United States. Between 1990 and 2010, more than 70 billion dollars were spent attempting to restore three million hectares of wetlands (marshes, bogs, and swamps) in North America (Copeland, 2010). More recently and on the global scale, the United Nations has declared 2021–2030 as the Decade on Ecosystem Restoration to ameliorate the impacts of climate change, land use change, and the loss of wildlife habitat, biodiversity, and other ecosystem services (UN General Assembly 73rd Session, 2019). This renewed focus is expected to lead to an increase in the restoration of tidal marshes and associated ecosystem services such as fishery production. However, research to better understand and inform how to effectively recover tidal marsh ecosystems in terms of functioning ecosystems, and not just size, is still in its early stages.

In the San Francisco Bay-Delta ("Bay-Delta"), California, USA, widespread diking, draining, and dredging transformed the landscape from a tidal marsh-dominated ecosystem to an open-water dominated ecosystem by the mid-1900s (Nichols et al., 1986; Whipple et al., 2012), resulting in an estimated 77% loss in wetland habitats (primarily tidal marshes), 94% loss in net primary productivity, and 89% loss in carbon flow to herbivores (Cloern et al., 2021). Accompanying these ecosystem losses is the highest documented rate of biological invasions in any estuary in the world (Cohen & Carlton, 1998). However, over the last two decades, hundreds of square kilometers of reclaimed tidal marshes have been tidally restored via levee breaches, and numerous multiagency restoration projects are underway or planned, with the goal of restoring over 120 km^2 of marshland by 2050 (California EcoRestore, 2020). A primary objective of these projects is to recover native fishes, many of which are threatened and declining due to habitat alteration and food limitation (Herbold et al., 2014). Recent advances in understanding food-web dynamics come from stable isotope studies that quantify the relative contribution of energy pathways to primary and secondary consumers (Howe & Simenstad, 2011; Schroeter et al., 2015; Young et al., 2021). These approaches show that tidal marshes can support diverse food webs, owing to complex channel networks with mixed residence times (Enright et al., 2013; Stumpner et al., 2021) and a combination of "brown" and "green" energy pathways (i.e., fueled by decomposing terrestrial plant matter and phytoplankton, respectively; Colombano et al., 2021; Brown et al., 2024). While food-web-focused approaches in evaluating restoration outcomes can be promising, they are still precursory in restoration ecology (Loch et al., 2020; Palmer et al., 2016).

Restoration age often predicts successional stage (Moreno-Mateos et al., 2012) and provides a rationale for comparing sites that were restored at different points in time in the past as an indicator of a restoration trajectory (i.e., *chronosequence*). However, the geographic and environmental contexts of a restoration site also play important roles. For example, a global meta-analysis of response ratios between restored and reference tidal marshes showed that biodiversity recovered at relatively faster rates in sites with higher levels of hydrologic connectivity (e.g., tidal and riverine systems), warmer climates (e.g., temperate and subtropical environments), and larger tidal marsh habitats (Moreno-Mateos et al., 2012). In the Bay-Delta, a stable isotope study showed that restored marshes ranging from 11 to 73 years old had recovered emergent vegetation communities capable of supporting a diverse array of invertebrates and fishes via the brown pathway, however the specific organic matter sources shifted with location along the salinity gradient (Howe & Simenstad, 2011). Studies combining newly restored marshes (<10 years old) with older ones, paired with relevant, local references, could help understand how the reliance of fishes on algal versus detrital pathways may change as succession advances. Evidence from other systems suggests that mobile taxa (e.g., invertebrates and birds) tend to reestablish quickly, but carbon and nitrogen cycling, and organic matter accumulation, recover slowly (Meli et al., 2014; Moreno-Mateos et al., 2012; Ruhí, Fairchild, et al., 2016). Similarly, energy pathways may also recover at different rates: phytoplankton communities may reestablish immediately after tidal hydrology is restored, but vascular plants supporting detrital pathways may take longer (Ballantine & Schneider, 2009; Howe & Simenstad, 2015). We hypothesize that when the strength of the detrital pathway is not yet fully recovered in a restored marsh, its capacity to support primary and secondary consumers may remain limited to those using the algal pathway, in turn reducing food availability for piscivorous fishes (see Figure 1A).

A wide range of life history and foraging strategies are common among estuarine fishes due to the dynamic nature of the environment, which shifts rapidly at diel to interannual scales (Rountree & Able, 2007). Many primary consumers can exploit resources from both the brown and algal energy pathways (e.g., by collecting detritus deposited on the benthos, or by filtering particles from the water column; Kreeger & Newell, 2000). Additionally, some resident fishes live in the marsh for their entire life, while others do so during certain life stages (e.g., as juveniles) or opportunistically, moving into marshes on a tidal or daily basis in search of food and cover (Kneib, 1997; Rountree & Able, 2007). Finally, introduced species, commonly generalists, often exploit a wide diversity and abundance of prey relative to their more specialist, native counterparts (Matern et al., 2002). Because all trophic levels in the Bay-Delta system have been heavily invaded, most predator–prey relationships are novel from an evolutionary standpoint (Matern & Brown, 2005). This high diversity in foraging strategies and life histories likely provides stability to the fish assemblage (Colombano et al., 2022) but also challenges any assessment of food-web structure, given the high degree of omnivory and temporal variability.

Our study sought to assess whether tidal marsh restoration leads to the recovery of diverse energy pathways that support estuarine fishes. We evaluated restoration sites of different ages (*new*, *young*, *old*; spanning 1–150 years) along the Bay-Delta's estuarine salinity gradient (seaward, middle, and landward). Building on previous work (Grimaldo et al., 2009; Howe & Simenstad, 2015; Wozniak et al., 2006; Young et al., 2021), we tracked energy flows among key components of the aquatic food web using the stable isotopes $\delta^{13}C$ (to assess the carbon source), $\delta^{15}N$ (to determine trophic position), and $\delta^{34}S$ (to track marine influence), and we characterized individual fish populations as well as the whole community (Layman et al., 2012).

We first asked, how does food-web structure differ between restored and reference tidal marshes? We tested this question by calculating food chain length (FCL) and isotopic niche volume for fish communities collected at restored and reference sites. Theory posits that disturbance frequency, nutrient limitation, and habitat size reduction can all shorten food chains (Post, 2002). While breaching levees may immediately restore tidal hydrology and increase phytoplankton production, stores of particulate and fine organic matter are slow to build and may limit detrital pathways after the initial influx of decaying terrestrial plants and associated productivity, or "trophic surge" (Baer, 2016; Ballantine & Schneider, 2009; Howe & Simenstad, 2015). Thus, we hypothesized that young restoration sites would support fish communities that are structurally simpler, that is, with lower trophic positions and with less diverse (or "compressed") isotopic niches relative to reference marshes (Figure 1A,B). Second, we asked, to what extent do fishes rely on algal versus detrital pathways, and does restoration shift reliance? We tested this question by running Bayesian mixing models with terrestrial vegetation and phytoplankton as sources. We hypothesized that fishes in restored sites may largely rely on the "green" or algal pathway, as detrital pathways are slower to establish (Ballantine & Schneider, 2009; Howe & Simenstad, 2015). We believe this pattern could be due to a well-recognized lag in the recovery of biogeochemical functioning after tidal marsh ecosystem restoration (Moreno-Mateos et al., 2012). Third, what role do the associated origins (i.e., introduced vs. native) and life histories of fishes (i.e., resident vs. transient) play in potentially shifting food-web structure, for example, by changing community membership and "sequestering" energy? We tested this question by comparing these groups' niche volumes, and their resulting niche overlaps. We hypothesized that the introduced fish assemblage would have a larger and more unique isolated niche volume than the native assemblage (Figure 1B), due to the region's long history of invasions (Cohen & Carlton, 1998) and the fact that introduced species are often generalist feeders or occupy unique niches (Comte et al., 2016; Schroeter et al., 2015; Young et al., 2017). Additionally, resident species that typically reside in marshes may rely on terrestrially derived organic matter that is available year-round (Davis et al., 2024; Young et al., 2021). Answering these questions could help calibrate expectations for how native fishes may benefit from tidal marsh restoration efforts via the recovery of trophic pathways, in the San Francisco Bay-Delta and beyond.

METHODS

Study system and sample design

The San Francisco Bay-Delta is the largest drowned river valley estuary on the west coast of North America. It is located at the confluence of the Sacramento and San Joaquin rivers—the two major watersheds draining California's Sierra Nevada. As a result of the Mediterranean climate consisting of cool, wet winters and hot, dry

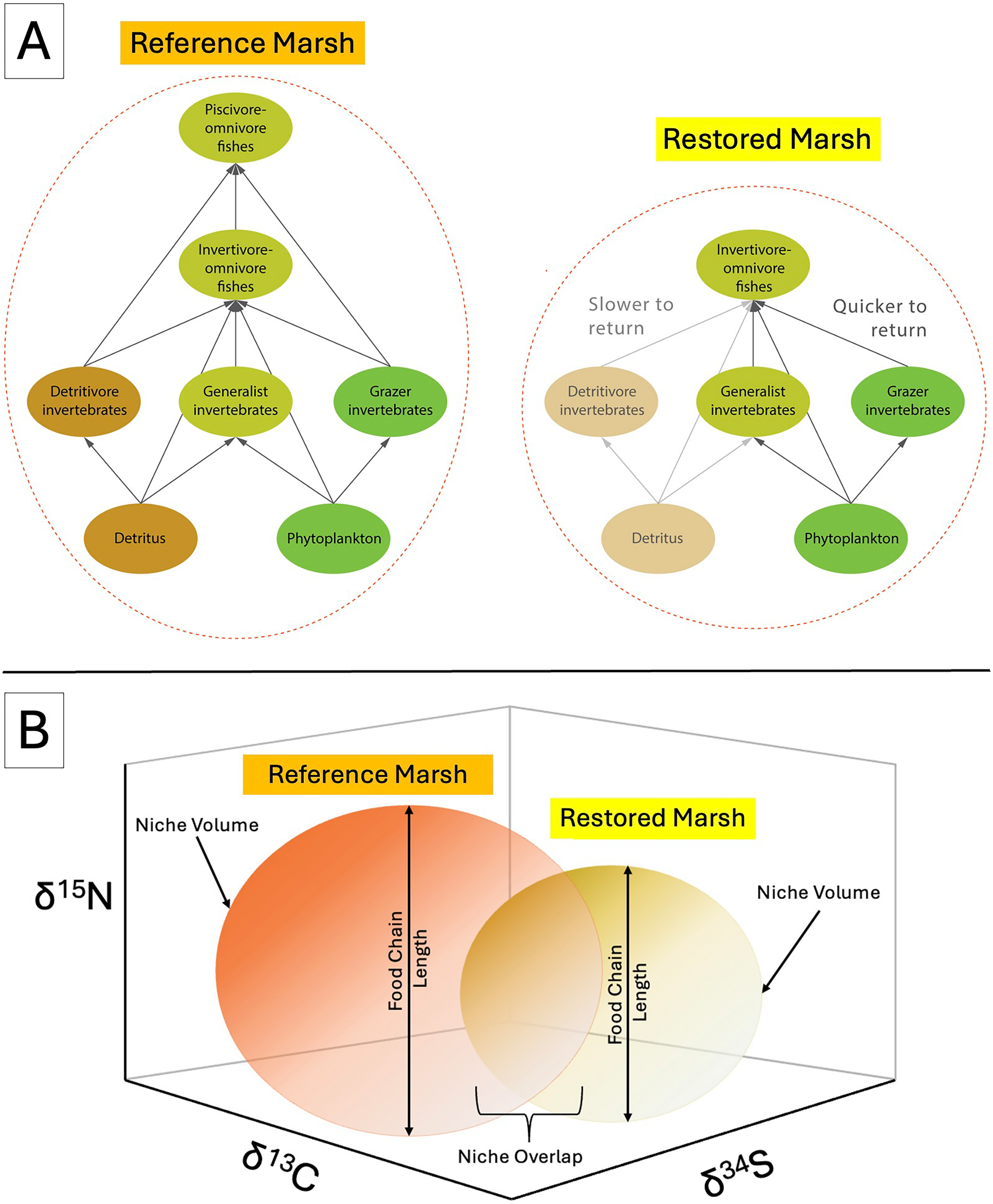

FIGURE 1 Hypothesized energy pathways in a reference versus a restored marsh food web and associated stable isotope analysis metrics. (A) Conceptual diagram representing the main energy pathways in a tidal marsh food web, in reference (continuously hydrologically connected) versus restored conditions (hydrologically fragmented and then reconnected). (B) Associated metrics of vertical structure and total trophic niche size. Food chain length (FCL) is measured as the number of trophic levels between a top predator and the basal resources that support their prey (both on the algal and detrital sides). Niche volume is measured as the isotopic volume encompassing all δ^{13}C, δ^{15}N, and δ^{34}S samples, while niche overlap represents the intersecting volume between two niches.

