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Zooplankton Trends in the Cache-Lindsey Slough Complex, 2014-2021

By

KIMBERLY LUKE
THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

Animal Biology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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Committee in Charge

2023

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Finally, thank you to my partner Kellen and both our families, who have supported and encouraged me throughout my degree.

Abstract

Zooplankton are a central aspect to most aquatic food webs but are often overlooked in monitoring and restoration. California's San Francisco Estuary (SFE), one of the most altered and invaded estuaries in North America, is one of few estuaries with a robust and long-term zooplankton sampling effort. Yet while major scientific studies have occurred in the mainstem of the estuary, backwater areas such as the Cache-Lindsey slough complex (CLC) of the north Delta have generally been neglected. These backwater areas are hotspots for zooplankton density and can often be more productive than mainstream channels.

We present the longest time series analysis (2014-2021) of zooplankton in the CLC. To understand temporal and spatial shifts in zooplankton density and its impact as a food resource, we focused on monthly springtime (March - May) zooplankton samples, when juvenile fish abundance (key planktivores) is often highest. We identify spatial zones of particularly high zooplankton density, document temporal shifts in density, and explore factors driving density changes overall. In addition to temperature and chlorophyll-α concentrations, drought conditions had a significant impact on zooplankton density. Within the CLC, the Cache network is consistently identified as an area of high zooplankton production, but there was a significant decline in zooplankton density alongside a decline in chlorophyll-α concentration.

Given the reduction of plankton and planktivorous fishes, restoration design in the region might consider prioritizing actions aimed at boosting fish food production. Many restoration sites in the SFE have full tidal exchange with mainstream channels, but our findings indicate how actions that increase hydraulic retention time can be beneficial. For example, constrained hydrologic connectivity, especially towards backwater locations, extends residence time and plankton production, and therefore could benefit restoration.

Zooplankton Trends in the Cache-Lindsey Slough Complex, 2014-2021

Introduction

Zooplankton are critical links in the trophic ecology of aquatic ecosystems. For example, because of their small size and temporally variable densities, they are important foundational food web resources for many consumer organisms (Michel and Oberdorff 1995; Medeiros and Arthington 2008; Nunn et *al*. 2011). Fishes often rely on zooplankton for prey during juvenile stages, and some pelagic fishes like the endangered Delta Smelt (*Hypomesus transpacificus*), feed on zooplankton throughout their life (Moyle 2002, Thomson et *al*. 2010). Therefore, consistent and abundant levels of zooplankton promote rapid growth and increased survival of fishes (Welker et *al*. 1994; Slater and Baxter 2014). Effects of zooplankton cascade bi-directionally through ecosystems, and classic ecosystem ecology has focused intensely on the strength and importance of these linkages (Carpenter and Kitchell 1993, Pace et al. 1999). For example, planktivorous and juvenile fishes support higher trophic levels, including larger fishes, birds, and small mammals (Moyle 2002; Takekawa et *al*. 2011; Johnson 2000). Declines in zooplankton may negatively impact higher trophic levels, or alternatively, induce conditions that favor harmful algal blooms (Baxter et *al*. 2008, Chakraborty et *al*. 2022).

Despite their ecological relevance, zooplankton are less studied compared to other aquatic trophic levels and are often omitted from long-term monitoring programs, even though

they offer a cost-effective way to understand ecosystem ecology and climate impacts (Richardson 2008; Jeppesen et *al.* 2011). These biases are particularly relevant in estuaries, as many long-term zooplankton studies focus on lake and open ocean ecosystems (Bashevkin et *al*. 2022). Estuaries are a highly valued ecosystem type, providing services like nursery habitat and viable fisheries (Barbier et al. 2011; Thrush et al. 2014), and increased long-term conservation and monitoring is needed to ensure their future sustainability (Baird 2005).

The San Francisco Estuary (SFE, California, USA), is one of few estuaries with a zooplankton sampling effort dating back to 1972 as a part of the Interagency Ecological Program (IEP), run by the California Department of Fish and Wildlife (Winder and Jassby 2011). Over time, the number and extent of IEP studies that include zooplankton sampling has increased, providing long-term data that encompasses much of the estuary (Bashevkin et *al*. 2022).

Zooplankton production can be regulated by both biotic and abiotic controls, including food availability, nutrients, species introductions, competition, predation, salinity, temperature, turbidity, dissolved oxygen, and flow (Landry 1978; Carpenter et *al*. 1987; Kimmerer et *al*. 1994; Morgan et *al*. 1997, Winder and Jassby 2011; Michalec et *al.* 2017; Işkın et al. 2020). In the SFE, there have been long-term declines in zooplankton productivity caused by reductions in phytoplankton densities, the one of most note being due to the grazing effect of the invasive overbite clam *Potamocorbula amurensis* in the 1980's (Orsi and Mecum 1986; Carlton et *al*. 1990; Alpine and Cloern 1992; Kimmerer 2002). *Potamocorbula amurensis* competes with zooplankton for phytoplankton, but also directly consumes copepods during filter feeding (Kimmerer & Lougee 2015). Zooplankton densities in the upper SFE are positively affected by lower velocities and higher residence times (Young et. *al* 2020; Smits et *al*. 2023), while

community structure and composition are influenced by salinity, flow, temperature, and season (Orsi and Mecum 1986; Bollens et *al*. 2014).

Although there are many ongoing zooplankton monitoring programs in the SFE, few have focused on the Cache-Lindsey Slough Complex (CLC), located in the North Delta. The CLC is comprised of the Lindsey and Cache slough networks, and although they are close in proximity, each constitutes distinct watershed land uses, water quality characteristics, submerged and floating aquatic vegetation densities, surrounding landscapes, and fish assemblages. These slough networks represent a powerhouse of zooplankton production compared to the south Delta and the brackish Suisun Marsh, especially during a recent five-year drought (Montgomery 2017). In particular, the terminal, upstream reaches of the sloughs in the CLC showed the highest densities in the complex (Jasper 2020).

Our study asked: (1) How did zooplankton density in upstream slough sites change over the period from 2014 to 2021 during the spring months of March, April, and May? (2) How did water year type affect zooplankton? (3) Did certain sites have higher zooplankton density than others? and (4) What drove differences in zooplankton density among the upstream reaches of the CLC?

The following hypotheses were formulated from our research questions.

(1) Zooplankton density will decline over time, reflecting other ecosystem shifts in the North Delta during this period.

(2) Zooplankton will have lower densities and later peaks in wet (high precipitation) years than moderate or dry years because of advection and dispersal processes related to increased water and flow. Zooplankton assemblages in wet years will have higher relative

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proportions of Cladoceran genera because overland flow from still moving water will transport them into the sloughs.

(3) The Cache network sites will have higher zooplankton densities than Lindsey network sites because of differences in chlorophyll-α concentrations, submerged aquatic vegetation (SAV) volumes, water inputs, and lack of major water diversions.

(4) Chlorophyll-α and temperature drive the differences in density at upstream ends of the two slough networks, consistent with other studies in the San Francisco Estuary (Orsi and Mecum 1986; Bollens et. *al* 2014). Secondary drivers include the period of the study (i.e., during or after the drought), and the slough network (Lindsey or Cache).

Our study represents the longest time series analysis of zooplankton dynamics in the upstream sloughs of the CLC. Earlier studies highlighted higher production potential for zooplankton in the CLC (Durand et al. 2020), but this work occurred over brief timescales. Large ecosystem shifts during the 2012-2016 drought, including proliferation of aquatic vegetation and changes in fish assemblage, call into question whether the high productivity of the CLC can be sustained over long time frames (Durand et al. 2020).

The period analyzed includes a transformative drought period and the years following it, allowing for a comparison of contrasting climatic cycles. This study focused on spring months March, April, and May because juvenile fish production is highest over this period, making zooplankton the critical resource link for the ecosystem during this time (Moyle 2002).

