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RESEARCH

Flow Augmentations Modify an Estuarine Prey Field

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ABSTRACT

Zooplankton density and community composition in estuaries can be affected by variation in freshwater inputs, with important implications for higher trophic levels. In the San Francisco Estuary, management agencies have initiated autumn flow augmentations in the form of changes to reservoir releases or to exported water from the South Delta to increase and improve available habitat for endangered Delta Smelt, *Hypomesus transpacificus*, during the season when their body condition most influences fecundity. Autumn flow augmentation only occurs in years with higher precipitation, effectively moving the Low-Salinity Zone (LSZ) downstream to key foraging habitats for Delta Smelt in Suisun Bay and Suisun Marsh. To assess whether augmented flow enhanced prey resources for Delta Smelt, we compared autumn zooplankton abundance, biomass, spatial distribution, and community composition in years when flow was augmented (2017, 2019) with reference years when flow was not augmented (2018, 2020). In augmented years, we detected higher total zooplankton abundance and altered community composition in Suisun Bay and Suisun Marsh. Increased freshwater in these regions was associated with higher abundance of *Pseudodiaptomus forbesi*, a preferred prey of Delta Smelt, while species associated with higher salinities—*Acartiella sinensis* and *Tortanus dextrilobatus*—were less abundant. Thus, autumn flow augmentations can influence foraging habitat and prey availability for Delta Smelt, underscoring the complex responses of estuarine zooplankton communities to changes in response to flow and salinity regimes. This study is management- relevant because it shows that important Delta Smelt prey items increase in downstream regions when X2 is lower. Whether that results in a response in Delta Smelt abundance remains to be seen.

KEY WORDS

zooplankton, X2, outflow, estuarine hydrology, Delta Smelt

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INTRODUCTION

Tidal estuaries are highly dynamic, productive environments that provide critical habitat for many ecologically and economically important species (Johnston et al. 2002; Kimmerer 2004; Ray 2005; Barbier et al. 2011; Sheaves et al. 2015). Biotic interactions at the tidal interface of fresh and marine waters shape estuarine planktonic prey communities, which in turn influence habitat suitability for estuarine fishes (Kimmerer 2002b; Jassby 2008; Ziegler et al. 2019; Connelly et al. 2020). For example, zooplankton availability as prey for fishes in the Columbia River estuary was dominated by relationships with season, flow, and salinity (Bottom and Jones 1990; Connelly et al. 2020). Such effects of river flows can interact with physical habitat and biota in complex ways. In the Skeena River estuary in British Columbia, calanoid copepod abundance was positively correlated with salinity but that of harpacticoid copepods was linked to eelgrass habitat (Arbeider et al. 2019). Consequently, changes in flow regime can affect zooplankton composition as well as overall abundance. In tidal estuaries with managed freshwater flows, understanding this dynamic environment is critical for developing water-management strategies that can effectively protect estuarine and diadromous fishes (Peterson 2003). These strategies will be increasingly important with climate change, which will continue to affect marine and freshwater ecosystems independently, thereby compounding the effect of flow management on estuaries (Lotze et al. 2006; Barbier et al. 2011; Elliott and Whitfield 2011; Gillanders et al. 2011).

The San Francisco Estuary (henceforth "the estuary") is one of the largest estuaries on the west coast of North America, and it has undergone anthropogenic alterations that have changed the ecological community (Nichols et al. 1986). Its watershed extends from the Sierra Nevada Mountain range to the Pacific Ocean at the Golden Gate Bridge, an area that covers over 150,000 square kilometers and nearly 40% of the state of California. Within the estuary, Suisun Bay and Suisun Marsh, situated just west of the confluence of the Sacramento–San Joaquin Delta (the Delta), form the largest tidal marsh on the US West coast (Figure 1). Freshwater from natural runoff and reservoir releases flows into the Delta. Flows out of the Delta (outflow), which is itself a complex and highly managed water-conveyance system, are controlled by diversions at two pumping stations in its southern extent. In addition to an altered hydrology (Kimmerer 2008; Grimaldo et al. 2021), the estuary and Delta's pelagic fish and zooplankton community has been affected by loss of tidal wetland (Nichols et al. 1986; Brown 2003; Whipple et al. 2012) and introductions of non-native prey, competitors, and predators (Alpine and Cloern 1992; Winder and Jassby 2011).

Delta Smelt, *Hypomesus transpacificus*, is a native fish that has been at the forefront of water-resource management concerns because of its decline in abundance (USFWS 2019). Delta Smelt are a small-bodied, annual, planktivorous species, which live in cool, turbid waters (Moyle et al. 2016). The most common phenotype of larval Delta Smelt is semi-anadromous, hatching in the spring and early summer (March through June) in the freshwater Delta, and moving into brackish waters (0.5 to 6 practical salinity units [psu]), during the summer and fall (July through December). Depending on flow conditions during summer and fall, this brackish zone can be as far west as Suisun Bay and Suisun Marsh, or at the confluence of the Sacramento and San Joaquin rivers, or even further upstream. There, Delta Smelt grow and mature on once-abundant food resources, before reaching spawning condition in the early winter, when they move back into the fresher water of the Delta to spawn during January through March (Bennett 2005; Moyle et al. 2016). There are also less common Delta Smelt phenotypes that complete their life cycle entirely in either brackish or fresh water (Hobbs et al. 2019). Regardless of the specific life-history pathway, the decline of Delta Smelt may have resulted from a reduction in freshwater flow and associated changes in the estuary's salinity regime that shape zooplankton abundance and community composition (Moyle et al. 2018). Consequently, targeted flow augmentations—by managing reservoir releases or export water pumped from the South Delta—increase

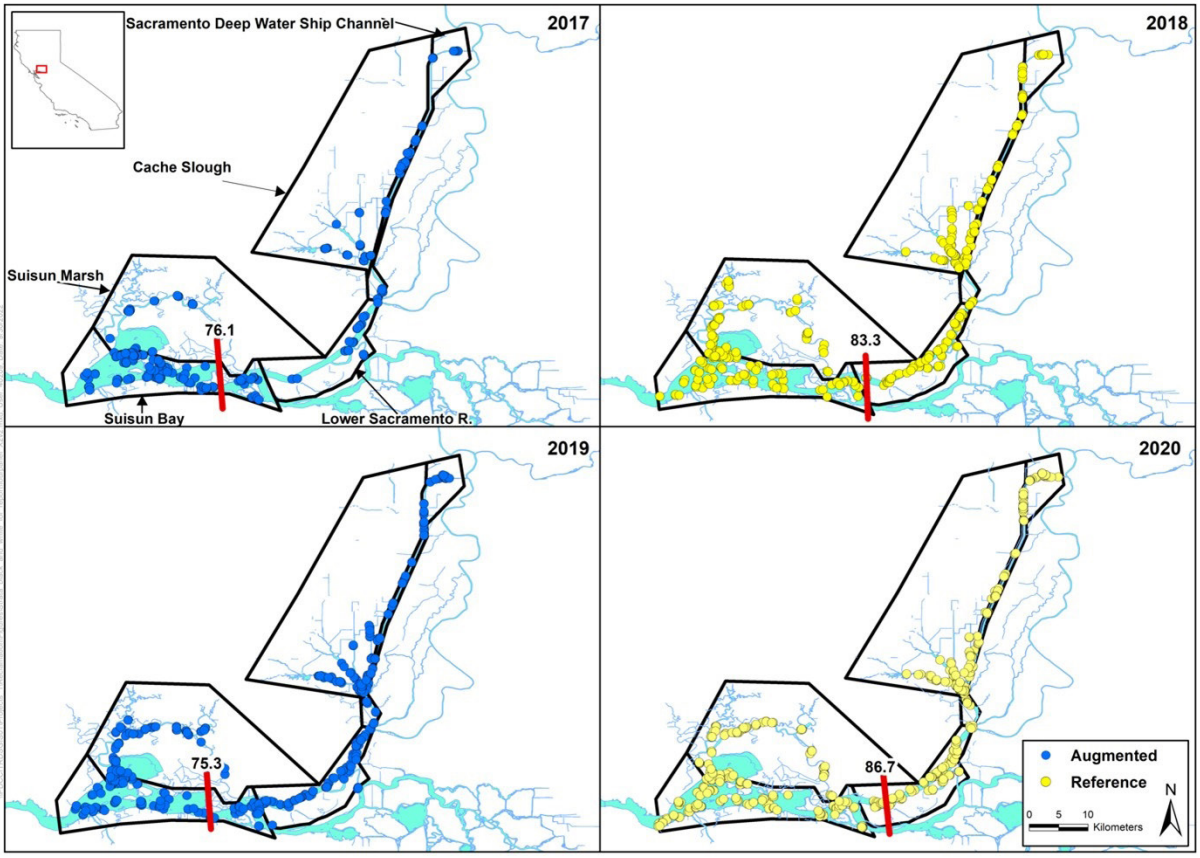

Figure 1 Map of sampling locations (*points*) for each target region (*polygons*) in the San Francisco Estuary across four years. *Red lines* and values represent the location of the mean X2 line (km) for augmented (*blue*) and reference (*yellow*) years. The *red square* in the inset map depicts the extent of the study area in California.

net freshwater outflow from the Delta to the estuary to improve habitat quality and increase zooplankton prey availability at time-periods critical for Delta Smelt.

Increased food availability in autumn is correlated with higher survival of pre-spawning Delta Smelt (Rose et al. 2013a, 2013b; FLOAT–MAST 2015). Consequently, augmented outflow during autumn months of years classified as wet or above normal, based on a Sacramento Valley Index water year type (USFWS 2008), are intended to allow Delta Smelt improved access to estuarine foraging areas. Delta Smelt preferentially reside in areas where salinity is less than 6 psu, concurrent with the position of a standard metric known as X2, which represents the distance (in km) from the Golden Gate Bridge to where salinity is a tidally averaged isohaline of 2 psu (Jassby et al. 1995). In these augmented years, outflow in September and October maintained X2 near 80 km, thereby expanding the low-salinity environment for Delta Smelt downstream to estuarine habitats in Suisun Bay and Suisun Marsh, where most Delta Smelt historically occurred (Feyrer et al. 2007, 2011; Merz et al. 2011; Bever et al. 2016; Hendrix et al. 2023). Outflow augmentation is also hypothesized to change environmental conditions within the targeted regions by increasing material fluxes of sediment, nutrients, and chlorophyll-*a*, which can benefit Delta Smelt via lower trophic levels (Kimmerer et al. 2002b; Brown et al. 2014).

The scarcity of Delta Smelt makes it challenging, if not impossible, to observe their foraging habitat use directly. Instead, we focused on understanding how dynamic habitats and

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hydrology influence zooplankton communities in areas where Delta Smelt were known to occur.

Delta Smelt occupy estuarine channel habitats (Sommer and Mejia 2013), which can provide thermally stratified, deep, cold-water refuges in summer (Mahardja et al. 2022) but foraging, as indicated by higher stomach fullness, tends to occur closer to shallow, tidal wetlands (Hammock et al. 2019). Zooplankton undergo a diurnal vertical migration in response to tidal exchange (also known as vertical tidal migration), moving upward in the water column on the flood tide, enabling them to maintain position in the estuary (Kimmerer et al. 1998, 2002b). Increased outflows can alter zooplankton assemblages, affecting foraging habitat for estuarine fishes (Jassby et al. 1995; Kimmerer et al. 1998; Kimmerer 2002a; Cloern 2007). Understanding trends in distribution and relative abundance of zooplankton in this tidal estuary–marsh complex is important because of the ecological role of zooplankton in supporting estuarine fishes, especially those that are experiencing widespread population declines (Kimmerer et al. 2019; Hartman et al. 2021).

