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RESEARCH

I'm Not that Shallow – Different Zooplankton Abundance But Similar Community Composition Between Habitats in the San Francisco Estuary

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ABSTRACT

Wetland restoration is a key management tool for increasing food availability for at-risk fishes in the San Francisco Estuary. To characterize the benefits of restoration sites, it is critical to quantify the abundance and composition of fish food resources in and near the wetlands. Characterization of zooplankton communities is considered particularly important, but accurate analysis of zooplankton samples is time-consuming and expensive. The recently established Fish Restoration Program (FRP) Monitoring Team assessed whether data from existing long-term monitoring surveys could be used to characterize shallow-water zooplankton communities before restoration. During the springs of 2017 to 2019, the FRP collected zooplankton samples near the mouth of tidal wetland sites, or immediately outside future restoration sites, and compared them to concurrent samples collected in deep water by existing long-term monitoring surveys. We found very few differences in community composition between shallow and deep samples, though a few taxa were more abundant in shallow water. Seasonal and interannual differences in composition and abundance showed that restoration sites provide varying food resources over time. There was significantly higher total abundance of zooplankton in deep versus shallow water, which may be a result of differences in zooplankton production, migration, or fish predation. Inconsistencies in towing speed and gear type may also be driving this result, rather than true habitat differences. This study indicates that monitoring of wetland restoration sites must rely on multiple years of data collected on the site—rather than relying on adjacent open-water sampling—and should include monitoring of epiphytic and epibenthic invertebrates as well as zooplankton.

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INTRODUCTION

Zooplankton are a key primary consumer group in most estuarine and marine habitats.

Mesozooplankton (chiefly small crustaceans 150 to 500 microns in length) provide a trophic transfer between primary producers (including both phytoplankton and vascular plant detritus [Harfmann et al. 2019; Holmes and Kimmerer 2022]) and the fish community. Many mesozooplankton also consume smaller animals, bacteria, and protists, contributing to trophic transfer through alternative pathways (Kankaala et al. 2010; Kayfetz and Kimmerer 2017). As such, understanding zooplankton dynamics is an important part of characterizing the aquatic ecosystem, but a full understanding of drivers of zooplankton productivity and community composition in estuaries has remained elusive. Within the San Francisco Estuary (estuary), multiple monitoring programs have sampled zooplankton since the 1970s. However, until recently these data sets were analyzed separately, limiting statistical power (Bashevkin et al. 2022). It is therefore no surprise that publications focused on zooplankton lag significantly behind publications focused on fish (Hartman et al. 2021).

Analysis to date has identified a few key facts about zooplankton in the system. Zooplankton surveys, along with diet analyses performed on fish collected concurrently with zooplankton tows, have shown zooplankton are the primary diet of several threatened and endangered fish species, such as Delta Smelt *(Hypomesus transpacificus),* Longfin Smelt (*Spirinchus thaleichthys),* and juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) (Feyrer et al. 2003; Hobbs et al. 2006; Goertler et al. 2018; Slater and Baxter 2014; Sabal et al. 2016; Jungbluth et al. 2021). These surveys have also documented the shift in copepod community composition from native species to non-native species, such as *Pseudodiaptomus forbesi* and *Limnoithona tetraspina* (Winder and Jassby 2011), as well as the overall decline in zooplankton abundance caused by reduction in their food supply and predation on nauplii (Kimmerer et al. 1994; Orsi and Mecum 1996).

The zooplankton community in the open-water habitats of the estuary shifts over space and time. On daily time-scales, many species exhibit diurnal or tidal vertical migration, potentially allowing them to hold their position in the estuary (Manuel and O'Dor 1997; Forward and Tankersley 2001; Kimmerer et al. 2002), and avoid predation (Kimmerer et al. 2002; Rollwagen–Bollens et al. 2006). On annual scales, zooplankton species differ in the timing of their peak abundance, with *Eurytemora* spp. peaking in April or May and *Pseudodiaptomus* spp. peaking in July or August (Merz et al. 2016). In a spatial context, species may be restricted to certain regions of the estuary by salinity tolerance, biological interactions, or a combination of the two (Kayfetz and Kimmerer 2017).

While earlier zooplankton research focused on open-water processes, in recent years more effort has been taken to describe the importance of floodplains and tidal wetlands to the food web in this estuary. Wetlands once comprised over 60% of the area of the Delta (Whipple et al. 2012) and were home to a diverse community of native wildlife. Over the past 150 years, the Delta has lost 98% of its wetlands (Robinson et al. 2014). By some estimates, wetland vegetation provided most of the primary productivity in the Delta (Cloern et al. 2016). Therefore, natural resource managers have prioritized restoration of tidal wetlands and floodplains to achieve some of the productivity they once contained (Brown 2003).

While Cloern et al. (2016) assessed primary productivity from historic wetlands in the estuary and Cloern et al. (2021) estimated that marsh plants provide up to a quarter of the primary production in the Delta today, the amount of secondary productivity tidal wetlands provide is still poorly understood. Direct study of zooplankton communities in estuary wetlands is limited, and the studies that have been completed to date have been inconclusive. Some taxa, such as the copepod *Eurytemora carolleeae*, have slightly greater biomass in tidal wetlands (Grimaldo et al. 2004), but differences between regions of the estuary tend to overwhelm differences between wetlands and channels (Bollens et al. 2014). Zooplankton export was hypothesized to be a benefit of tidal wetlands; however, the limited observations on flux from wetlands show varying results, with either no net export, or varying between net positive and net negative, depending on time of year or time in the tidal cycle (Dean et al. 2005; Kimmerer–Ignoffo, Bemowski, et al. 2018). However, fish collected in regions with high area of tidal wetlands had fuller stomachs than would be expected, given zooplankton density in the channels, indicating they may be foraging within the wetlands rather than benefiting from export from wetlands (Hammock et al. 2019), though this is still speculative.

To understand zooplankton dynamics across habitats, increased monitoring of tidal wetlands is clearly needed, as is integrating these data with existing open-water samples. In this study, we compared zooplankton samples collected near or just inside reference wetlands and future restoration sites to zooplankton samples collected in nearby channels, in accordance with the Fish Restoration Program (FRP), which is tasked with assessing the effectiveness of tidal wetland restoration for Delta Smelt, Longfin Smelt, and juvenile Chinook Salmon. We chose to focus on differences between shallow sites and deeper sites, rather than wetland type or restoration status because of limitations in available sites, but we see this as the first step in understanding differences in zooplankton between habitats.

The channel samples were collected by the Interagency Ecological Program (IEP) 20-mm survey and Environmental Monitoring Program (EMP) zooplankton survey (*https://iep.ca.gov/Science-Synthesis-Service/Monitoring-Programs*). To see whether these samples were comparable, we tested the following study questions:

- Are there differences in zooplankton density between shallow, wetland-adjacent habitat and deeper habitats?
  - We hypothesized that shallow, wetland-adjacent habitat would have higher total zooplankton density.
- Are there differences in zooplankton community composition between shallow, wetland-adjacent habitat and deeper habitats?
  - We hypothesized that some taxa make up a larger proportion of the total zooplankton community in shallow water than in deep water.
- How do these differences change across the estuary and over time?
  - We hypothesized that sites further from the mouth of the estuary would have higher overall zooplankton density and relatively more freshwater taxa, such as cladocerans.
  - We hypothesized that overall zooplankton density would be highest later in the spring, but with substantial interannual variation.