summers, interannual variation in estuarine salinity occurs based on prevailing freshwater flow patterns that shift on seasonal and multiyear cycles (Dettinger et al., 2016). Sampling sites spanned a highly dynamic oligohaline–mesohaline region located seaward of the river confluence, where salinity may vary from 0 to 15 ppt within marshes (Jassby et al., 1995; see Table 1 for site-specific salinity ranges).

Prior to European colonization, the Bay-Delta was an extensive mosaic of tidal marshes and channels; however, widespread land use change resulted in over a 70% loss of primarily marsh habitat (Cloern et al., 2021) and a transition to mainly open-water habitat (Nichols et al., 1986). The remaining marshes are a patchwork of ancient, centennial, and restored marshes with different management histories and configurations. Focal sites in this study include Tule Red Tidal Restoration Project (hereafter Tule Red; restored) and its reference (Ryer Island); Wheeler Island Conservation Area (hereafter Wheeler Island; restored) and its reference (Chipps Island); and the southwest portion of Sherman Island (Sherman Island; restored) and its reference (Browns Island). Each site was classified based on its history of hydrologic connectivity. Reference marshes are those that were never cut off from their tidal flow, while restored marshes were once disconnected from tidal flow but then reconnected via levee breaching, either intentionally (Tule Red) or unintentionally (Wheeler Island and Sherman Island). Chipps Island and Wheeler Island are tidal marshes with mixed habitat use and history, but include significant parcels that are classified as reference or restored, respectively; sampling was limited to those areas.

Study sites spanned over two orders of magnitude in time since restoration (from 1 to 150 years): Tule Red's levee was intentionally breached in 2019, after careful planning and design ("new restoration"), Wheeler Island was breached in 2008 after levee failure ("young restoration"), and Sherman Island experienced a series of levee failures starting in 1870 ("old restoration"; Table 1). Our design paired each restored site with a nearby reference site to control for food-web structure differences that could be driven by the geographic and salinity gradient (seaward, middle, landward position) rather than by differences in age (Figure 2). At each site, we sampled three

TABLE 1 Study site characteristics including age (of restored sites), location along the estuarine gradient, parcel size, restoration history, average salinities, and landscape context of marsh sites.

Variable	Tule Red	Ryer Island	Wheeler Island	Chipps Island	Sherman Island	Browns Island
Status and age of restored site	Restored, New (2019)	Reference of New	Restored, Young (2008)	Reference of Young	Restored, Old (1870)	Reference of Old
Estuarine location	Seaward	Seaward	Middle	Middle	Landward	Landward
Size (km^2)	1.70	3.47	0.50[a]	3.45[a]	5.67	2.41
Restoration history	Intentional levee breach after channel excavation/revegetation	…	Levee failure	…	Levee failure	…
Salinity (psu), mean (min–max)	7.25 (3.70–13.61)	7.45 (3.47–13.28)	4.38 (1.19–9.73)	3.01 (0.93–7.11)	1.56 (0.29–4.79)	2.15 (1.15–5.67)
Average WY (2020)	6.16 (3.70–9.48)	5.81 (3.47–8.40)	2.70 (1.19–5.80)	1.75 (0.93–2.34)	0.69 (0.29–1.54)	1.61 (1.15–1.82)
Dry WY (2021)	8.33 (5.83–13.61)	9.10 (4.82–13.28)	6.06 (3.03–9.73)	4.27 (2.04–7.11)	2.44 (1.01–4.79)	3.42 (2.03–5.67)
Landscape context	Embedded in large marsh complex and connected to shallow open water/shoal habitat	Marsh island surrounded by shallow open water/shoal habitat	Embedded in large marsh complex and connected to shallow open water/shoal habitat. Other land uses occur on property	Marsh island surrounded by shallow open water/shoal habitat	Marsh island surrounded by shallow to deep open water habitat; located at the confluence of two major rivers	Marsh island surrounded by shallow to deep open water habitat; located at the confluence of two major rivers

Abbreviation: WY, water year.

[a] Sites with mixed habitat use and history, including the parcels that we sampled, classified as reference or restored.

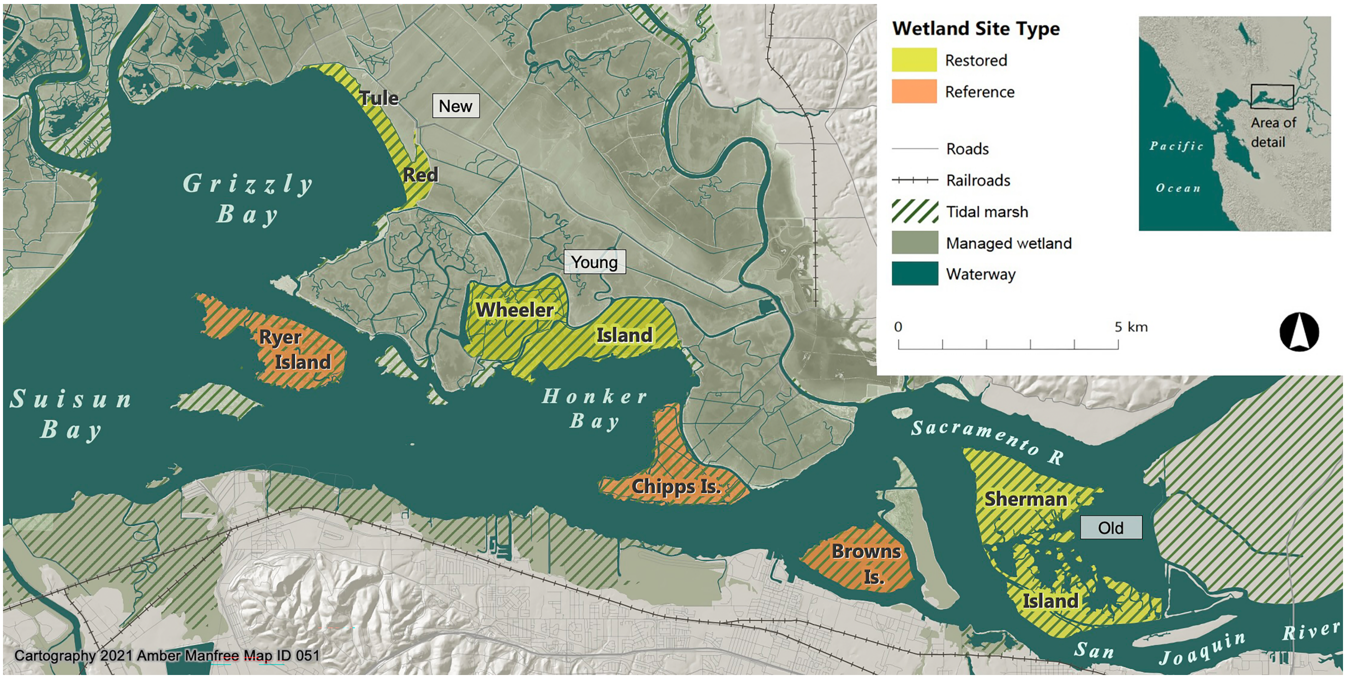

FIGURE 2 Study area. Study area in the San Francisco Bay-Delta (California, USA). Study sites include three restored tidal marshes (yellow) and three paired reference sites (orange) located between Grizzly Bay (seaward) and the Sacramento-San Joaquin confluence (landward). Tule Red and Ryer Island are the *New* restoration pair, Wheeler Island and Chipps Island are the *Young* restoration pair, and Sherman Island and Browns Island are the *Old* restoration pair. Map credit: Amber Manfree.

locations in both the exterior marsh edge and interior channels to capture microhabitat-level variation within and between sites during the winter (February–March) and summer visits (May–July). We sampled in 2020, an average water year, and again in 2021, an anomalously dry year when salinity levels were 2.2-fold higher on average (Table 1).

Field sample collection

We studied food webs by focusing on the upper trophic level (fish) and the basal resource level (phytoplankton and emergent vegetation) that support their prey. For all groups, we collected parallel samples to aid in taxonomic characterization and to gather enough biomass for stable isotope analyses. We targeted phytoplankton using 50 μm net-tows for 5 min, sieved through a 100-μm filter to remove any zooplankton, then filtered through a pre-combusted Whatman GF/F filter. This process was repeated in the interior and exterior of each site during an ebbing tide. We recognize that these samples contain, in addition to phytoplankton microalgae, small amounts of suspended particulate organic matter (SPOM) that could have multiple origins. For simplicity, we deemed this component to represent the algal pathway throughout our analyses. On average, ambient chlorophyll *a* concentration values in the system were 1.5–2.5-fold higher in the summer than in the winter samplings (Appendix S1: Table S1). With regard to emergent vegetation, we manually collected *Schoenoplectus* sp. and *Typha* sp. from three independent sampling locations in the interior and exterior of each site (if present).

Regarding fish collection, we combined minnow traps and 10-min otter trawls in the exterior and interior channels of each site, applying equal effort for tows and minnow traps across sites. We then identified and measured each fish, and we stored them at −20°C until further analyses. Our fish sampling was effective at targeting a wide range of small-to-medium-sized fish (approximately 10–400 mm in fork length; Table 2). After all fish were collected, counted, and measured, we devised a strategy to select species for stable analyses first, and then individuals for the selected species. Regarding species selection, we sought to include as many species and trophic strategies as possible, prioritizing those that were consistently present across sites, and with high replication (Appendix S1: Table S2). To select individual fish for stable isotope analysis, we used a decision tree aimed at maximizing coverage across seasons, habitats, and body size ranges. Specifically, if there were 15 individuals or fewer of a species at a given site and year, all 15 individuals were processed for stable isotope analyses. If there were over 15 individuals at a given site and year, we first grouped those individuals based on sampling

TABLE 2 Mean and SD of fork lengths (FL, in millimeters) by species, and associated numbers (N) of individual fish that were used in stable isotope analysis, caught in the 2020 (average water year) and 2021 (dry water year) winter and summer sampling seasons.