Delta Smelt inhabit a highly dynamic environment, displaying a wide response to various environmental conditions, but, as a result of their current low abundance, it is difficult to validate population responses to environmental changes (Hobbs et al. 2017). Our objective was to examine the effects of autumn flow augmentation during wet or above-normal water years on zooplankton communities in the estuary, as a proxy for how this targeted action could potentially affect Delta Smelt foraging opportunities. We compared environmental variables within the estuary and Delta, as well as autumn zooplankton assemblages that have historically comprised the prey base of Delta Smelt, to compare the effect of years with flow augmentation (2017, 2019) to reference years (2018 and 2020), when no flow augmentation occurred.

- First, we expected that environmental variables—such as turbidity, chlorophyll-*a* and nutrients—would increase in response to higher outflow, and that temperature, salinity, and ammonium would decrease in augmented years (Table 1).

- Second, we expected that zooplankton abundance and biomass would increase in Suisun Bay and Suisun Marsh, and that community composition would favor freshwater zooplankton species under flow augmentation.

Table 1 Predictions and results for the effect of increased outflow on environmental variables during managed flow augmentations within the estuary and Delta. Environmental variables in *italics* indicate agreement between prediction and results.

Environmental variable	Prediction	Results	Source
Temperature	Decrease	No significant change	Schultz et al. 2019
Turbidity	*Increase*	*Increase for Suisun Bay and Marsh*	Brown et al. 2014
Salinity	*Decrease*	*Decrease for Lower Sacramento, Suisun Bay and Marsh*	Brown et al. 2014
Chlorophyll *a*	Increase	Decrease for Lower Sacramento, Suisun Bay and Marsh	Brown et al. 2014
Nitrate	Increase	No significant change	Brown et al. 2014
Ammonium	Decrease	No significant change	Brown et al. 2014
Phosphate	*Increase*	*Increase for Sacramento Shipping Channel, Suisun Bay*	Heidel et al. 2006
Dissolved Organic Carbon	*Decrease*	*Decrease in Sacramento Shipping Channel, Lower Sacramento and Suisun Bay*	Downing et al. 2009
Zooplankton Abundance	*Increase*	*Increase for Suisun Bay*	Brown et al. 2014, Schultz et al. 2019
Zooplankton Biomass	Increase	Decrease for Suisun Bay	Brown et al. 2014, Schultz et al. 2019

- Third, we expected that zooplankton abundance and biomass would increase in shoals, where lower water velocity makes it easier for them to maintain position and where more food is retained, relative to channels under augmented conditions.

MATERIALS AND METHODS

Site Selection

We focused our study on the upper estuary where net outflow determines the position of low-salinity habitat (0.5 to 6 psu) that juvenile and sub-adult Delta Smelt occupy in higher densities than elsewhere in the estuary (Merz et al. 2011). Sampling locations were selected using a generalized random tessellated stratified (GRTS) sampling design across the upper estuary (Stevens Jr and Olsen 2004; Starcevich et al. 2016), focusing on five target regions: the Cache Slough Complex; the Sacramento Deep Water Ship Channel (DWSC); the lower Sacramento River; Suisun Bay; and Suisun Marsh (Figure 1). Sampling was conducted during autumn (September through November). Three stations in each region were sampled in tandem with the US Fish and Wildlife Service's Enhanced Delta Smelt Monitoring (EDSM) program (USFWS 2022). Each week, three new GRTS stations per region were selected and sampled. In 2017, sampling occurred on a biweekly basis; in 2018, sampling occurred weekly. In 2019 and 2020, paired sampling with EDSM extended, so that weekly sampling began in April and ended in November, but since the focus of this study is on autumn habitat conditions, only samples from September through November were used in this analysis.

Sampling Methods

At each of the 15 sampling stations, we conducted individual fixed-depth tows in three habitat types when present: the surface of channels, deep within channels (> 6 m), and on shoals (< 3 m), following methods in Schultz et al. (2019). We identified zooplankton samples using methods described in the Interagency Ecological Program's (IEP's) Environmental Monitoring Program (Kayfetz et al. 2020), except that we used 10 aliquot counts instead of 20 to account for higher sample densities that result from larger-volume nets, as described in (Schultz et al. 2019). We identified all organisms to the lowest possible taxonomic level, and we further separated zooplankton by life stage, hereafter referred to as taxa. Prey taxa noted in this study were confirmed in a gut content survey of Delta Smelt collected between 2011 and 2017 from September to November by Slater et al. (2019).

We took spot measurements of temperature (°C), turbidity (NTU), salinity (psu), dissolved oxygen (DO; mg L^{-1}), and chlorophyll-*a* (mg L^{-1}) for each habitat type using an EXO-2 multiparameter sonde (YSI, Yellow Springs, Ohio USA) before each zooplankton tow. Chlorophyll-*a* serves as a proxy for phytoplankton biomass, which is grazed down by zooplankton such as *Pseudodiaptomus forbesi*, an important prey for Delta Smelt (Kayfetz and Kimmerer 2017). We filtered water samples by vacuum pressure at < 10 mm Hg through 47-mm-diameter, 0.2-µm polycarbonate filters at each site at the surface. The UC Davis Ecosystem Ecology and Limnology Lab later analyzed the water samples using colorimetric assays for ammonium (NH_4^+, mg L^{-1}), nitrate (NO_3^-, mg L^{-1}), and phosphorous (PO_4^{3-}, mg L^{-1}) (Murphy and Riley 1962; Verdouw et al. 1978; Doane and Horwáth 2003). Dissolved organic carbon (DOC, mg L^{-1}) was analyzed by high-temperature catalytic oxidation (Bird et al. 2003). We obtained the computed net Delta outflow index (outflow) and estimated X2 values from the Dayflow program (CDWR 2022).

Data Analysis

Two measures of the zooplankton community were designated as response variables: abundance by volume (count m^{-3}) and biomass by volume (µg m^{-3}), herein referred to as abundance and biomass, respectively. Biomass of mesozooplankton (zooplankton 0.2 to 20 mm TL) was calculated by multiplying species-specific grams of carbon by the abundance value as outlined in Kayfetz et al. (2020) and using the dataset from Kimmerer et al. (2011, unreferenced, see "Notes"). While biomass and abundance were highly correlated in our study (Pearson's R value of 0.91), both values were

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used in analyses because these measurements can provide different information about food availability that can reflect changes in seasons (Atkinson et al. 2012), different life stages (Coyle and Pinchuk 2003), or reductions in body size (Cremona et al. 2020). Water-quality variables (temperature, turbidity, salinity, chlorophyll-*a*, nitrate, ammonium, phosphate, dissolved organic carbon), water year type, taxa, zooplankton abundance and biomass, and habitats were each compared across sampling sites during reference and augmented years using a non-parametric Kruskal–Wallis test (*H* stat) followed by a Dunn's multiple pairwise comparison. Dunn's tests were conducted with Bonferroni corrections for multiple comparisons of all covariates.

Non-metric multi-dimensional scaling (NMDS) ordinations were constructed using samples that were square-root-transformed, followed by Wisconsin double standardization to equalize emphasis of dominant sites and dominant taxa on the ordination space before calculating the Bray–Curtis dissimilarity matrix ('metaMDS') from the *vegan* package (Bray and Curtis 1957; Oksanen et al. 2022). Rare taxa (i.e., found in five or fewer sites) were removed from the analysis. A two-dimensional solution was selected as the final solution for all ordinations because it reduced solution stress below 0.16. The influence of environmental covariates was examined by fitting vectors to the ordination spaces using the function `envfit` from the *vegan* package (Oksanen et al. 2022).

The degree of dissimilarity of abundance and biomass between mesozooplankton in reference and augmented years was analyzed with Similarity Percentage (*simper vegan* package, Oksanen et al. 2022), in R version 3.5.3 (R Core Team 2020), with permutations following Clarke (1993) and Oksanen et al. (2022).

RESULTS

We analyzed a total of 1,401 samples from 2017 to 2020, across five regions, with three stations per region per week, each containing up to three habitat types per station (Table 2). Sampling extended from the northern terminus of the Sacramento DWSC, south and seaward to Carquinez Straits on the western edge of Suisun Bay (Figure 1; Table 2).

Physical Environment across Augmented and Reference Years

The position of X2 was more seaward in augmented years than in reference years: mean ± SD 75.7 ± 2.01 km vs. 85.3 ± 0.06 km, respectively (CDWR 2022). This 9.6-km difference

Table 2 Number of samples taken for each of three habitats (channel surface, channel deep, and shoal) in each of five regions during years with varying hydrologic conditions

		Regions				
		Cache Slough	Sacramento DWSC	Lower Sacramento River	Suisun Bay	Suisun Marsh
2017 (augmented)	Channel surface	11	19	10	34	6
	Channel deep	5	18	12	32	6
	Shoal	2	0	5	30	4
2018 (reference)	Channel surface	26	28	30	35	20
	Channel deep	16	27	28	32	16
	Shoal	5	1	7	24	23
2019 (augmented)	Channel surface	39	37	39	38	35
	Channel deep	25	37	38	36	29
	Shoal	6	3	9	33	20
2020 (reference)	Channel surface	33	37	33	44	25
	Channel deep	27	36	33	45	20
	Shoal	12	22	32	33	33

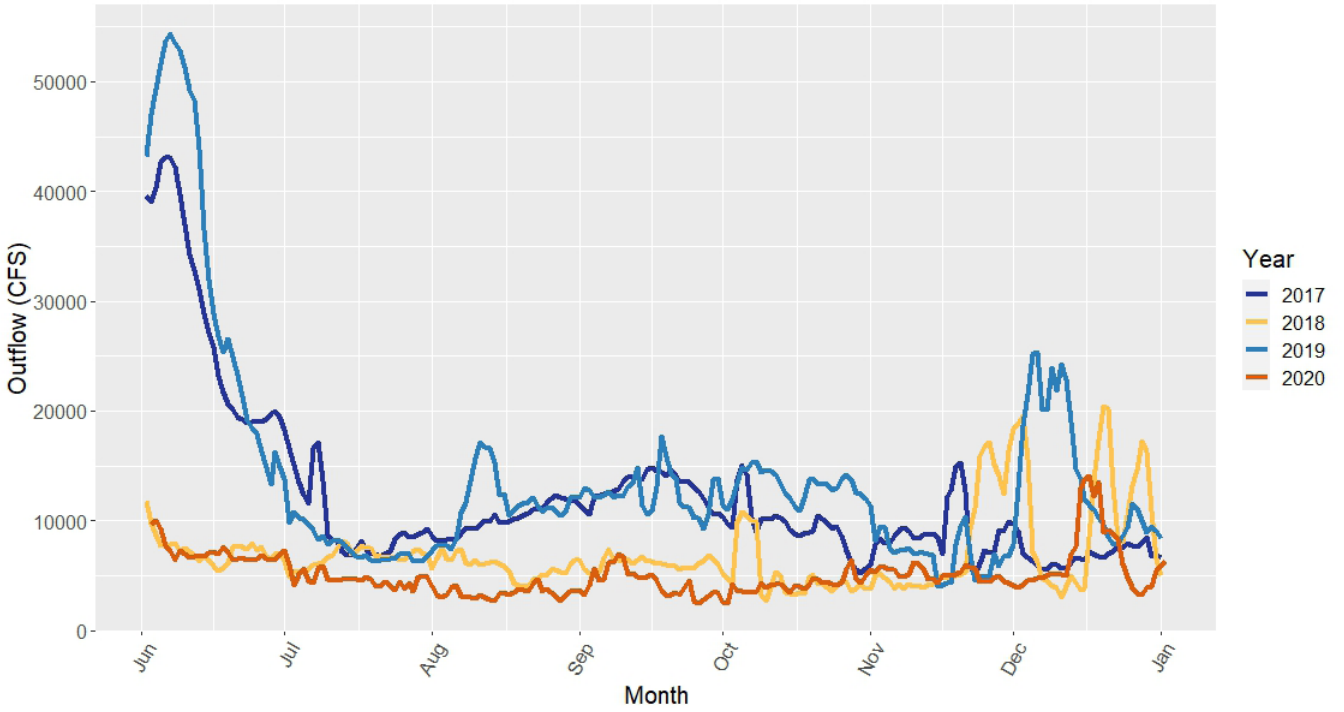

Figure 2 Outflow from June through January for years 2017-2020. *Blue lines* represent augmented years 2017 and 2019; *yellow* and *orange lines* represent reference years 2018 and 2020.