METHODS

Study Area

This study took place in the upper estuary—specifically in the Cache Slough Complex, Confluence, and Suisun Marsh (Figure 1, Table 1)—since these regions of the estuary are targeted for tidal wetland restoration because of their high abundance of native fishes and appropriate elevations (Moyle et al. 2012). The FRP has planned restoration projects spread throughout these regions on land that is currently managed wetland (where gates or pumps control all hydrologic connection), muted tidal wetland (where the wetland and surrounding channel are partially connected, but not enough for full tidal action), or dry farmland. The FRP has also selected existing tidal wetlands to use as reference sites to monitor the effectiveness of their restoration projects, though the Delta has relatively few patches of tidal wetlands remaining. All samples collected in shallow habitats were classified as 'shallow,' but future analysis should assess whether shallows outside wetlands of different ages differ from shallow areas not directly connected to wetlands.

Gear Descriptions

Environmental Monitoring Program

The Environmental Monitoring Program (EMP) survey monitors water quality, phytoplankton, meso-zooplankton, macro-zooplankton,

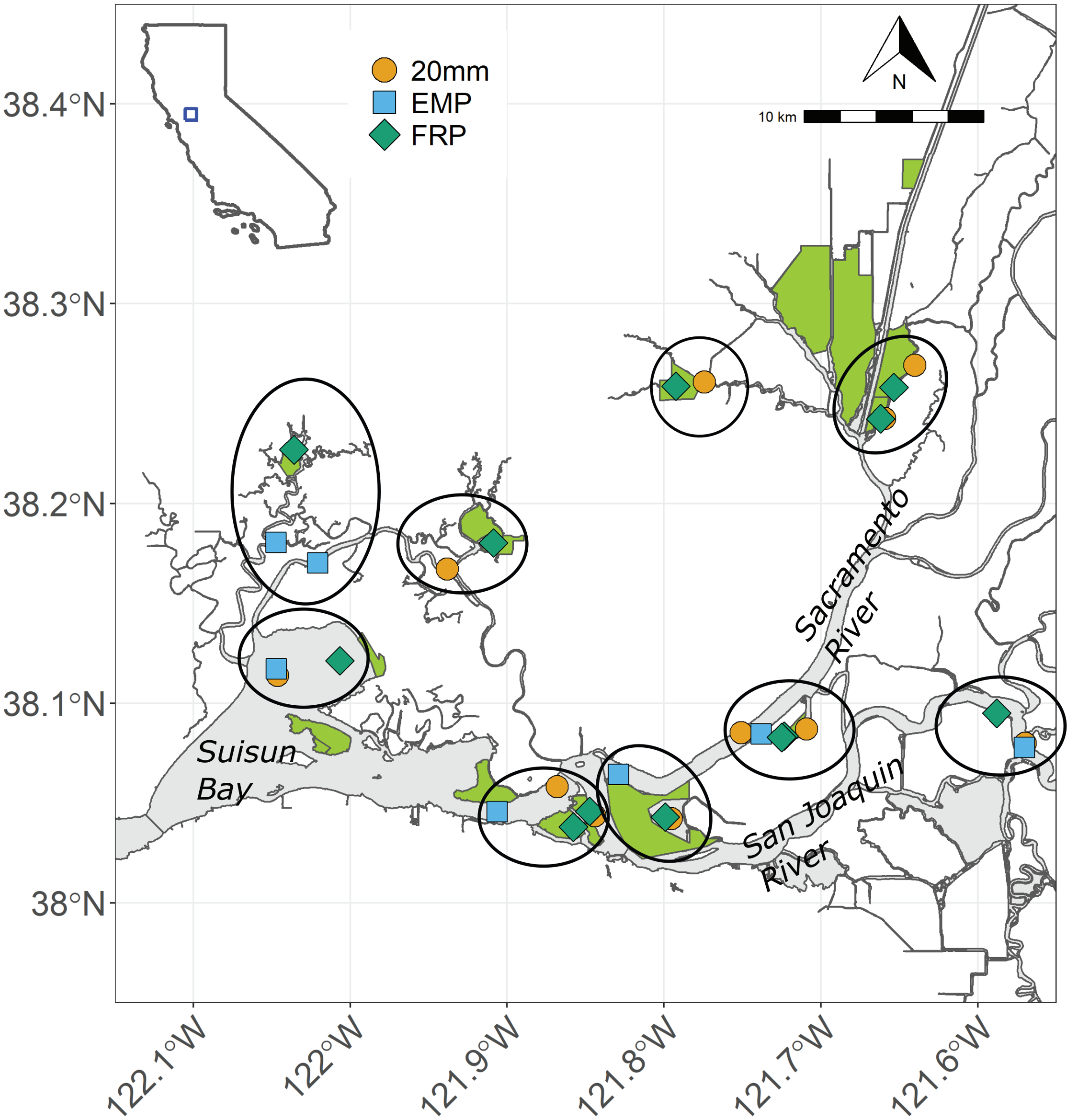

Figure 1 Map of study area with sampling sites marked. *Circles* indicate sampling sites, which each include two or more stations that were paired for analysis. *Green areas* indicate future FRP wetland restoration sites or existing wetland areas used for reference sites.

and benthic invertebrates in the upper estuary throughout the year. Zooplankton are collected using a steel sled with paired mesozooplankton (0.16-mm mesh net, 73 cm long, with a 12-cm-diameter net mouth) and macrozooplankton nets. The net is towed obliquely through the water column for 10 minutes. See Barros (2021b) for a full study description.

20-mm Survey

The 20-mm Survey monitors Delta Smelt distribution throughout their historical spring range in the Sacramento–San Joaquin Delta and San Francisco Estuary during the spring (Damon and Chorazyczewski 2021). The 20-mm Survey targets Delta Smelt in the post-larval and juvenile life stage at lengths >20 mm. Zooplankton is collected with a 0.16-mm-mesh modified Clarke-Bumpus net, 73 cm long with a mouth diameter of

Table 1 Sampling locations for each survey used in this analysis and years where data was collected. Sites are stations that were closed together and used as random effects in models. Distance is the distance from the Golden Gate Bridge measured by shortest water distance. Latitude and Longitude are WGS 84.

