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RESEARCH

Years of Drought and Salt: Decreasing Flows Determine the Distribution of Zooplankton Resources in the San Francisco Estuary

Arthur Barros*[1], Rosemary Hartman [2], Samuel M. Bashevkin [3], Christina E. Burdi [1, 2]

ABSTRACT

The San Francisco Estuary (estuary) and the Sacramento–San Joaquin Delta (the Delta) in California face significant challenges in managing water resources during extended droughts. Zooplankton are a vital trophic link between phytoplankton producers and higher-level consumers such as predatory zooplankton and fish. However, there is still much to be learned about what drives zooplankton abundance and how they respond to drastic changes in environmental conditions, such as droughts. We found that during drought years zooplankton abundance and distribution changes varied for examined taxa. Significant declines in the abundance of *Daphnia* spp. and the copepod *Pseudodiaptomus forbesi* occurred in the Suisun Marsh and Suisun Bay regions. In contrast, abundance of the non-native copepod *Limnoithona tetraspina* increased in Suisun Marsh and the South-Central Delta during those same drought conditions. Salinity is a strong determinant of the presence and abundance of the studied taxa, and we showed that changes in the distribution of salinity as a result of low outflow conditions were an important factor in the regional abundance of zooplankton. Because of the expected increase in the frequency and severity of regional droughts, understanding how these conditions affect zooplankton in the estuary will benefit scientists and resource managers who aim to improve conditions for native fishes.

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INTRODUCTION

Extended droughts present a significant challenge in managing water resources available to the San Francisco Estuary (estuary). There have been documented declines of many fish species of concern, correlated with decreases in freshwater outflow in the estuary (Kimmerer 2002; SWRCB 2017), but the mechanisms behind these declines are often poorly understood. As the primary consumers of phytoplankton, zooplankton facilitate a vital trophic link between phytoplankton producers and higher-level consumers. In this region, zooplankton are a key food source for several important fish species, notably Delta Smelt (*Hypomesus transpacificus*) (Slater and Baxter 2014; Slater et al. 2019), Longfin Smelt (*Spirinchus thaleichthys*) (Barros et al. 2022; Jungbluth et al. 2021), juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) (Goertler et al. 2018; Tiffan et al. 2014), and the larval stages of other fishes (Hunter 1981). Because of their importance in fish diets, zooplankton have been studied extensively. However, more knowledge is needed to understand what drives zooplankton abundance and how they respond to environmental conditions (Hartman et al. 2021). One key question is how zooplankton respond to extremes such as high- and low-outflow years.

This paper is one of a series produced by the Interagency Ecological Program (IEP) Drought Synthesis Team (Hartman, Stumpner et al., this issue), which formed in 2021 in response to the critically dry water year. The team analyzed how drought affected a broad suite of environmental parameters, including hydrology, water quality, phytoplankton, invertebrates, and fish. While there is no single agreed-upon definition for "drought," droughts in California generally occur when there are multiple years of low precipitation and a resulting water supply shortage (CDWR 2020). In this series, the authors define "drought" as 2 or more consecutive years with a Sacramento Valley Water Year Hydrological Index (SVI) classifications of "Below Normal", "Dry," or "Critical," similar to the delineation in Mahardja et al. (2021). "Wet" years are defined as 2 or more consecutive years with a SVI classification of "Above Normal" or "Wet." Each paper in this edited volume can stand alone, but many of the papers refer to each other and provide complementary information.

Zooplankton have been monitored regularly in the estuary since 1972, when the California Department of Fish and Wildlife (CDFW) Environmental Monitoring Program (EMP) Zooplankton Survey began (Bashevkin et al. 2022). Long-term monitoring has enabled the detection of key changes in the zooplankton community—most notably, the significant decrease in zooplankton abundance coinciding with the introduction and spread of the invasive clam, *Potamocorbula amurensis,* in the mid-1980s (Carlton et al. 1990; Kimmerer et al. 1994). In addition, the introduction of several non-native zooplankton species (e.g., the cyclopoid copepod *Limnoithona tetraspina*, the calanoid copepod *Pseudodiaptomus forbesi*, and the mysid *Hyperacanthomysis longirostris*) has resulted in drastic shifts in community composition (Winder and Jassby 2011). Declines in zooplankton abundance and changes in community composition have been linked to major declines in the pelagic fishes of the estuary known as the "Pelagic Organism Decline" (Winder and Jassby 2011; Brown et al. 2016; Moyle et al. 2016). Increases in the occurrence of drought conditions (Diffenbaugh et al. 2015) could compound stressors in an already heavily disturbed ecosystem.