in mean X2 moved the LSZ from the downstream area of the lower Sacramento River in reference years to within Suisun Bay in augmented years (Figure 1). During augmented years, outflow rapidly decreased during the summer months to levels comparable to outflow in 2018, a reference year, before increasing from August through October (Figure 2). Environmental conditions differed in Suisun Bay and Suisun Marsh; years with augmented flow had increased turbidity, lower salinity, and lower values of chlorophyll-*a*, DOC, and phosphate than in other years (Figure 3). However, temperature, nitrate, and ammonium did not significantly vary within the same region between reference and augmented years.

Zooplankton Abundance, Biomass, and Distribution

Zooplankton mean abundance tended to be higher in augmented than reference years in all regions, but only significantly so in Suisun Bay (Figure 4, $p < 0.05$). Zooplankton mean biomass was lower in augmented years in Suisun Marsh. The Sacramento DWSC and Cache Slough generally had the highest regional zooplankton abundance and biomass.

Zooplankton Community Composition

Non-metric multi-dimensional scaling (NMDS) revealed that in augmented years, zooplankton communities became more homogenous, and the Suisun Bay community more strongly overlapped with those of the lower Sacramento River, Sacramento DWSC, and Cache Slough. Regionally, communities differed most strongly along a salinity gradient (Figure 5).

The three species driving community patterns among regions and across reference and augmented years were *Pseudodiaptomus forbesi*, *Acartiella sinensis,* and *Tortanus dextrilobatus* (Figure 6). *P. forbesi* adults and copepodites contributed the most to dissimilarity between reference and augmented years. *P. forbesi* was the dominant species in the lower Sacramento River, Sacramento DWSC, and Cache Slough (Figure 7). *P. forbesi* was a smaller component of the community in Suisun Bay and Suisun Marsh,

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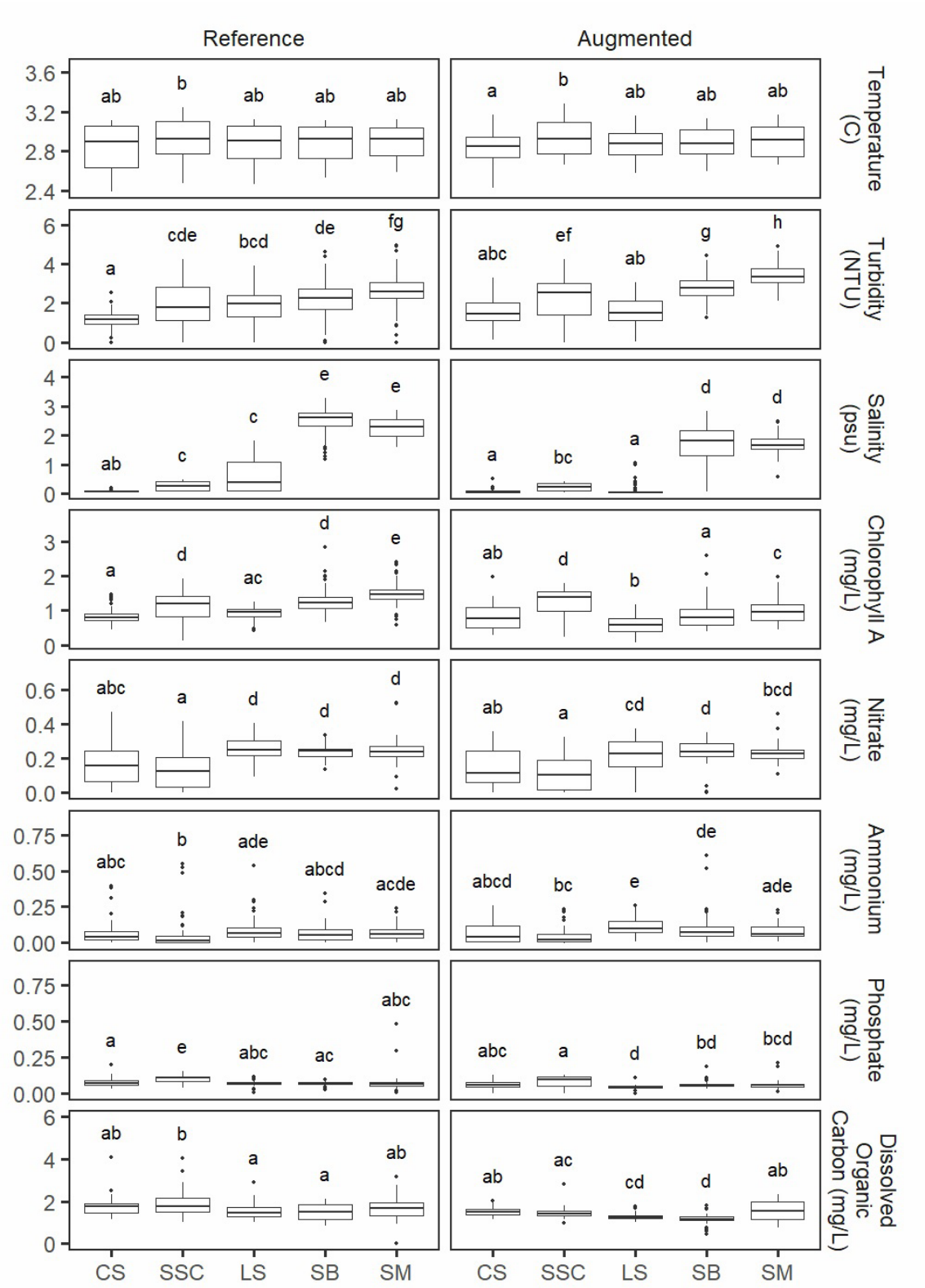

Figure 3 Differences in water quality within five regions of the estuary for years with variable flow. All values are on the log + 1 scale to aid in visualization. The same *lowercase letters* indicate that no significant differences were observed between regions or flow types as determined by Dunn's multiple comparison post-hoc test (p-value > 0.05, see Table 3). Nitrate, ammonium, phosphate, and dissolved organic carbon were taken only in surface waters; the other water-quality metrics were taken across all habitat types. Abbreviations: CS-Cache Slough, SSC-Sacramento Deep Water Ship Channel, LS-Lower Sacramento River, SB-Suisun Bay, SM-Suisun Marsh.

Table 3 Kruskal–Wallis Rank Sum test results for water quality variables, total abundance, total biomass, for five regions and in habitats within regional subsets in the northern San Francisco Estuary during the 4 years of varying hydrology. Abbreviations: CS-Cache Slough, SSC- Sacramento DWSC, LSR-Lower Sacramento River, SB-Suisun Bay, SM-Suisun Marsh.

Predictor variables	Response variable	Subset	Chi-squared statistic	DF	*p*-value	Figure number
Region, year type	Temperature		27.2	9	<0.05	Figure 3
Region, year type	Turbidity		485.4	9	<0.05	
Region, year type	Salinity		1126.9	9	<0.05	
Region, year type	Chlorophyll-*a*		598.5	9	<0.05	
Region, year type	Nitrate		135.7	9	<0.05	
Region, year type	Ammonium		84.4	9	<0.05	
Region, year type	Phosphate		162.2	9	<0.05	
Region, year type	Dissolved organic carbon		171.3	9	<0.05	
Region, year type	Total abundance		219.6	9	<0.05	Figure 4
Region, year type	Total biomass		183.47	9	<0.05	
Region, year type	Total abundance	SM	13.3	5	<0.05	Figure 8
Habitat, year type	Total abundance	SB	24.2	5	<0.05	
Habitat, year type	Total abundance	LS	47.5	5	<0.05	
Habitat, year type	Total abundance	SSC	38.9	5	<0.05	
Habitat, year type	Total abundance	CS	7.6	5	0.18	
Habitat, year type	Total biomass	SM	34.9	5	<0.05	
Habitat, year type	Total biomass	SB	66.2	5	<0.05	
Habitat, year type	Total biomass	LS	67.4	5	<0.05	
Habitat, year type	Total biomass	SSC	60.1	5	<0.05	
Habitat, year type	Total biomass	CS	16.0	5	<0.05	

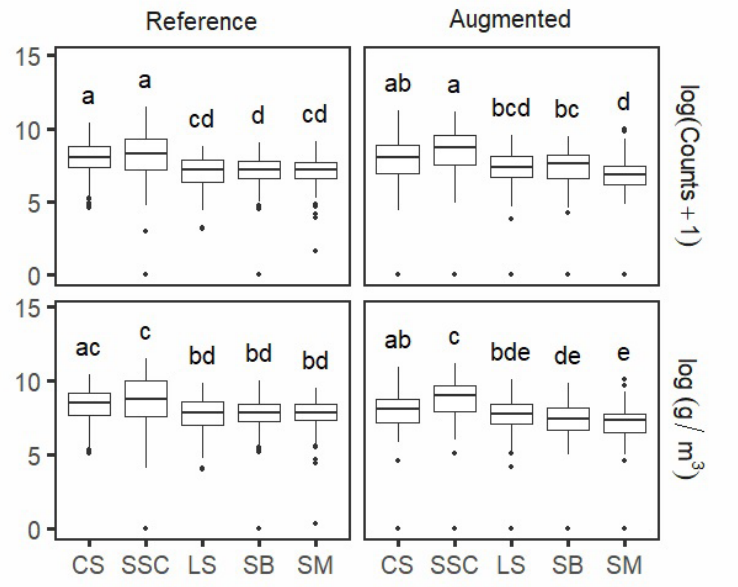

Figure 4 Mean and standard error for total abundance (*top row*) and total biomass (*bottom row*) for five regions within the estuary in years with varying hydrology. *Lowercase shared letters* indicate no significant differences were observed between regions as determined by Dunn's multiple comparison post-hoc test (*p*-value > 0.05, see Table 3). Group membership is comparable across hydrology types, not between metrics. Abbreviations: CS-Cache Slough, SSC-Sacramento Deep Water Ship Channel, LS-Lower Sacramento River, SB-Suisun Bay, SM-Suisun Marsh.