Site	Distance (KM)	Survey	Habitat	Depth (m)	Salinity (PSU)	Station	Longitude	Latitude	Years
Grizzly Bay	61	20mm	Deep	1.6	2.33	602	–122.0462	38.1140	All
Grizzly Bay	61	EMP	Deep	1.2	2.03	NZ028	–122.0472	38.1172	All
Grizzly Bay	61	FRP	Shallow	1.1	2.11	602 FRP	–122.0067	38.1213	All
Browns Island	70	20mm	Deep	15.2	0.57	513	–121.8680	38.0583	All
Browns Island	70	EMP	Deep	6.6	0.68	NZ054	–121.9064	38.0458	All
Browns Island	70	FRP	Shallow	1.6	0.60	Browns Channel	–121.8578	38.0381	All
Winter Island	73	20mm	Deep	7.6	0.34	801	–121.844	38.0437	All
Winter Island	73	EMP	Deep	6.2	0.19	NZ060	–121.8289	38.0644	All
Winter Island	73	FRP	Shallow	1.2	0.20	Winter	–121.8475	38.0459	All
Wings Landing	74	EMP	Deep	2.7	1.01	NZS42	–122.0472	38.1805	2018, 2019
Wings Landing	74	FRP	Shallow	1.9	0.90	Wings 1	–122.0359	38.2269	2018, 2019
Little Honker Bay	76	20mm	Deep	1.2	0.95	609	–121.9380	38.1672	All
Little Honker Bay	76	EMP	Deep	4.6	1.05	NZ032	–122.0208	38.1703	All
Little Honker Bay	76	FRP	Shallow	1.1	1.10	Blacklock	–121.9088	38.1803	All
Sherman Lake	77	20mm	Deep	2.2	0.15	703	–121.79522	38.0422	2017
Sherman Lake	77	FRP	Shallow	1.9	0.17	Sherman	–121.79921	38.0431	2017
Horseshoe Bend	84	20mm	Deep	5.1	0.09	705	–121.70917	38.0871	All
Horseshoe Bend	84	20mm	Deep	9.1	0.12	706	–121.75069	38.0852	All
Horseshoe Bend	84	EMP	Deep	5.17	0.07	NZ064	–121.7381	38.0847	All
Horseshoe Bend	84	FRP	Shallow	1.1	0.06	Decker Breach	–121.7234	38.0836	All
Horseshoe Bend	84	FRP	Shallow	1.2	0.07	North Decker	–121.7251	38.0829	All
Webb Tract	100	20mm	Deep	2.8	0.10	815	–121.5698	38.0800	All
Webb Tract	100	EMP	Deep	6.6	0.11	NZ086	–121.5703	38.0778	All
Webb Tract	100	FRP	Shallow	1.8	0.10	Webb	–121.5879	38.0950	All
Prospect Island	102	20mm	Deep	9.0	0.08	726	–121.6400	38.2691	All
Prospect Island	102	20mm	Deep	5.5	0.08	724	–121.6594	38.2425	All
Prospect Island	102	FRP	Shallow	2.9	0.08	Prospect Breach	–121.6619	38.2424	All
Prospect Island	102	FRP	Shallow	2.8	0.09	Miner Side Channel	–121.6535	38.2581	All
Lindsey Slough	110	20mm	Deep	3.2	0.21	720	–121.7742	38.2607	2017
Lindsey Slough	110	FRP	Shallow	1.9	0.22	Lindsey Breach	–121.7925	38.2587	2017

12 cm, mounted on top of a larger fish-sampling net with its own flowmeter. The survey samples at 47 stations throughout the estuary and completes three 10-minute tows at each station. Zooplankton are sampled during one of these tows, typically the first (Damon and Chorazyczewski 2021).

Fish Restoration Program

FRP gear and methods were designed to be readily comparable to the EMP and 20-mm methods. FRP mesozooplankton samples are collected with 0.15-mm mesh net, 68 cm long, with a mouth diameter of 15 cm. The primary difference between gear methodologies is that the FRP tows immediately beneath the surface of the water for 5 minutes instead of 10 minutes, to reduce the potential for take of listed fishes. While using a surface tow instead of an oblique tow may introduce an additional source of variation, oblique tows were logistically infeasible in shallow wetland habitats, and previous studies found relatively little difference between surface and bottom tows in the estuary (Hartman 2019; Schultz 2019). Where tidal channels or marsh habitat were too small to conduct a full 5-minute tow, the tow time was reduced. In some cases, the gear was held in the mouth of a tidal channel to sample water flowing out of the channel on an ebb tide, instead of being towed.

Sampling Design

To compare deep-channel samples collected for the EMP survey and the 20-mm survey to the shallow samples collected by the FRP, FRP staff selected ten shallow sites (mean depth 1.8 m) that were inside or adjacent to future tidal wetland restoration sites or existing tidal wetlands (Figure 1, Table 1). All these sites had either an EMP station (mean depth 4.7 m), a 20-mm station (mean depth 5.7 m) or both in close proximity (average water distance between paired sites was 1.77 km, maximum was 6.7 km, minimum was 0.3 km). The furthest sites were in Suisun Marsh, and they were far enough to have little tidal exchange between them. The distance between sites could have been the source of additional error in our sampling framework; however, we were limited by the existing sampling network, which does not have extensive coverage in Suisun Marsh. The FRP sampled monthly from March through June in 2017, 2018, and 2019 as close in time as possible (within 5 days) to the longer-term (EMP and 20-mm) surveys. FRP sampling in 2017 occurred within hours of the other two surveys, but early data analysis showed community composition to be very similar, so the time-frame was relaxed.

Laboratory Methods

For a full description of laboratory methods used by each survey, see Kayfetz et al. (2020). In brief: zooplankton samples were preserved in 10% formalin (EMP and 20-mm) or 70% ethanol (FRP), dyed with rose Bengal, and brought back to the laboratory for enumeration and identification. Samples were rinsed of chemicals using a 0.15-mm sieve under low-pressure tap water. Organisms were then transferred into a beaker and diluted with tap water to a target concentration of 200 to 400 organisms per milliliter. A mechanical pipette was used to stir the diluted sample until organisms were evenly suspended. One-milliliter aliquots were drawn and placed onto a Sedgewick Rafter slide. All zooplankton were then identified to the lowest taxonomic group possible using a compound microscope. Some taxa were identified to species, others to genus or family, depending on their role in fish diets and the difficulty of identification. A minimum of five aliquots and a maximum of 20 aliquots were analyzed, so that 6% of the sample—or 600 to 4,000—individual organisms were identified. Taxonomic level of identification differed somewhat among the three surveys, but levels were standardized in the data analysis process.

Data Analysis

We calculated catch-per-unit effort (CPUE) for each taxon in each sample using the formula:

$$CPUE = \left(\frac{n * v}{s}\right)/V$$

where:

V = volume of water sampled as calculated by flowmeter
n = number of organisms counted in sub-sample
v = volume of sample when processed
s = sub-sample percentage

Data were combined using methods described in Bashevkin et al. (2020). In brief, taxa that were not consistently counted by all three surveys (e.g., insect larvae) were removed, taxa that were not quantitatively sampled by 0.15-mm mesh were removed (e.g., rotifers and copepod nauplii), and taxonomic resolution was standardized between surveys. The combined data set only included samples from the selected stations with at least one paired shallow (FRP) and one deep (EMP or 20-mm) sample per month. These paired stations were grouped into 'sites' as shown in Figure 1. All data manipulations and analyses were performed using R version 4.1.1 (R Core Team 2021).

To create a variable that signified the position of each site along the salinity gradient of the estuary, we calculated the centroid of all stations within a site and calculated the in-water distance from the center of the site to the Golden Gate Bridge using the ‘GGDist’ function in the ‘spacetools’ R package (Bashevkin 2022).

