Hydrodynamics drive pelagic communities and food web structure in a tidal environment

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Abstract
Hydrodynamic processes can lead to the accumulation and/or dispersal of water column constituents, including sediment, phytoplankton, and particulate detritus. Using a combination of field observations and stable isotope tracing tools, we identified how hydrodynamic processes influenced physical habitat, pelagic communities, and food web structure in a freshwater tidal system. The pelagic habitat of a terminal channel differed spatially, likely aligning with differences in hydrodynamics. Three zones that we classified by exchange with downstream habitat had distinct water quality characteristics, supported different densities of zooplankton and nekton, and exhibited disparate support from benthic and pelagic trophic pathways to pelagic consumers. Hydrodynamically driven zones and their emergent characteristics appeared sensitive to hydrology, as elevated runoff was correlated with a shift in hydrodynamic habitat and organismal distributions. The results of our study highlight the relationship between hydrodynamic processes, biological responses, and climate, and suggest that understanding the physical process can improve understanding of pelagic habitats and communities.

KEYWORDS
benthic–pelagic coupling, hydrodynamics, phytoplankton, San Francisco Estuary, stable isotopes

1 | INTRODUCTION

Estuarine hydrodynamics influence productivity through a variety of mechanisms and across multiple spatial and temporal scales (Largier, 1993). Upstream hydrologic inputs (Filardo & Dunstan, 1985; Jassby & Powell, 1994) and exchange with downstream marine environments (Cloern & Jassby, 2010, 2012; Raimonet & Cloern, 2017) can stimulate estuarine productivity, as can within-estuary circulation patterns (Jassby & Powell, 1994; Moon & Dunstan, 1990). These broad hydrodynamic drivers can influence productivity, and the distribution thereof, on estuary-wide scales. For example, phytoplankton can be abundant up- and/or downstream of an estuarine turbidity maximum (ETM), while detritus can accumulate within the ETM (Suzuki et al., 2012). The hydrodynamic variability associated with ETMs can be important for local invertebrate productivity and fish recruitment (North & Houde, 2001, 2003; Suzuki et al., 2009). These classical ETMs are created by a combination of gravitational circulation and tidal pumping (Allen et al., 1980), but turbidity fronts caused by other mechanisms can also be associated with elevated organic matter densities (Jago et al., 2006; Nakatsuka et al., 2002).
Phytoplankton, detritus, benthic algae, and other carbon sources are important to estuarine consumers (Deegan & Garritt, 1997; Peterson et al., 1985), but the relative value of each can be highly variable within and among estuaries (Chanton & Lewis, 2002; Deegan & Garritt, 1997). Large-scale estuarine hydrodynamics demonstrably affect these productivity pathways and food web structure, particularly with respect to ETMs. For example, in many systems, the abundance of mixotrophic and heterotrophic organisms is elevated in ETMs relative to other habitats (Chikugo River estuary, Islam et al., 2005; Columbia River estuary, Crump & Baross, 1996; Chesapeake Bay, Lee et al., 2012), suggesting variability in the organic carbon sources available to consumers. In the Chikugo River estuary, Suzuki et al. (2012) identified the differential distribution of phytoplankton and plant detritus with respect to the ETM, whereby phytoplankton was more abundant up- and downstream of the ETM while plant detritus was more abundant in the ETM. This matches the findings of Suzuki et al. (2009), who noted elevated abundance of the mysid *Hyperacanthomysis longirostris* in the Chikugo River estuary ETM, a species tied to detrital food sources (Schroeter et al., 2015). Similarly, the copepod *Acartia tonsa* consumed detritus within the Río de la Plata ETM and phytoplankton outside of it (Derisio et al., 2014), and in the Columbia River estuary detritus was the dominant contributor to food webs in the ETM (Simenstad et al., 1990).

Physical processes other than gravitational circulation and tidal pumping, such as tidal asymmetries, can also influence the distribution of suspended particles and organic material in estuaries. Tidal asymmetries (i.e., flood-ebb bias in velocity) can elevate suspended sediment concentration at or near the extent of the tidal excursion (Dronkers, 1986) and be associated with elevated organic matter concentrations (Jago et al., 2006). Tidal asymmetries can be found in peripheral and terminal channels in both saline and freshwater portions of estuaries, and it occurs as the tidal wave transitions from progressive wave to standing wave and is reflected off the end of the terminal channel. Tidal asymmetry and associated dissipation of tidal energy along terminal channels causes incomplete exchange with surrounding habitats, and thus retention of water across daily, spring/neap, and seasonal time scales (Fagherazzi et al., 2008). Incomplete exchange creates gradients in physical properties such as residence time and variable within-channel exchange that act as a mechanism to either accumulate or disperse water constituents (P. R. Stumpner, Burau, et al., 2020), including water column or marsh-derived organic matter. Gradients in physical properties can create significant variability in chemical and biological properties and thus establish habitat gradients along the longitudinal axis of a slough or channel (McLusky & Elliott, 2004). Thus, localized processes driven by interactions between tidal currents and local topography can lead to high suspended sediment concentrations, elevated productivity, and/or accumulated organic matter.

As part of dendritic tidal marshes, terminal sloughs, and channels dominate peripheral habitats in many estuaries and can provide a crucial ecological function (Kneib, 1997). In many estuaries, anthropogenic impacts have altered or destroyed these peripheral habitats (Kennish, 2002), eliminating their ecological benefits and obscuring relationships between underlying physical processes and ecological responses. One such estuary, the San Francisco Estuary (SFE), has been severely altered in a variety of ways, including the loss of 98% of its historical tidal wetland (Nichols et al., 1986; Whipple et al., 2012). Despite the disruption of habitat loss, recent research in the SFE has identified regions where the hydrodynamic processes associated with terminal channels can still impact pelagic communities (Feyrer et al., 2017; Montgomery, 2017). The distribution of both plankton and nekton in a long terminal channel were associated with a local turbidity maximum caused by flood-dominated tidal currents (Morgan-King & Schoelhamer, 2013). This nekton includes pelagic fish, such as the endemic, endangered Delta Smelt *Hypomesus transpacificus*, which is present in the channel and similar habitats year-round (Hobbs et al., 2019; Moyle et al., 2016; Sommer & Mejia, 2013).

This turbidity maximum and associated habitat gradient represent variability in the accumulation and/or dispersal of water quality constituents, which could also include variation in productivity available to local consumers, specifically in situ primary production and local detrital accumulation. The term detritus here is meant to incorporate the actual detrital organic material and associated bacteria and microzooplankton essential for detrital nutrient cycling (Azam et al., 1983). Zooplankton and pelagic nekton in the San Francisco Estuary are ultimately fueled by multiple carbon sources contingent on availability, including phytoplankton (Grimaldo et al., 2009; Müller-Solger et al., 2002) and detrital-derived sources (Harfmann et al., 2019; Howe & Simenstad, 2011; Young et al., 2020), and so further understanding of hydrodynamic mechanisms that drive the availability of these two different trophic pathways can inform habitat management for Delta Smelt and species-specific habitat management.

In our study, we sought to identify how gradients in hydrodynamic exchange can structure pelagic habitat and influence community and food web structure by addressing the following: (1) the relationship between hydrodynamic conditions and pelagic habitat; (2) the distribution of pelagic zooplankton and nekton among habitats that vary in hydrodynamic exchange; and (3) the importance of trophic pathways to consumers across hydrodynamically driven pelagic habitats. Understanding the role of hydrodynamics with respect to local food webs provides important insight into the causes of food web spatiotemporal variability. This spatiotemporal variability can stabilize complex food webs (Polis et al., 1997; Winemiller, 1996) and maintain consistent support for higher trophic levels (McCann et al., 2005).