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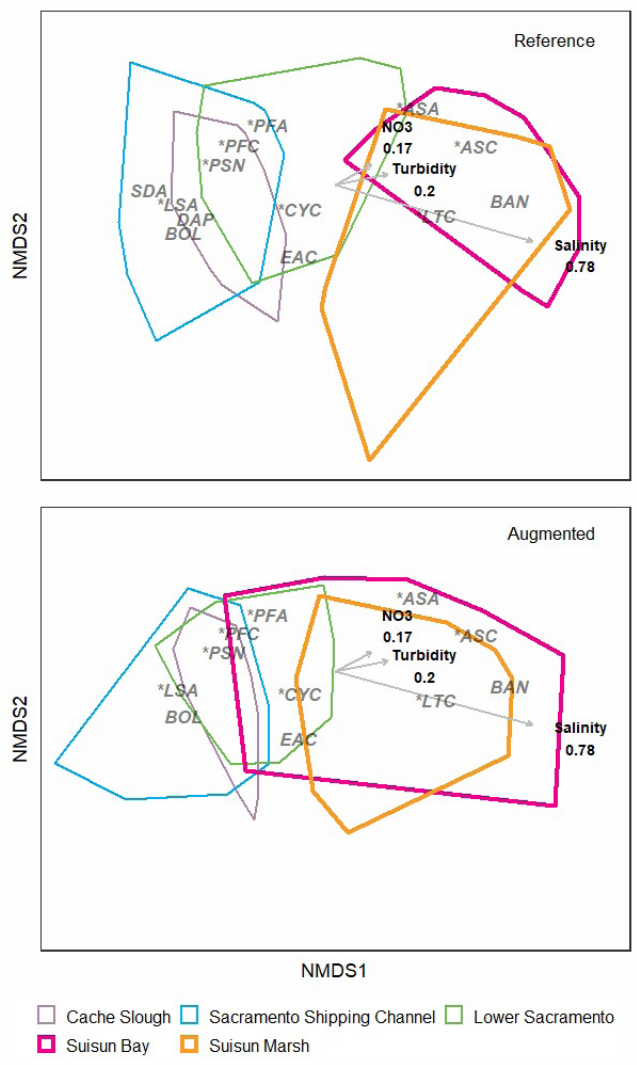

Figure 5 NMDS ordinations depicting differences in 58 lower trophic taxa abundance across five regions in reference (*top*) and augmented (*bottom*) years in the San Francisco Estuary (stress = 0.16). *Arrows* indicate direction with positive change for water-quality variables. Taxa names are in *gray*, and *asterisks* preceding names indicate known prey items for Delta Smelt in the fall. Abbreviated taxa names are defined as follows, where life stages are indicated by adult (a), copepodites (c), and nauplii (n): ASA- *Acartiella sinensis* (a), ASC- *A. sinensis* (c), BAN- Barnacle (n), BOL- *Bosmina longirostris*, CYC- Cyclopoid (c), EAC- *Eurytemora affinis* (c), LSA- *Limnoithona sinensis* (a), LTC- *Limnoithona tetraspina* (c), PFA- *Pseudodiaptomus forbesi* (a), PFC- *P. forbesi* (c), PSN- *Pseudodiaptomus* (n).

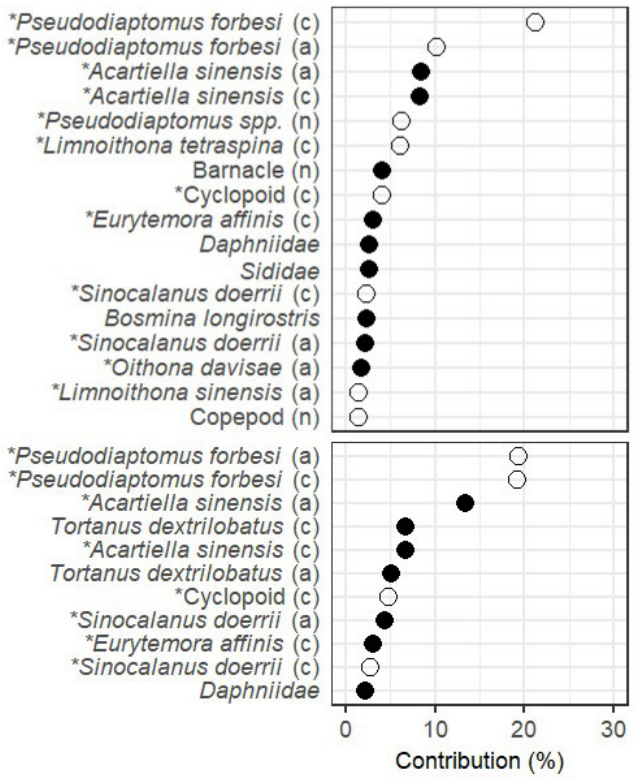

Figure 6 Average contribution to dissimilarity between lower trophic community abundance (*top*) and biomass (*bottom*) during reference and augmented years. A cut-off of 90% cumulative dissimilarity is shown. Taxa with higher abundance/biomass in augmented years are *white*; those with higher abundance/biomass in reference years are *black*. *Asterisks* preceding the names of taxa indicate known Delta Smelt fall prey items. Life stages are indicated for adult (a), copepodite (c), and nauplii (n).

but in augmented years, *P. forbesi* increased in abundance and biomass. *A. sinensis* was rarely found in the lowest-salinity regions of the Sacramento DWSC and Cache Slough and was most abundant in Suisun Bay and Suisun Marsh (Figure 7). Its abundance and biomass decreased in Suisun Bay and Suisun Marsh in augmented years and increased in the lower Sacramento River region in reference years. *T. dextrilobatus* is a larger-sized calanoid copepod species and—similar to the increased presence of *A. sinensis*—contributed more to dissimilarity in biomass than abundance (Figures 6 and 7), which in turn influenced significantly higher biomass observed in Suisun Marsh during reference years. *T. dextrilobatus* was only observed in Suisun Bay

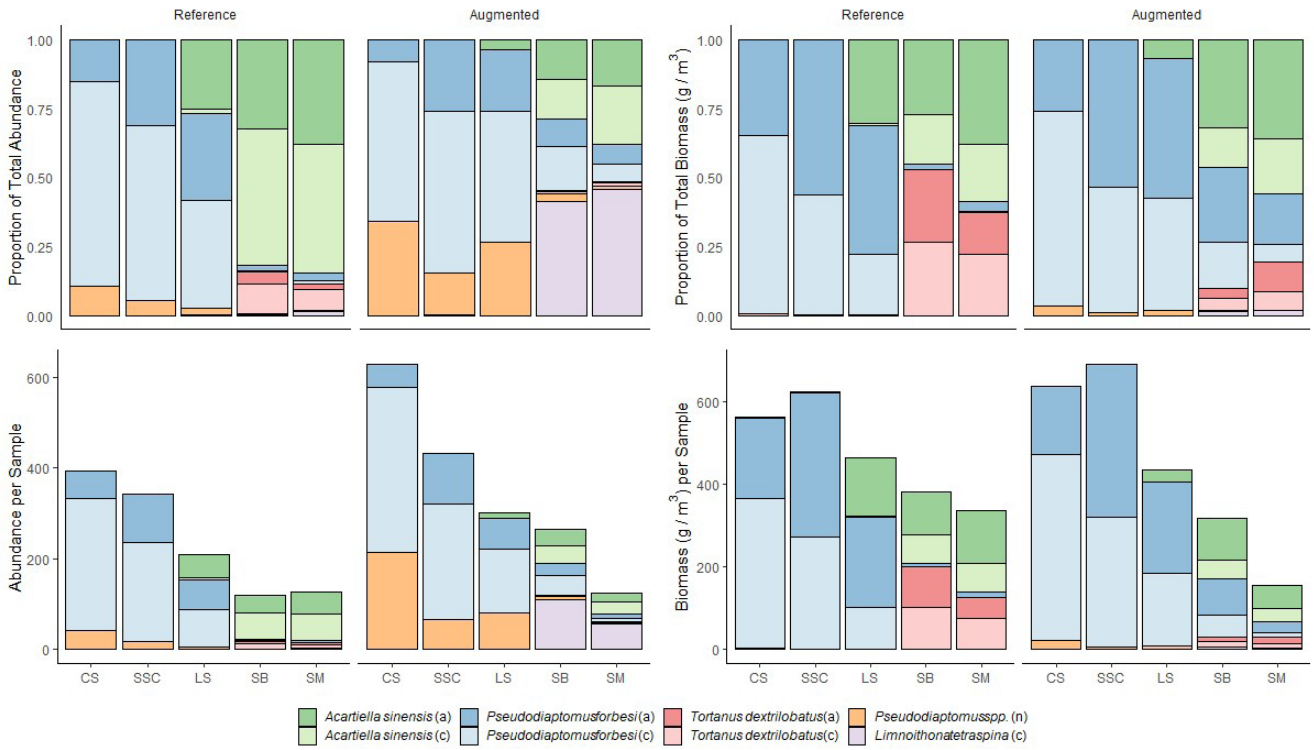

Figure 7 Mean abundance (*left*) and biomass (*right*) for zooplankton taxa in reference and augmented years. Proportion of total shown on *top*; counts are on *bottom*.

and Suisun Marsh, and infrequently in the lower Sacramento River, and it decreased in abundance and biomass in augmented years (Figure 7).

Differences in Zooplankton Abundance, Biomass, and Community by Habitat Type

Overall, zooplankton abundance was consistent among habitat types and across years with reference and augmented flows (Figure 8). Zooplankton biomass and abundance followed similar patterns with few exceptions, one of which was lower biomass in the shoal habitat of Suisun Marsh in augmented years. Among habitats within a region and across reference and augmented years, biomass was higher in deep channels compared to surface and shoal habitats in the lower Sacramento River, Suisun Bay, and Suisun Marsh. There was no difference in biomass across habitats in Suisun Marsh during reference years.

DISCUSSION

During augmented years, the position of X2 moved 9.6 km seaward into Suisun Bay and Suisun Marsh. Decreased salinity in this area resulted in a more freshwater zooplankton community in which the Delta Smelt's most frequently consumed prey species, *P. forbesi* (Slater et al. 2019), was more abundant. Simultaneously, species typically found in higher salinity—*A. sinensis* and *T. dextrilobatus*—and therefore less frequently consumed by Delta Smelt, became less abundant. It remains unclear whether the increase in *P. forbesi* in the Suisun Bay and Suisun Marsh region gives Delta Smelt a sufficient foraging benefit to enhance survival, growth, and reproductive potential.