To test for differences in zooplankton density between shallow and deep water, as well as characterize trends over space and time, we used model selection using Akaike’s information criterion corrected for small sample sizes (AICc) to evaluate the following predictor variables that were chosen *a priori* as potentially important drivers of zooplankton abundance:

- Habitat (shallow vs. deep)
- Survey (EMP vs. 20-mm vs. FRP)
- Month (as a continuous variable, to test for changes over the course of the season)
- Year (as a factor)
- Distance from the Golden Gate Bridge (as a proxy for position along the salinity gradient)
- The interaction of habitat and month
- The interaction of habitat and year

We regressed all combinations of these predictor variables against the log-transformed total zooplankton CPUE using the ‘dredge’ function from the MuMIn package in R (Barton 2018). Sampling site (with paired deep and shallow samples) was included as a random effect in all models. When sites contained multiple shallow or deep samples, all samples were included. We ranked these models using AICc to choose a final explanatory model and tested the significance of each term included in the top model using the ‘lme4’ and ‘lmerTest’ packages in R (Bates et al. 2022). For factorial variables with more than two levels, we computed estimated marginal means of all pairwise comparisons using the package ‘emmeans’ (Lenth et al. 2021).

Testing for an effect of shallow vs. deep habitat addresses our primary research question (differences in zooplankton abundance), testing for an effect of survey addresses potential differences in sampling methodology, testing for an effect of month and year addresses our question of temporal patterns, and testing for an effect of distance to the Golden Gate Bridge addresses our question of spatial patterns. Inclusion in the top-ranked model provides support for a factor being important in driving zooplankton density.

To evaluate differences in community composition, we calculated the relative abundance of each taxon in each sample by dividing CPUE for each taxon by the total CPUE in each sample. This allowed us to see whether there were differences in which taxa are present while controlling for the total CPUE within the sample. We then performed a permutational multivariate analysis of variance (PERMANOVA) using the ‘adonis’ function from the ‘vegan’ package in R (Oksanen et al. 2020). We modeled the relative abundance matrix using habitat, month (as a continuous variable), distance to the Golden Gate Bridge, and year (as a factor) as predictor variables while blocking by Site with 999 free permutations.

For a better understanding of how individual species within the community change with the predictor variables, we used Hierarchical Modelling of Species Communities (HMSC), a joint species distribution modeling framework developed by Ovaskainen and Abrego (2020). We fitted a lognormal Poisson model with the R-package HMSC (Tikhonov et al. 2020) on relative abundance of taxa within each sample (as calculated for the PERMANOVA analysis) with Month (as a continuous variable), Habitat, Distance to the Golden Gate Bridge, and Year (as a factor) as predictor variables, blocking by Site, and assuming the default (uninformative) prior distributions. We sampled the posterior

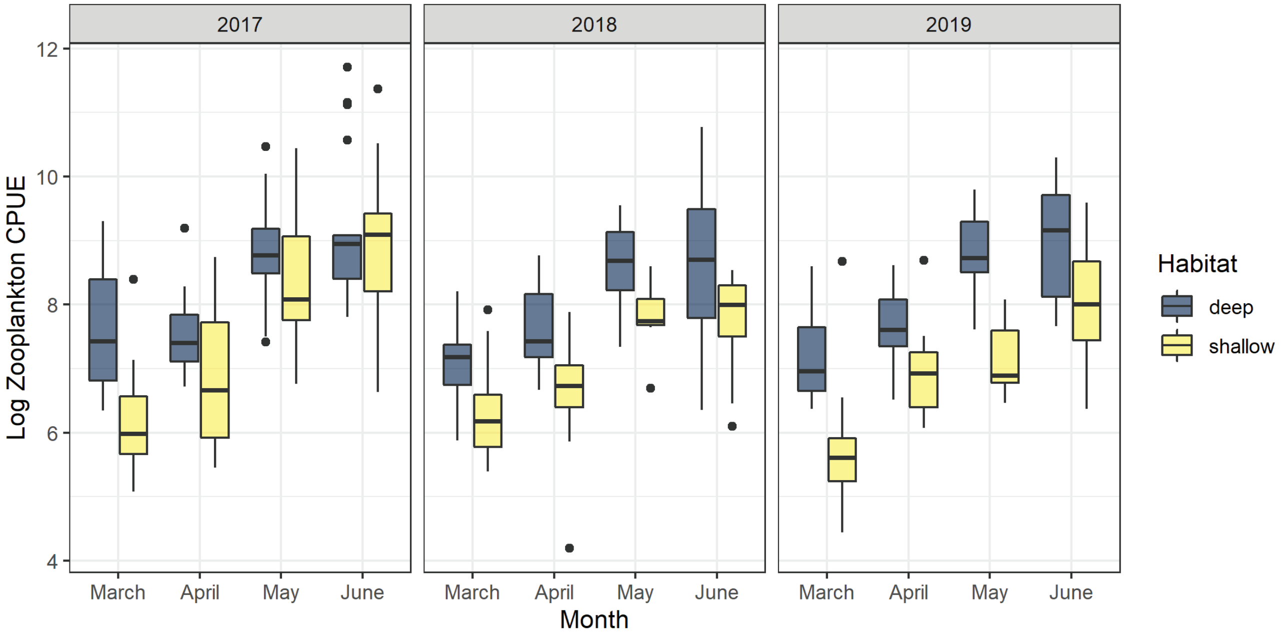

Figure 2 Total zooplankton CPUE by month, year, and habitat (shallow samples collected by FRP, deep samples by EMP and 20-mm surveys)

distribution with two Markov Chain Monte Carlo (MCMC) chains, each of which was run for 501,000 iterations, of which the first 1,000 were removed as burn-in. The chains were thinned by 100 to yield 5,000 posterior samples per chain, and so 10,000 posterior samples in total. We examined MCMC convergence by examining the potential scale reduction factors of the model parameters (Gelman and Rubin 1992).

We examined the responses to the predictor variables by plotting which species showed a positive or negative association with each predictor with at least a 95% posterior probability. To compute explanatory power, we made model predictions based on models fitted to all data and computed the pseudo-R^2 as the squared Spearman correlation between observed and predicted values, multiplied by the sign of the correlation (Tikhonov et al. 2020). We then graphed the pseudo-R^2 for each species and predictor variable to visualize which predictor variables had the strongest relationships with which species.

RESULTS

Plots of total zooplankton CPUE show differences between shallow and deep habitats, though these are not consistent for all time-periods (Figure 2). Shallow habitats (collected by the FRP), usually have lower CPUE than deep habitat (collected by the 20-mm or EMP surveys), but the differences are lower in June than earlier in the season (Figure 2).