Methods

Study Area

California maintains a Mediterranean climate that includes dry summers and wet winters and extended periods of drought. The California Department of Water Resources classifies water years (October 1-September 30) using an index and includes the designations 'wet', 'above normal', 'below normal', 'dry', and 'critical' (DWR 2023). For our study, DWR's classifications are simplified into three water-year types; critical and dry years were referred to as 'dry', below normal was redefined as 'moderate', and above normal and wet years were determined as 'wet'.

The Sacramento-San Joaquin River Delta (Delta) represents the most inland portion of the SFE (Lund et *al.* 2010), and has been highly altered for agriculture, water conveyance, recreation, and conservation. The North Delta, located within the Delta proper, is a tidal, primarily freshwater system filled with a mosaic of deep, dredged channels bordered by levees, shallow subtidal lakes, emergent wetlands, agriculture, and slough networks. The CLC is located in the North Delta and is made up of the Lindsey network (Lindsey), comprised of Lindsey, Barker, and Calhoun Cut sloughs; and the Cache network (Cache), comprised of Cache, Hass, and Ulatis sloughs.

Lindsey has limited flow inputs, receiving water from Big Ditch, Campbell Lake, and Jepson Prairie overflows. In addition to inputs, water is also exported from the slough network at Barker Slough Pumping Plant, into the North Bay Aqueduct. The landscape mosaic surrounding Lindsey includes riparian, agriculture, open intertidal, and a restoration site. The Lindsey network has an elevated level of submerged and floating aquatic vegetation relative to other parts of the CLC.

Cache has elevated flows compared to Lindsey due to its connection to Ulatis Creek, which also increases turbidity. Sloughs are highly leveed without restoration sites (although some are planned or in construction during the study, namely Lookout Slough). Cache network has less submerged and floating aquatic vegetation compared to Lindsey network, but since the start of the study more vegetation has become established (Jasper 2020).

Sampling

Zooplankton

Beginning in 2012, monthly zooplankton samples were collected in both Cache and Lindsey networks and included upstream and downstream locations, as well as the confluence of the two sloughs (Figure 1). This study only analyzed samples taken at the upstream dead-end sites of five sloughs: Barker Slough (BK1), Cache Slough (CA1), Calhoun Cut Slough (CC1), Hass Slough (HS1), and Ulatis Slough (UL1). Zooplankton were collected with a 50-μm-mesh, conical 2m long net with a 0.5m diameter mouth. Attached at the mouth of the net was a General Oceanics mechanical flowmeter to estimate water volume sampled. The flowmeter display was recorded immediately before and after the net was towed. Once deployed, the net was hand-towed for 20m against the current. The contents of the net were rinsed into the cod end of the net, transferred to a 1-liter Nalgene bottle, stained with 1% rose bengal, and fixed with 5% formaldehyde.
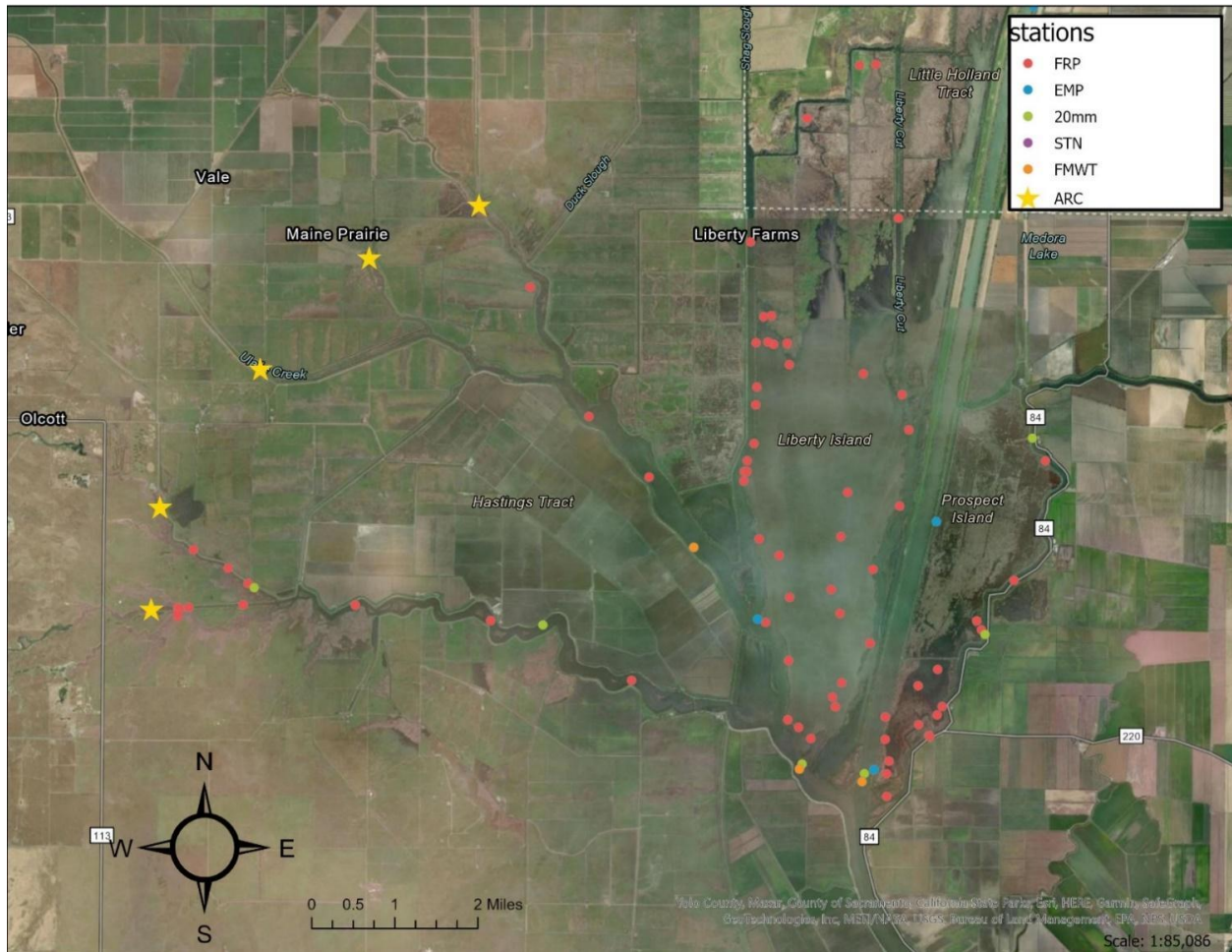
Figure 1. Map of the North Delta, SFE, USA contrasting IEP zooplankton study sites and ARC zooplankton study sites. Legend describes different IEP project sites (colored circles) & ARC sites (stars).

In the lab, samples were set to a uniform volume of 500mL, and subsamples were taken starting at 5mL. Zooplankton were counted and identified to genera under a dissecting microscope. Sufficient subsamples were processed so that counts of the three most abundant genera exceeded 100 individuals. Counted individuals were identified as copepodites, adults, or gravid females within their respective genera. Egg counts were estimated until 25 gravid females were counted in a genus.

To determine counts per sample, genera counts were tallied for each subsample and added across all subsamples for a total count. Total counts were multiplied by the inverse proportion of the subsampled volume to the uniform volume and divided by the tow volume to

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calculate zooplankton density (individuals per cubic meter). Tow volume was initially calculated

using the start and stop flowmeter numbers recorded in the field with the following formulas

from the General Oceanics flowmeter user manual:

$$DISTANCE\ in\ meters = \frac{Difference\ in\ COUNTS\ (final\ -\ initial)\ (x)\ Rotor\ Constant}{999,999}$$

$$VOLUME\ cubic\ meters = \{3.14159\ (x)\ (Net\ Mouth\ Radius)^2\ \}\ (x)\ Distance$$

However, there were errors with the flowmeter values which resulted in unrealistic

volumes and zooplankton densities. As a result, a standardized tow volume was developed to

account for error in flowmeter values. The standardized volume was calculated by first

determining a percent yield for volumes calculated with flowmeter values. The sum of all sample

volumes calculated using flowmeter numbers was divided by the summation of maximum

geometric volume for each sample. Geometric volume was calculated with the General Oceanics

formula, but instead of using flowmeter values to calculate distance, the distance was set to 20m.

