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RESEARCH

The Influence of Zooplankton Availability on Delta Smelt Condition and Foraging Across Habitat Contexts

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ABSTRACT

Strategies for endangered species conservation may have different outcomes depending on the habitat context in which they are implemented. Understanding these context-dependent effects can help optimize and target management efforts. In this analysis, we investigate how environmental and food-web conditions interactively affect condition and foraging of Delta Smelt (*Hypomesus transpacificus*), an endangered fish endemic to the San Francisco Estuary (the estuary). Food limitation, in terms of pelagic zooplankton availability, is considered a main factor that contributes to the decline in Delta Smelt abundance. Our overarching objective was to examine whether the effect of zooplankton on Delta Smelt depended on habitat context. Specifically, we hypothesized that zooplankton would less positively affect Delta Smelt condition—as measured by hepatosomatic index (HSI)—and foraging success in areas with nearby tidal wetlands, because these adjacent habitats may provide access to prey items from the epibenthos and fringing vegetation. In contrast, in regions with limited proximity to wetlands, we hypothesized that Delta Smelt would rely more on pelagic prey, which would manifest as a more positive effect of zooplankton on body condition and foraging success for Delta Smelt. Using models that accounted for habitat in multiple ways, we found little evidence that zooplankton and habitat interactively influenced Delta Smelt condition or gut fullness. Rather, the influence of zooplankton on HSI and gut fullness was generally positive across habitat contexts. Given the well-documented food limitation in the estuary, promoting the availability of pelagic zooplankton is a rational, albeit complex, management aim. Furthermore, our results suggest that efforts to increase zooplankton would broadly benefit Delta Smelt across a wide range of habitat contexts.

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INTRODUCTION

Ecological relationships can vary depending on local environmental conditions, and this context dependence has implications for conservation (Catford et al. 2022). For instance, the net effects of managing local stressors can depend on the context of stressors at larger spatial scales (Brown et al. 2013). As an illustrative example, marine reserves may have the largest conservation effect on sensitive species if they occur in refuges from climate warming (Brown et al. 2013). In a similar vein, the outcomes of habitat restoration for threatened species may depend on other environmental conditions (e.g., physiological stress imposed by poor water quality, competition or predation pressure from invasive species). Moreover, the capacity for management is finite, so resources must be strategically allocated to maximize conservation outcomes (Cote et al. 2016). Understanding how environmental factors interact to influence target species can help optimize conservation and management actions, in addition to better understanding their basic ecology.

The Delta Smelt (*Hypomesus transpacificus*) is a fish endemic to the Sacramento–San Joaquin Delta and San Francisco Estuary (hereafter the estuary), which is a physically, politically, and hydrodynamically complex ecosystem. The population of Delta Smelt has sharply declined and is nearly extinct in the wild (Moyle et al. 2016), to the point that annual supplementation of the wild population with hatchery-raised fish began in December 2021 (Hung et al. 2022). Population reductions of Delta Smelt and other pelagic fishes in the estuary are thought to be caused by a variety of proximate factors, including low recruitment, habitat and water quality degradation, increased mortality, and food limitation (Sommer et al. 2007; Moyle et al. 2016). Currently, substantial effort and resources are being invested in conservation and supplementation of Delta Smelt. Understanding the factors that influence Delta Smelt health and condition under a variety of ecological contexts is fundamental to informing which management strategies may have the most positive conservation outcomes.

Here we focus on food limitation as a key factor linked to the imperiled status of Delta Smelt. Pelagic zooplankton are a critical prey resource for Delta Smelt (Slater and Baxter 2014; Slater et al. 2019), but zooplankton abundance has declined across the estuary (Winder and Jassby 2011; Cloern and Jassby 2012) and has remained consistently low since around 1990 (Hammock, Moose, et al. 2019; Bashevkin et al. 2022). Given the uncertainties and expense of management actions, it is critical to understand whether alleviation of food limitation may affect Delta Smelt differently across habitat contexts. For example, in highly channelized, relatively homogeneous areas such as the Sacramento River Deepwater Ship Channel (DWSC), zooplankton may be particularly beneficial to Delta Smelt if the species is highly dependent on prey in the water column. In Suisun Marsh, in contrast, Delta Smelt may depend less on prey within the water column if they forage along adjacent tidal wetlands, the proximity of which correlates with foraging success of Delta Smelt (Hammock, Hartman et al. 2019). Understanding the possible context dependence of the relationship between zooplankton abundance and Delta Smelt could guide managers in deciding how, where, and when to focus actions to bolster bottom-up pathways of the pelagic food web.

In our analysis we consider whether zooplankton abundance affects Delta Smelt condition and foraging success differently across habitat contexts. We characterize habitat with three related variables within the estuary (salinity, tidal wetland proximity, and region), and we hypothesized that there would be an interactive effect between zooplankton biomass and each of these habitat variables on Delta Smelt condition and foraging success. Specifically, we hypothesized that the effect of total zooplankton biomass would be more positive in freshwater habitats (which are generally more channelized), in habitats with limited proximity to tidal wetlands, and that the effect of zooplankton would vary regionally, depending on the extent of tidal wetlands in each (e.g., in the DWSC, zooplankton biomass would have a strongly positive influence). In contrast, we hypothesized that zooplankton would less positively affect Delta Smelt in brackish habitats, habitats adjacent to tidal wetlands, and regions more influenced by tidal wetlands (such as Suisun Marsh). The proposed mechanism is the same in each context: in habitats with greater tidal wetland influence, fish may forage within or along tidal wetlands, making them less dependent on zooplankton for food. In more channelized habitat, fish may depend more on zooplankton, because wetlands (and any associated prey) are less accessible.

METHODS

Dataset

We analyzed condition and foraging success of Delta Smelt collected from August 2011 to September 2020 from the estuary. In considering Delta Smelt condition, we examined hepatosomatic index (HSI):

$$HSI = (liver\ wt) \times (total\ body\ wt)^{-1} \times 100 \qquad \textbf{Eq 1}$$

HSI reflects short-term energy reserves available to fishes (Mehner and Wieser 1994; Peragón et al. 1999; De Pedro et al. 2003), and is sensitive to food limitation in Delta Smelt, responding to fasting within 4 days at 16 °C (Hammock et al. 2020). To assess Delta Smelt foraging success, we examined gut fullness:

$$\text{Gut fullness} = (gut\ content\ wt) \times (total\ body\ wt)^{-1} \times 100 \qquad \textbf{Eq 2}$$

Gut fullness provides a snapshot of material ingested by fish; however, it does not necessarily correlate with prey quality, nor does it indicate what will be assimilated as fish tissue. Both the California Department of Fish and Wildlife (CDFW) and the US Fish and Wildlife Service (USFWS) collected Delta Smelt. The CDFW conducts several long-term fish-monitoring fish surveys—namely, the Summer Townet (STN), the Fall Midwater Trawl (FMWT), and the Spring Kodiak Trawl (SKT) —two of which collect zooplankton concurrently (the STN and FMWT). After a sharp decline in the abundance of Delta Smelt in the wild, more intensive sampling carried out by USFWS was initiated in December 2016 (i.e., Enhanced Delta Smelt Monitoring; EDSM). Beginning in 2017, the consulting company ICF began conducting surveys to complement the EDSM sampling by collecting zooplankton, phytoplankton, and water-quality samples. Sampling by ICF does not completely overlap with EDSM surveys; it occurred from September to November in 2017–2018 and from April to November in 2019–2020 (Schultz and Kalmback 2023).