		Mean ± SD fork length (N individuals)			
Species	**(Scientific name)**	**Winter 2020**	**Summer 2020**	**Winter 2021**	**Summer 2021**
Resident					
Golden shiner[a]	(*Notemigonus crysoleucas*)	90 ± 29 (13)	112 ± 30 (17)	100 ± 23 (9)	115 ± 38 (2)
Menidia sp. silverside[a]	(*Menidia* sp.)	64 ± 9 (11)	80 ± 7 (7)	61 ± 17 (14)	62 ± 20 (34)
Prickly sculpin	(*Cottus asper*)	65 ± 10 (4)	73 ± 18 (35)	76 ± 18 (35)	66 ± 19 (33)
Threespine stickleback	(*Gasterosteus aculeatus*)		39 ± 9 (29)	41 ± 11 (4)	42 ± 6 (3)
Tridentiger sp. goby[a]	(*Tridentiger* sp.)	76 ± 17 (4)	68 ± 16 (12)	66 ± 19 (24)	62 ± 14 (30)
Tule perch	(*Hysterocarpus traskii*)	122 ± 32 (18)	64 ± 40 (38)	133 ± 6 (7)	51 ± 20 (21)
Yellowfin goby[a]	(*Acanthogobius flavimanus*)	132 ± 39 (9)	77 ± 25 (25)	142 ± 44 (15)	77 ± 21 (58)
Transient					
American shad[a]	(*Alosa sapidissima*)	89 ± 11 (22)	123 ± 12 (13)	100 ± 0 (2)	89 ± 37 (46)
Clupeidae[a]	(*Clupeidae*)		34 ± 4 (31)		
Longfin smelt	(*Spirinchus thaleichthys*)		31 ± 3 (28)		
Northern anchovy	(*Engraulis mordax*)				77 ± 4 (22)
Sacramento splittail	(*Pogonichthys macrolepidotus*)	128 ± 13 (30)	176 ± 40 (18)		
Striped bass[a]	(*Morone saxatilis*)	122 ± 19 (21)	120 ± 56 (14)		90 ± 64 (25)
Threadfin shad[a]	(*Dorosoma petenense*)	87 ± 7 (23)			

Note: Species are grouped by life history (resident or transient).

[a] Non-native status.

season (winter vs. summer), then habitat (interior vs. exterior), and finally by size class. Each of these groupings is hereafter referred to as a "stratum." We then gave identification numbers to the individual fish and selected them randomly within each stratum until we reached 15 "replicates" for the stratum. After selection, we checked via logistic regression that variation in size among individuals of that species did not influence the probability of a given individual being selected. We found no significant effect of size on selection probability in any species except for threespine stickleback (*Gasterosteus aculeatus*) (Appendix S1: Table S3).

Laboratory sample processing

We processed a total of 915 samples for δ^{13}C, δ^{15}N, and δ^{34}S isotope analysis, encompassing fish ($n = 806$), phytoplankton ($n = 37$), and emergent vegetation ($n = 72$; Appendix S1: Figure S1, Table S4). For fish, we thawed and dissected the left posterior dorsal muscle tissue of all fish collected. For all other samples, we thawed and rinsed them with deionized water to remove contaminants. We dried all samples at 50°C for a minimum of 72 h or until constant weight was reached, then ground samples into a homogeneous powder via a ball mill grinder or a mortar and pestle. We then weighed all homogenized powders via a 6-place microbalance (Mettler Toledo XPE206DR), loaded the appropriate amount of sample (1.5–1.8 mg for animal tissue and 2.0–2.4 mg for basal resources) into tin capsules, and placed them onto 96-well culture plates. Samples were analyzed at the Center for Stable Isotope Biogeochemistry (CSIB) on the UC Berkeley campus (Berkeley, CA). At CSIB, δ^{13}C, δ^{15}N, and δ^{34}S isotopic values and percentages were determined by continuous flow (CF) triple isotope analysis using a mass spectrometer (CHNOS elemental analyzer interfaced to an IsoPrime100 [Isoprime Ltd]). A total of 62 samples (>7% of the pool) were randomly selected to assess instrument precision; for these samples, we ran three analytical replicates ("subsamples") for each. We found these subsamples to be within 0.07‰ (for C), 0.06‰ (for N), and 0.21‰ (for S) of each other (average deviations), in line with the reported precision of the instrument (±0.10‰, ±0.20‰, and ±0.40‰, respectively).

Data analysis

Restoration effects on FCL and niche volume

To test whether restored sites have shorter food chains, we calculated FCL using the Maximum Trophic Position convention (Equation 1), calculated as the trophic position of the species with the highest average δ^{15}N for each site, relative to its baseline (Post et al., 2000; Vander Zanden & Fetzer, 2007; Walters & Post, 2008):

$$\text{Maximum Trophic Position} = \frac{(\delta^{15}\text{N top predator}) - (\delta^{15}\text{N baseline})}{3.4} + 1. \quad (1)$$

δ^{15}N values for top predators (within the size class targeted by our fishing gear) represent each individual fish from the species with the highest average δ^{15}N per site and year (Post et al., 2000) (Appendix S1: Table S5). To calculate δ^{15}N of the baseline, we first averaged δ^{15}N of emergent vegetation (detritus) and phytoplankton (algae) for each site and year. We then calculated a weighted average of those values for each focal fish species based on their percent use of detrital versus algal sources, as calculated via the MixSIAR models (see *Restoration effects on the importance of detrital versus algal pathways*, below). This procedure allowed controlling for potential biases that would occur if different fish species showed different degrees of detrital versus algal reliance, and if these resources differed systematically in their δ^{15}N values. We used *t*-tests to calculate whether FCL differed between sites of each tidal marsh pair.

We then calculated the isotopic niche volume for each fish community, across sites and over time (seasons and years). Isotopic niche volume represents the total, three-dimensional space encompassing all δ^{13}C, δ^{15}N, and δ^{34}S isotope values of fish in the local food web—thus, it captures the diversity of trophic pathways present in a local food web. Lipid normalization was deemed unnecessary as the average bulk C:N ratio for our fish was 3.2, lower than the commonly accepted threshold of 3.5, above which normalization is recommended (Logan et al., 2008; Skinner et al., 2016). Isotope niches of fish communities were calculated by measuring the "standard ellipse volume" around the δ^{13}C, δ^{15}N, and δ^{34}S data of each marsh's fish community, using the "nicheROVER" package in R (Lysy et al., 2014; Rossman et al., 2016). These isotopic niche volumes were then compared across pairs of sites across all visits.

Notably, both variation in species richness (i.e., species-poor vs. species-rich communities) and variation in abundance (i.e., large vs. small populations in each species) can influence the amount of variation in isotopic values, and thus variation in isotopic niche volume (Appendix S1: Figure S1). To determine whether observed patterns were more driven by differences in abundance or in species richness within the fish community, we implemented a resampling algorithm that allowed controlling for abundance (i.e., all marsh pairs had the same number of total individuals in the community) or richness (i.e., all marsh pairs had the same species list represented). By comparing resampled model outputs, we then inferred whether differences in isotopic niche volume would still be observed if all communities were equally abundant (same total N), or equally rich. While any process involving the selection of a species pool from the community can bias results (Martinez, 1991), our sets of 1000 iterations likely accounted for potential effects of random selection. Finally, we compared niche volumes within paired sites via Cohen's *D*, to measure restoration effect sizes. A large effect size (Cohen's $D \geq |0.80|$) indicates the "signal" or mean difference between sites is much greater than the variability or "noise" (Cohen, 1988). In turn, medium ($|0.50| \leq$ Cohen's $D < |0.80|$) and small effect sizes ($|0.20| \leq$ Cohen's $D < |0.50|$) indicate smaller signal or difference between sites, likely outweighed by noise in the data (Cohen, 1988).

Restoration effects on the importance of detrital versus algal pathways

To quantify the reliance of fish on detrital versus algal energy pathways, and compare reliance between restored and reference sites, we focused on two basal resource endpoints: emergent vegetation to characterize the detrital pathway, and phytoplankton to characterize the algal pathway (see *Field sample collection*). We ran Bayesian mixing models to estimate reliance on each pathway (and associated uncertainty) via the "MixSIAR" package in R (Stock et al., 2022). MixSIAR uses inputs of biological tracers, such as stable isotope data, and quantifies the reliance of a consumer on different prey sources. The model requires the input of trophic discrimination factors (TDFs; the difference between the isotopic value of the tissue of a consumer and its diet). We used the TDFs of 2.1 ± 6.6‰ for δ^{13}C and 3.1 ± 7.5‰ for δ^{15}N (from the Canseco et al., 2022 meta-analysis), and 1.27 ± 1.31‰ for δ^{34}S (from the Raoult et al., 2024 meta-analysis). Given all our focal fish were planktivore or omnivore at the collected size classes and given the absence of species-specific TDFs for our species, we used the same trophic discrimination factors across multiple taxa when running the MixSIAR models (Canseco et al., 2022; McCutchan et al., 2003; Raoult et al., 2024). However, we assessed the influence of TDFs via a sensitivity analysis, where in addition to the selected TDFs, we used the most extreme values found in the literature which included δ^{34}S (Appendix S1: Figure S2). For the lowest TDF values we used 0.6 ± 1.3‰ for δ^{13}C, 2.5 ± 1.7‰ for δ^{15}N, and −0.53 ± 0.3‰ for δ^{34}S (Canseco et al., 2022; McCutchan et al., 2003). For the highest TDF values we used

3 ± 1.2‰ for δ^{13}C, 4.6 ± 1.9‰ for δ^{15}N, and 4 ± 0.22‰ for δ^{34}S (Barnes & Jennings, 2007; Canseco et al., 2022).

To compare how individual species' reliance on detrital material differs if they are found in reference or restored sites (Davis et al., 2024), the model was run using δ^{13}C, δ^{15}N, and δ^{34}S data of each fish species with corresponding data on phytoplankton (algal pathway) and emergent vegetation (detrital pathway) as sources. We included all fish used in the community analysis except for fish found in two or fewer marsh sites and fish in larval or fry life stages. Non-senesced emergent vegetation tissue was used as a proxy to represent the brown pathway as it can be assumed the isotopic composition of the live form of the tissue would closely mirror the detrital form of the tissue (Cloern et al., 2002; Young et al., 2021). No priors were included in the model, and the output was plotted as the mean proportion of the diet explained by each source. Finally, we ran a paired *t*-test and Cohen's *D* test for effect size to see whether detrital reliance differed significantly between native and introduced species.

Effects of fish origins and life histories

To examine the influence of introduced and transient consumers on food-web structure, we calculated isotopic niche volume and niche volume overlap for the collected fish assemblages, following the same method described above. Niche volume overlap represents the probability that an individual represented within species' A niche volume is found within species' B niche volume, thus reflecting similarities in resource use and potential resource competition (James et al., 2020). Niche volume (‰^{3}) and percent overlap (%) were calculated by year and across years. We then assessed differences in these metrics between introduced and native fishes, and between resident and transient fishes, using Cohen's *D* effect sizes. All data were analyzed in R version 4.2.2 (R Core Team, 2023).