## METHODS

### 2.1 Study area

Our study took place within the northern Sacramento–San Joaquin Delta, CA, USA (Figure 1). The Sacramento–San Joaquin Delta (Delta) is formed by the confluence of the Sacramento and San Joaquin Rivers and comprises the freshwater tidal extent of the SFE. Anthropogenic impacts have led to the loss of many geomorphic
features, such as intertidal floodplain and tidal marsh with complex dendritic channels, and generally reduced heterogeneity (Whipple et al., 2012). Physical alteration has been concomitant with changes to the pelagic community and declines in native species (Feyrer et al., 2007; Kimmerer et al., 1994). These changes have resulted in localized hotspots of native fish abundance and/or diversity, typically associated with some remnant element of the natural landscape or ecological process (Moyle et al., 2012). Sampling was conducted within one such hotspot, the Sacramento Deep Water Shipping Channel (channel), with a documented residence of the endangered Delta Smelt (Moyle et al., 2016; Sommer & Mejia, 2013). The channel is a unique, man-made channel built in 1963 to allow large, ocean-going vessel traffic to access the Port of Sacramento. The channel is long (~42 km), has a uniform, consistent bathymetry (a central lane ~11 m deep with narrow benches ~2 m deep), and is terminal, meaning that it has no hydrologic inputs except at the downstream mouth. The upstream end is disconnected from the Sacramento River by artificial channel gates and accumulated sediment. Municipal stormwater flows into the upstream end, and agricultural inputs are small but present throughout the length of the channel.

We selected sampling sites downstream, within, and upstream of the turbidity maximum observed by Feyrer et al. (2017). Each of these sites was contextualized by the underlying hydrodynamic processes (advection and dispersion) that define exchange zones (P. R. Stumpner, Burau, et al., 2020). Each site corresponded to specific U.S. Coast Guard navigation markers within the channel (see Figure 1; Moderate Turbidity, High-Exchange—CM 56; Turbidity Maximum, Low-Exchange—CM 66; and Turbidity Minimum, No-Exchange—CM 84). Exchange zones are defined based on the range of tidal excursions, or the distance a water parcel travels upstream from the mouth of the channel over a spring-neap period, and the average concentrations from numerical simulations (P. R. Stumpner, Burau, et al., 2020). The high-exchange zone is located from the mouth of the channel to the minimum tidal excursion, that is, the distance a water parcel moved on the weakest flood tide in a spring-neap cycle. In this zone, exchange is due to advection and occurs every tidal period (~12.5 h). The moderate-exchange zone (not sampled) is located between the range of minimum and maximum spring-neap tidal excursions; in this zone, exchange is due to advection and occurs over a period of 1–7 days during the transition from neap to spring tides. The low-exchange zone is located from the maximum tidal excursion upstream to the location where dispersive exchange with the downstream channel is negligible; in this zone, exchange is due to dispersion and occurs on timescales >7 days. The no-exchange zone is defined as the location where dispersive exchange with the downstream channel is negligible, to the end of the channel; exchange in this zone is due to dispersion, largely insignificant with the downstream channel, and occurs on the order of weeks or longer.

2.2 | Field data collection

We collected samples in three seasons, Spring (May–June), Summer (August–September), and Winter (January–February) of 2 consecutive years (Summer 2016 through Spring 2018). During each season, we collected 10 samples at each site (described below) across several days as conditions allowed (3–15) and across the full range of tidal conditions. Catch of endangered species necessitated reduced sampling at certain sites and seasons (Table 1), particularly in Spring 2018, where CM 56 was not sampled and only three samples were collected at the other two sites. Sampling of pelagic nekton was conducted at each sampling location using a closed cod end midwater trawl with a square mouth opening of 3.6 m height and width, length of 17.6 m, and nine tapered panels of stretch mesh sized from 14.7 cm near the mouth to 1.3 cm near the cod end. The total trawl volume was determined using a mechanical flowmeter (General Oceanics model 2030RC) suspended over the side of the boat. Trawls were 15-min oblique tows conducted in the center of the channel, beginning near the bottom and ending at the surface. Across all
net tows a subsample of collected nekton species were frozen and retained for later stable isotope analysis. Two zooplankton samples were collected at each trawl location via a vertical net tow. The net had an opening of 50 cm, mesh size of 125 μm, and was towed through the water column at approximately 0.3 m/s. One sample was preserved in 10% formalin for later enumeration, and one sample was frozen for stable isotope analysis. Zooplankton sample enumeration was conducted by EcoAnalysts Inc. following the methods of Beaver et al. (2014) and included biovolume measurement. Before sampling at each location, we collected samples of primary producers such as dominant aquatic vegetation and suspended particulate organic matter (POM), including phytoplankton. POM was collected as seston vacuum-filtered onto pre-combusted 47 mm GF/F filters. Primary producer and POM samples were frozen and kept for stable isotope analysis.

Physical habitat parameters (water quality) were collected at the surface using a handheld multiparameter sonde (YSI EXO2; Yellow Springs Instruments Inc.). The physical measurements taken included temperature (°C), turbidity (FNU), specific conductance (μS/cm), chlorophyll α (μg L⁻¹), fluorescent dissolved organic matter (fDOM; μg L⁻¹), an indicator of bioavailable detrital material, and dissolved oxygen concentration (mg L⁻¹). We also took vertical water quality profiles to ensure that the water column was well-mixed. Hydrodynamic (i.e., water velocity and discharge) and hydrologic (i.e., tidally filtered discharge) data were obtained from U.S. Geological Survey operated water quality monitoring stations located nearby (see Data Availability). All sondes were calibrated and checked before and after sampling bouts to ensure measurement accuracy according to USGS operating procedures (U.S. Geological Survey, 2018).

### 2.3 Laboratory data collection

#### 2.3.1 Sample preparation

Primary producers were rinsed with deionized water to remove contamination. To obtain enough material for zooplankton stable-isotope analysis, individuals were pooled, with up to 300 individual calanoid copepods or cladocerans for each sample. All fish were filleted, with left posterior dorsal muscle tissue removed. Fish stomachs were then removed and placed in 90% ethanol. Shrimp muscle was extracted from the tail. Plant and animal tissues for stable-isotope analysis were oven-dried for 48–96 h at 60°C and then ground to a homogeneous powder. Glass fiber filters containing POM filtrate were oven-dried for 3–6 h at 60°C, desiccated for 18 h with a container of 5 ml 12 M hydrochloric acid to remove carbonates, and then oven-dried for another 3–6 h at 60°C before sample submission.

#### 2.3.2 Diet analysis

All invertebrates in fish stomach contents were identified to the lowest practical taxonomic level and enumerated. Fish diets were analyzed by EcoAnalysts Inc.

#### 2.3.3 Isotope analysis

We weighed the powdered samples on a microbalance and placed them in tin capsules for isotope analysis. All samples were analyzed for δ¹³C.
and δ¹⁵N at the University of California, Davis, Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (IRMS; Sercon Ltd). Long-term standard deviation for the laboratory is 0.2 permil (‰) for δ¹³C and 0.3‰ for δ¹⁵N. All isotope values are expressed in standard delta notation (δ) relative to international standards Vienna PeeDee Belemnite (V-PDB) and air for carbon and nitrogen, respectively (Sharp, 2017). Due to high C:N ratios we used the equation presented in Post et al. (2007) to normalize δ¹³C values for lipid content, where δ¹³C(normalized) = δ¹³C(unsaturated) – 3.32 + 0.99 × C:N.

Due to the difficulty in isolating stable isotope signatures for phytoplankton in seston-rich systems (Marty & Planas, 2008), we used the POM sample with the highest chlorophyll a concentration collected in each season (ranging from 4.3 to 9.3 µg L⁻¹) to represent the isolated phytoplankton signature. Season-specific estimates were selected as dissolved inorganic carbon fractionation can differ by season (Finlay & Kendall, 2007). This is undoubtedly not a pure phytoplankton signature as other constituents were included in each of those samples; however, by selecting samples with known elevated phytoplankton concentrations we were able to conservatively estimate the relative contribution of phytoplankton to consumers.