Our objective required examining the relationships between zooplankton availability and the condition and foraging success of Delta Smelt. Thus, we restricted our dataset to Delta Smelt that were collected with a complementary zooplankton tow, such that our observations were coupled in time and space. Accordingly, the dataset included fish from STN and FMWT surveys, which collect zooplankton and fish samples concurrently at a subset of survey sites. Similarly, we only included fish collected by EDSM trawls that had an accompanying zooplankton tow from the same date and station. Thus, our analysis focuses on juvenile through sub-adult fish and does not include the more mature fish collected during spring, which lack concurrently collected zooplankton data (e.g., during the SKT). Details on collection methods for Delta Smelt and zooplankton are described elsewhere (Feyrer et al. 2007; Sommer and Mejia 2013; Damon et al. 2016; Kayfetz et al. 2020; Bashevkin et al. 2022; White and Baxter 2022).

Immediately after collection, fish were wrapped in labeled aluminum foil, flash-frozen in liquid nitrogen kept on each boat, and later transferred to the University of California–Davis. At UC Davis, fork length and body weight were recorded, and specimens were dissected (see Teh et al. 2016 for details). The liver and gut were excised, and the liver was weighed. The gut was preserved in ethanol and transferred to the CDFW Diet Study Laboratory where gut contents were identified and counted, and gut content weight was estimated (see Slater and Baxter 2014; Slater et al 2019).

Zooplankton data from tows collected during the STN and FMWT surveys were downloaded using the ‘`zooper`’ R package (Bashevkin et al. 2022; Bashevkin, Hartman, Alstad, et al. 2023; Bashevkin, Hartman, Thomas, et al. 2023). The “catch per unit effort” data (CPUE or catch m^{-3}) were converted to “biomass per unit effort” (BPUE; µg C m^{-3}) using taxon-specific conversion factors (Kayfetz et al. 2020; Burdi et al. 2021).

Response Variables

Our analysis consisted of six linear models with Gaussian distributions, in which either HSI or gut fullness was the response variable (for each response variable there were three models using one of three habitat predictor variables). We aggregated fish data by averaging to the station–date level to match the resolution of the zooplankton data. For HSI, 174 observations from 74 stations (each with observations on 1 to 19 different dates) had corresponding data for zooplankton. However, a small subset of these lacked certain habitat data ($n = 7$), such that sample size varied slightly among our models. The EDSM samples at randomly selected station locations, so each station location is only sampled once. Of the 74 stations, 47 were these stations sampled once by EDSM.

For gut fullness, data aggregated to the station–date level were available for 136 observations. Gut fullness values were arcsine-square-root-transformed to improve normality of residuals. Model assumptions were checked by examining plots of residuals (Pierce and Shafer 1986). Delta Smelt are visual predators, so gut fullness increases with time of day (Hobbs et al. 2006; Hammock et al. 2017). We adjusted for this effect by linearly regressing transformed fullness against time-of-day; we then subtracted the time-of-day slope coefficient times the time-of-collection from each fullness observation, and added the product of that slope times the average hour of collection across the dataset. That is, we used the following equation to adjust each gut fullness value for time of collection:

$$AGF_i = GF_i - b\,[Time_i] + b\,[mean\,(Time)] \tag{Eq 3}$$

where AGF_i is adjusted stomach fullness for the ith fish, GF_i is the transformed stomach fullness value for the ith fish, b is the slope parameter of the regression for transformed stomach fullness~time of day, $Time_i$ is the time of collection for the *ith* fish, and $mean(Time)$ is the average time across the dataset. We use these time-adjusted, arcsine-square-root-transformed gut fullness data in our analysis, but we simply refer to these data as gut fullness. In figures that depict gut fullness, arcsine-square-root values are plotted, but to improve interpretability we back-transform the axis labels so that they show gut fullness percentages.

Predictor Variables

The six models were created using an *a priori* hypothesis testing framework in which “habitat” was specified in three different ways to assess the hypothesis that zooplankton would interact with habitat to influence HSI and gut fullness. Each model included zooplankton biomass and season—known predictors of HSI—and gut fullness for Delta Smelt. Zooplankton biomass had a right-skewed distribution, so we used ln-transformed zooplankton biomass in our models. In terms of season, HSI of wild Delta Smelt is lowest in fall (Hammock et al. 2022). Additionally, seasonal effects can be habitat-dependent (e.g., salinity by season interaction), with fuller guts being observed in freshwater habitat in the summer but in brackish habitats in the fall (Hammock et al. 2017). Furthermore, zooplankton abundance and composition can shift seasonally throughout the estuary (Ambler et al. 1985). For example, two calanoid copepod species that are important prey for Delta Smelt (Slater and Baxter 2014) show contrasting seasonal patterns in abundance, with *Pseudodiaptomus forbesi* being abundant in summer–fall, and *Eurytemora carolleeae* (formerly *E. affinis*; Jungbluth et al. 2020) being abundant in the winter–spring and rare in summer–fall (Durand 2010; Merz et al. 2016). Thus, seasonal effects on Delta Smelt condition and foraging success may act indirectly through their effects on the zooplankton community. We include season as a categorical variable (summer or fall using a cutoff of 31 August, which corresponds to the transition from the STN to the FMWT). In supplemental analyses, we examine seasonal patterns in zooplankton biomass, HSI, and gut fullness using the datasets specific to our study—and compare the results to previously published studies (see Appendix A).

In addition to zooplankton and season, each model included one term that characterized habitat; this was either:

- a categorical salinity variable (freshwater or brackish, based on a salinity cutoff of 0.55 [measured during the trawl from which each fish was collected]; Hammock et al. 2017);
- a categorical wetland prevalence (low, medium, high; cutoffs were based on the distributions of wetland area within a 2-km radius of the station; Figure 1; justification in Hammock, Hartman et al. 2019); or
- a categorical variable for five regions of the estuary (Cache Slough, the Confluence, Suisun Bay, Suisun Marsh, and the DWSC; Figure 2), which encompass much of the recent distribution of Delta Smelt (Moyle et al. 2016).