This value represents volume calculated if the 20m tow was unaffected by wind, detritus, or

flow. The geometric volume was multiplied by the percent yield number to create standardized

volume.

$$volume\ percent\ yield = \frac{\Sigma\ sample\ volume\ calculated\ with\ flowmeter\ distance}{\Sigma\ sample\ geometric\ volume}$$

$$standardized\ volume = geometric\ volume * volume\ percent\ yield$$

Water Quality

Monthly water quality measurements were collected from below the water's surface at each site in tandem with zooplankton sampling. A Hach Hydrolab 5 sonde was used from the start of the study until October 2018 and then a YSI EXO2 sonde used to take point measurements and determine temperature and other standard water quality parameters at each sampling event. Surface water grabs were collected in 1 liter Nalgene and stored in ice for later lab analysis run by the biogeochemistry lab at UC Davis. Lab analysis measured chlorophyll-α concentration, a proxy for phytoplankton density, and nutrient concentrations (nitrate, ammonium, phosphate, and total nitrogen and phosphate) and other water quality parameters. Chlorophyll-α concentrations were determined using a modified version of standard protocols (Clesceri et *al*. 1998). A subsample of each water grab was filtered through a Whitman porous filter with a vacuum filtration apparatus. Filter papers were placed into individual vials and freeze dried for lyophilization. Freeze dried samples were suspended in 90% ethanol and heated in a warm bath to extract chlorophyll-α from the filter paper. The standard method was altered by using 90% ethanol for extraction instead of 90% acetone, and the glass fiber filters were freeze dried (Sartory & Grobbelaar, 1984). Ethanol solutions were placed in a Turner Trilogy Laboratory Fluorometer to measure relative fluorescence units, RFU.

Analysis

Zooplankton

To test how zooplankton density changed from 2014-2021, how water-year type affects zooplankton, and how zooplankton density varied across space we used the Kruskal-Wallis test, a nonparametric analog to one-way ANOVA, which compares average ranks between groups

(Kruskal & Wallis 1952). We chose this method because our data violated the ANOVA assumption of normality, even after log transformation. In a Kruskal-Wallis test, the null hypothesis assumes all samples derive from similar populations, and it is rejected if a p-value of 0.05 or less is produced (Hecke 2012). Kruskal-Wallis tests that reject the null hypothesis were followed up with Dunn's tests to parse out which groups differed significantly. The Dunn's test, a nonparametric pairwise multiple comparison, specifies which groups have a significant difference in their average rankings (Dunn, 1964). A Bonferroni p-adjustment was used in the Dunn's calculation to account for type I errors due to the problem of multiple pairwise comparisons (Dunn 1961, Dinno 2015).

Drivers of Zooplankton Density

To answer our fourth question regarding drivers of zooplankton, general linear models were used to understand the influence and covariance of water quality parameters, and spatial and temporal differences on zooplankton density. Zooplankton densities were log transformed to achieve normal distribution and reduce skewness, and all independent and dependent variables were z-score standardized to achieve uniformness across variables (Gelman and Hill, 2007). Thus, zooplankton densities were the dependent variable, chlorophyll-α and temperature were continuous independent variables, and period and network were categorical variables. The independent variables chosen for modeling were based on *a priori* knowledge of the system and preliminary model exploration. Variables determined to not be important from preliminary model exploration included turbidity, submerged aquatic vegetation volume, and water-year type.

All possible models using our chosen variables were generated and compared using Akaike information criterion (AIC) and Bayesian information criterion (BIC) metrics. AICc, a type of AIC, was selected because it assists in correcting for small sample size. Both metrics compare models, assign values, and rank models based on best fit, while penalizing complexity. The model with the lowest assigned value is considered to be the best fit model. AIC prioritizes predictive accuracy in its model selection, whereas BIC prioritizes selecting a model that is the most consistent as sample size increases (Aho et *al.* 2014). Both metrics were considered to determine the best fit model.

Kruskal-Wallis and Dunn's tests were also run for chlorophyll-α concentration and temperature to look for correlations with zooplankton densities and improve our understanding of their influence on zooplankton variation. As with our zooplankton analyses, we looked at chlorophyll-α concentration and temperature differences across years of the study, water-year type, and space.

Results

Zooplankton

Temporal Density Trends

During 2014 to 2021, springtime zooplankton densities in upstream slough sites declined (Figure 2A). There was a severe decrease in median density and density variability after 2016, and density remained relatively low for the rest of the study. The highest median density occurred during 2014, while 2017 and 2019 had the lowest median zooplankton densities. The greatest variability in density values was in 2016 and the lowest was in 2017. The Kruskal-

Wallis test showed significant differences between years (p=0.0089), and the Dunn's test determined zooplankton densities in the year 2014 were significantly different from years 2019 and 2021 (p-value=0.0155).

Effects of Water-Year Type

Water-year type affected median zooplankton density and variability, peaks in density throughout the springtime, and zooplankton community composition. When comparing water-year types, zooplankton density was highest and had the most variability in dry years (Figure 2B). Moderate water years had the second highest median and second most variability and were relatively similar to dry years. Wet years had the lowest median density and the least variability in zooplankton abundances. There were significant differences in zooplankton densities across water-year types (p =0.0063), but only between dry and wet years (p =0.0053).

Peaks in springtime zooplankton density and differences in density between months also appear to be influenced by water-year type. During wet and moderate years, springtime zooplankton density typically increased each month and densities were highest in May (Figure 3). March and April densities were relatively low compared to May densities in moderate and wet years. During dry years, densities were generally highest in April and there was less variation between the three months compared to wet and moderate water years (Figure 3).

Across all water-year types, zooplankton assemblage was composed of a mixture of three clades, Cyclopoida, Calanoida, and Cladocera, but the proportions differed between water-year types (Figure 4). Genera present included *Acanthocyclops* and *Limnoithona* (Order Cyclopoida)*; Eurytemora, Pseudodiaptomus, Sinocalanus, Acartia,* and *Tortanus* (Order Calanoida); and *Daphnia, Ceriodaphnia, Diphanosoma, Moina, Simocephalus, Chydorid*, and *Bosmina* (Superorder Cladocera).

During dry years, >50% of the community composition was comprised of calanoid copepods *Eurytemora* and *Pseudodiaptomus*. Cyclopodia and Cladocera roughly split the remaining percent of community composition equally. *Acanthocyclops* was the most abundant cyclopoid zooplankton and *Bosmina* was the most abundant cladoceran zooplankton.

During moderate water years, Cladocera made up the majority of the composition, with *Bosmina* and *Ceriodaphnia* being the most abundant genera. Calanoid copepods, majority *Eurytemora*, were the second most abundant clade. Cyclopoida contributed the least to community composition and only *Acanthocyclops* was present.

In wet years, community composition was more evenly distributed among the three clades relative to dry and moderate years. Cladocera contributed the most to community composition, followed by calanoid copepods, and then cyclopoids contributing the least. The most abundant genus for each clade was *Bosmina, Eurytemora,* and *Acanthocyclops.* The calanoid *Pseudodiaptomus,* abundant in dry years, became scarce during wetter years. Conversely, *Limnoithona* appeared only during wet years.