RESULTS

Restoration effects on FCL and niche volume

Food chains in restored sites were shorter than in reference sites, in agreement with our hypothesis that restoration sites would support structurally simpler fish communities. This pattern was true for the new and old restored sites when pooling data across years (Figure 3A) and when looking into year-specific patterns in many cases (Figure 3B), with half of them being statistically significant. We observed substantial variation in the identity of the top predator setting FCL across sites and over time. For example, in the *new* restored site, the native transient Sacramento splittail (*Pogonichthys macrolepidotus*) had the highest average trophic position in the wet year, 2020, but Northern anchovy (*Engraulis mordax*), a native marine transient, held that position in dry 2021 (Appendix S1: Table S5). Non-native fishes, both transient and resident, often displayed the highest average δ^{15}N in restored and reference sites alike: the striped bass (*Morone saxatilis*), transient, and the *Tridentiger* sp. goby, resident, each set FCL in 25% of the cases (Appendix S1: Table S5).

Overall, fishes in the *young* and *old* restored sites had significantly compressed niche volumes (37% smaller on average) than their references—a pattern that was hypothesized and held true in both pooled and individual years (Cohen's $D > |0.80|$; Figure 4). However, the *new* restored site showed the opposite trend (11% larger niches), emerging from a significantly larger niche than its reference in 2020 (Cohen's $D = 0.82$) and a slightly smaller niche in 2021 (Cohen's $D = -0.59$; Figure 4A,B). When controlling for abundance, patterns remained consistent with those described above for all sites, with large effect sizes (Cohen's $D > |0.80|$) (Figure 4C,D). However, resampling to control for variation in species richness removed these differences, partially or totally, in all pairs (Figure 4E,F). This observation suggests that variation in community richness between restored and reference sites, not variation in abundance, drove the observed differences in niche volumes.

Restoration effects on the importance of detrital versus algal pathways

We observed that detrital reliance was high overall (grand mean: 70.9% ± 33.4%), but also highly variable across fish species and sites (Figure 5). Notably, fishes found in restored sites relied 7.4% less on the detrital pathway than species found in reference sites (paired *t*-test; $t_{10} = 3.43$, $p = 0.006$). We found no significant differences in detrital reliance between native and introduced species after controlling for site-level effects ($t_5 = -0.935$, $p = 0.391$). However, resident species relied 12.2% more on the detrital pathway than transient species after also controlling for site-level effects ($t_5 = 3.059$, $p = 0.028$; Figure 5; Appendix S1: Table S6).

Effects of fish origins and life histories

We assessed whether native and introduced fishes showed overlap or partitioning of their trophic niches. Introduced species displayed significantly larger niche

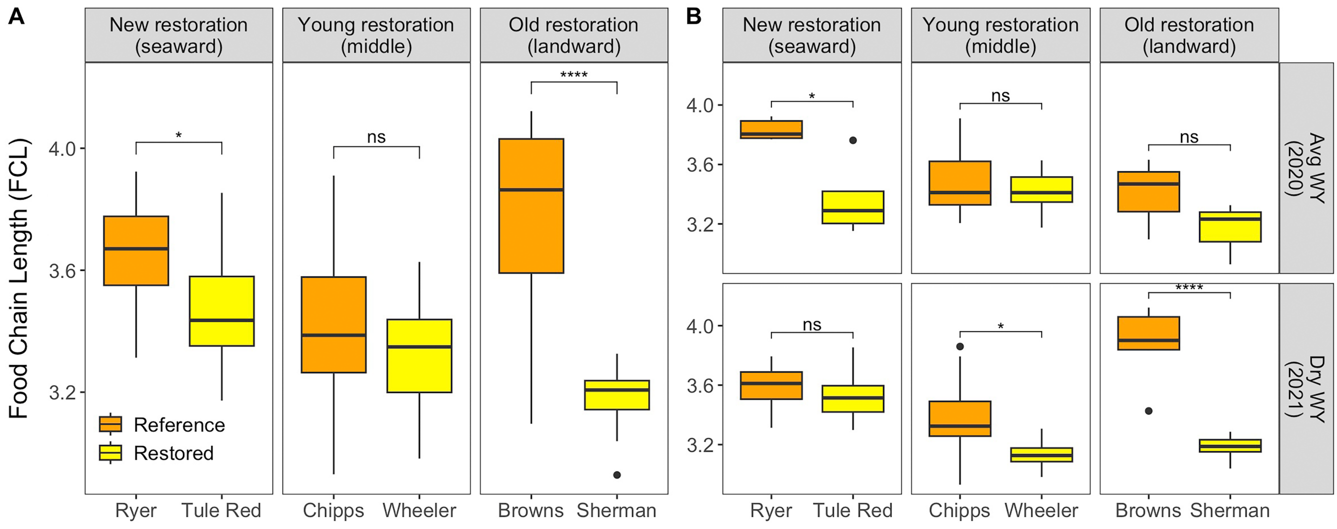

FIGURE 3 Food-chain length. Distribution of food-chain lengths, based on the trophic position of individuals of the species with the highest average δ^{15}N per site and sampling season, relative to its local baseline. Species-specific, local baselines were calculated based on the δ^{15}N of emergent vegetation (for the detrital pathway) and phytoplankton (for the algal pathway), and the reliance on each pathway as estimated via MixSIAR models. WY = water year. Sites pooled by year include the two species with the highest average δ^{15}N in 2020 and 2021. Asterisks denote significant differences from *t*-test between paired sites; *ns* denotes no significant differences. Boxplot lines denote median and interquartile range (IQR), whiskers denote the largest and smallest value outside the IQR but still within the 95% CI, and open circles denote outliers.

volumes than native species (Cohen's $D = -7.87$; Figure 6A). An average of 82.6% of the introduced species' niche volume overlapped with that of the native species, while an average of 96.7% of the native species' niche volume overlapped with that of the introduced species (Cohen's $D = 8.36$; Figure 6B,C). These patterns were consistent across years, both for niche volume (Cohen's $D = -6.68$ in 2020 and -6.86 in 2021) and for niche overlap (Cohen's $D = 7.84$ in 2020 and 7.30 in 2021) (see Appendix S1: Figure S3A,B). These results support our hypothesis that the introduced assemblage would have a larger niche that substantially overlaps with the native one.

Finally, we looked at whether life history (resident vs. transient) had an influence on niche volume and overlap. Overall, transient species had larger niche volumes than resident species (Cohen's $D = 3.86$, Figure 6D). However, patterns differed between years, with resident species displaying larger niches in 2020 and vice versa in 2021 (Cohen's $D = -0.83$; Appendix S1: Figure S3D). An average of 85% of the transient assemblage's niche volume overlapped with that of the resident one, whereas an average of 93.9% of the resident's niche volume overlapped with that of the transient one (Cohen's $D = -5.17$; Figure 6E,F). These results support the hypothesis that transient species may have a larger prey base due to different feeding patterns within and/or outside tidal marsh habitat.

DISCUSSION

A major goal of ongoing and planned tidal marsh restoration projects is to recover native fish populations, many of which have been declining over the last half century across US estuaries (Cloern & Jassby, 2012; Fournier et al., 2024; Sommer et al., 2007). Although tidal marsh restorations can produce similar, if not elevated, levels of invertebrate prey (Hartman et al., 2019; Woo et al., 2018), it remains largely unknown whether tidal marsh restoration leads to the recovery of robust and diverse aquatic food webs that support native fishes (Moreno-Mateos et al., 2012; Vander Zanden et al., 2016). To address this knowledge gap, our study leveraged sites spanning restoration ages, sampling them seasonally in two hydrologically contrasting years (average vs. dry water year). We found that food chains in all restored sites were (~8%) shorter than their paired reference site. Additionally, the *young* and *old* restored sites had smaller niche volumes than their references (37% on average), but the *new* restored site had an 11% larger niche volume than its reference site, suggesting that early succession may still be influencing the energy flows at the newest restoration site. When assessing the relative importance of the "detrital" (brown) versus "algal" (green) pathways, fishes strongly relied on detrital energy overall, with reliance being particularly strong in fishes found in reference

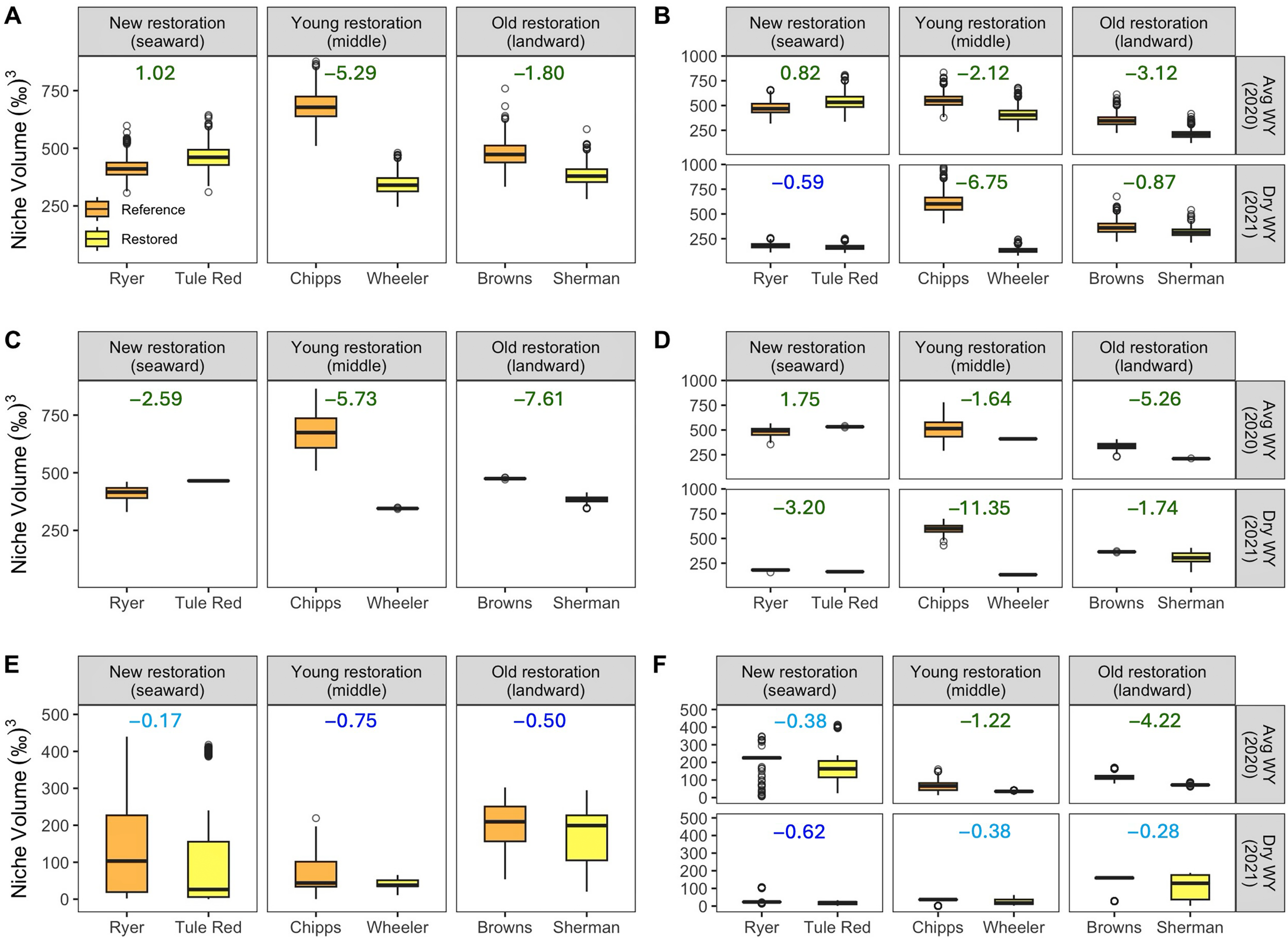

FIGURE 4 Isotopic niche volume. (A, B) The isotopic niche volume represents the total, three-dimensional volume encompassing all $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotope values of consumers in the local food webs of reference (orange) and restored (yellow) tidal marshes. Recalculated niche volumes that control for (C, D) abundance and (E, F) species richness allowed examining the influence of variation in community abundance (i.e., sampled number of individuals) or community richness (i.e., sampled numbers of species). Water years are 2020 (hydrologically average) and 2021 (dry). Cohen's *D* effect sizes are represented as small (light blue), medium (dark blue), or large (green). See *Methods* for more details. Boxplot lines denote median and interquartile range (IQR), whiskers denote largest and smallest value outside the IQR but still within the 95% CI, and open circles denote outliers.