Salinity was categorized as fresh or brackish to improve interpretability of potential interactions. In addition, a previous analysis found that categorizing salinity into two categories produced fish condition models with lower AICc than a continuous salinity variable or one with more categories (Hammock et al. 2021). Similarly, tidal wetland area was categorized to improve interpretability of possible interactions with zooplankton biomass. Wetland category thresholds were based on a histogram of sites (Figure 1). Categorization of our study sites reveals that our habitat characterizations are interrelated (Figure 3); for example, all sites in the Cache Slough and the DWSC region were freshwater, while all but one site from Suisun Bay and Suisun Marsh were brackish. Additionally, brackish habitats were generally associated with more abundant wetland habitat (Figure 3; Hammock, Hartman et al. 2019). Thus, although our hypothesis most specifically focused on tidal wetlands, the related habitat variables—salinity and region—were also included to test the hypothesis more broadly (i.e., to exhaustively test the hypothesis that zooplankton effects depend on habitat context [wetlands, salinity, and region]). Finally, all models included an interaction term between zooplankton biomass and the habitat variable, the primary parameter of interest in this study. Thus, the six models were in this form:

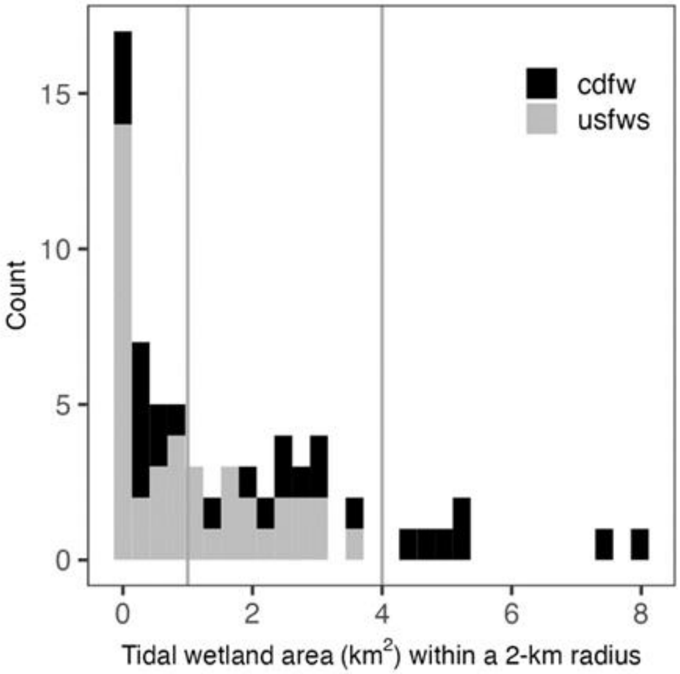

Figure 1 Distribution of the abundance of tidal wetland within a 2-km radius of each station included in our study ($n = 74$). Stations include those surveyed by the CDFW (STN and FMWT) and USFWS (EDSM surveys). The *vertical lines* indicate the thresholds used to categorize stations into "low, "medium," and "high" wetland categories.

HSI or gut fullness ~ zoop + habitat + season + zoop × habitat

where "habitat" was "salinity," "region," or "tidal wetland area."

Statistical significance was determined based on $\alpha = 0.05$. Results are reported from type-III F-tests unless noted. In some situations (e.g., an over-parameterized model), the significance of

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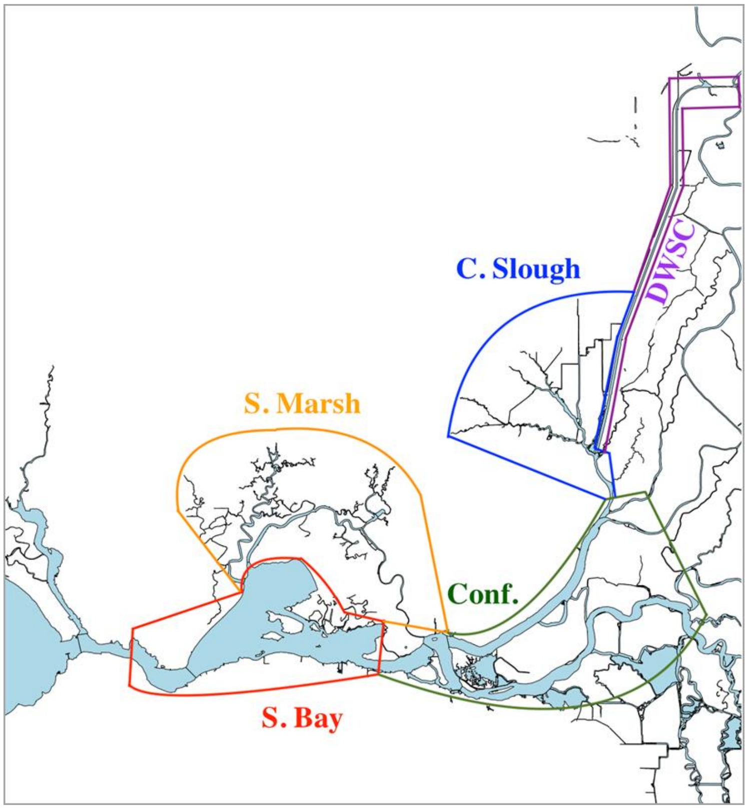

Figure 2 Map of the Sacramento–San Joaquin Delta and San Francisco Estuary. The recent range of Delta Smelt is divided into the five regions depicted, including the Sacramento River Deepwater Ship Channel (DWSC), Cache Slough (C. Slough), the Confluence (Conf.), Suisun Bay (S. Bay), and Suisun Marsh (S. Marsh). Note that boundaries are not necessarily geographically accurate and were selected to maximize sample size. For example, several Delta Smelt from the Carquinez Strait (strait just west of Suisun Bay) were lumped into Suisun Bay.