Spatial Density Trends

Zooplankton densities were generally highest at Cache network sites, CA1, HS1, and UL1 and lowest at Lindsey network sites, BK1 and CC1. Comparing site differences, median zooplankton density was highest at CA1 and lowest at CC1 (Figure 2C). HS1 had the greatest variability in zooplankton density compared to the other sites and BK1 had the least variability. Statistical analysis did not support the visual patterns of the box plot and determined zooplankton densities did not differ greatly, although the p-value on the cusp of the value that determines significance (p =0.051). Median density and variability of density was greater in Cache network than in Lindsey network (Figure 2D), but as with site differences, statistical

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analysis determined the difference in zooplankton density between networks was not significant (p =0.072).

Drivers of Zooplankton

The general linear model with the lowest AIC and BIC score was one that included temperature, chlorophyll-α concentration, and period as independent variables (Table 1). The model explained ~38% of variation in the data, and all variables had statistically significant relationships with zooplankton density (Table 2). Temperature and chlorophyll-α concentration both had positive effects on zooplankton density across both periods (2014-2016 and 2017-2021), but densities were lower in the latter period as indicated by the lower intercept value (Figure 5 & 6). The effect of temperature was consistent across both periods, but chlorophyll-α concentration had a greater effect on density during the second period as indicated by the steeper slope. However, an interactive effect between chlorophyll-α concentration and period was not included in the best fit model; thus the differences in slopes between periods were not significantly different.

Trends in Water Quality Parameters

Chlorophyll-α Concentration

Over the course of the study median spring chlorophyll-α concentration appeared to decrease. Median chlorophyll-α concentration decreased after 2015 and again after 2017 and stayed relatively low compared to the start of the study (Figure 7A). Variability in chlorophyll-α concentration also decreased after 2015 and stayed relatively low for the rest of the study. The greatest variability observed was in 2015, and the least was in 2021. There was no significant difference in chlorophyll-α concentration across years (p=0.32).

Among water year types, median spring chlorophyll-α concentration was similar for dry and moderate years, while wet years had the lowest median concentration (Figure 7B). Dry years had the highest variability in concentration, and wet years had the least variability. There was no statistical significance in chlorophyll- α concentration between water year-types (p=0.6).

Among sites, median chlorophyll-α concentration was highest at CA1 and lowest at CC1 (Figure 7C). CA1 had the greatest variability in chlorophyll-α concentration, followed by UL1, and CC1 had the least variability. Differences were significant (p=<0.0001), and chlorophyll-α concentration at CA1 differed significantly from HS1 (p=0.0026), BK1 (p=0.0029,), and CC1 (p=<0.0001), and concentration at UL1 differed significantly from CC1 (p=0.013). Median chlorophyll-α concentration and variability in concentration was higher in Cache network than Lindsey network (Figure 7D), and statistical analysis concluded there were significant differences in the chlorophyll-α concentration between networks (p=<0.0001).

Temperature

Comparing spring temperatures across years, there was little difference in median temperature but there was some difference in temperature variations (Figure 8A). The greatest temperature variations were in 2021, and the least was in 2017. There were no significant differences in water temperatures between years of the study (p=0.46).

Median temperatures were similar across all three water year types, but variability in temperatures differed between dry, moderate, and wet years (Figure 8B). Moderate water years had the greatest variability, dry years had intermediate variance, and wet years had low variability in water temperatures. Consistent with results of the analysis across all years, there were no significant differences in water temperatures among water-year types (p=0.14).

Across sites, median water temperatures and variability in temperature was relatively

consistent (Figure 8C). Median temperature was highest at UL1 and lowest at CC1 but there

were no statistically significant differences in temperature at sites (p=0.32). Comparing

networks, median temperatures were similar, but variability in temperatures was greater in Cache

network than in Lindsey network (Figure 8D). Statistical analysis concluded that differences in