When all possible models of total zooplankton CPUE were assessed with AICc, the top- ranked model included Habitat (shallow versus deep), Month (as a continuous variable) and Year (as a factor). All interaction terms and the term for Distance from the mouth of the estuary were not supported (Table 2). The top-ranked model showed a statistically significant increase in zooplankton CPUE by Month (March through June, $p < 0.0001$, Table 3, Figure 2). Samples collected in shallow habitats had significantly lower CPUE than deep habitats ($p < 0.0001$, Table 3, Figure 2). The estimated marginal means for Year found that 2017 had significantly higher CPUE than 2018 ($p = 0.0032$, Table 4). 2017 had slightly higher CPUE than 2019 with marginal significance ($p = 0.053$, Table 4). There was no

Table 2 Top twelve models of total CPUE ranked by AICc, with degrees of freedom (df), log likelihood, AIC, Change in AIC, and relative weight of each model

Rank	Model	df	logLikelihood	AICc	deltaAICc	weight
1	Month + Habitat + Year	7	−436.531	887.4	0	0.528
2	Month + Habitat	5	−439.661	889.5	2.1	0.185
3	Month + Habitat + Year + Month*Habitat	8	−437.02	890.5	3.08	0.113
4	Month + Habitat + Year + Year*Habitat	9	−436.224	891	3.6	0.087
5	Month + Habitat + Month*Habitat	6	−439.838	891.9	4.53	0.055
6	Month + Habitat + Year+ Year*Habitat + Month*Habitat	10	−436.817	894.3	6.91	0.017
7	Month + Habitat + Year + Distance	8	−439.672	895.8	8.38	0.008
8	Month + Habitat + Distance	6	−442.679	897.6	10.21	0.003
9	Month + Habitat + Year + Distance + Month*Habitat	9	−440.178	898.9	11.51	0.002
10	Month + Habitat + Year + Distance + Year*Habitat	10	−439.367	899.4	12.01	0.001
11	Month + Habitat + Distance + Habitat*Month	7	−442.882	900.1	12.7	0.001
12	Month + Habitat + Year + Distance + Habitat*Month + Habitat*Year	11	−439.975	902.8	15.36	0

Table 3 Fixed effects for top-ranked model of log-transformed total zooplankton CPUE, with standard errors, estimated degrees of freedom, *t*-value, *p*-value, and 95% confidence intervals. Formula: log(CPUE) ~ Habitat + Month + Error(Site). 333 observations grouped into 10 sites. Variance of site (random effect): 0.3325 (SD = 0.5766). Residual variance 1.018 (SD = 1.009).

Effect	Estimate	Std. Error	df	t value	P value	Lower CI	Upper CI
Intercept: Deep, 2017	5.418	0.236	119.278	22.965	< 0.0001	4.959	5.874
Month	0.660	0.043	317.379	15.424	< 0.0001	0.577	0.744
Shallow	−0.875	0.099	318.731	−8.842	< 0.0001	−1.069	−0.682
2018	−0.382	0.116	327.284	−3.295	0.00109	−0.607	−0.154
2019	−0.280	0.120	327.904	−2.341	0.01985	−0.514	−0.472

Table 4 Results of estimated marginal means of each pairwise comparison of years included in the model of total zooplankton CPUE (Table 3)

Contrast	Ratio	Std. Error	df	*t* ratio	*P* value
2017/2018	1.465	0.170	327	3.284	0.0032
2017/2019	1.323	0.159	328	2.331	0.0530
2018/2019	0.903	0.108	321	−0.855	0.6690

significant difference between 2018 and 2019 ($p = 0.669$, Table 4).

When examining a stacked bar plot of community composition, the clearest trend is an increase in *Pseudodiaptomus* spp. in later months (Figure 3). There were more *Eurytemora* spp. in 2018 and 2019 than in 2017, and more *Daphnia* spp. and *Bosmina* spp. in 2017. There are some differences between shallow and deep habitats in certain months (such as proportionally more *Bosmina* in shallow water in June of 2017), but these differences are not as large as the differences between months. The PERMANOVA results reinforced these observations, showing significantly different communities by Habitat, Month, Distance, and Year (Table 5). Of the predictor variables included in the PERMANOVA, Month had the greatest effect on community composition ($R^2 = 0.26$), followed by Year ($R^2 = 0.07$), followed by Distance ($R^2 = 0.05$), followed by Habitat ($R^2 = 0.02$).

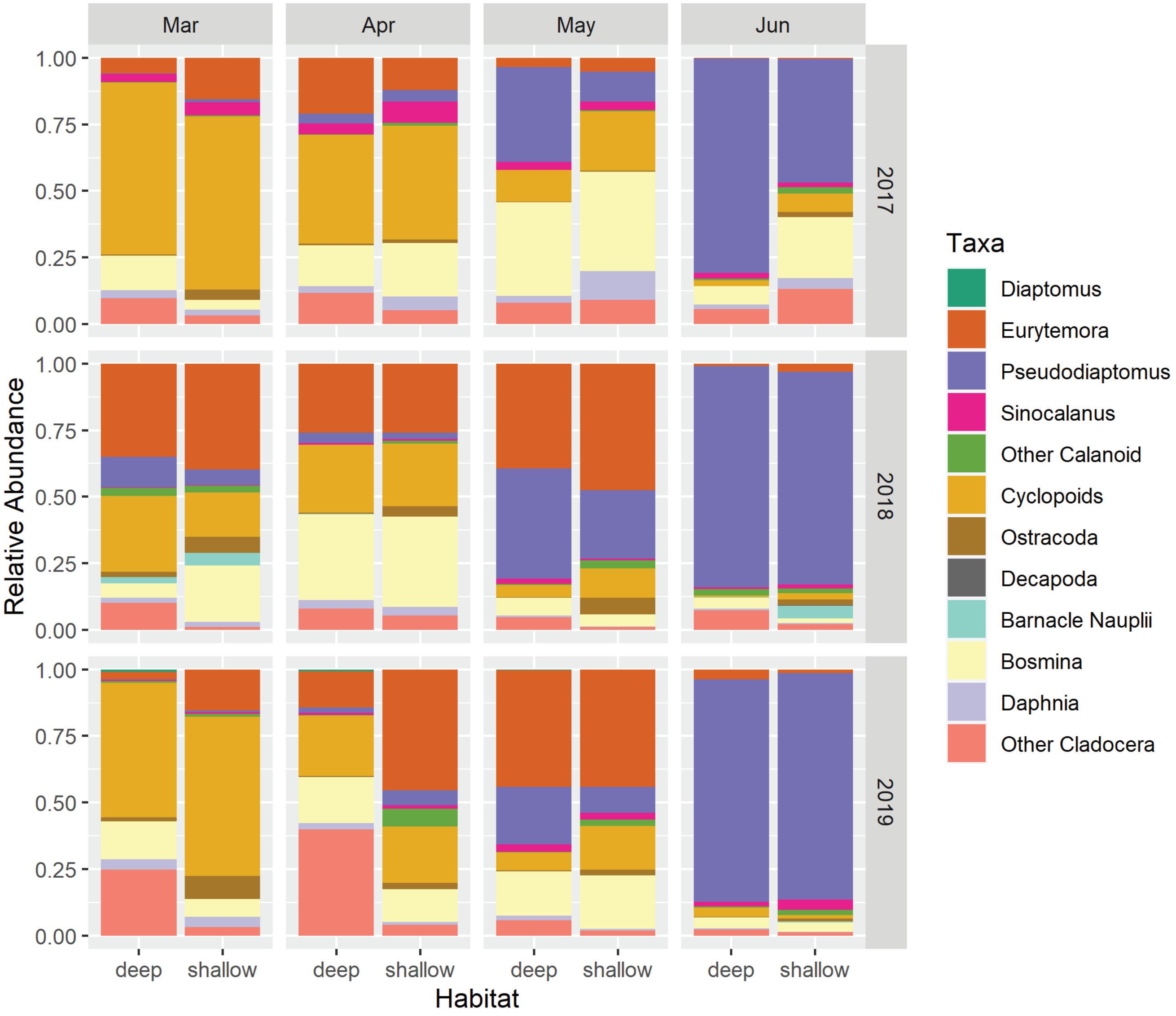

Figure 3 Stacked bar plot showing average community composition by month, year, and habitat. Juveniles and adults were combined for ease of plotting. Copepods in the rare genera *Acartia, Acartiella,* and *Tortanus* were combined in the 'other calanoid' group, and the rare *cladoceran Diaphanosoma* was combined with 'other cladocera' for ease of plotting.