Mechanistic explanations for why Delta Smelt abundance may not respond to increased prey abundance are varied and complex. Most

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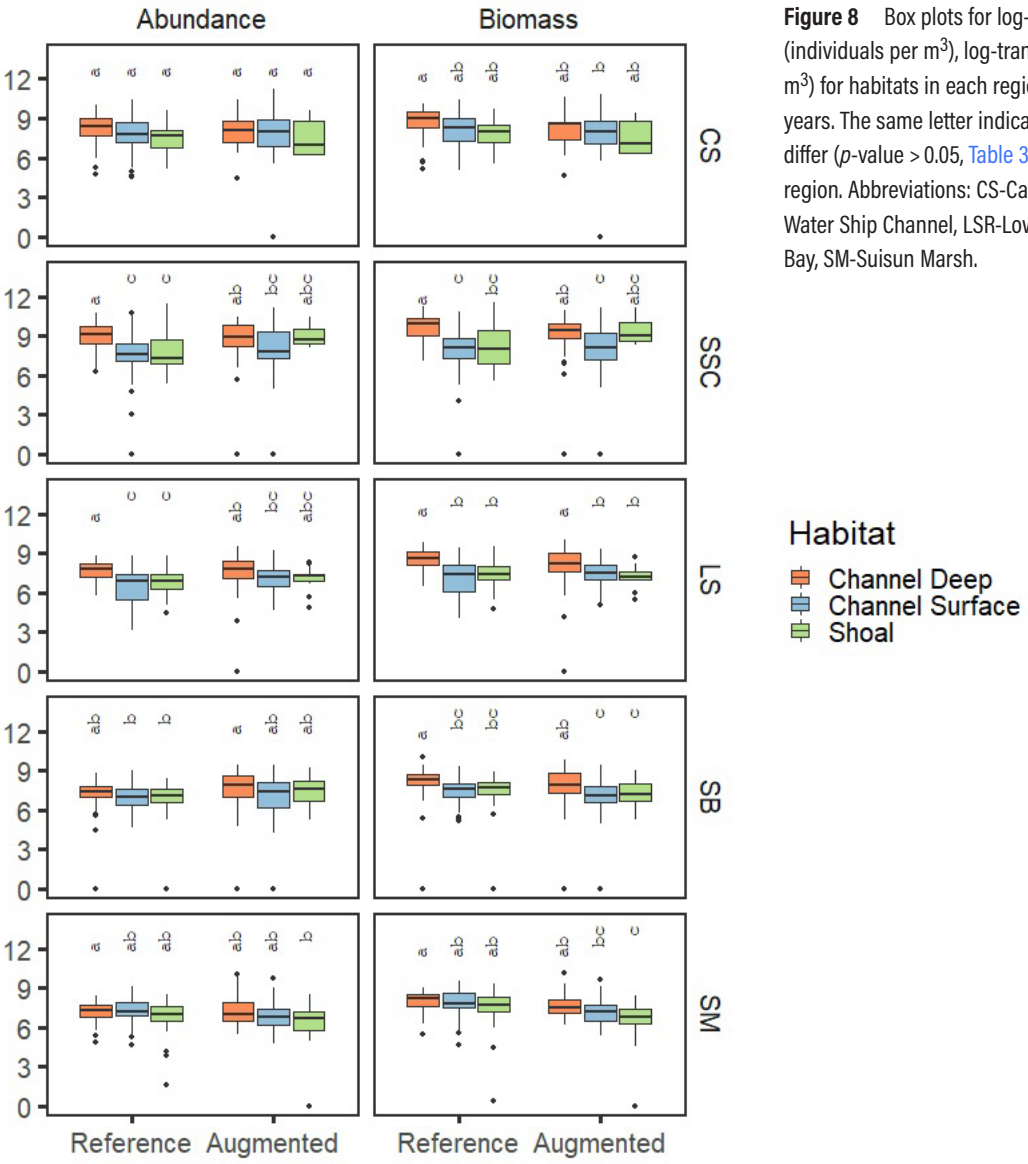

Figure 8 Box plots for log-transformed total abundance (individuals per m^3), log-transformed total biomass (µg C per m^3) for habitats in each region across reference and augmented years. The same letter indicates groups that do not significantly differ (p-value > 0.05, Table 3) which is only comparable within a region. Abbreviations: CS-Cache Slough, SSC-Sacramento Deep Water Ship Channel, LSR-Lower Sacramento River, SB-Suisun Bay, SM-Suisun Marsh.

importantly, variation in abundance of organisms as a function of flow does not appear to occur through upward trophic transfer (Jassby et al. 1995; Kimmerer 2002a). Recent work reinforces the idea that food-web interactions are not a linear chain as postulated by Brandt (1901) in the "agricultural model," connecting flow to phytoplankton to zooplankton, and so on to Delta Smelt. Rather, they are a network complicated by species invasions that rearrange food-web interactions (Mac Nally et al. 2010; Thomson et al. 2010) that can be observed by clam grazing (Kimmerer et al. 1994) and food-web responses after the introduction of predatory copepods to the upper estuary (Kratina et al. 2014), shifting distributions of northern anchovies out of the LSZ (Kimmerer 2006), and creating a dependence on subsidies of copepods from freshwater sources (Kimmerer et al. 2019). All considered, there is little reason to believe that nutrient enrichment alone increases secondary production in estuarine systems (*sensu lato* Nixon et al. 1986) because trophic dynamics have fundamentally altered the feeding environment for Delta Smelt in ways that the effect of overbite clam,

Potamocorbula amerensis, invasions (Kimmerer 2002a) alone cannot explain.

Despite knowledge of how invasions of non-native species have fundamentally altered networks of biotic interactions, conventional thought continues to be that flow augmentation alters environmental conditions, which could indirectly work in ways that can benefit Delta Smelt (Table 1). For example, increased turbidity from sediment loading during high flows was observed in the Suisun Bay and Suisun Marsh during augmented years and might benefit Delta Smelt by making them less visible to predators (Ferrari et al. 2014; Moyle et al. 2016). It may also improve foraging efficiency by creating a backdrop against which prey movement can be detected from suspended particles (Hasenbein et al. 2013; Moyle et al. 2016). However, high turbidity also inhibits zooplankton from feeding on phytoplankton and reduces survival and egg production in copepods (Sellner and Bundy 1987; Gasparini and Castelt 1997; Kang 2012).

While some environmental variables changed as predicted during augmented years, other variables such as nutrients and chlorophyll-*a* did not increase as predicted. Decreased water residence time and increased advection reduces chlorophyll-*a* production, thereby potentially reducing available biomass for herbivores (Jassby et al. 2002; Kimmerer 2004; Wan et al. 2013). On the other hand, the phytoplankton community in an augmented year (2017) was higher in nutritionally valuable diatoms, whereas the reference year (2018) was dominated by less nutritious taxa (Brett and Müller–Navarra 1997; Kalmbach et al. 2021). A higher proportion of nutritionally favorable diatoms may make up for lower overall phytoplankton biomass, particularly if there are benefits to herbivorous zooplankton such as *P. forbesi*, which selectively consume diatoms in other systems (Bowen et al. 2015).

Salinity is an important—if not the most important—driver of differences in zooplankton communities in tidal estuaries (Laprise and Dodson 1994; Hall and Burns 2002; Gao et al. 2008; Bollens et al. 2014). The San Francisco Estuary is no exception, and zooplankton communities segregate most clearly along a longitudinal salinity gradient (Kimmerer 2004; Bollens et al. 2014). Therefore, it is not surprising that a change in salinity (indexed by X2) from flow augmentation is the primary factor that explains differences in zooplankton communities in Suisun Bay and Suisun Marsh relative to reference years. In benthic assemblages across multiple flow regimes, salinity was the main factor that drove alterations in species assemblages (Peterson and Vayssieres 2010). Osmotic tolerance limits can restrict the range of zooplankton in more saline water (Schallenberg et al. 2003; Svetlichny and Hubareva 2014). When salinity tolerances of predators, competitors, and prey overlap, changes in these ecological interactions can also influence the range in which a given zooplankton species is observed (Kayfetz and Kimmerer 2017).

The increase of *P. forbesi* abundance in Suisun Bay during augmented years is best explained by upstream subsidies from highly abundant freshwater sources into Suisun Bay and Marsh (Kimmerer et al. 2018b, 2019; Hassrick et al. 2023). While *P. forbesi* may appear to be a freshwater species, historically, its distribution extended into higher-salinity regions. However, the overbite clam, an invasive species first detected in 1986, severely reduced phytoplankton and zooplankton in Suisun Bay (Alpine and Cloern 1992; Greene et al. 2011; Kimmerer and Thompson 2014; Hammock et al. 2019). The invasion continued with *A. sinensis,* a predatory copepod first detected in 1993 (Orsi and Ohtsuka 1999). These invasives are both brackish species, and since their introduction, the population center of *P. forbesi* has shifted further upstream away from Suisun Bay and Suisun Marsh (Kayfetz and Kimmerer 2017). When flow augmentation shifts X2 over Suisun Bay and Suisun Marsh, it effectively limits the range of *A. sinensis* (Slaughter et al. 2016; Kayfetz and Kimmerer 2017). Large outflow events in the spring can limit *P. amurensis* recruitment, and stress adults enough to reduce grazing in autumn (Thompson and Parchaso 2010; Perry and Wells 2021; FLOAT–MAST 2022). This could indirectly benefit *P. forbesi* during augmented years when their realized

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niches less strongly overlap with overbite clams and predatory copepods.

Arrival of invasive species has transformed the food web in the estuary to the detriment of native fishes (Kimmerer and Thompson 2014; Kratina et al. 2014). In the mid-1980s, the introduction of overbite clams caused a cascade of changes that coincided with temporal shifts in peak primary productivity in response to increased water clarity from their ability to efficiently filter the water column (Merz et al. 2016). After that, within the span of a year in 1993, an invasive and highly abundant small-bodied cyclopoid copepod, *Limnoithona tetraspina*, replaced larger calanoid copepods, *P. forbesi* and *Eurytemora affinis*, in the LSZ, accounting for almost 95% of the median total adult copepod abundance (Bouley and Kimmerer 2006). Juvenile Delta Smelt do not readily consume *L. tetraspina*, perhaps because the energetic cost of pursuing, capturing, and digesting such a small prey item has questionable benefits (Bouley and Kimmerer 2006; Baxter et al. 2010; Slater and Baxter 2014). Additionally, invasive predatory copepods such as *A. sinensis* are less energy-efficient food for Delta Smelt compared to herbivores such as *P. forbesi* (Kratina and Winder 2015). Thus, it is likely that the prey community during reference years in Suisun Bay and Suisun Marsh did not benefit Delta Smelt.

Zooplankton change their location in the water column in response to daily and seasonal changes in habitat. In the estuary and Delta, zooplankton have been observed to exhibit demersal behavior during the daytime to avoid predators in low-turbidity areas (Lampert 1989; Kimmerer and Slaughter 2016). Zooplankton also maintain their position in the estuary by rising in the water column during the flood tide and sinking back down on the ebb tide (Kimmerer et al. 1998, 2002). Although turbidity increased in Suisun Bay and Suisun Marsh during augmented years, patterns in zooplankton abundance and biomass changed little across habitats, suggesting that increased turbidity did not alter copepod habitat use or their position in the water column. Zooplankton biomass tended to be higher in deep channels across all regions sampled, compared to the surface of channels and shoal habitat. Hartman et al. (2022) also found that deep water habitat had higher zooplankton abundance compared to shallow water sites. While zooplankton abundance was not significantly higher in channel-deep habitat, biomass differed significantly (Figure 8). This may be because adult copepods (which have higher biomass) tend to use deep habitat, as Yelton et al. (2022) discovered in the Cache Slough region. Demersal behavior is also primarily observed in adult *P. forbesi* females, which are larger and therefore more vulnerable to visual predators (Fancett and Kimmerer 1985).