temperatures networks were not significant (p=0.062).
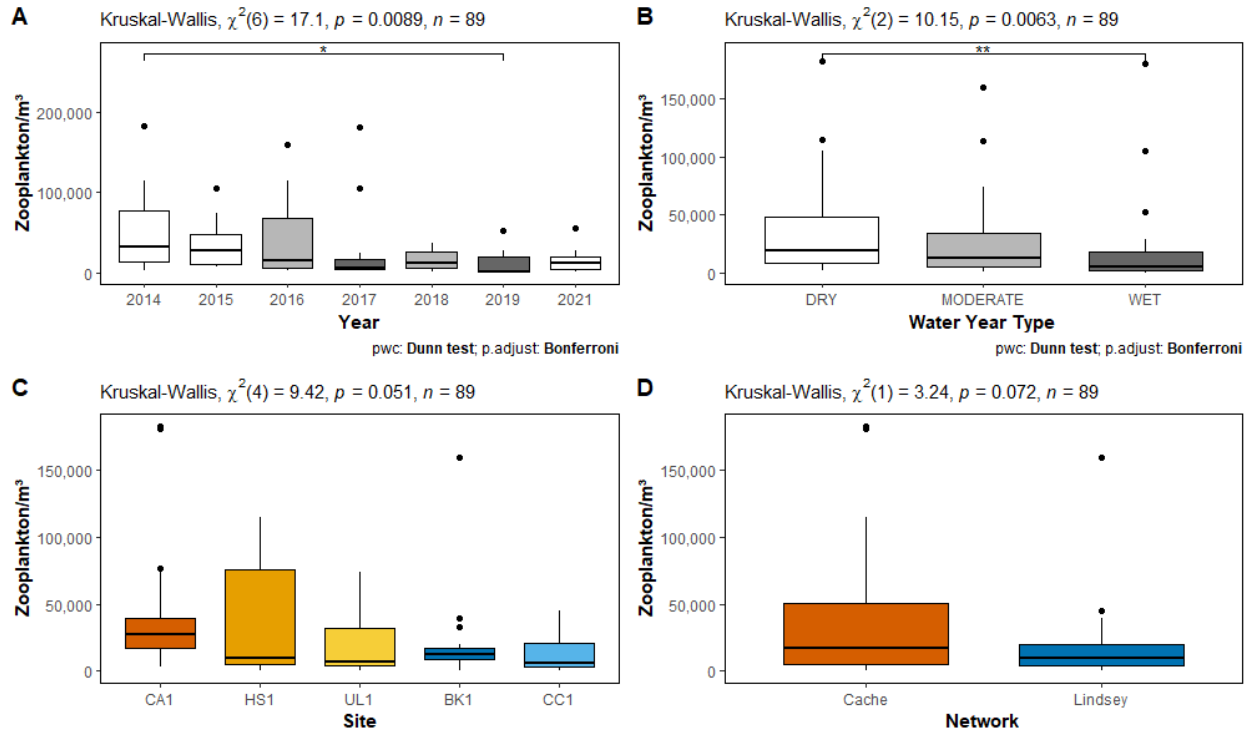
Figure 2. Box plots comparing median zooplankton density across years (A), water-year type (B), site (C), and network (D). Kruskal-Wallis statistical analysis is displayed above chart,
with chi-squared value ($\chi2$), p-value (*p*), and number of observations (*n*). Pairwise comparisons displayed within the plot and are indicated by brackets between groups that differ significantly. Significance codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Site and complex are color coded where Cache network=orange-yellow shades, Lindsey network=blue shades. Year and water-year type bars are colored by water year type: dark grey=wet year, light grey=average year, white=dry year**.
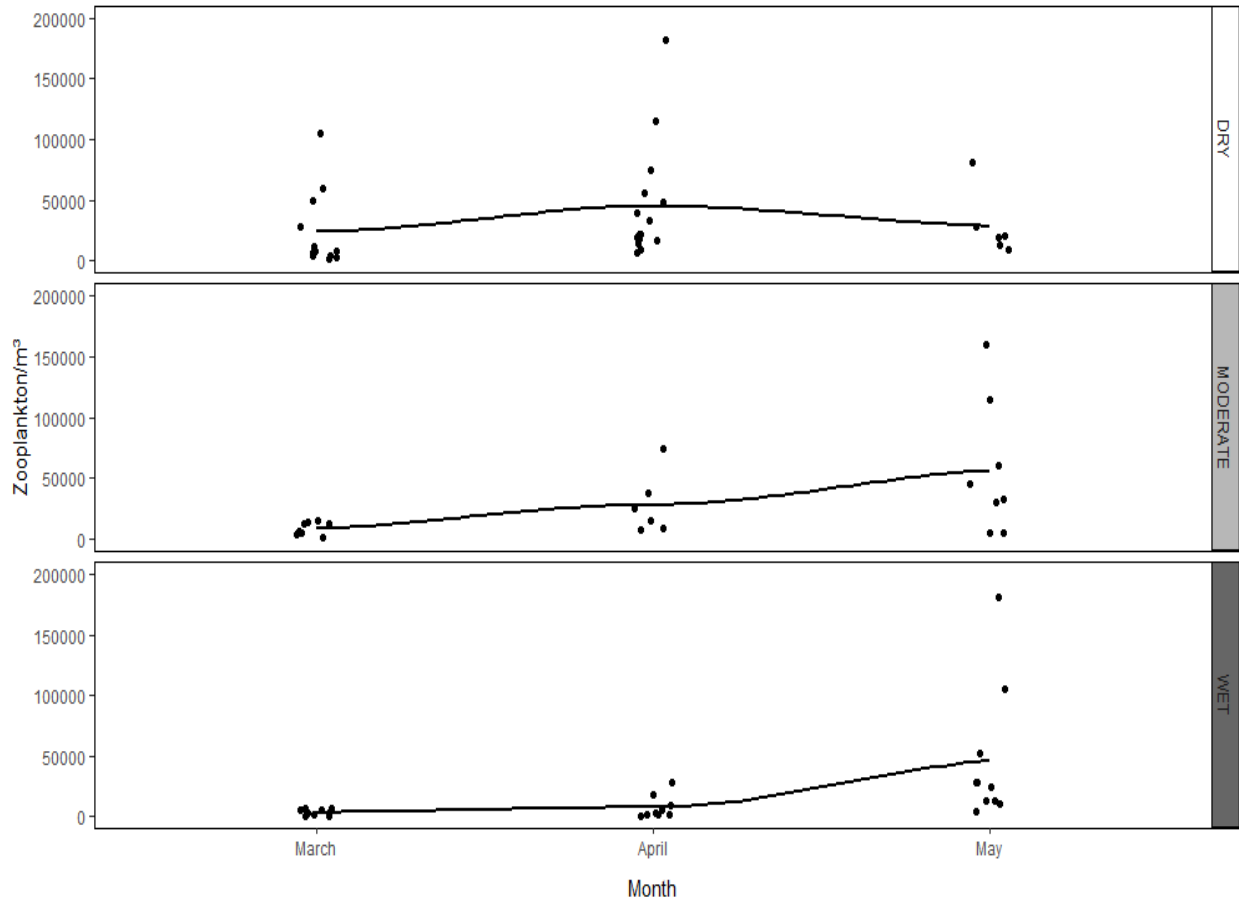
Figure 3. Individuals sample densities plotted across springtime months, faceted by water-year type. Each scatterplot is fitted with a LOESS trend line using geom_smooth in R Studio. Year label is shaded by water year type: dark grey=wet year, light grey=average year, white=dry year.
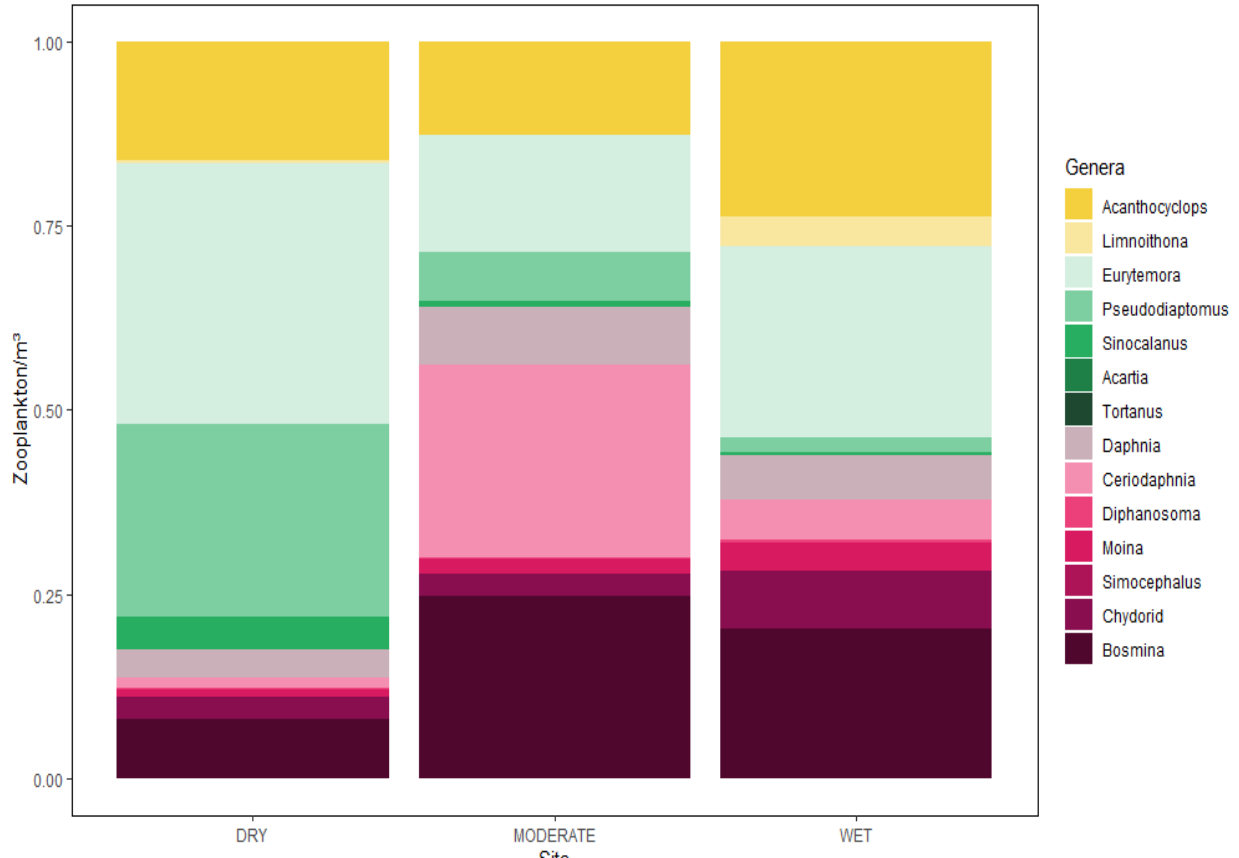
Figure 4. Stacked bar graphs for each water year type showing percent of each zooplankton genera. Bars are made up of total zooplankton density for each water year-type. Bars are colored by zooplankton clade: yellows= Cyclopoida, greens =Calanoida, and pinks= Cladocera.