Table 5 Results of PERMANOVA on community matrix vs. habitat (shallow vs. deep), month of the year (as a continuous variable), Year (as a factor), and Distance from the Golden Gate Bridge with degrees of freedom (df), sum of squares, mean squares, f-value, and *p*-value for each predictor

Predictor	df	Sums of Sqs	MeanSqs	*F*-value	R^2	*p*-value
Habitat	1	1.549	1.549	11.166	0.021	0.001
Month	1	19.700	19.700	142.035	0.261	0.001
Year	2	5.307	2.653	19.130	0.070	0.001
Distance	1	3.598	3.589	25.878	0.048	0.001
Residuals	327	45.354	0.139		0.601	
Total	332	75.499			1	

Figure 4 Joint Species Distribution Model matrix showing the relationships of each taxa with predictor variables. The intercept (*left-most*) column shows which species have higher relative abundance when compared with the other species at the intercept for the continuous variables (Month and Distance) and the baseline values (2017, Deep) for the discrete variables. The other columns show the direction of the effect of each predictor variable on the relative abundance of each species. *Red* indicates a positive relationship with a predictor variable; *blue* indicates a negative relationship.

The Hierarchical Modeling of Species Communities (HMSC) model demonstrates which species drive the observed differences in community composition (Figure 4). The potential scale-reduction factors for the β-parameters of the MCMC convergence on the HMSC model (that measure the responses of the species to environmental covariates; Ovaskainen et al. 2017) were on average 1.20 (maximum 3.60). Only 13 taxa had significantly different relative abundance between Habitats, whereas over 20 taxa had significantly different relative abundance between months and years. An additional 19 taxa had different relative abundance at different distances along the estuary. The model had a mean pseudo-R^2 of 0.30, though there was considerable range in R^2 by species, with the best fit being for juvenile *Pseudodiaptomus* spp. ($R^2 = 0.62$), cyclopoid juveniles (0.592), other cladocera ($R^2 = 0.51$), adult

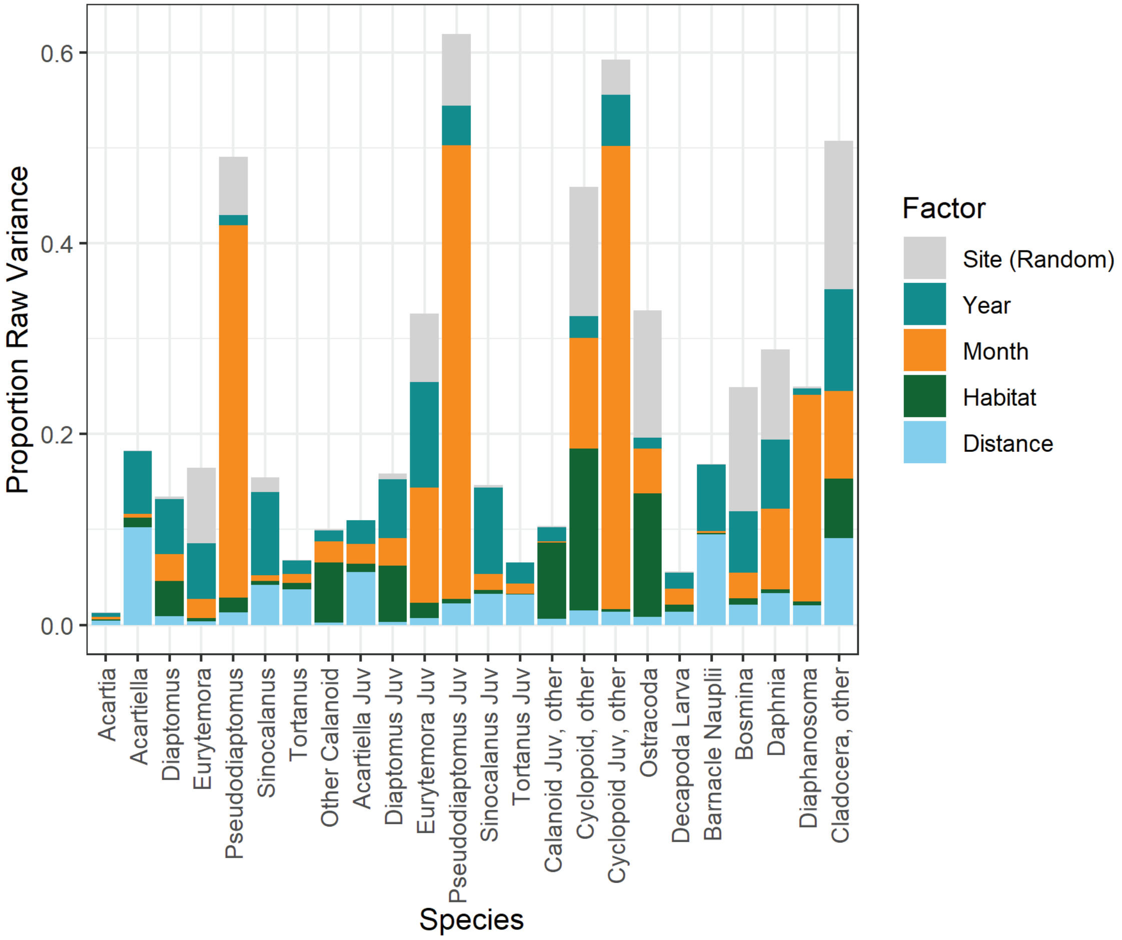

Figure 5 Proportion of variance explained by each of the explanatory factors included in the HMSC model as calculated by pseudo-R^2 of the Joint Species Distribution Model

Pseudodiaptomus spp. ($R^2 = 0.49$), and cyclopoid adults. Of the species with the highest R^2, Month explained the greatest proportion of the variance for *Pseudodiaptomus* (juveniles and adults) and cyclopoid juveniles. Habitat explained the greatest proportion of the variance for cyclopoid adults and Distance explained the greatest proportion of the variance for cladocerans (Figure 5).

DISCUSSION

We found multiple differences between zooplankton communities across seasons, years, regions of the estuary, and habitat types. However, seasonal changes in both community composition and CPUE were the strongest and most consistent patterns. Shallow-water habitats, including habitats adjacent to existing and future tidal wetlands, had slightly lower total CPUE of zooplankton, indicating productivity from tidal wetlands may be channeled through other chains in the food web (such as the epiphytic community), but trophic interactions, differences in sampling efficiency, sample collection, and sample processing may also be involved. Notably, this study examined only zooplankton CPUE and community composition and did not account for rates of zooplankton productivity or other processes.