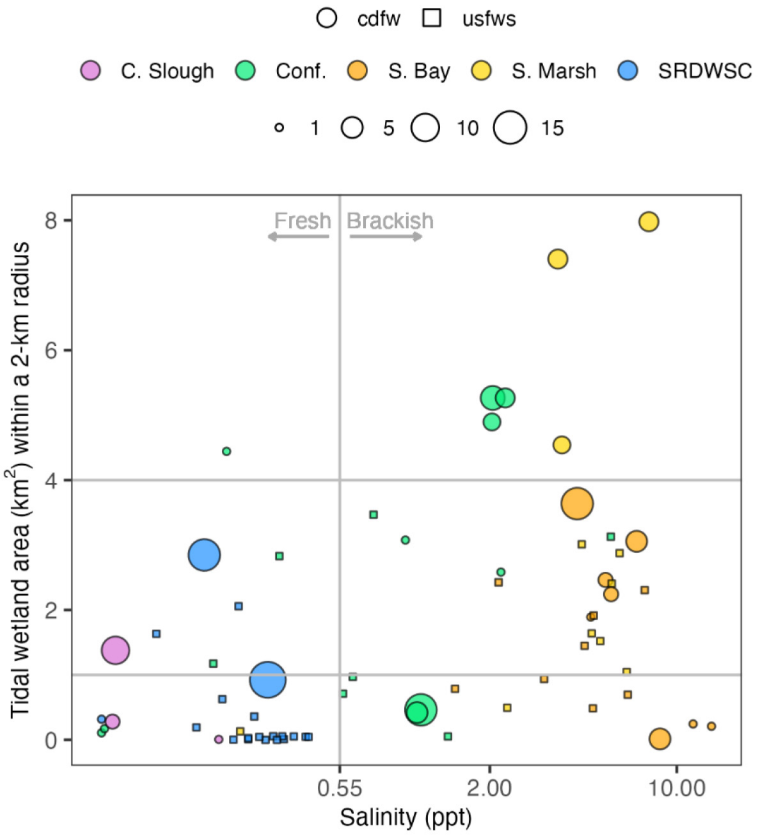

Figure 3 Habitat categorizations for each station (n = 74) included in our study. *Colors* indicate the assigned region for each station. *Shapes* indicate the agency associated with the station. *Size of points* indicate the number of dates on which the station was sampled (note: USFWS stations are sampled a single time). Stations to the *left of the vertical line* (salinity < 0.55) were classified as freshwater, and those *to the right* as brackish; *x*-axis is shown on a ln-scale to show spread of the freshwater sites. The *horizontal lines* depict the thresholds used to classify stations as "low," "medium," or "high" wetland abundance.

a main effect can depend on the inclusion of a non-significant interaction effect. Thus, we also report type-II F-test results if the interpretation of a main effect differed compared to that from a type-III F-test. F-tests were performed with the ‘`car`’ package (Fox and Weisberg 2019). All analyses were conducted in R version 4.2.1 (R Core Team c2022).

RESULTS

Similar to previous studies, (1) meso-zooplankton biomass was 2.9-fold higher in freshwater than in brackish water in summer, and 1.9-fold higher in freshwater in fall (Figure A1); (2) HSI declined from summer into fall in both freshwater and brackish water by 1.3-fold for both fresh and brackish habitats (Figure A2); and (3) gut fullness declined in freshwater from summer into fall but showed the opposite trend in brackish water (Figure A3). Our analysis of zooplankton biomass showed muted seasonal effects (Figure A1) compared to previous studies which analyzed zooplankton abundance (e.g., Hammock et al. 2017). However, a gradual temporal decline in meso-zooplankton biomass generally occurred in fall (Figure A4), while HSI declined abruptly from summer into fall in both freshwater and brackish habitat (Figure A4; Hammock et al. 2017, 2022). Additional details are in the results in Appendix A, and each of these effects are accounted for in the models below.

HSI Models

We examined the influence of zooplankton biomass on Delta Smelt HSI in various habitat contexts. The adjusted R^2 of the HSI models ranged from 0.21 to 0.29 (Table 1).

In the model that included salinity as the habitat variable, the zooplankton by salinity interaction effect was non-significant (Table 1A, Figure 4). The main effect of zooplankton biomass on HSI was non-significant in the type III F-test (Table 1A), but results from a type II F-test—which does not consider (in this case, non-significant) interaction effects—supported a positive effect of zooplankton biomass, regardless of salinity ($F = 5.4$, $p = 0.021$; Figure 4). HSI values were significantly lower in fall compared to summer (Table 1A; Figure 4). Overall, we found no support for zooplankton having a more positive effect on HSI in freshwater than in brackish habitat, as hypothesized.

Table 1 Effects of zooplankton biomass, habitat, and seasonality on hepatosomatic index (HSI). Results are shown for three separate models. Each model had a variable that represented habitat: salinity, wetland prevalence, or region—all of which are categorical variables. Results are from type-III F-tests.

	Model sample size	Predictor	F	p-value	Adj. R^2
A	n = 174	Zooplankton	2.15	0.145	0.21
		Salinity	0.11	0.744	
		Season	33.36	<0.001	
		Zooplankton × Salinity	0.14	0.706	
B	n = 167	Zooplankton	0.35	0.553	0.29
		Wetland	4.14	0.018	
		Season	32.21	<0.001	
		Zooplankton × Wetland	4.88	0.009	
C	n = 167	Zooplankton	4.52	0.035	0.23
		Region	1.19	0.316	
		Season	28.79	<0.001	
		Zooplankton × Region	1.21	0.310	

In the model that included wetland prevalence as our habitat variable, the zooplankton by wetland interaction was statistically significant (Table 1B; Figure 5). Specifically, zooplankton biomass had an overall positive effect on HSI, with the effect being most positive in sites in the “medium” wetland category (Figure 5). The range of the zooplankton predictor was notably wider for the medium wetland sites, because both the minimum and maximum observed zooplankton biomass values occurred in this category. To evaluate whether these points were unduly influencing the results, we re-ran the model without these two points. While the trend was slightly muted without these points (i.e., higher *p*-values), the zooplankton by wetland interaction remained statistically significant ($F = 3.89$, $p = 0.022$; Figure A5). HSI was lower in fall than

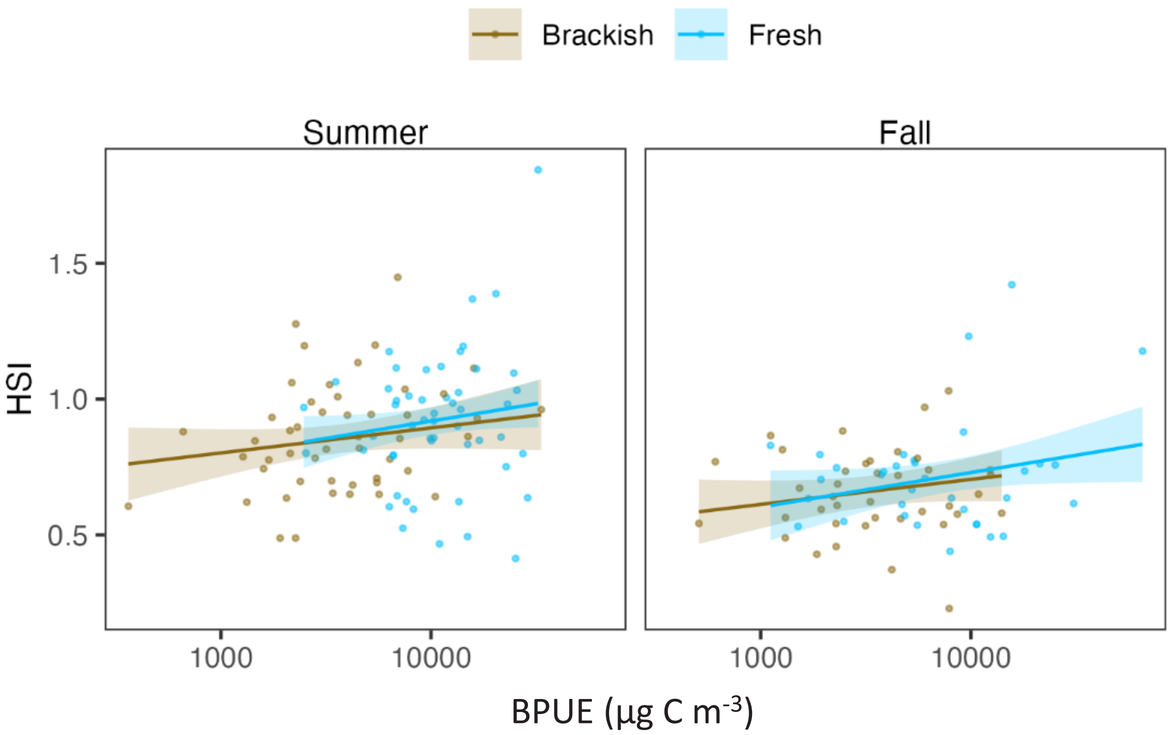

Figure 4 Hepatosomatic index (HSI) shown as a function of zooplankton biomass (BPUE; log-scale), salinity, and season. *Lines* show model fits with shaded regions showing 95% confidence intervals.