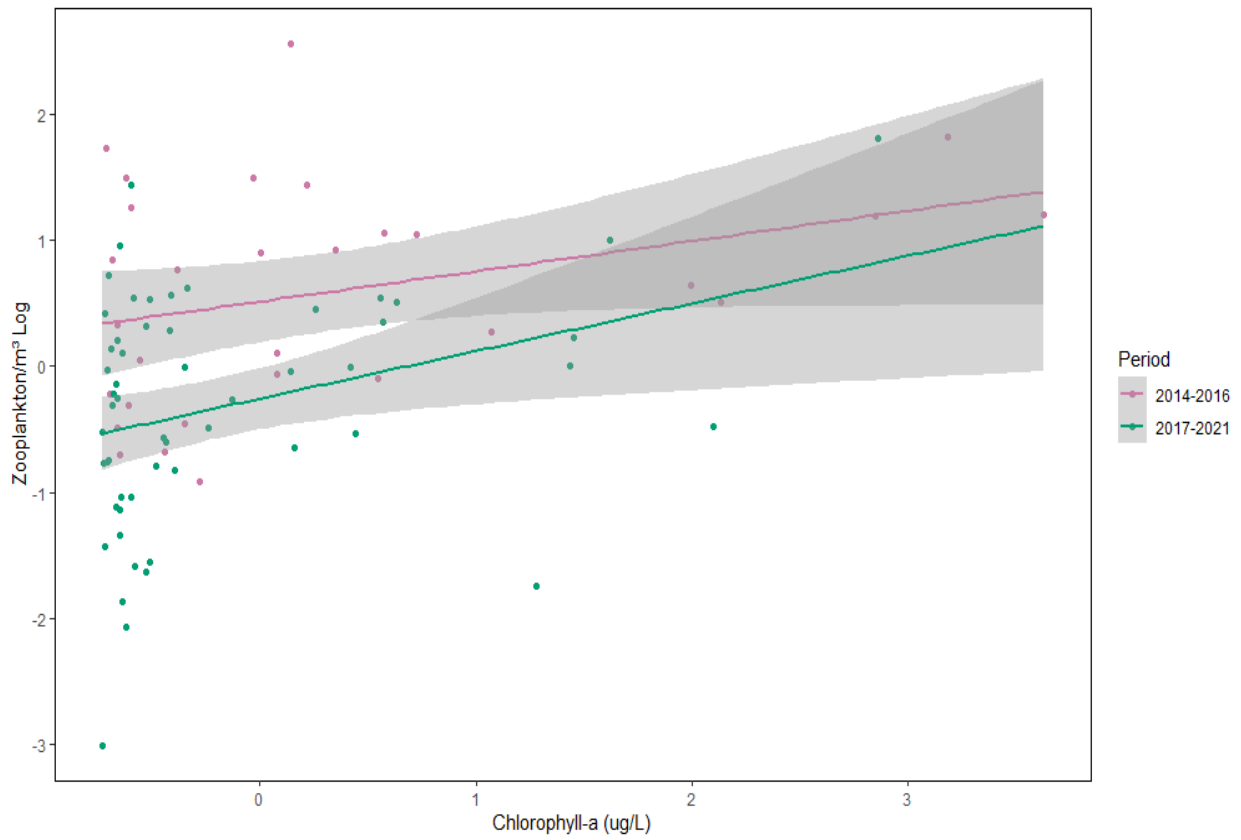
Figure 5. Effect of chlorophyll-α concentration on log zooplankton density for each period of the study. Chlorophyll-α concentration and log zooplankton density values were z-score standardized.
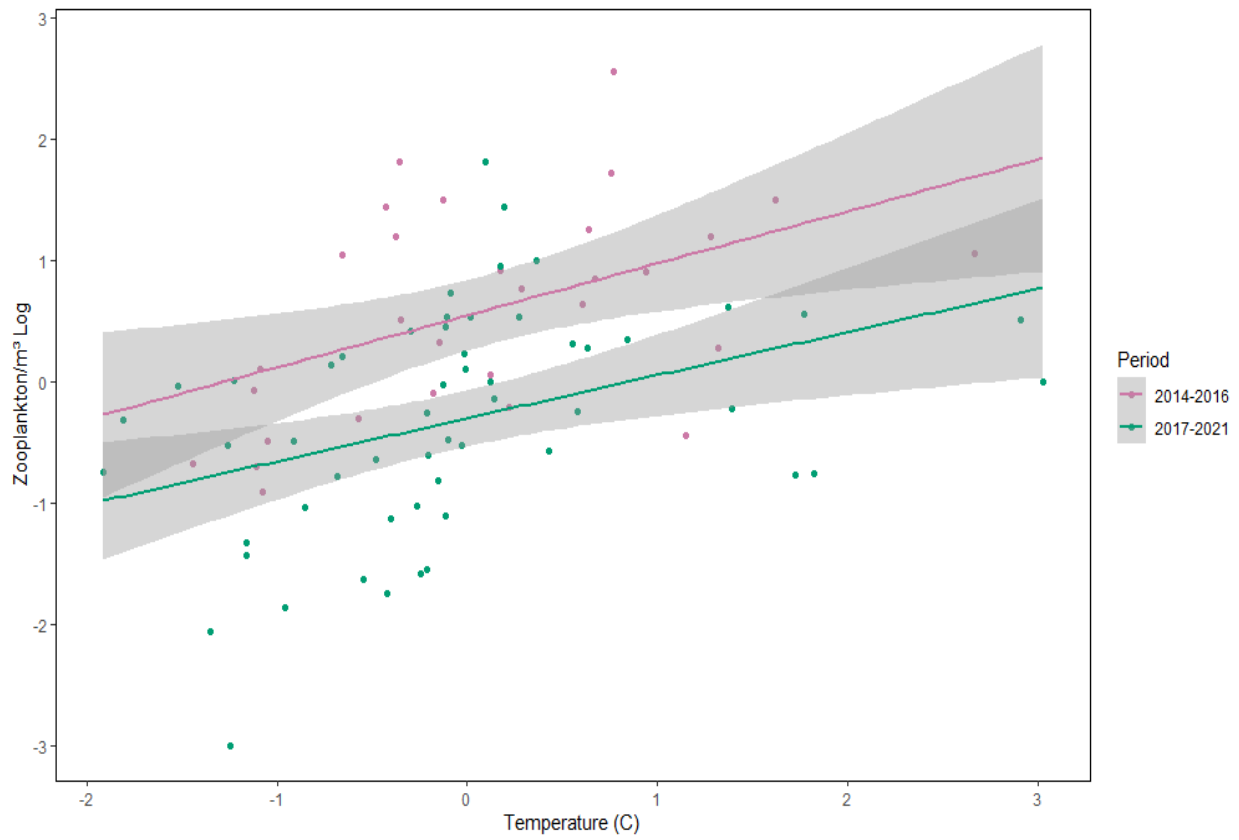
Figure 6. Effect of temperature on log zooplankton density during each period of the study. Temperature and log zooplankton density values were z-score standardized.
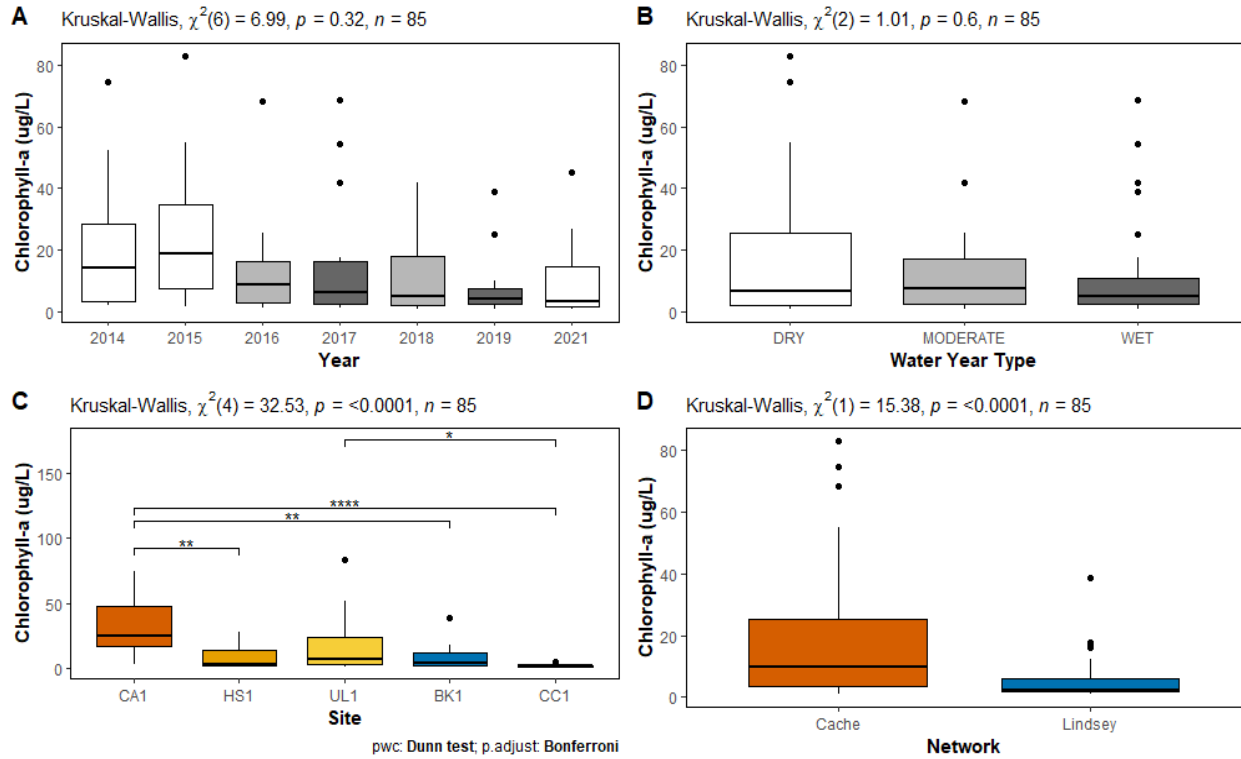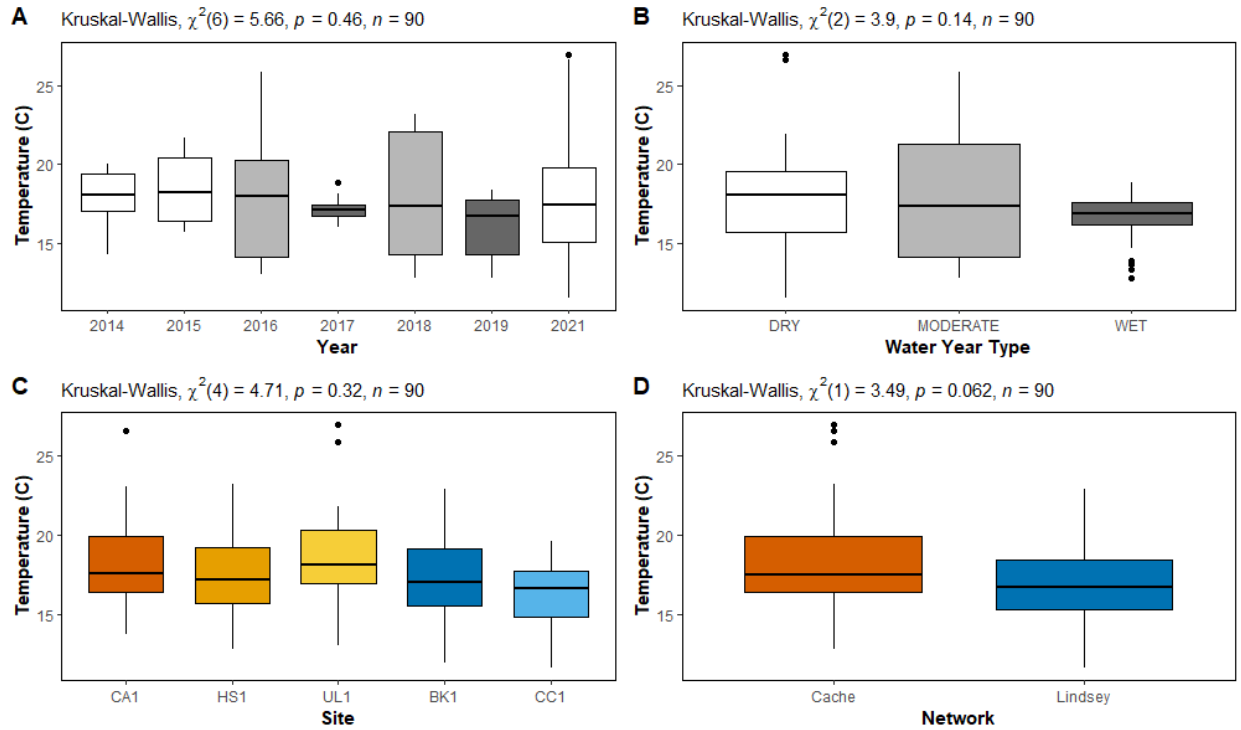
Figure 7. Box plots comparing median chlorophyll-α concentration across years (A), water-year type (B), site (C), and network (D). Kruskal-Wallis statistical analysis is displayed above chart, with chi-squared value (χ2), p-value (*p*), and number of observations (*n*). Pairwise comparisons displayed within the plot and are indicated by brackets between groups that differ significantly. Significance codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Site and complex are color coded where Cache network=orange-yellow shades, Lindsey network=blue shades. Year and water-year type bars are colored by water year type: dark grey=wet year, light grey=average year, white=dry year.**