2.4  |  Data analysis

2.4.1  |  The relationship between hydrodynamic conditions and pelagic habitat

The tidal excursion (i.e., integrated velocity between slack water) was estimated using the mean cross-sectional velocity collected at the mouth of the channel (site number 11455335). Tidal excursion estimates were corrected with a scaling factor of 1.5 based on comparison with tidal excursion measured with neutrally buoyant global positioning system drifters. The extent of the tidal excursion from the mouth of the channel was estimated for every tide for a spring–neap cycle centered around each of the six study periods. The range of tidal excursions was used to define three exchange zones: high, low, and no exchange, from the mouth to the upstream end of the channel (based on P. R. Stumpner, Burau, et al., 2020). We used these results to validate sampling site location relative to hydrodynamic exchange zones (high, low, and no exchange). To assess the influence of hydrodynamic process on pelagic habitat, we compared physical (specific conductance, temperature, turbidity) and biological (chlorophyll a and fDOM) water quality variables using two-way ANOVA with site and season as factors. All analyses were done in Program R (R Core Team, 2019).

2.4.2  |  The distribution of pelagic zooplankton and nekton

Densities of zooplankton and nekton were compared using two-way ANOVA with site and season as factors. Zooplankton and fish communities were compared using permutational multivariate analysis of variance (PerMANOVA) with site and season as factors. Fish diets were compared using permutational multivariate analysis of variance (PerMANOVA) on prey item counts with site and season as factors where sample sizes were appropriate (n > 10 for at least two of the three sites). All analyses were done in Program R (R Core Team, 2019) with the package “vegan” (Oksanen et al., 2019).

Biomass and total carbon were calculated for zooplankton and nekton (i.e., shrimp and fish). Zooplankton carbon was calculated by converting biovolumes measured during identification to carbon with the relationship: log BV = −1.429 + 0.808 log C, where BV is zooplankton biovolume (mL m⁻³) and C is zooplankton carbon (mg C m⁻³; Kimmel et al., 2006; Wiebe et al., 1975). Shrimp wet biomass was calculated using the following equation derived from collected samples: B = CL × 0.0255 + 0.213, where CL is carapace length (mm) and B is wet biomass (g). Biomass was converted to carbon following relationships for other caridean shrimp, where carbon is approximately 20% of wet biomass (Torres et al., 1994). We calculated fish wet biomass using published relationships for the San Francisco Estuary (Kimmerer et al., 2005). We converted fish biomass into carbon assuming 10% of fish biomass is carbon (Nixon et al., 1986).

2.4.3  |  The importance of trophic pathways to consumers across hydrodynamically driven pelagic habitats

We used the package MixSIAR 3.1 (Stock & Semmens, 2016) in Program R (R Core Team, 2019) to determine the relative proportion of different primary productivity pathways to sampled pelagic consumers. This modeling technique incorporates uncertainty in source contributions, including trophic enrichment (Phillips et al., 2014). We ran each model independently for zooplankton, shrimp, and each fish species, with taxonomic group and site as random effects and used both δ¹³C and δ¹⁵N. The model included both process error, by considering source and consumer variation, and residual error except for when the sample size was equal to one. Each model was set to run three chains for 100,000 Markov Chain Monte Carlo simulations, with a burn-in of 50,000. Trophic discrimination factors (TDFs; a measure of isotopic enrichment across trophic levels) were assigned by functional group from McCutchan et al. (2003), with reported standard errors converted to standard deviation per MixSIAR requirements. Enrichment factors for zooplankton were assigned based on generic values for aquatic species from (McCutchan et al., 2003; δ¹³C—mean 0.4, standard deviation 1.2; δ¹⁵N—2.3 ± 1.6). For Eucalanoplone modestus we used mean values for other caridean shrimp (Yokoyama et al., 2005; δ¹³C—mean 2.05; δ¹⁵N—3.75). Standard deviation values for caridean shrimp-specific TDFs were unavailable, and so we used a conservative standard deviation of 2.0 (larger than that for generic values for aquatic species, see above) for modeling purposes. For fishes, we added the value for fish muscle tissue to that for invertebrate omnivores (McCutchan et al., 2003; δ¹³C—1.7 ± 1.51; δ¹⁵N—6.25 ± 2.01).
Five groups of primary producers were analyzed for stable isotopes; four groups of vascular macrophytes (emergent vegetation, floating aquatic vegetation, submersed aquatic vegetation, terrestrial vegetation) and phytoplankton. Where there was high overlap in stable isotope values, subsequent statistical modeling pooled these vegetation groups. We included two groups of primary producers in the mixing models, benthic/littoral vegetation and phytoplankton. It is unlikely that consumers are directly consuming benthic/littoral vegetation, so this benthic/littoral vegetation represents both vegetation and associated detritus, bacteria and microzooplankton, which is assumed to have similar isotopic composition (Currin et al., 1995; Fellerhoff et al., 2003). Phytoplankton estimates (see Laboratory Data Collection) yielded stable isotope values consistent with published data for the area (Kendall et al., 2015) and were consistent with the signatures of obligate herbivores in the study, a method often used to derive primary producer estimates (Marty & Planas, 2008). There was no overlap between estimated phytoplankton stable isotope values and other vegetation types. Four broad categories of consumers were analyzed for stable isotopes; two categories of zooplankton (calanoid copepods and Cladocera) and two categories of nekton (shrimp and fishes). Mixing model results were propagated through carbon totals for each consumer group to evaluate the relative contribution of each primary producer to pelagic carbon. Where mixing model results were not available, season/region-specific averages from species in the same consumer category (i.e., zooplankton, pelagic fish) were applied for carbon estimates.

3 | DATA AVAILABILITY

All USGS gauging data are available in the USGS National Water Information System (NWIS; U.S. Geological Survey, 2019). Freshwater outflow (i.e., tidally filtered discharge) data are available at https://waterdata.usgs.gov/monitoring-location/11455350. Hydrodynamic (i.e., water velocity and discharge data) are available at https://waterdata.usgs.gov/monitoring-location/11455335. Original data collected for our study are available in the U.S. Geological Survey’s ScienceBase catalog at https://doi.org/10.5066/P9VCNYAZ (Larwood et al., 2019).

4 | RESULTS

4.1 | The relationship between hydrodynamic conditions and pelagic habitat

The downstream sampling site (CM 56) was within the high-exchange zone in every sample season except for Winter 2017, where CM 56 was located in the moderate-exchange zone. For all sampling periods, both the middle site (CM 66) was located in the low-exchange zone, and the upstream sampling location (CM 84) was located in the no-exchange zone. Each year was hydrologically distinct, with regionally heavy precipitation in Winter 2017 and virtually no precipitation in Winter 2018 (Figure 2a). The exchange zones along the channel, for each study period, show similar variability based on either the amount of freshwater flow or by season (Figure 2b). Due to seasonal similarities in the tidal forcing (extent and range of tidal excursions) and hydrology Summer 2016 and Summer 2017 were pooled for further summary and analysis, as are Spring 2017 and Spring 2018. Winter 2017 (wet) and Winter 2018 (dry) were analyzed as separate periods. Vertical profiles indicated no evidence of stratification, so presented values are water column averages, except for Winter 2017, where only surface water measurements are available.

Physical water quality characteristics of the sampled habitats were consistently and significantly different across sites (Specific conductance $F_{2,135} = 510.8$, $p < .001$; Temperature $F_{2,134} = 80.7$, $p < .001$; Turbidity $F_{2,135} = 50.3$, $p < .001$) and seasons (Specific conductance $F_{5,135} = 5.9$, $p < .001$; Temperature $F_{5,134} = 1448.5$, $p < .001$; Turbidity $F_{5,135} = 4.5$, $p < .005$). Specific conductance increased from downstream to upstream in most seasons, except in Winter 2017 and Spring 2017, where specific conductance was highest in the middle site (Table 1). Specific conductance differed across seasons but never exceeded 1050 $\mu$S cm$^{-1}$. Temperature generally increased from downstream to upstream, except in Winter 2017, where the temperature was similar at the middle and upstream sites. Temperature values differed across seasons. Turbidity exhibited a clear peak at the middle site except in Winter 2017, where the downstream site was most turbid (Figure 3). The upstream site was always the least turbid.