SUMMARY: MANAGEMENT IMPLICATIONS

The Fall X2 action was a flow augmentation intended to increase suitable Delta Smelt habitat in Suisun Bay and Suisun Marsh in various ways, including a hypothesized increase in zooplankton prey resources (Brown et al. 2014). Our results suggest that while more nutritious species tend to occupy downstream habitat in higher-flow conditions, the population of Delta Smelt did not increase in response to this shift in food resources during and after years with augmented flow. High water temperatures during 2017 may have suppressed recruitment and survival (FLOAT–MAST 2020). Another possibility is that lower food-web dynamics impart a bottom-up effect on Delta Smelt through reductions in microzooplankton abundance from clam predation. The removal of microzooplankton may be disrupting the link between bacteria and phytoplankton to higher trophic levels (Greene et al. 2011). Microzooplankton remain an under-studied component of the food web in the estuary and the Delta even though they are thought to be an important source of food for copepods (Gifford et al. 2007; Brown et al. 2016).

Estuary-wide benefits to Delta Smelt from reduced clam competition may be confounded by increasing frequency of drought conditions that could facilitate overbite clam recruitment (Crauder et al. 2016; Baumsteiger et al. 2017). Studies on the abundance and distribution of *P. amurensis* during augmented years are needed to determine how they respond to changes in

autumn outflow and the effect of their response on the Delta Smelt prey field.

Cache Slough and the Sacramento DWSC had high zooplankton abundance and biomass in both reference and augmented years. These regions can be highly productive, particularly in terminal channels (Feyrer et al. 2017; Kimmerer et al. 2018a), and serve as source populations to Suisun Bay and Suisun Marsh (Kimmerer et al. 2019; Hassrick et al. 2023).

CONCLUSION: FUTURE DIRECTIONS

Continued research into why Cache Slough and the Sacramento DWSC have such high zooplankton populations, despite being highly modified, may provide further insight into the effects of the autumn outflow action on habitat–zooplankton dynamics.

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REFERENCES

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr. [accessed 2023 Mar 31];37(5). *https://doi.org/10.4319/lo.1992.37.5.0946*

Arbeider M, Sharpe C, Carr–Harris C, Moore JW. 2019. Integrating prey dynamics, diet, and biophysical factors across an estuary seascape for four fish species. Mar Ecol Prog Ser. [accessed 2023 Mar 31];613:151–169. *https://doi.org/10.3354/meps12896*

Atkinson A, Ward P, Hunt BP, Pakhomov EA, Hosie GW. 2012. An overview of Southern Ocean zooplankton data: abundance, biomass, feeding and functional relationships. Commission for the Conservation of Antarctic Marine Living Resources Sci. [accessed 2023 Mar 31];19. Available from: *https://www.ccamlr.org/en/publications/science_journal/ccamlr-science-volume-19/171-218*

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecol Monogr. [accessed 2023 Mar 31];81(2). *https://doi.org/10.1890/10-1510.1*

Baumsteiger J, Schroeter RE, O'Rear T, Cook JD, Moyle PB. 2017. Long-term surveys show invasive overbite clams (*Potamocorbula amurensis*) are spatially limited in Suisun Marsh, California. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];15(2). *https://doi.org/10.15447/sfews.2017v15iss2art6*

Baxter R, Breuer R, Brown L, Conrad L, Feyrer F, Fong S, Gehrts K, Grimaldo L, Herbold B, Hrodey P, et al. 2010. Interagency Ecological Program 2010 pelagic organism decline work plan and synthesis of results. Sacramento (CA): IEP for the San Francisco Estuary. [accessed 2023 Mar 31]. 259 p. Available From: *https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/docs/cmnt091412/sldmwa/baxter_etal_iep_2010.pdf*

Bennett WA. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];3(2). *https://doi.org/10.15447/sfews.2005v3iss2art1*

Bever AJ, MacWilliams ML, Herbold B, Brown LR, Feyrer FV. 2016. Linking hydrodynamic complexity to Delta Smelt (*Hypomesus transpacificus*) distribution in the San Francisco Estuary, *USA*. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];4(1). *https://doi.org/10.15447/sfews.2016v14iss1art3*

Bird SM, Fram MS, Crepeau KL. 2003. Method of analysis by the US Geological Survey California District Sacramento Laboratory—determination of dissolved organic carbon in water by high temperature catalytic oxidation, method validation, and quality-control practices. Sacramento (CA): US Geological Survey. [accessed 2023 Mar 31]. 14 p. *https://doi.org/10.3133/ofr03366*

Bollens SM, Breckenridge JK, Cordell JR, Simenstad CA, Kalata O. 2014. Zooplankton of tidal marsh channels in relation to environmental variables in the upper San Francisco Estuary. Aquat Biol. [accessed 2023 Mar 31];21(3). *http://doi.org/10.3354/ab00589*

Bottom DL, Jones KK. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River Estuary. Prog Oceanogr. [accessed 2023 Mar 31]25(1–4). *https://doi.org/10.1016/0079-6611(90)90009-Q*

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Mar Ecol Prog Ser. [accessed 2023 Mar 31];324:219–228. *https://doi.org/10.3354/meps324219*

Bowen A, Rollwagen–Bollens G, Bollens SM, Zimmerman J. 2015. Feeding of the invasive copepod *Pseudodiaptomus forbesi* on natural microplankton assemblages within the lower Columbia River. J Plankton Res. [accessed 2023 Mar 31];37(6). *https://doi.org/10.1093/plankt/fbv078*

Brandt K. 1901. Life in the ocean. Washington (USA): Smithsonian Institute. Annual Report of the Board of Regents of the Smithsonian Instituition, showing the operations, expenditures, and condition of the institution for the year ending June 30, 1990. [accessed 2023 Mar 31]. 15 p. Available from: *http://aquaparadox.obs-vlfr.fr/html/PFD/Taxonomic%20Monographs/Brandt1901.pdf*

Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr. [accessed 2023 Mar 31];27(4). *https://doi.org/10.2307/1942268*

Brett M, Müller–Navarra Dör. 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshw Biol. [accessed 2023 Mar 31];38(3). *https://doi.org/10.1046/j.1365-2427.1997.00220.x*

Brown L. 2003. Will tidal wetland restoration enhance populations of native fishes? San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];1(1). *https://doi.org/10.15447/sfews.2003v1iss1art2*

Brown L, Baxter, Castillo G, Conrad, Culberson S, Erickson, Feyrer, Fong, Gehrts, Grimaldo L et al. 2014. Synthesis of studies in the fall low-salinity zone of the San Francisco estuary, September–December 2011. Reston (VA): US Geological Survey. Scientific Investigations Report 2014–5041. [accessed 2023 Mar 31]. 136 p. *https://doi.org/10.3133/sir20145041*

Brown LR, Kimmerer WJ, Conrad JL, Lesmeister S, Mueller–Solger A. 2016. Food webs of the Delta, Suisun Bay, and Suisun Marsh: an update on current understanding and possibilities for management. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];14(3). *https://doi.org/10.15447/sfews.2016v14iss3art4*

[CDWR] California Department of Water Resources. 2022. Dayflow results 1997–2020.csv [website, accessed 2023 Mar 31]. *https://data.cnra.ca.gov/dataset/dayflow*

Clarke KR. 1993. Non–parametric multivariate analyses of changes in community structure. Austral J Ecol. [accessed 2023 Mar 31];18(1). *https://doi.org/10.1111/j.1442-9993.1993.tb00438.x*

Cloern JE. 2007. Habitat connectivity and ecosystem productivity: implications from a simple model. Am Nat. [accessed 2023 Mar 31];169(1). *https://doi.org/10.1086/510258*

Connelly KA, Rollwagen–Bollens G, Bollens SM. 2020. Seasonal and longitudinal variability of zooplankton assemblages along a river-dominated estuarine gradient. Estuar Coast Shelf Sci. [accessed 2023 Mar 31];245. *https://doi.org/10.1016/j.ecss.2020.106980*

Coyle KO, Pinchuk AI. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish Oceanogr. [accessed 2023 Mar 31];12(4–5). *https://doi.org/10.1046/j.1365-2419.2003.00256.x*

Crauder JS, Thompson JK, Parchaso F, Anduaga RI, Pearson SA, Gehrts K, Fuller H, Wells E. 2016. Bivalve effects on the food web supporting Delta Smelt: a long-term study of bivalve recruitment, biomass, and grazing rate patterns with varying freshwater uutflow. Reston (VA): US Geological Survey. Open-File Report 2016-1005. [accessed 2023 Mar 31]. 216 p. *http://doi.org/10.3133/ofr20161005*

Cremona F, Agasild H, Haberman J, Zingel P, Noges P, Noges T, Laas A. 2020. How warming and other stressors affect zooplankton abundance, biomass and community composition in shallow eutrophic lakes. Clim Change. [accessed 2023 Mar 31];159. *https://doi.org/10.1007/s10584-020-02698-2*

Doane TA, Horwáth WR. 2003. Spectrophotometric determination of nitrate with a single reagent. Anal Lett. [accessed 2023 Mar 31];36(12). *https://doi.org/10.1081/AL-120024647*

Downing BD, Boss E, Bergamaschi BA, Fleck JA, Lionberger MA, Ganju NK, Schoellhamer DH, Fujii R. 2009. Quantifying fluxes and characterizing compositional changes of dissolved organic matter in aquatic systems *in situ* using combined acoustic and optical measurements. Limnol Oceanogr: Methods. [accessed 2023 Mar 31];7(1). *https://doi.org/10.4319/lom.2009.7.119*

Elliott M, Whitfield AK. 2011. Challenging paradigms in estuarine ecology and management. Estuar Coast Shelf Sci. [accessed 2023 Mar 31];94(4). *https://doi.org/10.1016/j.ecss.2011.06.016*

Fancett M, Kimmerer WJ. 1985. Vertical migration of the demersal copepod *Pseudodiaptomus* as a means of predator avoidance. J Exp Mar Biol Ecol. [accessed 2023 Mar 31];88(1). *https://doi.org/10.1016/0022-0981(85)90199-6*

Ferrari MC, Ranåker L, Weinersmith KL, Young MJ, Sih A, Conrad JL. 2014. Effects of turbidity and an invasive waterweed on predation by introduced Largemouth Bass. Environ Biol Fishes. [accessed 2023 Mar 31];97(1). *https://doi.org/10.1007/s10641-013-0125-7*

Feyrer F, Newman K, Nobriga M, Sommer T. 2011. Modeling the effects of future outflow on the abiotic habitat of an imperiled estuarine fish. Estuar Coast. [accessed 2023 Mar 31];34. *https://doi.org/10.1007/s12237-010-9343-9*

Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci. [accessed 2023 Mar 31];64(4). *https://doi.org/10.1139/f07-048*

Feyrer F, Slater SB, Portz DE, Odom D, Morgan–King T, Brown LR. 2017. Pelagic nekton abundance and distribution in the northern Sacramento–San Joaquin Delta, California. Trans Am Fish Soc. [accessed 2023 Mar 31];146(1). *https://doi.org/10.1080/00028487.2016.1243577*

[FLOAT–MAST] Flow Alteration Management Analysis and Synthesis Team. 2015. An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish. Sacramento (CA): Interagency Ecological Program. Technical Report #90. [accessed 2023 Mar 31]. 206 p. Available from: *https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/california_waterfix/exhibits/docs/petitioners_exhibit/dwr/part2/DWR-1089%20IEP_MAST_Team_2015_Delta_Smelt_MAST_Synthesis_Report_January%202015.pdf*