sites (as opposed to restored sites), and among resident species (as opposed to transient ones). Native fish occupied a smaller niche volume compared to introduced fish, with most of their niche within the introduced niche. Finally, transient fish occupied a larger niche volume compared to resident fish with less niche overlap. Our results indicate that food-web structure does not immediately recover with tidal marsh restoration, despite short-term "trophic surges" after breaching, even if fish assemblages are species-rich. Our results also demonstrate that food-web studies can offer a valuable approach to assess tidal marsh function across different stages of restoration (as suggested in Loch et al., 2020), addressing a critical need given widespread loss of estuarine habitat and the regional and global efforts to restore wetland functions (Cloern et al., 2021; Moreno-Mateos et al., 2012).

Restoration effects on FCL and niche volume

Overall, measured food chains were shorter in restored sites, as hypothesized, with different species dictating the FCL at each site, and differences fluctuating among site pairs and years. The reference sites in the *young* and *old* pairs had the same top predators (striped bass in 2020 and *Tridentiger* sp. goby in 2021), contrasting with the *new* restoration pair, which had silversides (*Menidia* sp.) and Sacramento splittail (2020), and Northern anchovy

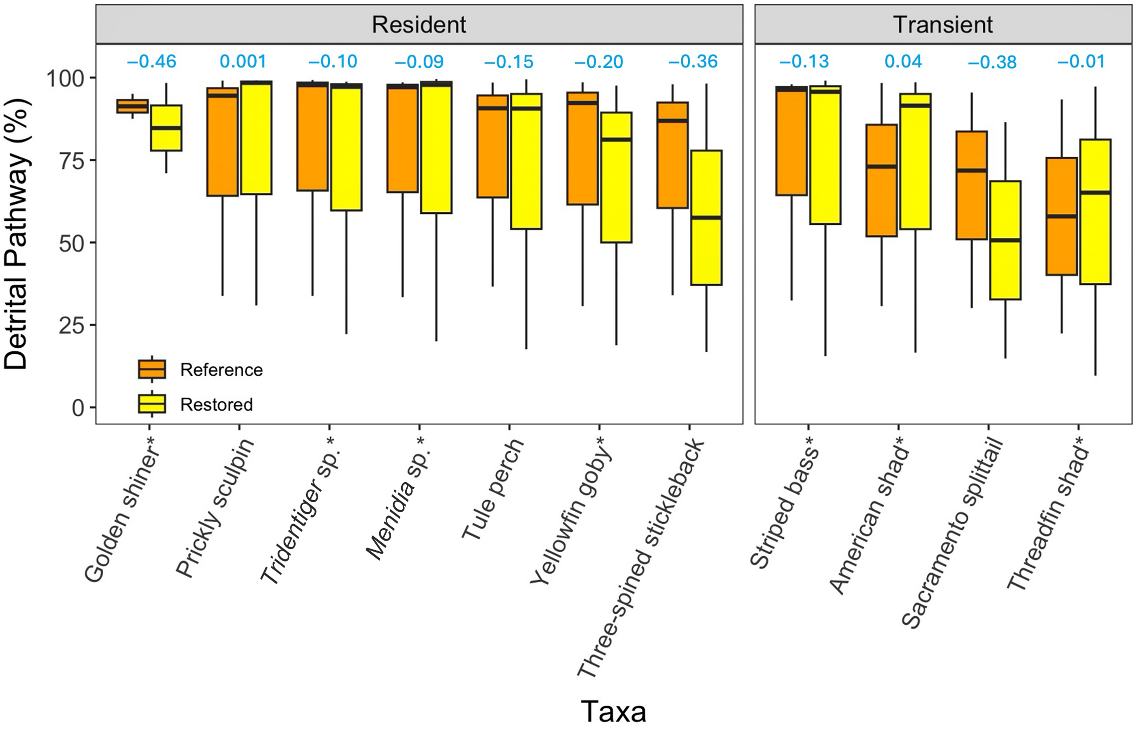

FIGURE 5 Species-specific detrital reliance between reference and restored sites. Percent detrital reliance (i.e., on the "brown" pathway) was estimated based on the isotopic signals of all individuals of each species. Species were grouped by life history, resident fishes (left panel) versus transient fishes (right panel). Colors denote individuals in reference (orange) versus restored (yellow) tidal marshes. Numbers reflect Cohen's *D* effect sizes, all of which were small (light blue). Asterisks denote non-native species. Boxplot lines denote median and interquartile range (IQR), whiskers denote largest and smallest value outside the IQR but still within the 95% CI, and open circles denote outliers.

(2021), as top predators. While it is possible that the high $\delta^{15}N$ of the Northern anchovy, a transient species that enters the estuary in late spring and early summer (Ervin, 2021), could reflect marine resources, we note that $\delta^{15}N$ values did not change significantly over 6 weeks (i.e., between individuals collected on 06/17 ($n = 12$) and those collected on 07/30/21 ($n = 10$); $z_{21} = -0.345$, $p = 0.73$). This observation leads us to believe that these fish may have already been at equilibrium with the new (estuarine) resources when we collected them in June–July. Finally, from our FCL results we also found that the *new* restored site, Tule Red, was the only site that supported native top predators (Sacramento splittail in 2020, Northern anchovy in 2021) in both years, species that tolerate high salinity levels. This observation suggests that salinity may be not only a driver of benthic and planktonic community dynamics in the Bay-Delta (Chang et al., 2018; Cloern et al., 2017) but also a major control of food-web structure—explaining fluctuations in FCL over time and space.

FCL has important implications for food-web stability (trophic cascades), pollutant bioaccumulation, and carbon exchange between freshwater ecosystems and the atmosphere (Post et al., 2000; Sabo et al., 2010; Schindler et al., 1997). We hypothesized that niche volume, a measurement of trophic compression, would be smaller (or less diverse) in restored sites than in reference sites. We found generally compressed niche volumes in restored relative to reference sites (Figure 4A), but these differences vanished when controlling for variation in community richness (Figure 4D,F). Contrary to our hypothesis, we found that in 2020, the *new* restoration site had a larger (less compressed) niche volume than its reference site, but this trend was reversed in 2021 (Figure 4B). This finding suggests that initial flooding temporarily promoted longer and more diverse food chains and fish communities with expanded isotopic niches, a pattern consistent with the "trophic surge hypothesis" (Monaghan et al., 2020; Turgeon et al., 2016). Specifically, levee breaching allowed the restoration of tidal hydrology, suddenly connecting pelagic and terrestrial nutrient sources and increasing production and organic matter exports. This observation supports the notion that carefully designed restoration plans, with excavated channel networks and marsh revegetation, could accelerate restoration trajectories relative to restoration sites with extensive ditching (Larkin et al., 2009; Oosterlee et al., 2018; Williamshen et al., 2021).

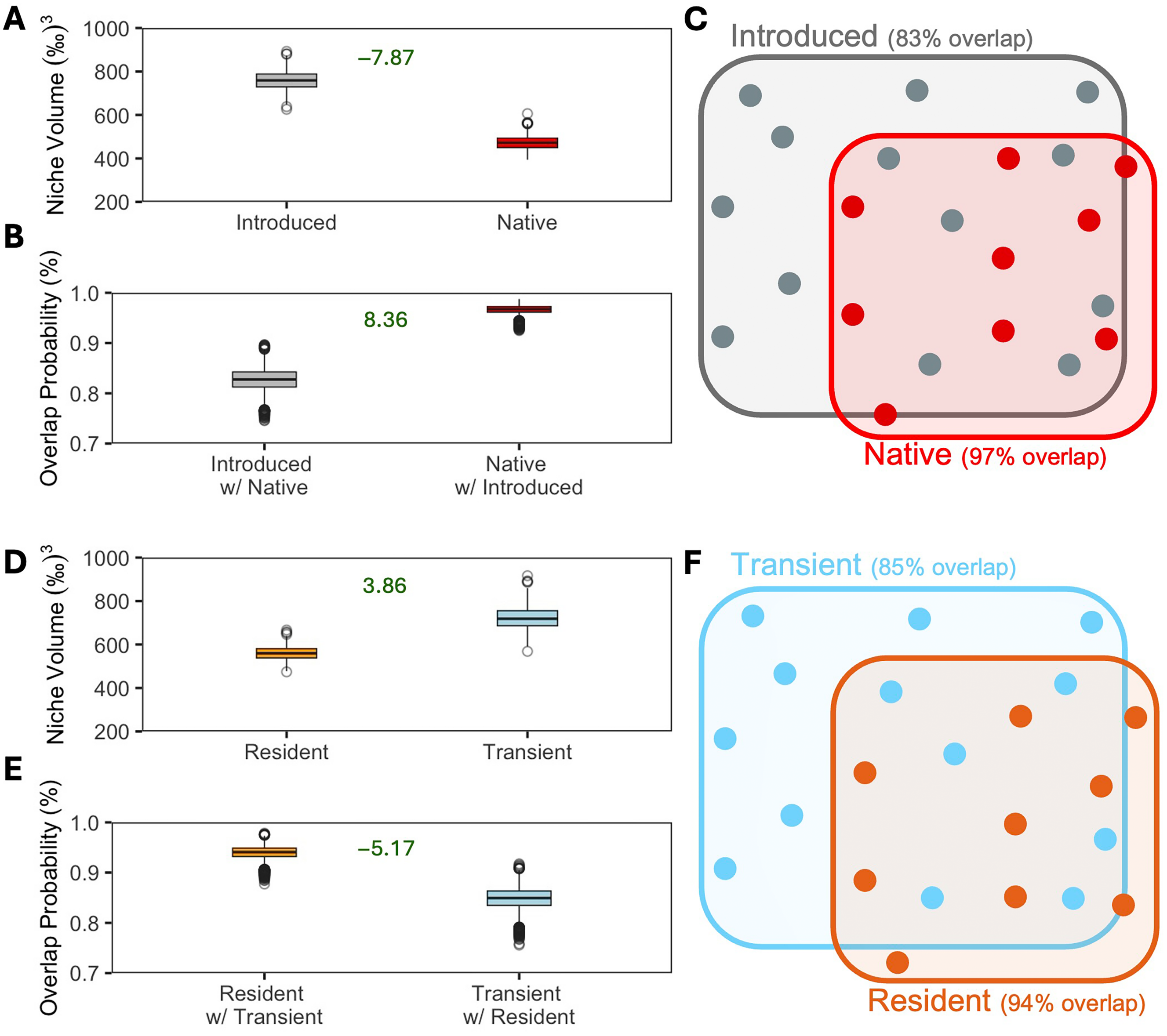

FIGURE 6 Niche volume and overlap by fish origin and life history. Niche volume (A, D), niche overlap (B, E), and diagram illustrating both results (C, F) comparing introduced versus native fish species, and resident versus transient species. This analysis pooled data across sampling years and sites. Numbers reflect Cohen's *D* effect sizes, all of which were large (green). Boxplot lines denote median and interquartile range (IQR), whiskers denote largest and smallest value outside the IQR but still within the 95% CI, and open circles denote outliers.