Biological water quality characteristics were also consistently and significantly different across sites (chlorophyll $\alpha$ $F_{2,135} = 32.9$, $p < .001$; fDOM $F_{2,135} = 17.3$, $p < .001$) and seasons (chlorophyll $\alpha$ $F_{5,135} = 3.6$, $p < .005$; fDOM $F_{5,135} = 76.0$, $p < .001$). Chlorophyll $\alpha$ generally increased from downstream to upstream, although in summer chlorophyll $\alpha$ concentrations were highest at the middle site (Figure 3). Seasonal chlorophyll $\alpha$ patterns were weak, although the highest values were observed in winter, and lowest values in summer. Fluorescent dissolved organic matter (fDOM) generally decreased from downstream to upstream, except in Winter 2017, where the trend was reversed (Figure 3). fDOM density was generally highest in winters.

4.2 | The distribution of pelagic zooplankton and nekton

4.2.1 | Zooplankton distribution

A total of 144 samples were collected across all sites and seasons. Total zooplankton densities generally increased from downstream to upstream, except in Winter 2017, where zooplankton densities were highest at the middle site (Figure 4). Calanoid copepods (e.g., *Pseudodiaptomus forbesi*, *Sinocalanus doerri*) and Cladocera, zooplankton groups known to be important to local pelagic fishes (Hobbs et al., 2006; Slater & Baxter, 2014), exhibited similar trends (Table 2).
PerMANOVA results showed significant community differences associated with both site ($F_{2,6} = 2.91, p = .014$) and season ($F_{3,6} = 2.23, p = .045$). Site differences were largely driven by greater density of cladocerans at the upstream site relative to downstream. Seasonal differences were driven largely by typical species turnover within the San Francisco Estuary (Kimmerer et al., 2018), with calanoid (*Pseudodiaptomus forbesi*) and cyclopoid (*Limnoithona tetraspina*) copepods dominating summer communities and other taxa dominating other seasons (Table 2).

### 4.2.2 Nekton distribution

In all, 13,965 individual organisms were sampled with the mid-water trawl representing pelagic nekton. The nektonic community was dominated by the Siberian Prawn *Palaemon modestus*, which comprised 89% of sampled organisms (84% of nekton biomass; Table 2). Siberian Prawn were overwhelmingly sampled at the middle site (>99% of individuals; 96% of biomass) in Summer (>99% of individuals; 75% of biomass). Fifteen species of fish were observed, of which Threadfin Shad *Dorosoma petenense* and American Shad *Alosa sapidissima* were the most abundant fish, together comprising 8% of nektonic organisms and 75% of sampled fishes. Two additional small-bodied pelagic fish species were collected, Delta Smelt *Hypomesus transpacificus* ($n = 6$) and Wakasagi *Hypomesus nipponensis* ($n = 4$). Collectively, these four species represent the sampled pelagic fish community, as other sampled species are littoral, benthic, or migratory. Pelagic fish densities were highest at the low exchange site in all seasons except for Winter 2018, where densities were highest at the high exchange, downstream location.

Pelagic nekton PerMANOVA results did not show significant community differences across sites ($F_{2,6} = 1.43, p = .096$) or seasons ($F_{3,6} = 1.11, p = .337$). Analyses were repeated without Siberian Prawn and nekton communities were still not significantly different across sites ($F_{2,6} = 1.43, p = .076$) and seasons ($F_{3,6} = 1.11, p = .331$). Nekton densities, but not communities, differed across sampled exchange zones. Sample sizes for Threadfin and American Shad were sufficient for diet analysis (i.e., $n > 10$ for at least two sites in a season). For both species diets were significantly different across sites (Threadfin Shad—$F_{2,56} = 6.51, p = .001$; American Shad—$F_{2,56} = 2.39, p = .004$) and seasons (Threadfin Shad—$F_{2,56} = 6.36, p = .001$; American Shad—$F_{1,46} = 3.66, p = .003$). Diet differences were largely driven by the abundance of Cladocera in no exchange, upstream diets and the abundance of ostracods (Threadfin Shad) and insects (largely Chironomidae; American Shad) in winter (Supplementary Information Material).
4.3 | The importance of trophic pathways to consumers across hydrodynamically driven pelagic habitats

4.3.1 | Stable isotope values

Mean δ¹³C values for vascular vegetation were relatively consistent across sampling regions and seasons (−22.3% to −29.6%) with high overlap in stable isotope values (Table 3). POM was typically more depleted than vascular vegetation, and phytoplankton estimates were always more depleted than vascular vegetation (Table 3). Zooplankton δ¹³C values were the most depleted of all sampled taxa (−29.3% to −38.9%; Figure 5), with little variability across zooplankton groups. Siberian Prawn were typically the most enriched relative to other taxa (−20.7% to −32.6%) while pelagic fish were generally intermediate, although with high variability (−19.5% to −35.8%).

Mean δ¹⁵N for vascular vegetation differed spatially, with more depleted values farther upstream (Table 3). Emergent vegetation exhibited seasonal variability in δ¹⁵N (1.46% to 9.1%; Figure 5), likely due to senescence (Cloern et al., 2002), with little evidence for seasonal variability in other macrophyte groups. POM was most...
FIGURE 4  Biomass of pelagic community constituents, with colored bars representing the mean and whiskers representing the standard error. Nekton are separated into shrimp and pelagic fish. Zooplankton densities have been converted to match nekton units; for zooplankton biovolume see Table 2. Colors as in Figure 1

TABLE 2  Mean biomass of sampled pelagic taxa by each season and exchange zone

| Taxa                        | Category | Spring High | Spring Low | Spring No | Summer High | Summer Low | Summer No | Winter 2017 High | Winter 2017 Low | Winter 2017 No | Winter 2018 High | Winter 2018 Low | Winter 2018 No |
|-----------------------------|----------|-------------|------------|-----------|-------------|------------|-----------|-----------------|----------------|---------------|----------------|----------------|---------------|
| *Pseudodiaptomus forbesi*   | Z        | 2.45        | 1.53       | 0.00      | 3.67        | 3.41       | 6.32      | 0.02            | 1.31           | 0.38          | 0.17           | 0.16           | 0.00          |
| *Sinocalanus doerri*        | Z        | 7.14        | 13.53      | 9.85      | 1.48        | 2.39       | 2.88      | 1.24            | 7.66           | 4.29          | 0.21           | 1.77           | 8.03          |
| Other Calanoida             | Z        | 0.04        | 0.07       | 5.55      | 0.05        | 0.32       | 1.85      | 0.12            | 0.54           | 0.22          | 0.00           | 0.03           | 0.94          |
| Calanoida (copepodites)     | Z        | 1.60        | 1.04       | 14.71     | 2.18        | 2.49       | 7.63      | 0.23            | 0.86           | 0.98          | 0.02           | 0.11           | 1.19          |
| Limnoithona tetraspina      | Z        | 0.02        | 0.25       | 7.15      | 1.02        | 5.44       | 8.79      | 0.09            | 2.37           | 2.06          | 0.01           | 0.11           | 3.72          |
| Cyclopoida (copepodites)    | Z        | 0.00        | 0.00       | 0.10      | 0.03        | 0.09       | 0.78      | 0.17            | 0.13           | 0.18          | 0.06           | 0.01           | 0.73          |
| Cladocera                   | Z        | 0.02        | 0.09       | 3.31      | 0.34        | 0.66       | 2.63      | 0.55            | 0.64           | 0.44          | 0.00           | 0.07           | 3.36          |
| Corbicula fluminea          | Z        | 0.00        | 0.01       | 0.00      | 0.04        | 0.15       | 0.00      | 0.00            | 0.00           | 0.00          | 0.04           | 0.00           | 0.00          |
| Other                       | Z        | 0.00        | 0.01       | 0.00      | 0.00        | 0.00       | 1.44      | 0.12            | 0.97           | 0.32          | 0.00           | 0.03           | 0.81          |
| Siberian Prawn Exopalaemon modestus | N | 0.00  | 1.31 | 0.00 | 0.00 | 18.90 | 0.00 | 0.93 | 3.45 | 0.12 | 0.02 | 0.40 | 0.00 |
| American Shad Alosa sapidissima | N | 0.00 | 0.00 | 0.00 | 0.04 | 0.09 | 0.01 | 0.00 | 0.00 | 0.00 | 0.34 | 0.01 | 0.05 |
| Delta Smelt Hypomesus transpacificus | N | <0.01 | <0.01 | 0.00 | 0.00 | <0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | <0.01 | 0.00 |
| Threadfin Shad Dorosoma petenense | N | 0.02 | 0.01 | 0.00 | 0.03 | 0.06 | 0.09 | 0.22 | 2.18 | 0.10 | 0.59 | 0.65 | 0.13 |
| Wakasagi Hypomesus nipponensis | N | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| Total zooplankton           |          | 11.26       | 16.53      | 40.67     | 8.81        | 14.96      | 32.32     | 2.54            | 14.48          | 8.88          | 0.50           | 2.30           | 18.78         |
| Total nekton                |          | 0.02        | 1.31       | 0.00      | 0.07        | 19.06      | 0.10      | 1.15            | 5.64           | 0.22          | 0.96           | 1.06           | 0.18          |