[FLOAT–MAST] Flow Alteration Management Analysis and Synthesis Team. 2020. Synthesis of data and studies relating to Delta Smelt biology in the San Francisco Estuary, emphasizing water year 2017. Sacramento (CA): Interagency Ecological Program. Technical Report #95. [accessed 2023 Mar 31]. 265 p. Available from: *https://calwatercenter.org/wp-content/uploads/2021/08/TR95-FLOAT-MAST-2017-Final-13JUL2021-compressed.pdf*

[FLOAT–MAST] Flow Alteration Management Analysis and Synthesis Team. 2022. White papers providing a synthesis of knowledge relating to Delta Smelt biology in the San Francisco Estuary, emphasizing effects of flow. Interagency Ecological Program. Technical Report #98. [accessed 2023 Mar 31]. 191 p. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=200748&inline*

https://doi.org/10.15447/sfews.2023v21iss2art1

Gao Q, Xu Z, Zhuang P. 2008. The relation between distribution of zooplankton and salinity in the Changjiang Estuary. Chin J Oceanol Limnol. [accessed 2023 Mar 31];26(2). https://doi.org/10.1007/s00343-008-0178-1

Gasparini S, Castelt J. 1997. Autotrophic and heterotrophic nanoplankton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*. J Plankton Res. [accessed 2023 Mar 31];19(7). https://doi.org/10.1093/plankt/19.7.877

Gifford SM, Rollwagen–Bollens G, Bollens SM. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Mar 31];348. https://doi.org/10.3354/meps07003

Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ. 2011. Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar Freshw Res. [accessed 2023 Mar 31];62(9). https://doi.org/10.1071/MF11047

Greene VE, Sullivan LJ, Thompson JK, Kimmerer WJ. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Mar 31];431. https://doi.org/10.3354/meps09099_

Grimaldo LF, Smith WE, Nobriga ML. 2021. Re-examining factors that affect Delta Smelt (*Hypomesus transpacificus*) entrainment at the State Water Project and Central Valley Project in the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];19(1). https://doi.org/10.15447/sfews.2021v19iss1art5

Hall CJ, Burns CW. 2002. Environmental gradients and zooplankton distribution in a shallow, tidal lake. Archiv Hydrobiol. [accessed 2023 Mar 31];154(3). https://doi.org/10.1127/archiv-hydrobiol/154/2002/485

Hammock BG, Moose SP, Solis SS, Goharian E, Teh SJ. 2019. Hydrodynamic modeling coupled with long-term field data provide evidence for suppression of phytoplankton by invasive clams and freshwater exports in the San Francisco Estuary. Enviro Manage. [accessed 2023 Mar 31];63. https://doi.org/10.1007/s00267-019-01159-6

Hartman, RK, Barros, A, Avila, M, Tempel, T, Bowles, C, Ellis, D, Sherman, S. 2022. I'm not that shallow–different zooplankton abundance but similar community composition between habitats in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];20(3). https://doi.org/10.15447/sfews.2022v20iss3art1

Hartman RK, Bashevkin SM, Barros A, Burdi CE, Patel C, Sommer T. 2021. Food for thought: connecting zooplankton science to management in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];19(3). https://doi.org/10.15447/sfews.2021v19iss3art1

Hasenbein M, Komoroske LM, Connon RE, Geist J, Fangue NA. 2013. Turbidity and salinity affect feeding performance and physiological stress in the endangered Delta Smelt. Integr Comp Biol. [accessed 2023 Mar 31];53(4). https://doi.org/10.1093/icb/ict082

Hassrick JL, Korman J, Kimmerer WJ, Gross ES, Grimaldo LF, Lee C, Schultz AA. 2023. Freshwater flow affects subsidies of a copepod (*Pseudodiaptomus forbesi*) to low-salinity food webs in the upper San Francisco Estuary. Estuar Coast. [accessed 2023 Mar 31];46. https://doi.org/10.1007/s12237-022-01142-1

Heidel K, Roy S, Creager C, Chih–fang C, Grieb T. 2006. Conceptual model for nutrients in the Central Valley and Scramento–San Joquin Delta. Lafayette (CA): Tetra Tech Inc. [accessed 2023 Mar 31]. 167 p. Available from: https://www.waterboards.ca.gov/centralvalley/water_issues/drinking_water_policy/final_nutrient_report_lowres.pdf

Hendrix AN, Fleishman E, Zillig MW, Jennings ED. 2023. Relations between abiotic and biotic environmental variables and occupancy of Delta Smelt (*Hypomesus transpacificus*) in autumn. Estuar Coast. [accessed 2023 Mar 31];46(1). https://doi.org/10.1007/s12237-022-01100-x

Hobbs J, Moyle PB, Fangue N, Connon RE. 2017. Is extinction inevitable for Delta Smelt and Longfin Smelt? An opinion and recommendations for recovery. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];15(2). https://doi.org/10.15447/sfews.2017v15iss2art2

Hobbs JA, Lewis LS, Willmes M, Denney C, Bush E. 2019. Complex life histories discovered in a critically endangered fish. Sci Rep. [accessed 2023 Mar 31];9:16772. https://doi.org/10.1038/s41598-019-52273-8

Jassby A. 2008. Phytoplankton in the upper San Francisco Estuary: recent biomass trends, their causes, and their trophic significance. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31]6(1). https://doi.org/10.15447/sfews.2008v6iss1art2

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient–rich tidal ecosystem. Limnol Oceanogr. [accessed 2023 Mar 31];47(3). *https://doi.org/10.4319/lo.2002.47.3.0698*

Jassby AD, Kimmerer WJ, Monismith SG, Armor C, Cloern JE, Powell TM, Schubel JR, Vendlinski TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. Eco Appl. [accessed 2023 Mar 31];5(1). *https://doi.org/10.2307/1942069*

Johnston RJ, Grigalunas TA, Opaluch JJ, Mazzotta M, Diamantedes J. 2002. Valuing estuarine resource services using economic and ecological models: the Peconic Estuary System study. Coast Manage. [accessed 2023 Mar 31];30(1). *https://doi.org/10.1080/08920750252692616*

Kalmbach A, Cox D, Lee C, Schultz AA. 2021. Comparison of phytoplankton community structure and nutrient conditions in the Sacramento River Delta during a fall flow action and non-action period. Chapter 8 In: Schultz AA, editor. Directed Outflow Project: Technical Report 2. Sacramento (CA): US Bureau of Reclamation. [accessed 2023 Mar 31]. p. 290–331. Available from: *https://www.usbr.gov/mp/bdo/docs/directed-outflow-project-tech-report2.pdf*

Kang H–K. 2012. Effects of suspended sediments on reproductive responses of *Paracalanus* sp.(Copepoda: Calanoida) in the laboratory. J Plankton Res. [accessed 2023 Mar 31];34(7). *https://doi.org/10.1093/plankt/fbs033*

Kayfetz K, Bashevkin SM, Thomas M, Hartman R, Burdi CE, Hennessy A, Tempel T, Barros A. 2020. Zooplankton integrated dataset metadata report. Sacramento (CA): California Department of Water Resources. IEP Technical Report 93. [accessed 2023 Mar 31]. 72 p. Available from: *https://deltacouncil.ca.gov/pdf/science-program/2020-11-09-iep-93-zooplankton-integrated-dataset-metadata.pdf*

Kayfetz K, Kimmerer WJ. 2017. Abiotic and biotic controls on the copepod *Pseudodiaptomus forbesi* in the upper San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Mar 31];581:85–101. *https://doi.org/10.3354/meps12294*

Kimmerer WJ. 2002a. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser. [accessed 2023 Mar 31];243:39–55. *https://doi.org/10.3354/meps243039*

Kimmerer WJ. 2002b. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries. [accessed 2023 Mar 31];25: 1275–1290. *https://doi.org/10.1007/BF02692224*

Kimmerer WJ. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];2(1). *https://doi.org/10.15447/sfews.2004v2iss1art1*

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Mar Ecol Prog Ser. [accessed 2023 Mar 31]*;324*. *https://doi.org/10.3354/meps324207*

Kimmerer WJ. 2008. Losses of Sacramento River Chinook Salmon and Delta Smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];6(2). *https://doi.org/10.15447/sfews.2008v6iss2art2*

Kimmerer WJ, Burau J, Bennett W. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnol Oceanogr. [accessed 2023 Mar 31];43(7). *https://doi.org/10.4319/lo.1998.43.7.1697*

Kimmerer WJ, Burau JR, Bennett W. 2002. Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. Estuaries. [accessed 2023 Mar 31];25(3). *https://doi.org/10.1007/BF02695979*

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Mar Ecol Prog Ser. [accessed 2023 Mar 31];113(1/2). Available from: *http://www.jstor.org/stable/24849580*

Kimmerer WJ, Gross ES, Slaughter AM, Durand JR. 2019. Spatial subsidies and mortality of an estuarine copepod revealed using a box model. Estuaries Coasts. [accessed 2023 Mar 31];42(1). *https://doi.org/10.1007/s12237-018-0436-1*

Kimmerer WJ, Ignoffo TR, Bemowski B, Modéran J, Holmes A, Bergamaschi B. 2018a. Zooplankton dynamics in the cache slough complex of the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];16(3). *https://doi.org/10.15447/sfews.2018v16iss3art4*

Kimmerer WJ, Ignoffo TR, Kayfetz KR, Slaughter AM. 2018b. Effects of freshwater flow and phytoplankton biomass on growth, reproduction, and spatial subsidies of the estuarine copepod *Pseudodiaptomus forbesi*. Hydrobiologia. [accessed 2023 Mar 31];807(1). Available from: *https://link.springer.com/article/10.1007/s10750-017-3385-y*

Kimmerer WJ, Slaughter A. 2016. Fine-scale distributions of zooplankton in the northern San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];14(3). *http://doi.org/10.15447/sfews.2016v14iss3art2*

Kimmerer WJ, Thompson JK. 2014. Phytoplankton growth balanced by clam and zooplankton grazing and net transport into the low-salinity zone of the San Francisco Estuary. Estuaries Coasts. [accessed 2023 Mar 31];37(5). *https://doi.org/10.1007/s12237-013-9753-6*

Kratina P, Mac Nally R, Kimmerer WJ, Thomson JR, Winder M. 2014. Human–induced biotic invasions and changes in plankton interaction networks. J Appl Ecol. [accessed 2023 Mar 31];51(4). *https://doi.org/10.1111/1365-2664.12266*

Kratina P, Winder M. 2015. Biotic invasions can alter nutritional composition of zooplankton communities. Oikos. [accessed 2023 Mar 31];124(10). *https://doi.org/10.1111/oik.02240*

Lampert W. 1989. The adaptive significance of diel vertical migration of zooplankton. Funct Ecol. [accessed 2023 Mar 31];3. *https://doi.org/10.2307/2389671*

Laprise R, Dodson JJ. 1994. Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence Estuary. Mar Ecol Prog Ser. [accessed 2023 Mar 31];107(1/2). *https://www.jstor.org/stable/24844779*

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JB. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science. [accessed 2023 Mar 31];312(5781). *https://www.science.org/doi/10.1126/science.1128035*