Seasonal Changes

Seasonal differences in both community composition and CPUE were the strongest patterns we observed, and the patterns were similar in shallow and deep habitats. Total CPUE increased over the course of the spring, potentially related to increases in temperature (Figure 2). The increased density is likely caused by increased phytoplankton availability, faster growth rates, and a shorter time to maturity and reproduction (Kimmerer, Ignoffo, Bemowski, et al. 2018; Gearty et al. 2021). Higher CPUE in June may also be from decreased outflow, which decreases transport of zooplankton out of the region (Kimmerer et al. 2014). High zooplankton abundance in June has been well described in this estuary and other estuaries across the globe (Grimaldo et al. 2004; Murrell and Lores 2004; Primo et al. 2009; Merz et al. 2016). The lack of support for a habitat × month interaction term in our study showed that the same pattern was equally apparent in both deep and shallow habitats.

The changes we observed in community composition over the course of the spring are well established in the literature of the estuary. The largest change in our study was the increase in both relative abundance and CPUE of the non-native copepod, *Pseudodiaptomus forbesi*, which is known to peak in the summer (Merz et al. 2016), and has become the most abundant calanoid copepod in much of the freshwater and low-salinity habitat in the Delta (Winder and Jassby 2011), and in the diet of many pelagic fishes (Slater and Baxter 2014; Sullivan et al. 2016 Jungbluth et al. 2021). Later months also saw an increase in relative abundance of the copepods *Tortanus* spp. and *Acartia* spp. *(*Figure 4*).* which may be a result of increased salinity intrusion as outflow decreases in May and June, since both taxa tend to be found at higher salinities (Lance 1963; Ohtsuka and Reid 1998; Ambler et al. 1985; Barros 2021a). This is also supported by increased abundance of these taxa closer to the Golden Gate Bridge (Figure 4). In contrast, the copepod *Eurytemora* spp. and the freshwater cladocerans—*Bosmina* spp. and *Daphnia* spp.—peaked earlier in the year and were found further from the Golden Gate Bridge (Figures 3 and 4).

Interannual Differences

We saw significant interannual differences in abundance and community composition. Because of California's Mediterranean climate, large swings in temperature and precipitation between years are common (Dettinger 2011), and these swings may have driven the changes to zooplankton abundance and community composition we observed. Specifically, 2017 was an extreme wet year, with the highest precipitation on record for California, and a Sacramento Valley Hydrologic Classification Index (an index of unimpaired runoff) of 14.9. The year 2018 was classified as "below-normal," with an index of 7.6, while 2019 was "wet," with an index of 10.6 (CDWR 2021). Previous research found that *Eurytemora* spp. and *Acartia* spp. increase in abundance with increased flow during the spring (Kimmerer 2002), and while *Pseudodiaptomus* spp. abundance does not vary with flow in fresh water, it increases with flow in low-salinity water (Kimmerer, Ignoffo, Kayfetz, et al. 2018), such as our western-most sites, which reached 2 psu during our study (Table 1), but can reach 10 to 15 psu later in the year (data not shown). The increase in these major groups of copepods likely drove the high total CPUE in 2017 and 2019, with a reduction in the below-normal year of 2018 (Figure 2). Our study looked at only 3 years of data, so the effect of water year type on zooplankton cannot be assessed statistically; however, other research conducted during 2017 saw similar overall increases in zooplankton abundance in the upper estuary that could be more conclusively tied to high flows (FLOAT-MAST 2021).

When assessing the relative abundance of each taxon, we found that 2017 had more of the cladocerans *Bosmina* spp. and *Daphnia* spp., cyclopoids, and the calanoid copepod *Sinocalanus* spp. than the following years. This is notable because these taxa have not been associated with high flows in the past, though the relative increase in these taxa may have been the result of decreased abundance of other taxa. The increase in the relative abundance of barnacle nauplii, *Tortanus* spp., and *Acartia* spp. in 2018 may have been the result of lower flows causing higher salinity to enter the western portion of our sampling sites and allowing these salt-tolerant taxa to thrive. *Pseudodiaptomus* spp. and *Eurytemora* spp. made up a larger proportion of the community in 2018 than 2017, which is somewhat unexpected because they have been shown to increase in absolute abundance (as opposed to relative abundance) during high flows (Kimmerer 2002; Kimmerer, Ignoffo, Kayfetz, et al. 2018). It may be that other taxa, such as cladocerans mentioned above, increased to an even greater degree in 2017.

Habitat Differences

We observed a lower abundance of zooplankton in shallow water. This runs counter to our hypothesis that zooplankton would be higher in shallow water, and counter to the conceptual model which suggests that restoring shallow tidal wetlands will provide an increased supply of food for at-risk fishes. Some previous studies of zooplankton in shallow water vs. deep water in the estuary did not find significant differences in abundance (Grimaldo et al. 2004; Kimmerer and Slaughter 2016). However, this is not consistent across all studies, because a recent study of zooplankton in Liberty Island found lower zooplankton catch within the wetlands (Steinhart et al. 2021).

Our results did not support our expectation that shallow habitats would provide increased zooplankton resources; however, this study looked only at zooplankton standing stock at a point in time, not total production rates or export. A recent synthesis of copepod growth and reproduction studies found that tidal wetlands in the Delta had some of the highest egg production rates and copepodite growth rates in the estuary (Gearty et al. 2021). Therefore, lower abundance in shallow water may be a result of transport dynamics, higher predation pressure, or other biotic interactions. Furthermore, most of the FRP sites had not been restored yet at the time of this study, and zooplankton biomass may increase with further wetland development. We did not have an adequate range of sites in various stages of development to explicitly include this in our model, so instead chose to focus on differences between shallow and deep habitats in general, rather than wetland restoration stages. Invertebrate communities in restored wetlands in other systems may take years—if not decades—to match reference wetlands (Fleeger et al. 2020), and restoration age may significantly affect food web structure in many systems (Wozniak et al. 2006; Howe and Simenstad 2015). When more of the FRP sites have been restored, allowing for a gradient of wetland age, this should be explored in more detail.

Our sampling sites were chosen based on existing sampling sites for EMP and 20-mm, and future tidal wetland restoration sites for FRP. While most of these sites were relatively close (less than 2 km, and within a tidal excursion of each other), some were further apart, with the maximum distance being over 7 kilometers. Comparing these sites may not be a true test of “deep” versus “shallow” habitat, because they may be far enough apart to have other changes in water quality, substrate, or hydrodynamics that dominate the observed patterns.

Tidal dynamics may be transporting zooplankton out of wetlands disproportionately, leading to lower abundance in the FRP’s samples. Calculating total zooplankton flux into and out of a tidal wetland is labor-intensive, so there have been few studies in the estuary. However, a study of zooplankton from Liberty Island (Lehman et al. 2010) found seasonal differences in zooplankton flux with net export during the spring (when our study occurred). Other studies have found variable results, with wetlands switching between sources and sinks at various times (Dean et al. 2005), or found data to be extremely noisy (Kimmerer, Ignoffo, Bemowski, et al. 2018). More intensive sampling is necessary to identify this as the mechanism behind our results.