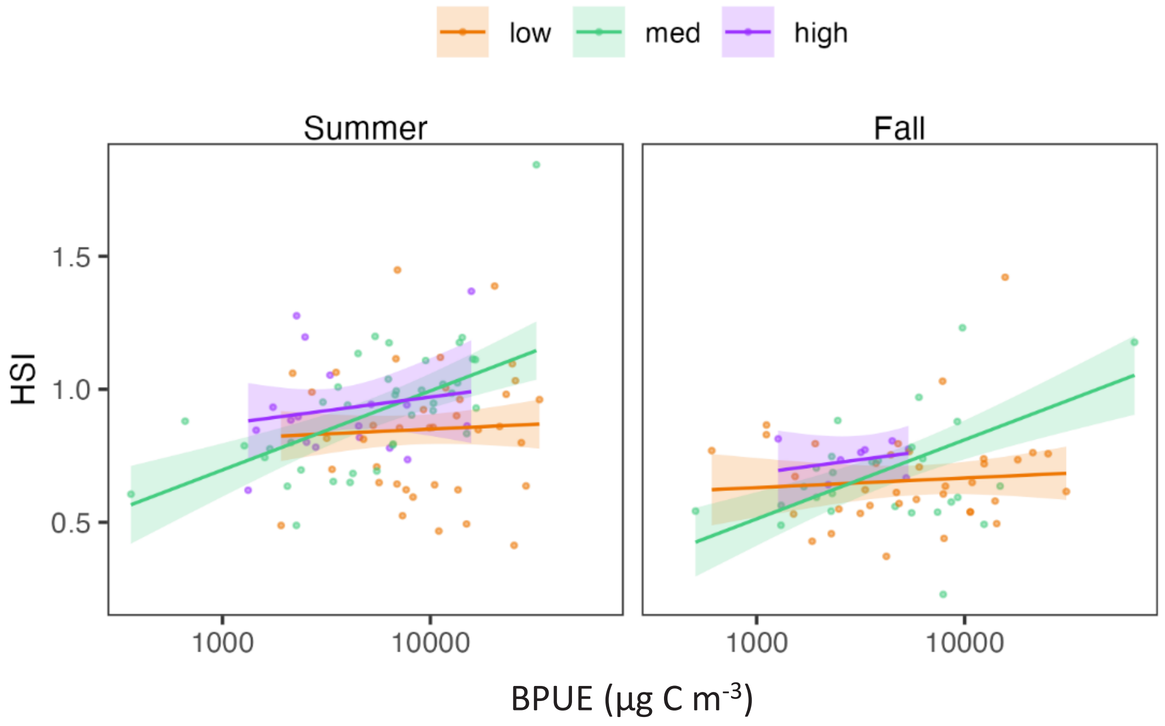

Figure 5 Hepatosomatic index (HSI) shown as a function of zooplankton biomass (BPUE; log-scale), season, and wetland abundance. *Lines* show model fits with shaded regions showing 95% confidence intervals.

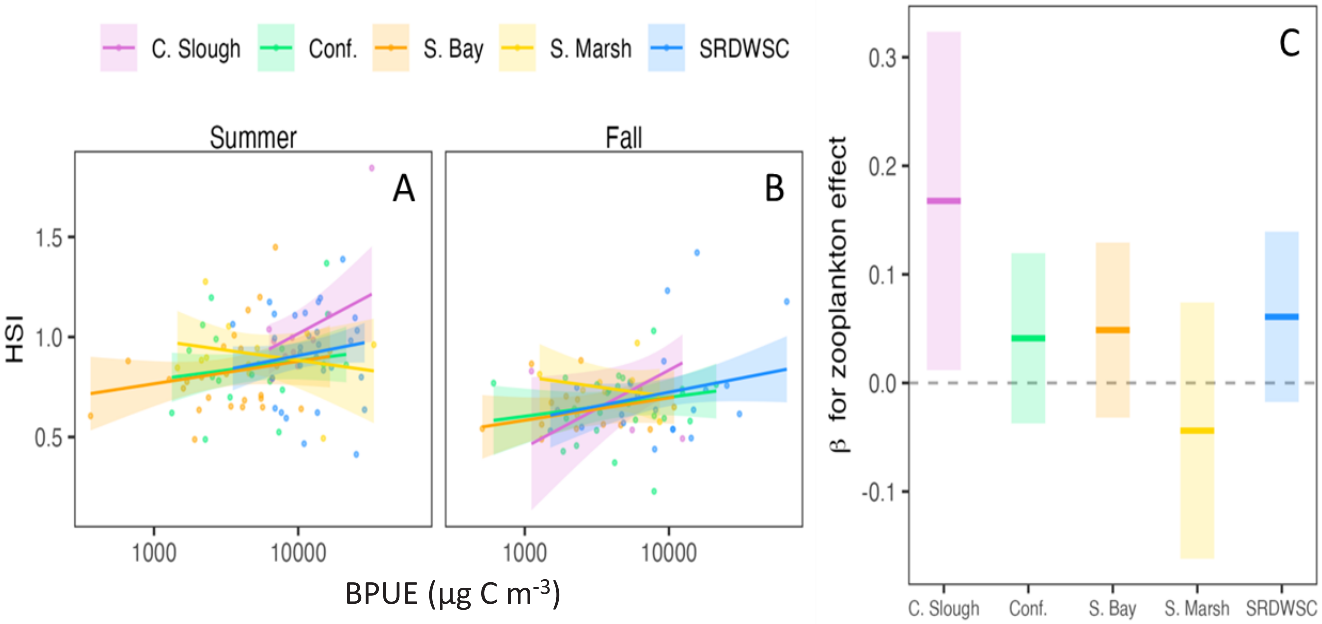

Figure 6 Panels **A** and **B** shows hepatosomatic index (HSI) as a function of zooplankton biomass (BPUE; log-scale), season, and region. *Lines* show model fits with shaded regions showing 95% confidence intervals. Panel **C** shows the parameter estimates from the model for each region.

in summer (Table 1B, Figure 5). Overall, results suggest that the magnitude of the zooplankton effect on HSI depended on wetland prevalence, but in a non-linear fashion (i.e., effect was most positive in the “medium” category).