Mahardja B, Bashevkin SM, Pien C, Nelson M, Davis BE, Hartman R. 2022. Escape from the heat: thermal stratification in a well-mixed estuary and implications for fish species facing a changing climate. Hydrobiologia. [accessed 2023 Mar 31];849. Available from: *https://link.springer.com/article/10.1007/s10750-022-04886-w*

Mac Nally R, Thomson JR, Kimmerer WJ, Feyrer F, Newman KB, Sih A, Bennett WA, Brown L, Fleishman E, Culberson SD, et al. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Eco Appl. [accessed 2023 Mar 31];20(5). *https://doi.org/10.1890/09-1724.1*

Merz JE, Bergman PS, Simonis JL, Delaney D, Pierson J, Anders P. 2016. Long-term seasonal trends in the prey community of Delta Smelt (*Hypomesus transpacificus*) within the Sacramento–San Joaquin Delta, California. Estuaries Coasts. [accessed 2023 Mar 31];39(5). *https://doi.org/10.1007/s12237-016-0097-x*

Merz JE, Hamilton S, Bergman PS, Cavallo B. 2011. Spatial perspective for Delta Smelt: a summary of contemporary survey data. Calif Fish Game. [accessed 2023 Mar 31];97(4). Available from: *https://www.baydeltalive.com/assets/06942155460a79991fdf1b57f641b1b4/application/pdf/CFG_097-4_2011-2-DeltaSmelt1.pdf*

Moyle PB, Brown LR, Durand JR, Hobbs JA. 2016. Delta Smelt: life history and decline of a once-abundant species in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];14(2). *https://doi.org/10.15447/sfews.2016v14iss2art6*

Moyle PB, Hobbs JA, Durand JR. 2018. Delta Smelt and water politics in California. Fisheries. [accessed 2023 Mar 31];43(1). *https://doi.org/10.1002/fsh.10014*

Murphy J, Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta. [accessed 2023 Mar 31];27. *https://doi.org/10.1016/S0003-2670(00)88444-5*

Nichols FH, Cloern JE, Luoma SN, Peterson DH. 1986. The modification of an estuary. Science. [accessed 2023 Mar 31];231(4738). *https://www.science.org/doi/10.1126/science.231.4738.567*

Nixon SW, Oviatt CA, Frithsen J, Sullivan B. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. J Limnol Soc S Afr. [accessed 2023 Mar 31];12(1–2). *https://doi.org/10.1080/03779688.1986.9639398*

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin P, O'Hara R, Simpson G, Solymos P. 2022. *vegan*: Community Ecology Package. R package version 2.6-2. [accessed 2023 May]. Available from: *https://cran.r-project.org/web/packages/vegan/vegan.pdf*

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biol Ecol. [accessed 2023 Mar 31];46(2). Available from: *http://www.plankton.jp/PBE/*

Perry S, Wells B. 2021. Benthic monitoring, 2019. In: IEP Newsletter. Sacramento (CA): Interagency Ecological Program for the San Francisco Estuary. [accessed 2023 Mar 31];40(1):61–68. Available from: *https://cadwr.app.box.com/s/3fo2sh8hnyx5rv6btmu2ydsqif12zp4l*

Peterson HA, Vayssieres M. 2010. Benthic assemblage variability in the upper San Francisco Estuary: a 27-year retrospective. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];8(1). *https://doi.org/10.15447/sfews.2010v8iss1art2*

Peterson MS. 2003. A conceptual view of environment–habitat–production linkages in tidal river estuaries. Reviews Fish Sci. [accessed 2023 Mar 31];11(4). *https://doi.org/10.1080/10641260390255844*

R Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: *https:/www.R-project.org/*

Ray GC. 2005. Connectivities of estuarine fishes to the coastal realm. Estuar Coast Shelf Sci. [accessed 2023 Mar 31];64(1). *https://doi.org/10.1016/j.ecss.2005.02.003*

Rose KA, Kimmerer WJ, Edwards KP, Bennett WA. 2013a. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: I. Model description and baseline results. Trans Am Fish. [accessed 2023 Mar 31];142(5). *https://doi.org/10.1080/00028487.2013.799518*

Rose KA, Kimmerer WJ, Edwards KP, Bennett WA. 2013b. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: II. Alternative baselines and good versus bad years. Trans Am Fish. [accessed 2023 Mar 31];142(5). *https://doi.org/10.1080/00028487.2013.799519*

Schallenberg M, Hall CJ, Burns CW. 2003. Consequences of climate-induced salinity increases on zooplankton abundance and diversity in coastal lakes. Mar Ecol Prog Ser. [accessed 2023 Mar 31];251. *https://doi.org/10.3354/meps251181*

Schultz AA, Grimaldo L, Hammock JL, Kalmbach AJ, Smith AG, Burgess O, Barnard D, Brandon J. 2019. Effect of isohaline (X2) and region on Delta Smelt habitat, prey and distribution during the summer and fall: insights into managed flow actions in a highly modified estuary. Chapter 9 In: Schultz AA, editor. Directed Outflow Project: Technical Report 1. Sacramento (CA): US Bureau of Reclamation. [accessed 2023 Mar 31]. p 237–301. Available from: *https://www.usbr.gov/mp/bdo/docs/directed-outflow-project-tech-report1.pdf*

Sellner K, Bundy M. 1987. Preliminary results of experiments to determine the effects of suspended sediments on the estuarine copepod *Eurytemora affinis*. Cont Shelf Res. [accessed 2023 Mar 31];7(11–12). *https://doi.org/10.1016/0278-4343(87)90051-3*

Sheaves M, Baker R, Nagelkerken I, Connolly RM. 2015. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries Coasts. [accessed 2023 Mar 31];38(2). Available from: *https://link.springer.com/article/10.1007/s12237-014-9846-x*

Slater S, Baxter R. 2014. Diet, prey selection, and body condition of age-0 Delta Smelt, *Hypomesus transpacificus*, in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];12(3). *http://doi.org/10.15447/sfews.2014v12iss3art1*

Slater S, Schultz AA, Hammock B, Hennessy A, Burdi C. 2019. Patterns of zooplankton consumption by juvenile and adult Delta Smelt (*Hypomesus transpacificus*). In: Schultz AA, editor. Directed Outflow Project: Technical Report 1. Sacramento (CA): US Bureau of Reclamation. [accessed 2023 Mar 31]. p 9–54. Available from: *https://www.usbr.gov/mp/bdo/docs/directed-outflow-project-tech-report1.pdf*

Slaughter AM, Ignoffo TR, Kimmerer WJ. 2016. Predation impact of *Acartiella sinensis*, an introduced predatory copepod in the San Francisco Estuary, USA. Mar Ecol Prog Ser. [accessed 2023 Mar 31];547. *https://doi.org/10.3354/meps11640*

Sommer T, Mejia F. 2013. A place to call home: a synthesis of Delta Smelt habitat in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 31];11(2). *https://doi.org/10.15447/sfews.2013v11iss2art4*

Starcevich L, DiDonato G, McDonald T, Mitchell J. 2016. A GRTS user's manual for the *SDrawNPS* package: a graphical user interface for generalized random tessellation stratified (GRTS) sampling and estimation. Fort Collins (CO): National Park Service. Natural Resource Report NPS/PWRO/NRR–2016/1233. [accessed 2023 Mar 31]. Available from: *https://irma.nps.gov/DataStore/Reference/Profile/2229965*

Stevens Jr DL, Olsen AR. 2004. Spatially balanced sampling of natural resources. J Am Stat Assoc. [accessed 2023 Mar 31];99(465). *https://doi.org/10.1198/016214504000000250*

Svetlichny L, Hubareva E. 2014. Salinity tolerance of alien copepods *Acartia tonsa* and *Oithona davisae* in the Black Sea. J Exp Mar Biol Ecol. [accessed 2023 Mar 31];461. *https://doi.org/10.1016/j.jembe.2014.08.012*

Thompson JK, Parchaso F. 2010. *Corbula amurensis* conceptual model. US Geological Survey. [accessed 2023 Mar 31]. 39 p. Available from: *https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=6635e2222f9ec8999aca3cb4a98b42eb3ee7591a*

Thomson JR, Kimmerer WJ, Brown LR, Newman KB, Nally RM, Bennett WA, Feyrer F, Fleishman E. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecol Appl. [accessed 2023 Mar 31];20(5). *https://doi.org/10.1890/09-0998.1*

[USFWS] US Fish and Wildlife Service. 2008. Formal Endangered Species Act consultation on the proposed coordinated operations of the Central Valley Project (CVP) and State Water Project (SWP). Sacramento (CA): USFWS.

[USFWS] US Fish and Wildlife Service. 2019. Biological Opinion for the Reinitiation of Consultation on the Coordinated Operations of the Central Valley Project and State Water Project. Sacramento (CA): USFWS.

[USFWS] US Fish and Wildlife Service, Senegal T, Mckenzie R, Speegle J, Perales B, Bridgman D, Erly K, Staiger S, Arrambide A, Gilbert M. 2022. Interagency Ecological Program and USFWS: San Francisco Estuary Enhanced Delta Smelt Monitoring Program data, 2016–2021 ver 8. Environmental Data Initiative. [accessed 2023-03-29]. *https://doi.org/10.6073/pasta/e1a540c161b7be56b941df50fd7b44c5*

Verdouw H, Van Echteld C, Dekkers E. 1978. Ammonia determination based on indophenol formation with sodium salicylate. Water Res. [accessed 2023 Mar 29];12(6). *https://doi.org/10.1016/0043-1354(78)90107-0*

Wan Y, Qiu C, Doering P, Ashton M, Sun D, Coley T. 2013. Modeling residence time with a three-dimensional hydrodynamic model: linkage with chlorophyll *a* in a subtropical estuary. Ecol Modell. [accessed 2023 Mar 29];268. *https://doi.org/10.1016/j.ecolmodel.2013.08.008*

Whipple A, Grossinger RM, Rankin D, Stanford B, Askevold R. 2012. Sacramento–San Joaquin Delta historical ecology investigation: exploring pattern and process. Richmond (CA): San Francisco Estuary Institute–Aquatic Science Center. SFEI Contribution No. 672. [accessed 2023 Mar 28]. 225 p. Available from: *http://www.sfei.org/DeltaHEStudy*

Winder M, Jassby AD. 2011. Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. Estuaries Coasts. [accessed 2023 Mar 28];34(4). *https://doi.org/10.1007/s12237-010-9342-x*

Yelton R, Slaughter AM, Kimmerer WJ. 2022. Diel behaviors of zooplankton interact with tidal patterns to drive spatial subsidies in the northern San Francisco Estuary. Estuaries Coasts. [accessed 2023 Mar 28];45(6). Available from: *https://link.springer.com/article/10.1007/s12237-021-01036-8*

Ziegler SL, Able KW, Fodrie FJ. 2019. Dietary shifts across biogeographic scales alter spatial subsidy dynamics. Ecosphere. [accessed 2023 Mar 28];10(12). *https://doi.org/10.1002/ecs2.2980*

NOTE

Kimmerer WJ, Ignoffo TR, Sullivan L. 2011. Length, weight, carbon, and nitrogen content of the common copepods in the San Francisco Estuary [dataset]. Tiburon (CA): Romberg Tiburon Center, San Francisco State University. [accessed 2023 Mar 31]. Available from: *kimmerer@sfsu.edu*.