Restoration effects on the importance of detrital versus algal pathways

By the mid-20th century, extensive diking and draining of vegetated tidal marshes in the Bay-Delta disconnected large parcels of land from the estuary and led to an estimated 94% loss in detritus production and energy transfer to herbivores (Cloern et al., 2021). Tidal marsh recovery can boost the detrital pathway of an aquatic ecosystem by supplying decaying terrestrial matter year-round (Howe & Simenstad, 2011), buffering consumers from seasonal declines in phytoplankton (Young et al., 2021). The observation that fish in restored sites relied less on the detrital pathway than in reference sites is consistent with our hypothesis that detrital pathways may be relatively slower to return (Figure 1). The relatively slow recovery of biogeochemical cycling often observed in restoring wetlands (Moreno-Mateos et al., 2012) also underscores the importance of tracking food-web trajectories with repeated sampling events—particularly in the Bay-Delta and other highly modified estuaries (Howe & Simenstad, 2011; Schroeter et al., 2015; Young et al., 2021). Additionally, transient species showed slightly lower detrital reliance than resident species overall (about 12%). In fact, all fishes except the transient threadfin shad (*Dorosoma petenense*) and Sacramento splittail showed high reliance (>60%) on the detrital pathway, in agreement with previous work (Young et al., 2021). Thus, while transient fish may source prey from both inside and outside the marsh, resident fish may strongly benefit from restoration-driven increases in the detrital food base—particularly over long timescales.

Influence of fish origins and life histories

As a result of the Bay-Delta's long history of invasion, reference and restored tidal marshes are threatened by the establishment and spread of introduced species (Boyer et al., 2023; Cohen & Carlton, 1998; Ruiz et al., 2011). These invasions have already caused profound changes in food-web structure and dynamics. For example, the introductions of the invasive filter-feeding overbite clam (*Potamocorbula amurensis*) and Asian clam (*Corbicula fluminea*) are associated with a marked reduction in phytoplankton biomass and associated consumer abundance (e.g., mysid shrimp) after the late 1980s (Feyrer et al., 2003). This trophic cascade is often touted as a major driver of the pelagic organism decline (POD) that started around the year 2000 and involved population declines of Delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), striped bass, and threadfin shad (Cloern et al., 2017; Sommer et al., 2007), the latter three of which are included in this study. Our study found the native species' niche is much smaller and is encompassed within the introduced species' niche. For instance, the introduced striped bass is often regarded as a functional analogue to native piscivorous fishes such as Sacramento pikeminnow (*Ptychocheilus grandis*; Stompe et al., 2020), and if striped bass are excluded, an entire trophic level of top predators may be missing. The larger and overlapping niche occupied by introduced species indicates that introduced species consume a wider range of food sources (Figure 6C). The high number of introduced invertebrates (and expanded prey base) in tidal marshes (Schroeter et al., 2015) may also support introduced fishes with high trophic plasticity (Comte et al., 2017). Our findings suggest that introduced species may be occupying niches that are unused by native species, likely through a combination of direct replacement of native species (i.e., formerly occupied niches) and in-filling of unused niche space.

The abundance and richness of invasive species, and the effects these exert on food webs, may change as a function of hydroclimatic fluctuations, as seen in other estuaries (Akin & Winemiller, 2006; Possamai et al., 2021). For example, when looking at all fish caught in the average water year 2020 for our study, approximately 38% of the individuals were introduced and 61% were native (1% were unidentified fry). However, in the dry year 2021, this trend reversed and ~63% of the fish caught were introduced. Similar patterns in hydroclimate control over negative covariation between native and introduced fishes have been reported from the Bay-Delta (Chang et al., 2018; Colombano et al., 2022), and it is a known phenomenon from riverine fish communities exposed to hydrologic extremes (Comte et al., 2021; Ruhí et al., 2015; Ruhí, Olden, & Sabo, 2016). Understanding the consequences of these relationships at the food-web level is important for predicting restoration outcomes under increasingly variable climates (Knowles & Cronkite-Ratcliff, 2018).

Because life history can greatly influence the extent and timing of reliance on different prey and basal resources (Kneib, 1997; Rountree & Able, 2007), we also sought to determine whether transient and resident fishes differed in their niche volumes and whether their volumes overlapped. The higher niche volume for transient species, when pooled across years, may be explained by a higher diversity of food sources consumed within tidal marsh habitats or consumed across habitats (e.g., when moving between tidal marsh and open water), which could allow them to take advantage of a wider range of food sources (e.g., both marine zooplankton and marsh benthic invertebrates). However, in any specific year, transient species had a lower niche volume than resident species (Appendix S1: Figure S3), a pattern that is likely explained by the high turnover in community composition observed for transient species between the average water year (e.g., longfin smelt, striped bass, threadfin shad, Sacramento splittail in 2020) and the dry water year (e.g., Northern anchovy in 2021). Indeed, the resident fish assemblage was compositionally similar between years—only one of the 12 species present in 2020 was not detected in 2021, and all species that were present in 2021 were also present in 2020 (a pattern consistent with long-term observations from Suisun Marsh; Colombano et al., 2020). In contrast, we observed substantial turnover in the transient assemblage, illustrated by the fact that four of the nine species present in the dry year 2021 had not appeared in 2020. These results suggest that transient fishes can take advantage of different resources interannually (Rountree & Able, 2007) and that droughts influence variation in fish origin, composition, and trophic overlap—the latter decreasing in dry years due to increased representation of transient, marine species.

Limitations and future directions

In the context of tidal marsh restoration research, our study is unique in terms of approach and replication, as it integrates about a thousand samples for three stable isotopes, collected seasonally for two years in tidal marshes spanning three orders of magnitude in age since restoration. However, it was not without limitations. First, our summer sampling season (May to July) likely captures a transition window from spring environmental conditions (cooler temperatures, heavier rainfall) to drier summer conditions. Second, because a few of the species studied undergo ontogenetic shifts (e.g., striped bass, threadfin shad, American shad, and Sacramento splittail), potentially confounding effects of body size could exist (Table 2). When assessing this effect, a posteriori, we found no significant variation in fish lengths (after controlling for species identity) between restored and reference sites (GLM, $F_{1,787} = 3.552$, $p > 0.05$). This result suggests that variation in size would not have systematically biased inferences on the effects of restoration on fish isotopic signals. Nevertheless, general associations between size and trophic position (δ^{15}N) are to be expected (Woodward et al., 2005). Third, by covering a large spatial scale, limitations arose in our ability to collect every component of each local food web, forcing us to focus on end members (resources) that were common across sites and overlooking those that may have been important at some but not all sites (Appendix S1: Figure S1). For instance, since we did not use gear targeting larger individuals, such as gill nets, we likely undersampled large piscivorous fish such as adult striped bass and Sacramento pikeminnow (Nobriga & Feyrer, 2007; Steinke et al., 2019; Young et al., 2022; Zeug et al., 2017), which could have led to underestimation of FCLs and niche volumes. Further studies that target the largest fish size classes could alter or refine our findings. Fourth, our system is strongly dominated by omnivory (i.e., feeding across multiple trophic levels). Fish feeding on both invertebrates and plants, or more generally, on multiple different trophic levels below them, can reduce variation in trophic position and thus measurements of FCL and trophic niche volume. Fifth, we used live plant tissue in our MixSIAR models instead of fine particulate organic matter (FPOM) to represent the detrital pathway, as FPOM signals overlapped with those of phytoplankton. While this is a common practice in the Bay-Delta and elsewhere (Howe & Simenstad, 2011; Schroeter et al., 2015; Young et al., 2021), the fractionation processes that occur with decomposition are likely not being adequately considered when using live tissue. Sixth, uncertainty in trophic discrimination factors required for the Bayesian mixing models can greatly influence results. Our sensitivity analysis examining how changing TDFs would change inferences on detrital reliance confirmed that such influence can be strong but also revealed that some general patterns would remain—including the consistently lowest detrital reliance of the *new* restoration pair (Appendix S1: Figure S2). In this manuscript, we utilized TDFs from Canseco et al., 2022 (δ^{13}C and δ^{15}N) and Raoult et al., 2024 (δ^{34}S). These values were calculated by combining TDFs from multiple species of fish and were very similar to the widely used TDFs suggested by McCutchan et al. (2003) for δ^{13}C and δ^{15}N. Finally, while isotopes are an indicator of diet, limitations such as overlap in signals of potential prey can influence niche volume and detrital reliance estimates. Here, by moving from two (δ^{13}C and δ^{15}N) to three stable isotopes (including δ^{34}S) we increased variation and the conclusive capacity of our results (Raoult et al., 2024; Appendix S1: Figure S1). Future research that ground-truths results with gut content analysis would help refine inferences based on stable isotope data alone.

Concluding remarks

Our findings illustrate that even if careful restoration design offers a path toward desirable restoration outcomes, food-web structure may not be immediately recovered with tidal marsh restoration. With more than 30,000 acres of habitat slated for restoration across the San Francisco Estuary (California EcoRestore, 2020), understanding how tidal marsh restoration may lead to food-web recovery is of key importance. The level of invasion and alteration of the San Francisco Bay–Delta is severe but not unique, and our results can inform restoration projects in other human-dominated settings (Cohen & Carlton, 1998; Gilby et al., 2021). Our study underscores the importance of understanding how energy pathways change with ecosystem restoration efforts (Palmer & Ruhi, 2019) and shows that incorporating the recovery of energy pathways as an indicator of restoration success would help refine the design and monitoring of wetland restoration projects.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Pagliaro et al., 2025a) are available in Dryad at https://doi.org/10.5061/dryad.79cnp5j5g. Code (Pagliaro et al., 2025b) is available in Zenodo at https://doi.org/10.5281/zenodo.13948464.

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REFERENCES

Akin, S., and K. O. Winemiller. 2006. "Seasonal Variation in Food Web Composition and Structure in a Temperate Tidal Estuary." *Estuaries and Coasts* 29: 552–567.

Baer, S. G. 2016. "Nutrient Dynamics as Determinants and Outcomes of Restoration." In *Foundations of Restoration Ecology* 333–364. Washington, DC: Island Press/Center for Resource Economics.

Ballantine, K., and R. Schneider. 2009. "Fifty-Five Years of Soil Development in Restored Freshwater Depressional Wetlands." *Ecological Applications* 19: 1467–80.

Barnes, C., and S. Jennings. 2007. "Effect of Temperature, Ration, Body Size and Age on Sulphur Isotope Fractionation in Fish." *Rapid Communications in Mass Spectrometry* 21(8): 1461–67.

Boyer, K., S. Safran, S. Khanna, and M. Patten. 2023. "Landscape Transformation and Variation in Invasive Species Abundance Drive Change in Primary Production of Aquatic Vegetation in the Sacramento–San Joaquin Delta." *San Francisco Estuary and Watershed Science* 20(4): 1–29. https://doi.org/10.15447/sfews.2023v20iss4art2.