Note: Zooplankton (category Z) are reported as biovolume (ml L⁻¹), nekton (category N) are reported as biomass (g 100 m⁻³).
TABLE 3  Mean and standard deviation of primary producer stable isotope values for each season and exchange zone

| Primary producer | δ13C (‰)   | δ15N (‰)   |
|------------------|------------|------------|
|                  | Spring     | Summer     | Winter 2017 | Winter 2018 | Winter 2017 | Winter 2018 |
| High             |            |            |            |            |            |            |
| EMV              | -27.7 ± 0.6| -27.7 ± 0.9| -28.3 ± 0.6| -27.5 ± 0.4| 3.1 ± 1.9  | 5.0 ± 1.9  | 7.1 ± 4.3  | 1.5 ± 1    |
| FAV              | -23.4 ± 0.5| -24.9 ± 0.1| -14.5 ± 0.6| -28.5 ± 0.4| 7.6 ± 0.5  | 9.7 ± 1    | -          | -          |
| SAV              | -28.4 ± 0.3| -28.7 ± 0.7| -25.0 ± 0.8| 5.1 ± 0.1   | 3.9 ± 1.9  | 4.8 ± 1.5  | 3.8 ± 0.9  | -          |
| TER              | -25.9 ± 2.3| -27.0 ± 1.5| -21.1 ± 1.4| 4.9 ± 2.7   | 6.2 ± 2.7  | 7.9 ± 3.9  | 4.9 ± 4.4  | -          |
| All Vegetation   | -33.2 ± 1.2| -31.3 ± 1.2| -33.6 ± 3.6| 5.9 ± 5.3   | 5.9 ± 5.9  |            |            |            |
| Est. Phyto       | -27.5 ± 0.5| -27.4 ± 1.1| -27.0 ± 0.9| 5.6 ± 0.5   | 9.1 ± 0.5  | 4.4 ± 3.1  | 3.4 ± 3.7  | -          |
| Low              |            |            |            |            |            |            |            |            |
| EMV              | -30.2 ± 0.5| -29.7 ± 0.5| -29.8 ± 3.7| -27.4 ± 0.3| 6.2 ± 1.7  | 8.3 ± 0.2  | 4.1 ± 0.8  | 2.2 ± 2.7  |
| FAV              | -28.4 ± 0.4| -20.5 ± 8.4| -35.7 ± 1.4| 5.9 ± 2.3   | 5.3 ± 1.4  | 5.4 ± 2.5  | 6.6 ± 0.5  | -          |
| SAV              | -32.1 ± 1.3| -31.2 ± 0.2| -23.9 ± 8.3| 5.8 ± 1.7   | 7.4 ± 1.6  | 2.1 ± 2    | 2.2 ± 2.7  | -          |
| TER              | -29.6 ± 1  | -28.8 ± 1.6| -27.4 ± 0.3| 5.9 ± 5.3   | 5.9 ± 5.9  |            |            |            |
| All Vegetation   | -33.2 ± 1.2| -31.3 ± 1.2| -33.6 ± 3.6| 5.9 ± 5.3   | 5.9 ± 5.9  |            |            |            |
| Est. Phyto       | -32.1 ± 1.3| -31.2 ± 0.2| -23.9 ± 8.3| 5.8 ± 1.7   | 7.4 ± 1.6  | 2.1 ± 2    | 2.2 ± 2.7  | -          |

Note: Primary producer categories include EMV, FAV, POM, SAV, and TER. All Vegetation represents mean and standard deviation of all non-POM producer categories.

Abbreviations: EMV, emergent vegetation; FAV, floating aquatic vegetation; POM, particulate organic matter; SAV, submersed aquatic vegetation; TER, terrestrial vegetation.

depleted downstream (3.81‰–5.07‰), with little difference between middle and upstream locations (5.33‰–7.33‰). Cladocera were more depleted (5.3‰–11.2‰) than calanoid copepods (7.6‰–14.2‰). Nekton were generally similar (Siberian Prawn–10.9‰–14.5‰; Fishes–9.7‰–15.7‰), although δ15N for both groups exhibited a generally positive relationship with individual size.

4.3.2  Mixing model results

Both zooplankton groups were reliant on similar trophic pathways, with phytoplankton a dominant contributor in all season/region combinations (mean = 76%; Figure 6). The contribution of vegetation to zooplankton was typically highest at the low exchange habitat in Winter. Both zooplankton groups (calanoid copepods and cladocerans) exhibited similar trends.

The contribution of primary producers to nekton was more variable (Figure 6). Shrimp were largely reliant on vegetation, and phytoplankton only dominated at the upstream site in Winter 2017. Fishes generally utilized both primary producer groups at different places and times. The contribution from phytoplankton was most consistent upstream and vegetation-based detritus pathways downstream, except in Spring where phytoplankton was the dominant contributor at all sites.

4.3.3  Source of pelagic carbon

The modeled contribution of the two trophic pathways was multiplied by calculated pelagic carbon associated with each consumer group. The contribution of the different trophic pathways to pelagic communities changed seasonally and across sites (Figure 7). The relative importance of phytoplankton to total pelagic biomass was always highest at the most upstream location and exceeded 50% at the downstream location in Spring and Summer. The contribution of vegetation at the middle site always exceeded 50% and dominated the downstream site during Winter. Location along the channel consistently influenced the value of different trophic pathways to consumers, particularly at the high exchange and no exchange ends.