Figure 8. Box plots comparing median temperature across years (A), water-year type (B), site (C), and network (D). Kruskal-Wallis statistical analysis is displayed above chart, with chi-squared value (χ2), p-value (*p*), and number of observations (*n*).

Pairwise comparisons displayed within the plot and are indicated by brackets between groups that differ significantly. Significance codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Site and complex are color coded where Cache network=orange-yellow shades, Lindsey network=blue shades. Year and water-year type bars are colored by water year type: dark grey=wet year, light grey=average year, white=dry year.**

Model	AICc	BIC	df
Chlorophyll-α+ Period+ Temp	207.372	218.826	5
Chlorophyll.α+ Period+ Temp+ Chlorophyll-α: Period	209.189	222.768	6
Chlorophyll.α+ Complex+ Period+ Temp	209.41	222.989	6

Table 1. Top three models from each model set with AICc and BIC scores and degrees of freedom (df)

Predictors	Estimates	CI	p-value
(Intercept)	0.47	0.18-0.76	0.002
Chlorophyll-a concentration	0.26	0.09-0.44	0.004
Temperature	0.35	0.18-0.53	<0.001
Period (2017-2021)	-0.73	-1.09-(-0.36)	<0.001
Observations	85		
R-squared	0.401		
R-squared adjusted:	0.379		

Table 2. Best fit linear model summary with estimates of change in log zooplankton density per change in unit of parameter, confidence intervals (CI), p-value for each parameter, number of observations, R-squared, and R-squared adjusted values. Parameter values were z-scored standardized.

Discussion

Temporal Changes

Our study supported our first hypothesis and showed declines in springtime zooplankton density at upstream slough sites of the CLC over a seven-year period. Densities decreased noticeably after 2016 and stayed consistently low regardless of water year type. Along with a decrease in zooplankton density, this study captured a decrease in chlorophyll-α concentration over time.

Ecosystem shifts during periods of drought have been observed in other estuaries, with some estuarine ecosystems shifting back to initial states following wetter years and others transitioning to an altered state (Dittman et *al.* 2014; Marques et *al.* 2014; Gomes & Bernardino 2020). In this study, densities in the CLC remained low even after wetter years indicating that the region may be transitioning to a different, reduced state of zooplankton density.

Continued monitoring is needed in the upstream sites of the CLC to continue following zooplankton density trends, with potential food web implications. And while these data are not nearly long enough to pick up early indictors of a regime shift, there were nonetheless signals of a change, particularly in the shifting variance of physical and biological data (Wooster and Zhang 2004, Lees et al. 2006). Future research in the Delta may seek to develop better predictive tools of early indictors of regime shifts.

Effects of Water-Year Type

Water-year type appeared to affect zooplankton density as we expected with lower densities occurring during wet years. Higher flows during wet years likely moved zooplankton downstream causing upstream sites to exhibit lower densities. In addition to advection, increased

inflow and precipitation during wet years also increased the volume of water at sites, diluting zooplankton densities.