Studies have yet to examine how extended droughts affect the distribution and abundance of zooplankton in the estuary, though there have been a few that focused on the relationship between zooplankton and outflow. Historically, the abundance of several important zooplankton species, such as *Neomysis mercedis,* was positively correlated with outflow (Jassby et al. 1995; Kimmerer 2002). However, not all species show this relationship (e.g., *Eurytemora affinis* was negatively correlated with outflow [Kimmerer 2002]), or the relationship has changed over time (e.g., the abundance of *N. mercedis* decreased with flow before 1987 and increased with flow afterwards [Kimmerer 2002], or it can vary by region [Bollens et al. 2011; Kimmerer et al. 2018b]).

During Drought years, freshwater outflows decrease drastically, and understanding the effect on the zooplankton community is key to understanding how water-management decisions affect zooplankton abundance. One possible mechanism for how reduced outflow in drought years can affect zooplankton is through shifts in the location of the estuary's low-salinity zone (LSZ), which is defined by the EMP as the region where salinity at the bottom of the water column is between 1 and 6 ppt. Before the invasion of the clam *P. amurensis*, positioning of the LSZ in the shallower areas of Suisun Bay (Figure 1) during spring and summer led to higher productivity as a result of higher water residence time and turbulent mixing, which reduces transport of phytoplankton seaward (Cloern et al. 1983). An alternative hypothesis for how outflow affected phytoplankton dynamics in Suisun was that during prolonged low outflow periods, increased salinity would promote higher benthic grazing from marine bivalves (Nichols 1985). Management decisions including upstream reservoir releases and the amount of water pumped out of the Delta by state and federal water projects can also profoundly affect the location of the LSZ in the estuary (MacWilliams et al. 2015). Increased freshwater exports, in combination with the invasive clam *P. amurensis,* have led to significant declines in pelagic phytoplankton biomass (Hammock et al. 2019). Since the invasion, chlorophyll concentration in Suisun Bay has dropped dramatically (Cloern 2019; Hammock et al. 2019), and Suisun now typically has lower chlorophyll concentrations than upstream regions in the Central and South Delta (Jassby 2008; Bosworth et al., this issue). Because of this decline in phytoplankton and zooplankton biomass, fish communities in the Suisun region now rely on transport of high densities of freshwater copepods, such as *P. forbesi*, from upstream to subsidize the food web (Kimmerer et al. 2018a; Kimmerer et al. 2018b).

The environmental conditions in each location—such as salinity, turbidity, dissolved oxygen, and temperature—can determine zooplankton presence. The distribution and abundance of many zooplankton species are strongly correlated to salinity gradients across the estuary (Ambler et al. 1985; Rollwagen–Bollens et al. 2011; Bollens et al. 2014), though inter-specific interactions may also control zooplankton distributions (Kayfetz and Kimmerer 2017). While many environmental and biological factors interact to influence zooplankton distribution, the salinity gradient is the factor that changes most dramatically during droughts (Hutton et al. 2017; Bosworth et al., this issue), so it is the most likely cause of zooplankton shifts during droughts.

Most zooplankton move with prevailing currents, although some taxa can use vertical migration to exploit vertical gradients in current speed and direction to position themselves in the estuary (Kimmerer et al. 1998). When seasonal abundances decrease in a particular geographic region of the estuary, it could represent either local changes in zooplankton production, changes to predation pressure and other mortality factors, or changes to transport of zooplankton from one region to another. For example, spatial subsidies of freshwater zooplankton from the Delta to Suisun Bay and Suisun Marsh are reduced during low-flow conditions (Kimmerer et al. 2018a; Kimmerer et al. 2019).

To better understand how years of drought affect zooplankton in the estuary, we examined three questions in relation to four of the most abundant taxa in the study area.

1. Do zooplankton taxon abundances change regionally between Drought and Wet years?

2. To what extent does salinity drive the presence and abundance of each taxon?

3. Do Drought years affect the abundance of each taxon within their primary salinity zone (the salinity zone in which they are the most abundant)?

METHODS

Target Taxa

We used four abundant target taxa in our analysis: the mysid *Hyperacanthomysis longirostris*, the calanoid copepod *Pseudodiaptomus forbesi*, the cyclopoid copepod *Limnoithona tetraspina,* and the cladoceran *Daphnia* spp.