Lastly, in the model that included region as the habitat variable, the zooplankton by region interaction term was non-significant (Table 1C; Figure 6). Zooplankton biomass positively affected HSI (Table 1C; Figure 6). Like the previous two models, season significantly affected HSI, with lower HSI in fall (Table 1C, Figures 6A and 6B). Overall, we found that the effect of zooplankton on HSI was generally positive and not statistically dependent on region of the estuary (i.e., overlap in the parameter estimates for each region; Figure 6C).

Gut Fullness Models

Models for gut fullness had relatively low fit, with adjusted R^2 ranging from 0.07 to 0.1 (Table 2). In the three gut fullness models across habitat contexts, we did not detect a statistical interaction between zooplankton biomass and habitat (salinity, wetland, or region; Table 2; Figures 7–9). In the model using wetland prevalence as the habitat variable, there was a positive effect of zooplankton biomass on gut fullness (Table 2B; Figure 8). For the models using salinity and region, the main effect of zooplankton was not significant for type-III tests (Tables 2A, 2C), but was for type-II tests (for salinity: $F = 10.00$, $p = 0.002$, Figure 7; for region: $F = 7.23$, $p = 0.008$; Figure 9). Thus, gut fullness increased with the biomass of zooplankton in the water column, and this effect was independent of habitat characteristics.

DISCUSSION

We aimed to understand whether local habitat characteristics influence the apparent effect of pelagic zooplankton availability on Delta Smelt condition and foraging success. Our hypothesis that zooplankton would more positively affect Delta Smelt condition and foraging in regions dominated by freshwater habitat and low wetland abundance was not supported. Overall, zooplankton biomass showed a positive effect on HSI and gut fullness, nearly regardless of habitat context. These results suggest that foraging and condition for juvenile through sub-adult Delta

Smelt would generally benefit from increased zooplankton biomass throughout its range.

The lone interaction detected in our study was between wetland prevalence and zooplankton biomass on HSI. This interaction was somewhat counter-intuitive, because zooplankton exerted the most positive influence on HSI at a moderate level of wetlands. Thus, the direction of the interaction was not aligned with our hypothesis, in which we predicted that zooplankton biomass would most strongly affect HSI at sites with limited proximity to wetlands. The effect of zooplankton biomass on HSI was nearly indistinguishable between sites with low and high wetland proximity. Perhaps the most plausible explanation is that the interaction is a statistical artifact, possibly from low sample size or variability of the data. The interaction did not follow the *a priori* hypothesis that higher zooplankton densities would most benefit the condition of Delta Smelt in channelized habitat.

Table 2 Effects of zooplankton biomass, habitat, and seasonality on gut fullness. Results are shown for three separate models. Each model had a variable that represented habitat: salinity, wetland prevalence, or region—all of which are categorical variables. Results are from type-III F-tests.

	Model sample size	Predictor	F	*p*-value	Adj. R^2
A	n = 136	Zooplankton	2.45	0.120	0.07
		Salinity	1.22	0.271	
		Season	3.19	0.077	
		Zooplankton × Salinity	1.09	0.297	
B	n = 136	Zooplankton	10.18	0.002	0.10
		Wetland	0.81	0.446	
		Season	3.08	0.082	
		Zooplankton × Wetland	0.49	0.613	
C	n = 136	Zooplankton	0.34	0.559	0.07
		Region	0.52	0.724	
		Season	2.96	0.088	
		Zooplankton × Region	0.55	0.699	

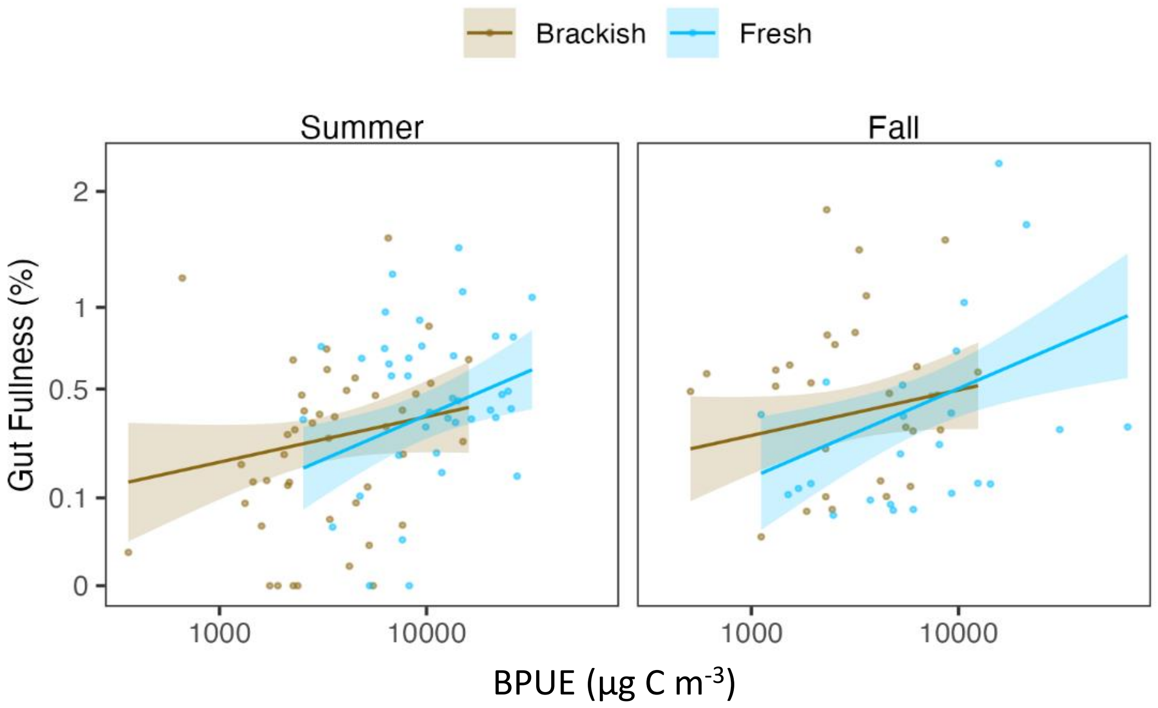

Figure 7 Gut fullness shown as a function of zooplankton biomass (BPUE; log-scale), salinity, and season. *Lines* show model fits with *shaded regions* showing 95% confidence intervals. Gut fullness data are shown as arcsine-square-root-transformed (as in the analysis), with *y-axis* ticks showing back-transformed values for reference.