5  DISCUSSION

5.1  Hydrodynamic controls on pelagic habitats

Pelagic habitats along the terminal channel were structured by hydrodynamic processes, with differential exchange corresponding with variability in various habitat characteristics. Elevated specific conductance in upstream habitats is indicative of evaporation and is
often due to low exchange and higher water age in this region (Downing et al., 2016; Gross et al., 2019). The gradient in specific conductance and elevated turbidity near the maximum extent of the tidal excursion support our characterizations of the three sites as high, low, and no exchange. Elevated chlorophyll $\alpha$ in the no exchange habitat is consistent with high residence time waters regionally (E. B. Stumpner, Bergamaschi, et al., 2020) but may also be related to water clarity, as elevated turbidity in the low exchange site may have limited phytoplankton growth (Cloern, 1987). Variability in phytoplankton community may also have affected in situ chlorophyll $\alpha$ measurement, as phytoplankton communities are noted to differ across regional habitats (E. B. Stumpner, Bergamaschi, et al., 2020). Notably, these mechanisms alone do not explain low chlorophyll $\alpha$ concentrations downstream of the turbidity maximum, which may be due to dispersion and low residence time in the high exchange habitat or other factors. Additionally, top-down controls may influence chlorophyll $\alpha$ trends, as high zooplankton densities in spring and summer may have limited chlorophyll $\alpha$ in the no exchange habitat in those seasons. Elevated fDOM concentrations downstream demonstrate the importance of external habitats as sources of detrital organic material, presumably originating in nearby tidal wetlands, fluvial floodplains, or the Sacramento River. Our study demonstrates that the influence of hydrodynamics on pelagic habitats can be sampled or measured on relatively small spatial scales, specifically in tidally influenced terminal channels.

5.2 | Habitats and distribution of pelagic zooplankton and nekton

The distribution of zooplankton and nekton within the channel was strongly correlated with the hydrodynamically driven habitat zones described above. The upstream zone characterized by no exchange with downstream habitats supported higher zooplankton densities, and higher densities of Cladocera, a group more abundant in low-velocity, freshwater habitats regionally (Frantzich et al., 2018; Kimmerer et al., 2018). The downstream, high exchange zone supported the lowest densities of zooplankton, which could reflect low phytoplankton abundance observed in the study or simply the relatively low densities of...
zooplankton present in many nearby SFE pelagic habitats (Kimmerer et al., 2018). Nekton were generally more abundant in the intermediate, low exchange zone. Shrimp were almost exclusively observed in the low exchange zone and at concentrations rarely observed in the San Francisco Estuary, particularly in pelagic habitats (T. Brown & Hieb, 2014; Young et al., 2017). This could reflect a strong affinity for turbidity, unmeasured food availability related to detrital accumulation, larval retention and local recruitment, or some other unmeasured habitat association. Pelagic fishes were most abundant in the low exchange zone and were generally positively associated with turbidity. Although this relationship has been observed with Delta Smelt, in many systems Threadfin Shad have negative relationships with turbidity (Bull et al., 1995). Given the high zooplankton densities upstream, low densities of pelagic fishes upstream run counter to expectations. This discrepancy suggests that turbidity might be more important than food availability in dictating the distribution of pelagic fishes, potentially reflecting the abundance of predatory species not sampled effectively by our gear (e.g., Striped Bass *Morone saxatilis*).

5.3 Hydrodynamics and benthic–pelagic coupling

Mixing model results showed that the contribution of different primary producer groups to consumers varied across the observed pelagic habitats, and when normalized by abundance of pelagic community constituents highlight the pivotal role the observed hydrodynamic processes have in driving primary producer contributions to pelagic habitats. Previous studies have identified productivity differences across habitats, including detrital and
organic matter accumulation in turbidity fronts (Jago et al., 2006; Suzuki et al., 2012) and variable phytoplankton densities across hydrodynamic habitats (E. B. Stumpner, Bergamaschi, et al., 2020). Our measurements of how these different organic matter sources are incorporated into pelagic consumers are consistent with those of Suzuki et al. (2012), which documented elevated detrital organic material in an ETM, and elevated phytoplankton densities up- and downstream of the ETM.

The predominant contribution of phytoplankton to both zooplankton groups is consistent with other local studies, which highlight the primacy of phytoplankton to zooplankton diets (Grimaldo et al., 2009; Müller-Solger et al., 2002). However, our conservative estimates of phytoplankton stable isotope signatures used in the mixing model are not pure phytoplankton but rather reflect a combination of phytoplankton and other POM of undefined origin. This uncertainty makes it difficult to precisely identify the relative contributions of phytoplankton and other primary productivity pathways; however, the occasional contribution of macrophyte-derived carbon to zooplankton should not be discounted, as it may provide additional resilience in a dynamic system (sensu Polis et al., 1997). Similar studies of the calanoid copepod *Acartia tonsa* have demonstrated plasticity in trophic support across an ETM gradient, whereby detritus is consumed within the ETM and phytoplankton on the edges (Derisio et al., 2014). The degree of detrital consumption may be variable across systems, as bioavailability and quality of detrital POM varies (Martineau et al., 2004; Sobczak et al., 2002).

Nekton exhibited high variability in the utilization of trophic resources other than phytoplankton in certain seasons and sites. Fish diet data also reflected this variability, as the importance of prey items other than zooplankton to pelagic fish was highly mutable in space and time. Notably, zooplankton were generally less prevalent in diets during winter, and at downstream locations, which is reflected in the importance of other trophic resources in those seasons and sites. Trophic variability, coupled with the variability in measured nekton biomass, drove high variability in the contribution of littoral/benthic productivity to the pelagic food web. The contribution of littoral/benthic productivity, in the form of vascular macrophytes and associated detritus, to pelagic consumers is widely recognized as an important element of pelagic food webs (Perissinotto et al., 2003; Vadeboncoeur et al., 2002). Littoral/benthic productivity can move across habitat boundaries (i.e., benthic–pelagic coupling) directly as either dissolved or POM or be transferred trophically as pelagic secondary consumers ingest littoral/benthic herbivores (Kneib, 2002).

In our study, the magnitude of benthic–pelagic coupling differed across hydrodynamic habitats and hydrologic regimes. Food webs with at least periodic subsidy from multiple productivity pathways are more resilient and robust to perturbation, either natural or anthropogenic (McMeans et al., 2016). Our study suggests that variable exchange along the channel increases pelagic food web complexity, and thus resilience. Further research identifying the contribution of different productivity pathways in more complex terminal systems (i.e., tidal marsh complexes) is needed to fully describe the value of hydrodynamic and physical habitat complexity to pelagic food web resilience.

### 5.4 Hydrology and ecosystem response

Hydrodynamically driven habitat zones and their emergent characteristics (i.e., water quality, zooplankton and nekton density) were sensitive to precipitation. Elevated runoff in Winter 2017 was associated with a shift in the local turbidity maximum and zooplankton distribution and is likely related to the relaxation of hydrodynamic controls (i.e., shift in tidal excursion) caused by increased outflow. Flood control infrastructure in the San Francisco Estuary likely caused the relaxation on hydrodynamic controls to the channel, as the largest observed habitat changes were associated with overtopping of a flood control weir and river bypass system that drains into the Delta near the mouth of the Sacramento Deep Water Shipping Channel. After runoff declined, the system returned to pre-precipitation water quality and organismal distribution patterns. Similar effects of hydrology on hydrodynamics would be expected in the absence of flood control infrastructure, only with more gradual transitions between phases.

Despite observed changes in water quality and organismal distribution, benthic–pelagic coupling was consistent across sites regardless of hydrologic variability. This consistency suggests that either there is minimal impact of hydrology on the importance of different trophic pathways or, more likely, the time scale of shift in the pelagic habitat was shorter than the time scale of biological response as measured in this study. Elevated outflow only modified local hydrodynamics briefly (approximately 1 month; Figure 2), and the influence of this perturbation on local food webs may have been brief and not captured by our sampling strategy, particularly given the punctuated nature of runoff impacts and delays in tissue turnover for many organisms (Vander Zanden et al., 2015). Hydrology is a common driver of food web structure in many habitats, including estuaries (Possamai et al., 2020), and so the potential for hydrologic disruption of hydrodynamic-driven food web structure should not be discounted.