Hyperacanthomysis longirostris, formerly described as *Acanthomysis bowmani* (Modlin and Orsi 1997), is a mysid shrimp native to the Ariake Sea in Japan (Suzuki et al. 2009). It was first documented in the estuary in 1993, where it was most likely

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introduced via ballast water (Modlin and Orsi 1997). After its introduction, *H. longirostris* quickly became the most abundant mysid in the estuary, replacing the native mysid, *Neomysis mercedis*, as the dominant catch in the CDFW EMP Zooplankton Survey and Fall Midwater Trawl mysid trawls (Avila and Hartman 2020; Barros 2021; Burdi et al. 2022). *Hyperacanthomysis longirostris* is found throughout the upper estuary, at higher temperatures and salinities than *N. mercedis*, and is smaller at maturity than the native *N. mercedis.* (Avila and Hartman 2020). *Hyperacanthomysis longirostris* abundance is usually highest in the summer (June–August), with lower abundances in fall, winter, and spring (Barros 2021). This species is relatively under-studied in the estuary; however, it has been shown to play an important role in fish diets, particularly Longfin Smelt (Lojakovic Burris et al. 2022).

The introduced calanoid copepod *P. forbesi* was first detected in 1988, and quickly became the most abundant calanoid in the upper estuary, generally replacing the once abundant *E. affinis* as the primary copepod prey of the endangered Delta Smelt (Moyle 1992; Slater and Baxter 2014; Slater et al. 2019). The introduction of another species in 1993, the predatory calanoid copepod *Acartiella sinensis*, is hypothesized to have narrowed the range of *P. forbesi* away from the LSZ and toward the freshwater zone of the upper estuary because of its predation on *P. forbesi* nauplii. (Slaughter et al. 2016; Kayfetz and Kimmerer 2017).

Limnoithona tetraspina is a brackish water cyclopoid copepod that was also introduced in 1993 (Orsi and Ohtsuka 1999), and rapidly became the most abundant copepod in the LSZ, especially during summer and fall (Bouley and Kimmerer 2006). Because of their high abundance, the total biomass of *L. tetraspina* in the estuary is similar to that of the larger calanoids *Eurytemora affinis* and *P. forbesi* combined, despite individual *L. tetraspina* being approximately one-tenth the mass (Bouley and Kimmerer 2006). Because of its small size, *L. tetraspina* could be important to larval fishes, especially during their earliest, pre-larval stage (CDFW Diet Study unpublished data, see “Notes”; Sullivan et al. 2016; Jungbluth et al. 2021). However, because of the small size of *L. tetraspina,* older and larger fishes would have to eat more of them (>1,000 individuals) to achieve the same biomass intake (CDFW Diet Study unpublished data, see “Notes”; Slater et al. 2019). Despite *L. tetraspina* being the most abundant copepod in the estuary, Delta Smelt select against or do not select for it (Slater and Baxter 2014; Sullivan et al. 2016), and it is only found in low amounts in Longfin Smelt diets (Jungbluth et al. 2021). This is possibly because of the copepod’s ability to avoid visual predators as a result of their small size and ability to remain relatively motionless in the water column (Bouley and Kimmerer 2006). *Limnoithona tetraspina’s* low energetic demand and predator avoidance behavior is likely what has contributed to its success in this region (Bouley and Kimmerer 2006; Gould and Kimmerer 2010).

Daphnia spp. is a globally distributed genus of cladocerans, primarily found in freshwater. Cladocerans (mostly *Daphnia* spp. and the smaller-bodied *Bosmina* spp.) historically dominated zooplankton biomass in the freshwater reaches of the estuary, but have declined by 6% per year from 1972 to 2008 (Winder and Jassby 2011). *Daphnia* spp. have increased abundance in off-channel (floodplain and rice field) habitats (Corline et al. 2021) and in the summer to late-fall months (Turner 1966). They are omnivorous, feeding on microplankton (e.g., ciliates) and phytoplankton (Gifford et al. 2007), but tend to provide lower nitrogen and fatty acid concentrations to fish predators compared to copepods (Kratina and Winder 2015). *Daphnia* spp. and other cladocerans make up a large portion of diets for fishes including Chinook Salmon (Goertler et al. 2018) and Delta Smelt (Slater et al. 2019), especially during wet years and seasons.