Brown, L. R., D. E. Ayers, B. Bergamaschi, J. R. Burau, E. T. Dailey, B. Downing, M. Downing-Kunz, et al. 2024. "Physics to Fish—Understanding the Factors that Create and Sustain Native Fish Habitat in the San Francisco Estuary (No. U.S. Geological Survey Open-File Report 2023–1087)."

California EcoRestore, and California Department of Water Resources. 2020. "California EcoRestore Highlights 2015 to 2020." https://water.ca.gov/Programs/All-Programs/EcoRestore.

Canseco, J. A., E. J. Niklitschek, and C. Harrod. 2022. "Variability in δ^{13}C and δ^{15}N Trophic Discrimination Factors for Teleost Fishes: A Meta-Analysis of Temperature and Dietary Effects." *Reviews in Fish Biology and Fisheries* 32: 1–17.

Chang, A. L., C. W. Brown, J. A. Crooks, and G. M. Ruiz. 2018. "Dry and Wet Periods Drive Rapid Shifts in Community Assembly in an Estuarine Ecosystem." *Global Change Biology* 24: e627–e642. https://doi.org/10.1111/gcb.13972.

Cloern, J. E., A. D. Jassby, T. S. Schraga, E. Nejad, and C. Martin. 2017. "Ecosystem Variability along the Estuarine Salinity Gradient: Examples from Long-Term Study of San Francisco Bay." *Limnology and Oceanography* 62: S272–S291. https://doi.org/10.1002/lno.10537.

Cloern, J. E., and A. D. Jassby. 2012. "Drivers of Change in Estuarine-Coastal Ecosystems: Discoveries from Four Decades of Study in San Francisco Bay." *Reviews of Geophysics* 50: 2012RG000397. https://doi.org/10.1029/2012RG000397.

Cloern, J. E., E. A. Canuel, and D. Harris. 2002. "Stable Carbon and Nitrogen Isotope Composition of Aquatic and Terrestrial Plants of the San Francisco Bay Estuarine System." *Limnology and Oceanography* 47: 713–729. https://doi.org/10.4319/lo.2002.47.3.0713.

Cloern, J. E., S. M. Safran, L. S. Vaughn, A. Robinson, A. A. Whipple, K. E. Boyer, J. Z. Drexler, R. J. Naiman, J. L. Pinckney, and E. R. Howe. 2021. "On the Human Appropriation of Wetland Primary Production." *Science of the Total Environment* 785: 147097.

Cohen, A. N., and J. T. Carlton. 1998. "Accelerating Invasion Rate in a Highly Invaded Estuary." *Science* 279: 555–58.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. New York: Routledge. https://doi.org/10.4324/9780203771587.

Colombano, D. D., A. Manfree, T. A. O'Rear, J. R. Durand, and P. B. Moyle. 2020. "Estuarine-Terrestrial Habitat Gradients Enhance Nursery Function for Resident and Transient Fishes in the San Francisco Estuary." *Marine Ecology Progress Series* 637: 141–157. https://doi.org/10.3354/meps13238.

Colombano, D. D., S. M. Carlson, J. A. Hobbs, and A. Ruhi. 2022. "Four Decades of Climatic Fluctuations and Fish Recruitment Stability across a Marine-Freshwater Gradient." *Global Change Biology* 28: 5104–20. https://doi.org/10.1111/gcb.16266.

Colombano, D. D., T. B. Handley, T. A. O'Rear, J. R. Durand, and P. B. Moyle. 2021. "Complex Tidal Marsh Dynamics Structure

Fish Foraging Patterns in the San Francisco Estuary." *Estuaries and Coasts* 44: 1604–18.

Comte, L., J. Cucherousset, and J. D. Olden. 2017. "Global Test of Eltonian Niche Conservatism of Nonnative Freshwater Fish Species between their Native and Introduced Ranges." *Ecography* 40: 384–392.

Comte, L., J. Cucherousset, S. Boulêtreau, and J. D. Olden. 2016. "Resource Partitioning and Functional Diversity of Worldwide Freshwater Fish Communities." *Ecosphere* 7: e01356.

Comte, L., T. Grantham, and A. Ruhi. 2021. "Human Stabilization of River Flows Is Linked with Fish Invasions across the USA." *Global Ecology and Biogeography* 30(3): 725–737.

Copeland, C. 2010. "Wetlands: An Overview of Issues (No. 37)." Congressional Research Service Reports.

Davis, M. J., I. Woo, S. E. W. De La Cruz, C. S. Ellings, S. Hodgson, and G. Nakai. 2024. "Allochthonous Marsh Subsidies Enhances Food Web Productivity in an Estuary and its Surrounding Ecosystem Mosaic." *PLoS One* 19: e0296836. https://doi.org/10.1371/journal.pone.0296836.

Dettinger, M., J. Anderson, M. Anderson, L. R. Brown, D. Cayan, and E. Maurer. 2016. "Climate Change and the Delta." *San Francisco Estuary and Watershed Science* 14(3): 1–26.

Enright, C., S. D. Culberson, and J. R. Burau. 2013. "Broad Timescale Forcing and Geomorphic Mediation of Tidal Marsh Flow and Temperature Dynamics." *Estuaries and Coasts* 36: 1319–39. https://doi.org/10.1007/s12237-013-9639-7.

Ervin, J. 2021. "Anchovy Alert! Spawning Anchovies Have Returned to Lower South San Francisco Bay." UC Davis - Fish in the Bay. Available at: https://www.ogfishlab.com.

Feyrer, F., B. Herbold, S. Matern, and P. Moyle. 2003. "Dietary Shifts in a Stressed Fish Assemblage: Consequences of a Bivalve Invasion in the San Francisco Estuary." *Environmental Biology of Fishes* 67: 277–288.

Fournier, R. J., D. D. Colombano, R. J. Latour, S. M. Carlson, and A. Ruhi. 2024. "Long-Term Data Reveal Widespread Phenological Change across Major US Estuarine Food Webs." *Ecology Letters* 27(12): e14441.

Gilby, B. L., M. P. Weinstein, R. Baker, J. Cebrian, S. B. Alford, A. Chelsky, D. Colombano, R. M. Connolly, C. A. Currin, and I. C. Feller. 2021. "Human Actions Alter Tidal Marsh Seascapes and the Provision of Ecosystem Services." *Estuaries and Coasts* 44: 1628–36.

Grimaldo, L. F., A. R. Stewart, and W. Kimmerer. 2009. "Dietary Segregation of Pelagic and Littoral Fish Assemblages in a Highly Modified Tidal Freshwater Estuary." *Marine and Coastal Fisheries* 1: 200–217. https://doi.org/10.1577/C08-013.1.

Hartman, R., S. Sherman, D. Contreras, A. Furler, and R. Kok. 2019. "Characterizing Macroinvertebrate Community Composition and Abundance in Freshwater Tidal Wetlands of the Sacramento-San Joaquin Delta." *PLoS One* 14: e0215421. https://doi.org/10.1371/journal.pone.0215421.

Herbold, B., D. M. Baltz, L. Brown, R. Grossinger, W. Kimmerer, P. Lehman, C. S. Simenstad, C. Wilcox, and M. Nobriga. 2014. "The Role of Tidal Marsh Restoration in Fish Management in the San Francisco Estuary." *San Francisco Estuary and Watershed Science* 12: 1–6.

Howe, E. R., and C. A. Simenstad. 2011. "Isotopic Determination of Food Web Origins in Restoring and Ancient Estuarine Wetlands of the San Francisco Bay and Delta." *Estuaries and Coasts* 34: 597–617.

Howe, E., and C. A. Simenstad. 2015. "Using Isotopic Measures of Connectivity and Ecosystem Capacity to Compare Restoring and Natural Marshes in the Skokomish River Estuary, WA, USA." *Estuaries and Coasts* 38: 639–658.

James, W. R., J. S. Lesser, S. Y. Litvin, and J. A. Nelson. 2020. "Assessment of Food Web Recovery Following Restoration Using Resource Niche Metrics." *Science of the Total Environment* 711: 134801. https://doi.org/10.1016/j.scitotenv.2019.134801.

Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. "Isohaline Position as a Habitat Indicator for Estuarine Populations." *Ecological Applications* 5: 272–289. https://doi.org/10.2307/1942069.

Junk, W. J., S. An, C. Finlayson, B. Gopal, J. Květ, S. A. Mitchell, W. J. Mitsch, and R. D. Robarts. 2013. "Current State of Knowledge Regarding the World's Wetlands and Their Future under Global Climate Change: A Synthesis." *Aquatic Sciences* 75: 151–167.

Kneib, R. T. 1997. "The Role of Tidal Marshes in the Ecology of Estuarine Nekton." *Oceanography and Marine Biology* 35: 154.

Knowles, N., and C. Cronkite-Ratcliff. 2018. "Modeling Managed Flows in the Sacramento/San Joaquin Watershed, California, Under Scenarios of Future Change for CASCaDE2." US Geol. Surv. Open-File Rep. 2018-1101 38.

Kreeger, D. A., and R. I. Newell. 2000. "Trophic Complexity between Producers and Invertebrate Consumers in Salt Marshes." In *Concepts and Controversies in Tidal Marsh Ecology* 187–220. Dordrecht: Springer.

Larkin, D. J., J. M. West, and J. B. Zedler. 2009. "Created Pools and Food Availability for Fishes in a Restored Salt Marsh." *Ecological Engineering* 35(1): 65–74.

Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, and L. A. Yeager. 2012. "Applying Stable Isotopes to Examine Food-Web Structure: An Overview of Analytical Tools." *Biological Reviews* 87: 545–562.

Loch, J. M. H., L. J. Walters, and G. S. Cook. 2020. "Recovering Trophic Structure through Habitat Restoration: A Review." *Food Webs* 25: e00162. https://doi.org/10.1016/j.fooweb.2020.e00162.

Logan, J. M., T. D. Jardine, T. J. Miller, S. E. Bunn, R. A. Cunjak, and M. E. Lutcavage. 2008. "Lipid Corrections in Carbon and Nitrogen Stable Isotope Analyses: Comparison of Chemical Extraction and Modelling Methods." *The Journal of Animal Ecology* 77: 838–846.

Lysy, M., A. D. Stasko, and H. K. Swanson. 2014. "nicheROVER: (Niche)(R)egion and Niche (Over)lap Metrics for Multidimensional Ecological Niches." R Package Version 1.

Martinez, N. D. 1991. "Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web." *Ecological Monographs* 61(4): 367–392.

Matern, S. A., and L. R. Brown. 2005. "Invaders Eating Invaders: Exploitation of Novel Alien Prey by the Alien Shimofuri Goby in the San Francisco Estuary, California." *Biological Invasions* 7: 497–507.

Matern, S. A., P. B. Moyle, and L. C. Pierce. 2002. “Native and Alien Fishes in a California Estuarine Marsh: Twenty-One Years of Changing Assemblages.” *Transactions of the American Fisheries Society* 131: 797–816. https://doi.org/10.1577/1548-8659(2002)131<0797:NAAFIA>2.0.CO;2.

McCutchan, J. H., Jr., W. M. Lewis, Jr., C. Kendall, and C. C. McGrath. 2003. “Variation in Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur.” *Oikos* 102: 378–390.