### 5.5 Conservation and management implications

Identifying hydrodynamic controls on pelagic habitats, communities, and food webs will aid in understanding distributions of pelagic communities at multiple spatial scales, and is important information needed for effective conservation and management. Characterizing hydrodynamic controls on pelagic habitats is a mechanistic approach that can be broadly applied. Without using hydrodynamic information, different pelagic habitats can easily be identified but predicting where or how these may form or change is difficult without knowing the underlying physical controls. For example, we can measure turbidity, but it is more difficult to predict where turbidity will be high...
as a result of restoration or other management actions. Delta Smelt, a pelagic fish endemic to the SFE, is strongly associated with turbid water throughout its extant distribution (Feyrer et al., 2007; Nobriga et al., 2008), and any factor influencing local turbidity may influence the distribution of these pelagic fishes. Similarly, the distribution of phytoplankton (and thus chlorophyll \( \alpha \)) is a known driver of zooplankton abundance (Ambler et al., 1985), important prey for Delta Smelt and other declining pelagic fishes. Chlorophyll \( \alpha \) concentration is easy to measure, but harder to predict, and enhanced understanding of physical controls on these processes can improve conservation management.

Current management priorities in the SFE focus on habitat restoration, specifically recreation of dendritic tidal wetland channels and associated floodplains (Herbold et al., 2014), and anthropogenic modifications to hydrology, primarily through manipulation of water releases and withdrawals (Luoma et al., 2015). Hydrodynamics can strongly influence pelagic habitat and associated biological responses at multiple spatiotemporal scales, which could provide crucial information for habitat restoration managers. This information could be used to inform restoration site placement and prioritization along existing hydrodynamically driven pelagic habitat gradients and assist with forecasting the development of hydrodynamically driven gradients within restored sites. By understanding the extent of exchange between channels or within a channel, we are better able to predict and understand the distribution of pelagic habitats within that channel and their subsequent effects on pelagic communities, resulting in greater confidence in forecasts of restoration outcomes.

Terminal channel systems with more complex inputs (e.g., terminal tidal marsh channels with adjacent tidal floodplain) may differ in many respects, but the influence of tidal hydrodynamics on terminal channel pelagic communities will likely still be profound. It is important to note that habitat restoration, levee failure, or other large-scale perturbations to regional hydrodynamics (including changing precipitation patterns) can alter tidal forcing and thus the location of pelagic habitats within tidal channels (Herbold et al., 2014). Although hydrologic influences on these gradients were limited to a single season in our study, further study of flow impacts on hydrodynamic features is needed to evaluate seasonal persistence and potential impacts of altered hydrology. Down-scaled global climate models predict increases in water temperature, salinity and sea level, and decreased precipitation and freshwater outflow (L. R. Brown et al., 2013; Cloern et al., 2011), which may also impact the persistence or location of these hydrodynamically driven habitats. The results of our study highlight the relationship between hydrodynamic processes and biological responses and suggest that understanding the physical process can improve the understanding of pelagic communities.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in the USGS National Water Information System (NWIS; https://doi.org/10.5066/F7P55KJN) and the USGS ScienceBase catalog (https://doi.org/10.5066/P9VCNYAZ).

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REFERENCES
Allen, G., Salomon, J., Bassoulet, P., Du Penhoat, Y., & De Grandpre, C. (1980). Effects of tides on mixing and suspended sediment transport in macrotidal estuaries. *Sedimentary Geology*, 26(1–3), 69–90. https://doi.org/10.1016/0037-0738(80)90066-8
Ambler, J. W., Cloern, J. E., & Hutchinson, A. (1985). Seasonal cycles of zooplankton from San Francisco Bay. In J. E. Cloern, & F. H. Nichols (Eds.), *Temporal dynamics of an Estuary: San Francisco Bay* (pp. 177–197). Springer.
Azam, F., Fenchel, T., Field, J. G., Gray, J., Meyer-Reil, L., & Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, 10, 257–263. https://www.jstor.org/stable/24814647
Beaver, J. R., Tausz, C. E., Renicker, T. R., Holdren, G. C., Hosler, D. M., Manis, E. E., Scotese, K. C., Teacher, C. E., Vitanye, B. T., & Davidson, R. M. (2014). The late summer crustacean zooplankton in western USA reservoirs reflects ecoregion, temperature and latitude. *Freshwater Biology*, 59(6), 1173–1186. https://doi.org/10.1111/fwb.12338
Brown, L. R., Bennett, W. A., Wagner, R. W., Morgan-King, T., Knowles, N., Feyrer, F., Schoelhamer, D. H., Stacey, M. T., & Dettinger, M. (2013). Implications for future survival of delta smelt from four climate change scenarios for the Sacramento–San Joaquin Delta, California. *Estuaries and Coasts*, 36(4), 754–774. https://doi.org/10.1007/s12237-013-9585-4
Brown, T., & Hieb, K. A. (2014). Status of the Siberian prawn, *Eupalaemon modestus*, in the San Francisco Estuary. *San Francisco Estuary and Watershed Science*, 12(1). https://doi.org/10.15447/sfews.2014v12is1art4
Bull, L., Fox, D., Brown, D., Davis, L., Miller, S., & Wullschleger, J. (1995). Fish distribution in limnetic areas of Lake Okeechobee, Florida. *Advances in Limnology*, 45, 333–342.
Chanton, J., & Lewis, F. G. (2002). Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, USA. *Limnology and Oceanography*, 47(3), 683–697. https://doi.org/10.4319/lo.2002.47.3.0683
Cloern, J. E. (1987). Turbidity as a control on phytoplankton biomass and productivity in estuaries. Continental Shelf Research, 7(11–12), 1367–1381. https://doi.org/10.1016/0278-4343(87)90042-2

Cloern, J. E., Canuel, E. A., & Harris, D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnology and Oceanography, 47(3), 713–729. https://doi.org/10.4319/lo.2002.47.3.0713

Cloern, J. E., & Jassby, A. D. (2010). Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuaries and Coasts, 33(2), 230–241. https://doi.org/10.1007/s12237-009-9195-3

Cloern, J. E., & Jassby, A. D. (2012). Drivers of change in estuarine–coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. Reviews of Geophysics, 50(4), 1–33. https://doi.org/10.1029/2012RG000397

Cloern, J. E., Knowles, N., Brown, L. R., Cayan, D., Dettinger, M. D., Morgan, T. L., Schoellhamer, D. H., Stacey, M. T., Van der Wegen, M., Wagner, R. W., & Jassby, A. D. (2011). Projected evolution of California’s San Francisco Bay–Delta–River system in a century of climate change. PLOS One, 6(9), e24465. https://doi.org/10.1371/journal.pone.0024465

Crump, B. C., & Baross, J. A. (1996). Particle-attached bacteria and heterotrophic plankton associated with the Columbia River estuarine turbidity maxima. Marine Ecology Progress Series, 138, 265–273. https://doi.org/10.3354/meps138265

Curren, C. A., Newell, S. Y., & Paerl, H. (1995). The role of standing dead Spartina alterniflora and benthic microalgal in salt marsh food webs: Considerations based on multiple stable isotope analysis. Marine Ecology Progress Series, 121, 99–116. https://doi.org/10.3354/meps121099

Deegan, L. A., & Garritt, R. H. (1997). Evidence for spatial variability in estuarine food webs. Marine Ecology Progress Series, 147, 31–47. https://doi.org/10.3354/meps147031

Deriso, C., Braverman, M., Gaitán, E., Hozbor, C., Ramírez, F., Carreto, J., Deegan, L. A., & Garritt, R. H. (1997). Evidence for spatial variability in estuaries and productivities in estuaries. Continental Shelf Research, 7(11–12), 1367–1381. https://doi.org/10.1016/0278-4343(87)90042-2

Finlay, J. C., & Kendall, C. (2007). Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. Stable Isotopes in Ecology and Environmental Science, 2, 283–333.