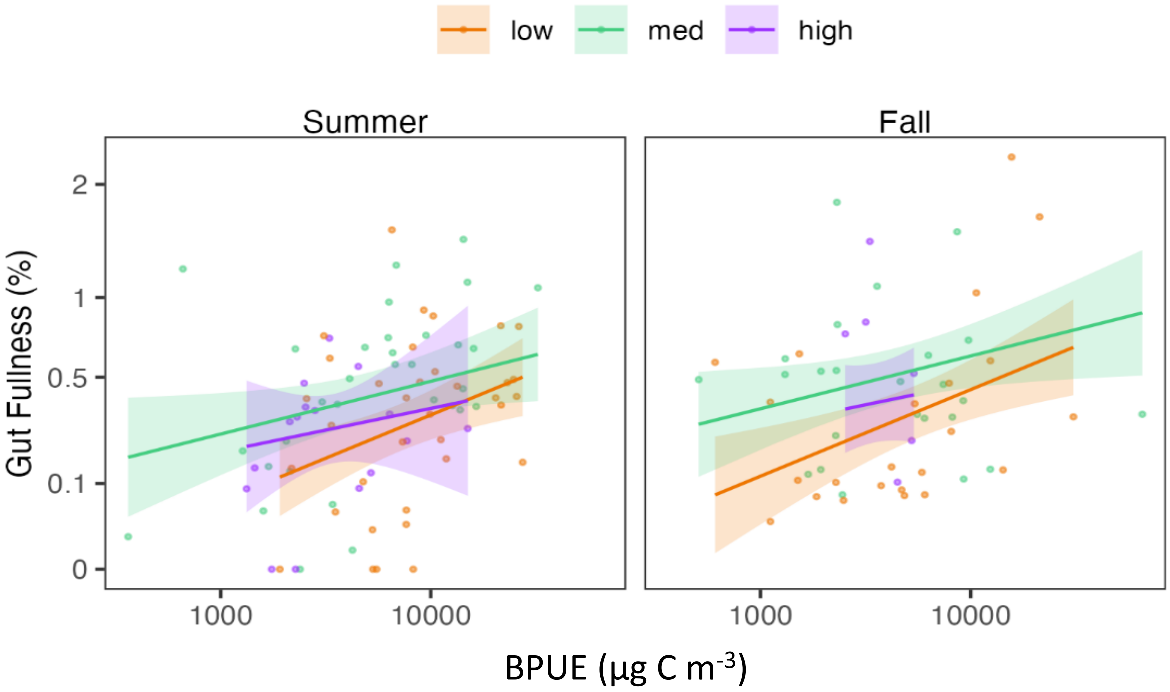

Figure 8 Gut fullness shown as a function of zooplankton biomass (BPUE; log-scale), season, and wetland abundance. *Lines* show model fits with *shaded regions* showing 95% confidence intervals. Gut fullness data are shown as arcsine-square-root-transformed (as in the analysis), with *y-axis ticks* showing back-transformed values for reference.

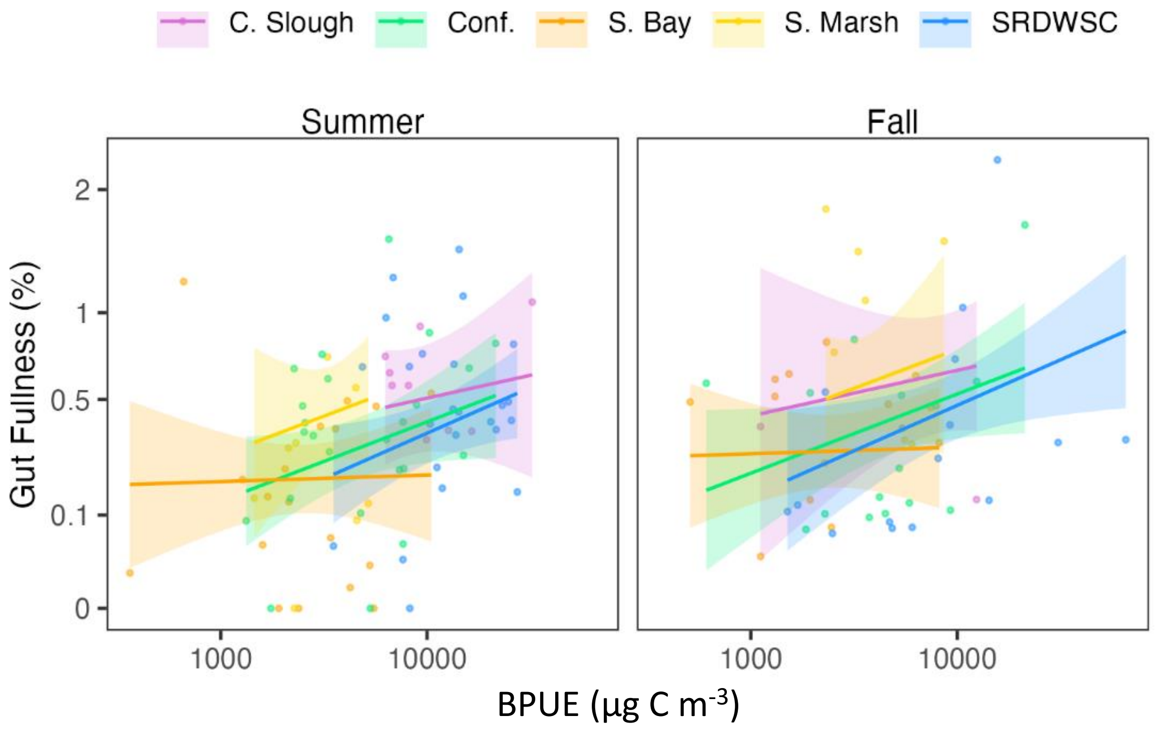

Figure 9 Gut fullness shown as a function of zooplankton biomass (BPUE; log-scale), season, and region. *Lines* show model fits with *shaded regions* showing 95% confidence intervals. Gut fullness data are shown as arcsine-square-root-transformed (as in the analysis), with *y-axis* ticks showing back-transformed values for reference.

Moreover, the gut fullness results showed that zooplankton density improved foraging success regardless of tidal wetland influence, so the mechanism by which we expected tidal wetlands to improve juvenile through sub-adult Delta Smelt HSI was not supported.

In all HSI models, Delta Smelt condition was lower in fall than in summer. This fall decline in HSI is also consistent across a wide range of water-year conditions (Hammock et al. 2022). Higher HSI in summer is somewhat surprising given the relative frequency of warm water temperatures in summer, which would be expected to depress HSI under food-limited conditions, e.g., Heidinger and Crawford (1977). Water temperatures over 21 °C are common, particularly in freshwater habitats, and Delta Smelt tend to experience thermal stress around 20 °C to 21 °C (Moyle et al. 2016). Thus, higher HSI values in summer occur despite somewhat sub-optimal abiotic conditions and may relate to relatively abundant zooplankton in summer in freshwater (Appendix A). Lusardi et al. (2020) described similar results with Coho Salmon (*Oncorhynchus kisutch*) growing quickly at water temperatures generally considered sub-optimal for the species, showing that abundant prey can offset negative effects of high water temperatures in the wild.