Meli, P., J. M. Rey Benayas, P. Balvanera, and M. Martínez Ramos. 2014. “Restoration Enhances Wetland Biodiversity and Ecosystem Service Supply, but Results Are Context-Dependent: A Meta-Analysis.” *PLoS One* 9: e93507.

Mitch, W., and J. Gosselink. 2007. *Wetlands*. Hoboken, NJ: John Wiley & Sons, Inc.

Monaghan, K. A., C. S. Agostinho, F. M. Pelicice, and A. M. Soares. 2020. “The Impact of a Hydroelectric Dam on Neotropical Fish Communities: A Spatio-Temporal Analysis of the Trophic Upsurge Hypothesis.” *Ecology of Freshwater Fish* 29: 384–397.

Moreno-Mateos, D., M. E. Power, F. A. Comín, and R. Yockteng. 2012. “Structural and Functional Loss in Restored Wetland Ecosystems.” *PLoS Biology* 10: e1001247.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. “The Modification of an Estuary.” *Science* 231: 567–573. https://doi.org/10.1126/science.231.4738.567.

Nobriga, M. L., and F. Feyrer. 2007. “Shallow-Water Piscivore-Prey Dynamics in California’s Sacramento–San Joaquin Delta.” *SFEWS* 5(2): 1–13. https://doi.org/10.15447/sfews.2007v5iss2art4.

Oosterlee, L., T. J. Cox, W. Vandenbruwaene, T. Maris, S. Temmerman, and P. Meire. 2018. “Tidal Marsh Restoration Design Affects Feedbacks between Inundation and Elevation Change.” *Estuaries and Coasts* 41: 613–625.

Pagliaro, M., S. De La Cruz, I. Woo, J. Sousa, N. Rich, L. Grimaldo, D. Colombano, and A. Ruhi. 2025a. “Does Tidal Marsh Restoration Lead to the Recovery of Trophic Pathways that Support Estuarine Fishes? [Dataset].” Dryad. https://doi.org/10.5061/dryad.79cnp5j5g.

Pagliaro, M., S. De La Cruz, I. Woo, J. Sousa, N. Rich, L. Grimaldo, D. Colombano, and A. Ruhi. 2025b. “Does Tidal Marsh Restoration Lead to the Recovery of Trophic Pathways that Support Estuarine Fishes?” Zenodo. https://doi.org/10.5281/zenodo.13948464.

Palmer, M. A., J. B. Zedler, and D. A. Falk. 2016. “Ecological Theory and Restoration Ecology.” In *Foundations of Restoration Ecology* 3–26. Washington, DC: Island Press/Center for Resource Economics.

Palmer, M., and A. Ruhi. 2019. “Linkages between Flow Regime, Biota, and Ecosystem Processes: Implications for River Restoration.” *Science* 365: eaaw2087. https://doi.org/10.1126/science.aaw2087.

Possamai, B., D. J. Hoeinghaus, and A. M. Garcia. 2021. “Environmental Factors Drive Interannual Variation in Estuarine Food-Chain Length.” *Estuarine, Coastal and Shelf Science* 252: 107241.

Post, D. M. 2002. “The Long and Short of Food-Chain Length.” *Trends in Ecology & Evolution* 17: 269–277.

Post, D. M., M. L. Pace, and N. G. Hairston, Jr. 2000. “Ecosystem Size Determines Food-Chain Length in Lakes.” *Nature* 405: 1047–49.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Raoult, V., A. A. Phillips, J. Nelson, Y. Niella, C. Skinner, M. B. Tilcock, P. J. Burke, P. Szpak, W. R. James, and C. Harrod. 2024. “Why Aquatic Scientists Should Use Sulfur Stable Isotope Ratios (δ34S) more Often.” *Chemosphere* 355: 141816. https://doi.org/10.1016/j.chemosphere.2024.141816.

Rossman, S., P. H. Ostrom, F. Gordon, and E. F. Zipkin. 2016. “Beyond Carbon and Nitrogen: Guidelines for Estimating Three-Dimensional Isotopic Niche Space.” *Ecology and Evolution* 6: 2405–13.

Rountree, R. A., and K. W. Able. 2007. “Spatial and Temporal Habitat Use Patterns for Salt Marsh Nekton: Implications for Ecological Functions.” *Aquatic Ecology* 41: 25–45. https://doi.org/10.1007/s10452-006-9052-4.

Ruhí, A., E. E. Holmes, J. N. Rinne, and J. L. Sabo. 2015. “Anomalous Droughts, Not Invasion, Decrease Persistence of Native Fishes in a Desert River.” *Global Change Biology* 21: 1482–96. https://doi.org/10.1111/gcb.12780.

Ruhí, A., G. W. Fairchild, D. J. Spieles, G. Becerra-Jurado, and D. Moreno-Mateos. 2016. “Invertebrates in Created and Restored Wetlands.” In *Invertebrates in Freshwater Wetlands: An International Perspective on Their Ecology* 525–564. Cham: Springer International Publishing.

Ruhí, A., J. D. Olden, and J. L. Sabo. 2016. “Declining Streamflow Induces Collapse and Replacement of Native Fish in the American Southwest.” *Frontiers in Ecology and the Environment* 14: 465–472. https://doi.org/10.1002/fee.1424.

Ruiz, G. M., P. W. Fofonoff, B. Steves, S. F. Foss, and S. N. Shiba. 2011. “Marine Invasion History and Vector Analysis of California: A Hotspot for Western North America.” *Diversity and Distributions* 17: 362–373. https://doi.org/10.1111/j.1472-4642.2011.00742.x.

Sabo, J. L., J. C. Finlay, T. Kennedy, and D. M. Post. 2010. “The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers.” *Science* 330: 965–67.

Schindler, D. E., S. R. Carpenter, J. J. Cole, J. F. Kitchell, and M. L. Pace. 1997. “Influence of Food Web Structure on Carbon Exchange between Lakes and the Atmosphere.” *Science* 277: 248–251.

Schroeter, R. E., T. A. O’Rear, M. J. Young, and P. B. Moyle. 2015. “The Aquatic Trophic Ecology of Suisun Marsh, San Francisco Estuary, California, during Autumn in a Wet Year.” *San Francisco Estuary and Watershed Science* 13(3): 1–18.

Skinner, M. M., A. A. Martin, and B. C. Moore. 2016. “Is Lipid Correction Necessary in the Stable Isotope Analysis of Fish Tissues?” *Rapid Communications in Mass Spectrometry* 30(7): 881–89.

Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, and B. Herbold. 2007. “The Collapse of Pelagic Fishes in the Upper San Francisco Estuary.” *Fisheries* 32: 270–77.

Steinke, D. A., M. J. Young, C. D. Smith, and F. V. Feyrer. 2019. “Diets of Striped Bass and *Sacramento pikeminnow* at Ryer Island, Suisun Bay, California, 2018: U.S. Geological Survey Data Release.” https://doi.org/10.5066/P9YGG46K.

Stock, B., B. Semmens, E. Ward, A. Parnell, A. Jackson, and D. Phillips. 2022. “MixSIAR: Bayesian Mixing Models in R.” R Package Version 3.1.12.

Stompe, D. K., J. D. Roberts, C. A. Estrada, D. M. Keller, N. M. Balfour, and A. I. Banet. 2020. “Sacramento River Predator Diet Analysis: A Comparative Study.” *San Francisco Estuary and Watershed Science* 18(1): 1–16.

Stumpner, P. R., J. R. Burau, and A. L. Forrest. 2021. “A Lagrangian-to-Eulerian Metric to Identify Estuarine Pelagic Habitats.” *Estuaries and Coasts* 44: 1231–49. https://doi.org/10.1007/s12237-020-00861-7.

Turgeon, K., C. T. Solomon, C. Nozais, and I. Gregory-Eaves. 2016. “Do Novel Ecosystems Follow Predictable Trajectories? Testing the Trophic Surge Hypothesis in Reservoirs Using Fish.” *Ecosphere* 7: e01617.

UN General Assembly 73rd Session. 2019. “United Nations Decade on Ecosystem Restoration (2021-2030): Resolution/Adopted by the General Assembly (No. A/RES/73/284).” United Nations.

Vander Zanden, J. M., and W. W. Fetzer. 2007. “Global Patterns of Aquatic Food Chain Length.” *Oikos* 116: 1378–88.

Vander Zanden, J. M., J. D. Olden, C. Gratton, and T. D. Tunney. 2016. “Food Web Theory and Ecological Restoration.” In *Foundations of Restoration Ecology* 301–329. Washington, DC: Island Press/Center for Resource Economics.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. “Human Domination of Earth’s Ecosystems.” *Science* 277: 494–99.

Walters, A. W., and D. M. Post. 2008. “An Experimental Disturbance Alters Fish Size Structure but Not Food Chain Length in Streams.” *Ecology* 89: 3261–67.

Whipple, A., R. M. Grossinger, D. Rankin, B. Stanford, and R. A. Ashevold. 2012. *Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and Process*. San Franc. Estuary Inst. Aquat. Sci. Cent. SFEI Contribution No. 672. Richmond, VA: SFEI.

Williamshen, B. O., T. A. O’Rear, M. K. Riley, P. B. Moyle, and J. R. Durand. 2021. “Tidal Restoration of a Managed Wetland in California Favors Non-Native Fishes.” *Restoration Ecology* 29: e13392. https://doi.org/10.1111/rec.13392.

Woo, I., M. J. Davis, C. S. Ellings, G. Nakai, J. Y. Takekawa, and S. De La Cruz. 2018. “Enhanced Invertebrate Prey Production Following Estuarine Restoration Supports Foraging for Multiple Species of Juvenile Salmonids (*Oncorhynchus* spp.).” *Restoration Ecology* 26: 964–975. https://doi.org/10.1111/rec.12658.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. “Body Size in Ecological Networks.” *Trends in Ecology & Evolution* 20(7): 402–9.

Wozniak, A. S., C. T. Roman, S. C. Wainright, R. A. McKinney, and M.-J. James-Pirri. 2006. “Monitoring Food Web Changes in Tide-Restored Salt Marshes: A Carbon Stable Isotope Approach.” *Estuaries and Coasts* 29: 568–578.

Young, M. J., K. A. Berridge, T. O’Rear, P. B. Moyle, and J. R. Durand. 2017. “Habitat Partitioning by Native and Alien Fishes and Decapods in Novel Habitats of the Upper San Francisco Estuary.” *Biological Invasions* 19: 2693–2710.

Young, M., F. Feyrer, C. Smith, and D. Valentine. 2022. “Habitat-Specific Foraging by Striped Bass (Morone saxatilis) in the San Francisco Estuary, California: Implications for Tidal Restoration”. *San Francisco Estuary and Watershed Science*, 20(3): 1–19. https://doi.org/10.15447/sfews.2022v20iss3art4.

Young, M. J., E. Howe, T. O’Rear, K. Berridge, and P. Moyle. 2021. “Food Web Fuel Differs across Habitats and Seasons of a Tidal Freshwater Estuary.” *Estuaries and Coasts* 44: 286–301.

Zedler, J. B., and S. Kercher. 2005. “Wetland Resources: Status, Trends, Ecosystem Services, and Restorability.” *Annual Review of Environment and Resources* 30: 39–74.

Zeug, S. C., F. V. Feyrer, A. Brodsky, and J. Melgo. 2017. “Piscivore Diet Response to a Collapse in Pelagic Prey Populations.” *Environmental Biology of Fishes* 100: 47–958.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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