Predation on zooplankton may be higher in shallow areas. Larval fishes have been found to be much more abundant in marsh-edge habitat in the estuary (Grimaldo et al. 2004), and most larval fish prey chiefly on zooplankton (Nobriga 2002; Sullivan et al. 2016; Jungbluth et al. 2021). The highly abundant, invasive Mississippi Silverside

(*Menidia beryllina*) are also more prevalent in shallow areas and wetlands than in deeper habitats, and they primarily eat copepods (Cohen and Bollens 2008). Delta Smelt that forage in regions with higher tidal wetland coverage tend to have fuller stomachs even when zooplankton tows show relatively low abundance of food (Hammock et al. 2019), so standing stock of biomass may not be the most appropriate measure of food resources.

Wetlands also have a greater abundance of non-zooplankton invertebrates, particularly epiphytic and epibenthic amphipods, drift invertebrates, and insects (all utilized for fish food), which may be competing with zooplankton for increased wetland production (Young et al. 2018; Hartman et al. 2019). Stable isotope analysis of amphipods and chironomids in shallow wetland habitat of the Delta shows a higher carbon contribution from submerged and emergent vegetation than copepods collected in the same habitat (Young et al. 2021). Because much of the increased production in wetlands is conveyed through emergent vegetation rather than phytoplankton, direct benefits of tidal wetlands may be found chiefly in the contribution of epiphytic invertebrates, rather than zooplankton.

We found that ostracods, *Eurytemora* spp. copepods, and other (rare/unidentified) calanoid copepods were somewhat more abundant in shallow water, with cyclopoids, *Diaptomus* spp., *Pseudodiaptomus* spp., and other (rare/unidentified) cladocerans somewhat less abundant (Figure 4); however, habitat explained less than 20% of the variance in any of these taxa (often much less than 20%; Figure 5), so it is not a strong correlation. *Eurytemora* spp. were found to be more abundant in wetlands than open-water habitat in one previous study of zooplankton in tidal wetlands (Grimaldo et al. 2004), but Grimaldo et al. did not find any significant difference in *Pseudodiaptomus* spp. or *Diaptomus* spp. and found cladocerans to be more abundant in the channel habitat. It is evident that more research on the differences between shallow- and deep-water zooplankton is needed before conclusions can be drawn. It is also evident that we cannot draw conclusions about one habitat by sampling in adjacent habitats.

We should also note that the zooplankton captured in our nets are only an approximation of the zooplankton community. Individual taxa may or may not interact, and those interactions may be part of what drove the patterns we saw in this paper (as seen by Kayfetz and Kimmerer [2017]). Future studies should look more closely at patterns of individual taxa and known inter-specific interactions. This paper took a coarse look at the zooplankton assemblage and relative percent abundance of zooplankton, but more detailed, species-specific models will be needed to fully understand their dynamics.

Sampling Differences

Most previous studies that compared zooplankton communities across habitats collected deep and shallow samples using the same boats and same personnel for all habitat types (Grimaldo et al. 2004; Bollens et al. 2014; Kimmerer and Slaughter 2016). While the FRP, 20-mm, and EMP surveys used very similar gear, small differences in deployment, processing, and analysis could contribute to the differences we observed. Each program used a different housing set-up for deploying the zooplankton net. The survey boats were different sizes, and were operated at different speeds, leading to differences in average volume per sample and potential differences in bow wakes that could alter net avoidance and sampling efficiency (Harris et al. 2000).

Even when the same gear is used in the same manner, sampling efficiency may change with water depth. Many zooplankton taxa migrate vertically to the surface at night and return to deep water or move to the bottom during the day (Dodson 1990; Kimmerer et al. 2002). The FRP conducted a pilot study before beginning this sampling program and found similar abundances in surface trawls and deep trawls (Hartman 2019), but further investigation may be warranted. If the water is shallow, zooplankters may migrate all the way to the sediment where they are out of the reach of the gear, and the highly abundant *Pseudodiaptomus* spp. has been found in highest abundance in the benthic sediment during the daytime (Yelton et al. 2022). If the water is deeper, they may only migrate to a darker part of the water column where they are still available to an oblique trawl. However, it is worth noting that the 20-mm zooplankton net is affixed to the top of the 1.39-m-diameter fish net, and the EMP sampling procedure does not generally allow the sled to hit the bottom at the beginning of the tow to avoid getting mud in the net. Thus, neither survey encompasses the entire water column.

Tidal dynamics may also affect the observed patterns. The EMP program always samples at high slack tide, whereas the 20-mm and FRP sample at varying tide stages, though generally close to high slack or early ebb tide (Kayfetz et al. 2020). Some zooplankton have vertical migration based on the stage of the tide, so differences in time of tide may cause different catch (Kimmerer et al. 2002). In some shallow lakes, horizontal diel migration has also been observed in zooplankton (Burks et al. 2002), where some taxa migrate to deeper water during the day and then re-colonize littoral areas at night. In the estuary, this has been observed in larval fishes (Bennett et al. 2002), but to date not been examined in invertebrate zooplankton.

Differences in preservative may cause further biases in community composition between surveys. The FRP preserves samples in ethanol, and the other surveys preserve in formalin. Ethanol is a somewhat less effective fixative (Harris et al. 2000), potentially contributing to the higher abundance of “Other Cyclopoids” and “Other Calanoids” in FRP samples. These groups comprised either rare species, or individuals that could not be identified to species because they were damaged. Alternatively, it may be that certain taxa considered “rare” in channel samples—so not identified to species—are more common in shallow habitat.

Management Implications

The drivers of zooplankton abundance and distribution can be used to help inform management actions aimed at increasing food supply for at-risk fishes, such as location and design of restoration sites or managed flow actions. For example, the high abundance of zooplankton (calanoid copepods in particular) in June provides an excellent source of food for fishes that rear in the fresh and low-salinity zone of the estuary, including Longfin Smelt and Delta Smelt (Slater and Baxter 2014; Grimaldo et al. 2020; Jungbluth et al. 2021). However, the summer peak in zooplankton biomass is after most juvenile salmonids (another species of management concern) have migrated out of the region and entered the ocean (Munsch et al. 2019). Therefore, juvenile salmonids may rely more heavily on macroinvertebrates such as amphipods and insects that are common in wetlands. Diet studies of juvenile salmonids in estuaries have found high percentages of insects, amphipods, and oligochaete worms, particularly when rearing on floodplains and tidal wetlands (David et al. 2016; Goertler et al. 2018), so zooplankton are not their only source of prey. Even traditionally planktivorous fishes, such as Delta Smelt, when collected near extensive tidal wetland habitat, are found eating insects and amphipods more frequently (Whitley and Bollens 2014). This may be observed more often, as more wetland restorations in the Delta are completed.

The interannual differences in both community composition and abundance indicate that any management action will need to be monitored for multiple years and under multiple water year types to assess its effectiveness. The differences we found in community composition and abundance between shallow- and deep-water habitat mean that evaluations of restoration effectiveness cannot rely solely on existing monitoring programs to understand zooplankton dynamics. Furthermore, evaluations of restoration effectiveness should not rely solely on zooplankton dynamics to measure success of restoration sites. Instead, zooplankton abundance should be measured in concert with measurements of phytoplankton biomass, macroinvertebrate abundance, and fish abundance, as the FRP is currently doing.

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