That is not to say that prey were sufficiently abundant for Delta Smelt in summer in freshwater. We detected a positive relationship between HSI and gut fullness with increasing zooplankton density in freshwater (Figure 7), implying that the population would have eaten more and had better condition had the prey density been higher (e.g., Silva–Castiglioni et al. 2016; Hammock et al. 2020). The seasonal decline in Delta Smelt HSI may be partly attributed to resource limitation; although, we only observed a decline in zooplankton biomass in freshwater habitats (see Appendix A, but note that this effect was non-significant). Additionally, HSI appears to decline more abruptly from summer to fall compared to zooplankton biomass (which shows a more gradual decline; Figure A4), suggesting that resource limitation is not the reason for the rapid decline in HSI in fall. Another possibility is that some amount of survivorship bias may occur in the summer, where only Delta Smelt with high HSI survive through this period of peak water temperature. A recent life-cycle analysis for Delta Smelt indicates that summertime survival had a strong influence on the species' population trajectory over recent decades (Polansky et al. 2024). Our study does not identify the specific mechanism(s) that drives the strong seasonal effect on HSI, but identifying this factor should improve understanding of the environmental controls on Delta Smelt condition.

We found that gut fullness was positively related to zooplankton biomass across habitats. The consistent lack of an interaction in our gut fullness models—regardless of the habitat variable—suggests that juvenile through sub-adult Delta Smelt forage on pelagic prey, regardless of habitat context. Interestingly, this positive effect of zooplankton on foraging success was observed despite substantial spatial differences in zooplankton community composition (Winder and Jassby 2011) and resulting composition of prey in the Delta Smelt gut contents across habitats (Slater et al. 2019). Additionally, Delta Smelt consume larger prey items that are not targeted by meso-zooplankton sampling (e.g., mysids, amphipods, larval fish) in both brackish and freshwater habitats (Slater et al. 2019). In short, despite the zooplankton tows that contained different prey assemblages across habitats, juvenile through sub-adult Delta Smelt seemed to consume prey biomass in relation to the prevalence of zooplankton in the water column.

Previous studies have suggested the importance of non-zooplankton prey items for Delta Smelt, particularly in areas with prevalent tidal wetlands (Hammock, Hartman, et al. 2019a). However, in our study we did not observe direct benefits of wetland proximity on gut fullness. Hammock, Hartman, et al. (2019) attribute 60% of the positive effect of tidal wetlands on gut fullness to predation on larval fish. The analysis in Hammock, Hartman, et al. (2019) included 69 Delta Smelt—mostly collected during winter and spring—with larval fish in their guts; however, in our study, larval fish were found in the gut contents of only five fish (out of approximately 500 individuals). Thus, an important caveat of our study is its exclusion of adult fish collected in January through May (because no concurrent zooplankton tows were collected during the SKT), such that we cannot infer the importance of wetland proximity for foraging of adult fish. Larger-bodied adult Delta Smelt are more likely to forage on larval fish than are the juveniles and sub-adults that dominate in summer and fall (Slater et al. 2019), and many larval fish rear in tidal wetlands (Baltz et al. 1993; Beck et al. 2001; Grimaldo et al. 2017). In addition, Hammock, Hartman, et al. (2019) conducted their analysis of the effect of tidal wetland area on gut fullness at the individual fish level. Thus, their sample size was much larger (n = 1,380) compared to the current study, which was conducted at the station–date level (n = 136). Thus, our study does not refute the association between tidal wetlands and Delta Smelt foraging success and condition, but suggests that tidal wetlands may be more important for adult foraging than for younger life stages. It is also worth noting that we found overall low fit for the gut fullness models, which indicates we were missing important predictors of gut fullness for juvenile to sub-adult Delta Smelt.

Overall, zooplankton biomass tended to positively affect Delta Smelt HSI and gut fullness across habitats. These results have relatively straightforward—albeit difficult to implement—management implications. That is, any management actions to increase zooplankton biomass should benefit Delta Smelt condition and foraging (Kimmerer and Rose 2018). Accounting for such food-web interactions has been recognized as a valuable management approach in fish conservation (Naman et al. 2022). Both HSI and foraging success eventually correlate with fitness in fishes (e.g., Brooker et al. 2013; Rodgveller 2019), so increasing zooplankton abundance is expected to aid the recovery of the population. However, one disconcerting possibility is that increasing zooplankton abundance may also benefit exotic predators (e.g., Mississippi Silverside [*Menidia audens*], Largemouth Bass [*Micropterus salmoides*]; Schreier et al. 2016) and competitors (e.g., Wakasagi [*Hypomesus nipponensis*]; Davis et al. 2022), potentially dampening or offsetting the positive effect of increased zooplankton. In addition, zooplankton taxa vary in nutritional composition (Kratina and Winder 2015), and an increase in total biomass could be from less nutritional or smaller prey (e.g., the cyclopoid *Limnoithona*) as opposed to larger and more nutritious prey (e.g., the calanoid copepod *P. forbesi* or *E. carolleeae*). So, despite increasing total zooplankton biomass, varying nutritional composition could affect Delta Smelt differently. Thus, other management actions targeted specifically for Delta Smelt—such as increasing turbidity or population supplementation—may be beneficial to the species, (Feyrer et al. 2007; Schreier et al. 2016; Hung et al. 2022; Pasparakis et al. 2023).

Despite these straightforward management implications for Delta Smelt, manipulating the productivity of the pelagic food web in the estuary is inherently challenging (Durand 2015). There is strong evidence for both bottom-up (Kimmerer et al. 2005; Gearty et al. 2021; Rogers et al. 2024) and top-down control of zooplankton (e.g., invasive clam consumption of nauplii; Kimmerer et al. 1994; Kimmerer and Lougee 2015). A single management action may also have contrasting results in different regions of the estuary. For example, increased periods of flow may decrease phytoplankton availability for zooplankton in the uppermost areas of the estuary (by reducing residence time; Delesalle and Sournia 1992; Hartman et al. 2024), while high flows may increase export of phytoplankton to downstream areas such as Suisun Bay (Jassby 2008; Kimmerer, Ignoffo, Kayfetz et all. 2018; Hassrick et al. 2023; Barros et al. 2024). Increased phytoplankton is associated with greater zooplankton biomass on annual time-scales in the estuary (Rogers et al. 2024), but increasing phytoplankton estuary-wide would likely require reducing grazing by clams and increasing residence time (Hammock, Moose, et al. 2019)—a politically difficult proposition. Tidal wetlands are associated with improved foraging success for Delta Smelt, but they are not considered significant sources of zooplankton for nearby channels (i.e., the Outwelling Hypothesis, Herbold et al. 2014), and can even be sinks (Kimmerer et al. 2018; Yelton et al. 2022). Consequently, management of zooplankton—with the goal of supporting Delta Smelt populations in a bottom-up manner—appears to simply require a higher density of zooplankton across the estuary.

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