Water-year type also affected community composition, but not in the exact way we expected. Our hypothesis speculated that wet years would have higher relative Cladocera density due to inflow from still water bodies that are Cladocera dominated. Yet while they did, it was during moderate years that the greatest relative densities of Cladocera occurred. Slower flows and longer residence times during moderate years compared to wet years may have given the cladoceran zooplankton a greater capacity for production (Viroux 1997; Viroux 2002). The study also captured a decrease in *Pseudodiaptomus,* and an increase in *Limnoithona* during wet years, indicating water-year type may play an important role in community composition at these sites.

Spatial Differences

Our study showed higher densities of zooplankton in the Cache Slough network as well as differences among sites within networks, supporting our third hypothesis. This pattern provides further support that upstream slough sites of the CLC, and the Cache network in particular, have a high zooplankton production capacity (Montgomery 2017, Jasper 2020). Higher densities in the Cache network correlated with higher chlorophyll-α concentration compared to Lindsey network. Chlorophyll- α concentration had a greater influence on zooplankton density after five-year drought than before, indicating that this water quality parameter is supporting and driving differences in zooplankton densities (Figure 11). Although analysis determined that the differences in zooplankton density across sites and networks weren't statistically significant, the strength of these patterns indicated there was a large difference which may be biologically significant (Yoccoz 1991).

Drivers of Zooplankton Density

Our best fit model determined chlorophyll-α concentration and temperature both have positive effects on zooplankton, mirroring previous studies in the Delta (Orsi and Mecum 1986; Müller-Solger et *al.* 2002). The model also showed how drought status, during or post extended drought, was an important factor, although high levels of chlorophyll-α concentration minimized the differences between periods (Figure 11). The decline in zooplankton density is likely due to a combination of factors that shifted between the two periods of the study that could include SAV volume, competition with invasive clams, upstream inflow, and residence time.

In the Delta, phytoplankton is the major source of primary production (Jassby et *al.* 2003) and can be in competition with SAV for nutrients and light (Pokorný et *al*. 1984; Vanderstukken et *al*. 2011). Increases in SAV can lead to declines in phytoplankton and zooplankton (Blindow 2001), so we initially thought the large increase seen in SAV CPUE in this area would significantly impact zooplankton trends. However, preliminary model exploration for this study determined SAV volume was not an important indicator of zooplankton density. While SAV was not important alone, it could still be a contributor at a macroscale, or to a combination of several factors affecting zooplankton density.

Another potential factor is the invasive clam Asian clam (*Corbicula fluminea*) which filter feeds phytoplankton and directly competes with zooplankton for food. *C. fluminea* is food limited in the western and northern parts of the Delta and has a lesser grazing capacity than *P. amurensis* (Foe and Knight 1985; Kimmerer and Thompson 2014) but can still have a strong negative impact on phytoplankton density, especially in shallow habitats like dead-end slough sites (Lopez et *al.* 2006). Therefore, the role of *Corbicula* in driving phytoplankton and zooplankton densities in the Delta should also be a topic of future research interest.

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While upstream inflow may push zooplankton downstream, these flows also represent an opportunity to transport nutrients into the system which supports the growth of phytoplankton for zooplankton consumption (Fackrell et *al.* 2022). Inflow from Ulatis creek and irrigation runoff from the surrounding agriculture can transport high concentrations of nutrients into the slough network (Weston et *al*. 2014; Jasper 2020). The influx of nutrients, like zooplankton, may be washed further downstream in wetter years which may dampen concentrations early in the spring. This may explain the relatively lower chlorophyll-α concentrations seen during wet years (Figure 7B).

Another hydrodynamic factor that may explain variability in phytoplankton and zooplankton densities is residence time, which often generates a positive effect (Ambler et *al.* 1985; Howarth 2000; Jassby 2008; Doubek et *al.* 2019). Studies completed in adjacent areas of the North Delta have shown higher isotopic water-ages at sites that are more upstream, dead end, and detached from the main inflow of the Sacramento River through Miner slough (Downing et *al.* 2016; Gross et *al.* 2019). Modeling from these studies showed the Lindsey network fully exchanges with Sacramento River water daily, but that the upper Cache network did not and had much higher water residence time (Durand et *al.* 2019). Hass Slough and parts of Cache Slough were partially composed of Sacramento River water, but upper Cache Slough sand Ulatis Slough had a negligible amount of river water exchange. This was likely due to other water inputs connected to these sloughs, such as Ulatis creek and agricultural inputs, and to a sand bar near the Hass-Cache confluence that prevents mixing with downstream sites.

Our study shows dead end areas of tidal sloughs, particularly those with higher chlorophyll-α concentrations and higher residence times, support high zooplankton densities. This pattern is true for other areas of the Delta, like the Deep-Water Shipping Channel, where the

dead end, upstream reaches have little to no tidal exchange and support higher zooplankton biomass (Young et *al.* 2020, Smits et *al.* 2023). Similar findings are also recorded in river systems, where backwaters lakes and sloughs with terminal ends have higher phytoplankton and zooplankton abundance compared to main channels or channels that are connected at both ends (Sampson et *al.* 2009, Burdis & Hoxmeier 2011, Dzialowski et *al.* 2013).

In the Cache network, it appears the higher chlorophyll-α concentration, distance from Sacramento River water input, and the sand bar that prevents total mixing creates the perfect scenario for increased zooplankton density at these dead-end slough sites. The upstream areas in the CLC also support higher abundances of fishes compared to downstream sites (Huntsman et al 2023), supporting the idea that areas with higher zooplankton densities are beneficial food sources for planktivorous and juvenile fishes (Beaugrand et al. 2003, Lomartire, Marques, and Gonçalves 2021).

Future Research & Management Implications

Taken together, our findings on zooplankton declines in upstream reaches of the CLC improve understanding of the North Delta and potential impacts of extended drought on the ecosystem. As climate change is expected to generate more frequent and extreme periods of drought and flood (Dettinger et *al.* 2016), there may be further ecosystem shifts in the north Delta. Another extended drought could cause further declines in zooplankton density and negatively impact fishes further through food resource limitation. Monitoring of water quality, zooplankton, and fish should continue in the CLC to capture and understand future shifts in the system.

Future research in the CLC should expand zooplankton analysis and include diet studies. Adding additional downstream sites to analyses will also create better understanding of

zooplankton densities in the area and the influence of hydrodynamics related to water-year type. Dry and moderate years may retain higher densities in downstream sites compared to wet years due to less advection.

To develop an understanding of biological significance in zooplankton density across sites and networks, diet studies might also be performed in tandem with zooplankton sampling. Gut contents of year-of-young and planktivorous fishes could be collected and analyzed to compare diet composition and gut fullness of fishes at different sites. This potential work can help isolate if there is a baseline of zooplankton density that correlates to gut fullness and increases in fish CPUE at sites. This baseline could also be used alongside continued monitoring to determine if zooplankton density at dead end sloughs decreases to a level that may negatively impact fish.

Our findings can also improve management and restoration decisions in the North Delta. Management of the CLC should include maintenance of the more productive areas within the Cache network. One way to maintain these areas is to consider the impact to chlorophyll-α concentrations, flow, inputs, and residence time in these sloughs when decisions regarding the current system or new restoration projects arise. New restoration projects for fishes in the North Delta that aim to promote increased hydrologic retention and higher productivity at lower trophic levels would be helpful. These actions will ultimately support fish consumers, and therefore the underlying ecological conditions in CA1 and UL1 might serve as an ecological template for managers to consider mimicking. Most elements that promote longer residence time, limited tidal exchange in upstream most reaches, local inflow, and limited aquatic vegetation could be incorporated into restoration designs in ways that ultimately benefit native fishes.

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