Frisnitz, J., Sommer, T., & Schreiber, B. (2018). Physical and biological responses to flow in a tidal freshwater slough complex. San Francisco Estuary and Watershed Science, 16(1). https://doi.org/10.15447/sfews.2018v16iss1art3

Grimaldo, L. F., Stewart, A. R., & Kimmerrer, W. (2009). Dietary segregation of pelagic and littoral fish assemblages in a highly modified tidal freshwater estuary. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 1, 200–217. https://doi.org/10.1577/C08-013.1

Gross, E., Andrews, S., Bergamaschi, B., Downing, B., Holleman, R., Burdick, S., & Durand, J. (2019). The use of stable isotope-based water age to evaluate a hydrodynamic model. Water, 11(11), 2207. https://doi.org/10.3390/w11112207

Harfmann, J., Kurobe, T., Bergamaschi, B., Teh, S., & Hersens, P. (2019). Plant detritus is selectively consumed by estuarine copepods and can augment their survival. Scientific Reports, 9(1), 1–9. https://doi.org/10.1038/s41598-019-45503-6

Herbold, B., Divol, D. M., Brown, L., Grossinger, R., Kimmerrer, W., Lehman, P., Simenstad, C. S., Wilcox, C., & Nobriga, M. (2014). The role of tidal marsh restoration in fish management in the San Francisco Estuary. San Francisco Estuary and Watershed Science, 12(1). https://doi.org/10.15447/sfews.2014v12iss1art1

Hobbs, J. A., Bennett, W. A., & Burton, J. (2006). Assessing nursery habitat quality for native smelts (Osmeridiae) in the low-salinity zone of the San Francisco estuary. Journal of Fish Biology, 69(3), 907–922. https://doi.org/10.1111/j.1095-8649.2006.01176.x

Hobbs, J. A., Lewis, L. S., Willmes, M., Denney, C., & Bush, E. (2019). Complex life histories discovered in a critically endangered fish. Scientific Reports, 9(1), 1–12. https://doi.org/10.1038/s41598-019-52273-8

Howe, E. R., & Simenstad, C. A. (2011). Isotopic determination of food web origins in restoring and ancient estuarine wetlands of the San Francisco Bay and Delta. Ecosystems and Coasts, 34(3), 597–617. https://doi.org/10.1007/s10023-011-9376-8

Islam, M. S., Ueda, H., & Tanaka, M. (2005). Spatial distribution and trophic ecology of dominant copepods associated with turbidity maximum along the salinity gradient in a highly embayed estuarine system in Ariake Sea, Japan. Journal of Experimental Marine Biology and Ecology, 316(1), 101–115. https://doi.org/10.1016/j.jembe.2004.11.001

Jaco, C., Ishak, A., Jones, S., & Goff, M. (2006). An ephemeral turbidity maximum generated by resuspension of organic-rich matter in a macrotidal estuary, S.W. Wales. Estuaries and Coasts, 29(2), 197–208. https://doi.org/10.1007/BF02781989

Jassby, A. D., & Powell, T. M. (1994). Hydrodynamic influences on interannual chlorophyll variability in an estuary: Upper San Francisco Bay-Delta (California, USA). Estuarine, Coastal and Shelf Science, 39(6), 595–618. https://doi.org/10.1016/S0277-7714(06)80012-0

Kendall, C., Young, M. B., Silva, S. R., Kraus, T., Peak, S., & Guerin, M. (2015). Tracing nutrient and organic matter sources and biogeochemical processes in the Sacramento River and Northern Delta: Proof of concept using stable isotope data. U. S. Geological Survey. https://doi.org/10.5066/F7Q17FCM

Kennish, M. J. (2002). Environmental threats and environmental future of estuaries. Environmental Conservation, 29(1), 78–107. https://doi.org/10.1017/S0376892902000061

Kimmel, D. G., Roman, M. R., & Zhang, X. (2006). Spatial and temporal variability in factors affecting mesozooplankton dynamics in Chesapeake Bay: Evidence from biomass size spectra. Limnology...
estuarine fishes. Estuaries and Coasts, 43, 880–893. https://doi.org/10.1007/s12237-019-00693-0

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montana, C. G. (2007). Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, 152(1), 179–189. https://doi.org/10.1007/s00442-006-0630-x

R Core Team. (2019). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/

Raimonet, M., & Cloern, J. E. (2017). Estuary–ocean connectivity: Fast physics, slow biology, Global Change Biology, 23(6), 2345–2357. https://doi.org/10.1111/gcb.13546

Schroeter, R. E., O’Rear, T. A., Young, M. J., & Moyle, P. B. (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). https://doi.org/10.15447/sfews.v13iss3art6

Sharp, Z. (2017). Principles of stable isotope geochemistry. University of New Mexico. https://doi.org/10.25844/h9q1-0p82

Simenstad, C. A., Small, L. F., & McIntire, C. D. (1990). Consumption

Suzuki, K. W., Kasai, A., Nakayama, K., & Tanaka, M. (2012). Year-round accumulation of particulate organic matter in the estuarine turbidity maximum: Comparative observations in three macrotidal estuaries (Chikugo, Midori, and Kuma Rivers), southwestern Japan. Journal of Oceanography, 68(3), 453–471. https://doi.org/10.1007/s10872-012-0109-9

Suzuki, K. W., Nakayama, K., & Tanaka, M. (2009). Horizontal distribution and population dynamics of the dominant mysid Hyperacanthomysis longirostris along a temperate macrotidal estuary (Chikugo River estuary, Japan). Estuarine, Coastal and Shelf Science, 83(4), 516–528. https://doi.org/10.1016/j.ecss.2009.04.023

Torr, J. J., Donnelly, J., Hopkins, T. L., Lancraft, T., Aarset, A., & Ainley, D. (1994). Proximate composition and overwintering strategies of Antarctic micronektonic crustacea. Marine Ecology Progress Series, 113, 221–232.

U.S. Geological Survey. (2018). National Field Manual for the Collection of Water-Quality Data. U.S. Geological Survey. https://doi.org/10.3133/twi09

U.S. Geological Survey. (2019). National Water Information System: U.S. Geological Survey web interface. https://doi.org/10.5066/F7P5SKJN. Accessed August 20, 2019.

Vadeboncoeur, Y., Vander Zanden, M. J., & Lodge, D. M. (2002). Putting the lake back together: Reintegrating benthic pathways into lake food web models: Lake ecologists tend to focus their research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral part of lake food webs. BioScience, 52(1), 44–54. https://doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. PLOS One, 10(1), e0116182. https://doi.org/10.1371/journal.pone.0116182

Whipple, A., Grossinger, R., Rankin, D., Stanford, B., & Askevold, R. (2012). Sacramento-San Joaquin Delta historical ecology investigation: Exploring pattern and process. SFEI Contribution No. 672. San Francisco Estuary Institute-Aquatic Science Center.

Wieber, P. H., Boyd, S., & Cox, J. L. (1975). Relationships between zooplankton displacement volume, wet weight, dry weight and carbon. Fishery Bulletin, 73, 777–786.

Winemiller, K. O. (1996). Factors driving temporal and spatial variation in aquatic foodplain food webs. In Food Webs (pp. 298–312). Springer. https://doi.org/10.1007/978-1-4615-7007-3_29

Yokoyama, H., Tanaki, A., Harada, K., Shimoda, K., Koyama, K., & Ishii, Y. (2005). Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Marine Ecology Progress Series, 296, 115–128. https://doi.org/10.3354/meps296115

Young, M. J., Berridge, K. A., O’Rear, T., Moyle, P. B., & Durand, J. R. (2017). Habitat partitioning by native and alien fishes and decapods in novel habitats of the upper San Francisco Estuary. Biological Invasions, 19(9), 2693–2710. https://doi.org/10.1007/s10530-017-1477-2

Young, M. J., Howe, E., O’Rear, T., Berridge, K., & Moyle, P. (2020). Food Web Fuel Differs Across Habitats and Seasons of a Tidal Freshwater Estuary. Estuaries and Coasts, 1–16. https://doi.org/10.1007/s12237-020-00762-9

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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