Study Area

This study focused on the upper San Francisco Estuary, limited by Carquinez Strait to the west, and the South-Central Delta to the east (Figure 1). This includes the regions of Suisun Bay, Suisun Marsh, the confluence of the Sacramento and

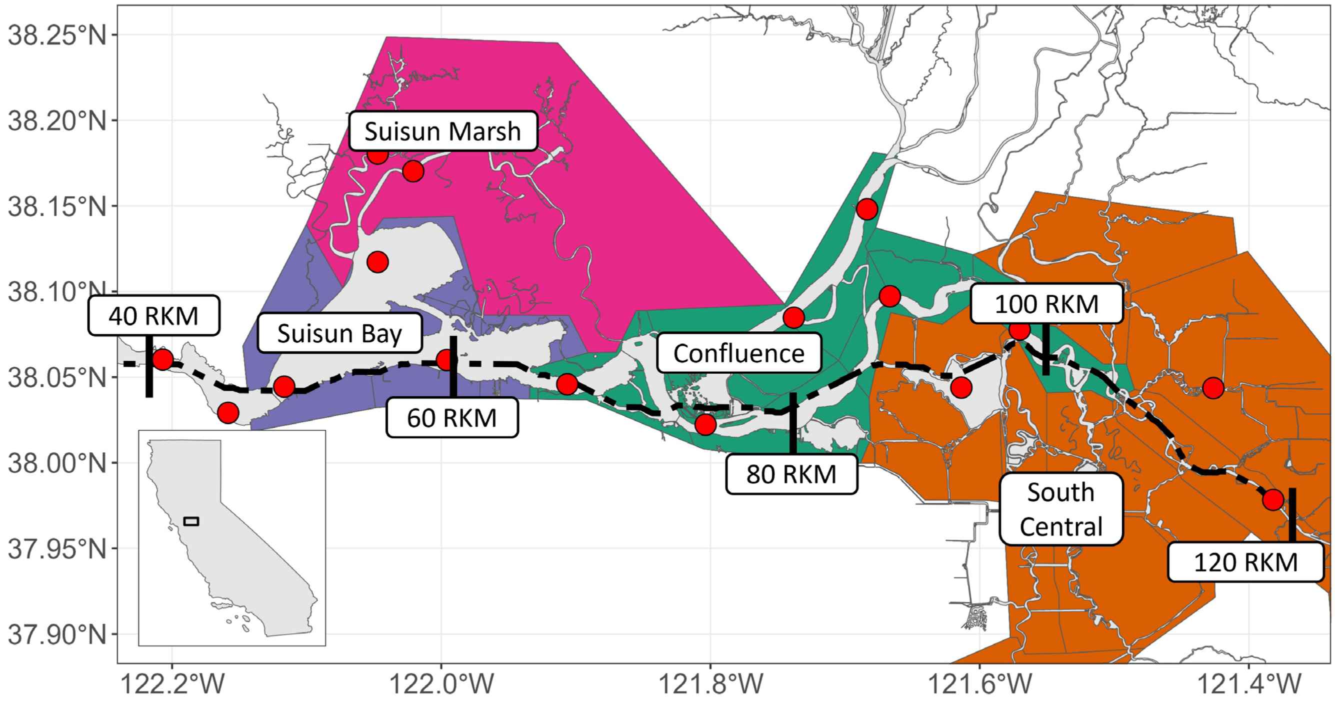

Figure 1 Map of sampling regions and stations (*red dots*) with the *dashed line* representing in-river distance from the farthest up-river station to the Golden Gate Bridge. RKM values represent distance in river kilometers to the Golden Gate Bridge.

San Joaquin rivers (confluence), and the South-Central Delta. One defining characteristic of most estuaries is their wide salinity range, which varies depending on the amount of fresh water entering the estuary from upstream sources (Kimmerer 2004). In the summer and fall, especially during Drought years, brackish water >2 ppt salinity can extend above the confluence. However, during Wet years with especially high outflows, the brackish water zone can be pushed further downstream, into Suisun Bay and Suisun Marsh.

Biomass Calculations

We downloaded zooplankton abundance (organisms m^{-3}) data for the CDFW EMP Zooplankton Survey using the 'zooper' package (*https://github.com/InteragencyEcologicalProgram/zooper*), an R package that synthesizes zooplankton data from multiple monitoring surveys (Bashevkin et al. 2022). We used abundance data from either the macro (500- to 505-µm mesh net tow), meso (150- to 160-µm mesh net tow), or micro (pumped into a 43-µm mesh net) gears, depending on which gear sampled each taxon most efficiently (Kayfetz et al. 2020). We then calculated adult biomass (carbon weight, µg m^{-3}) utilizing the conversions in Bashevkin et al (2022) for mesozooplankton (*P. forbesi* and *Daphnia* spp.) and microzooplankton (*L. tetraspina*), and the biomass for macrozooplankton (*H. longirostris*) using length-to-weight equations (Burdi et al. 2022). We focused on data from 1994 to 2021 since that is when all the examined taxa were present in the estuary and excluded winter months (December through February) because of inconsistent historical winter sampling. Sampling stations were assigned to regions (Suisun Marsh, Suisun Bay, the confluence, the North Delta, and the South-Central Delta using the 'deltamapr' package (Bashevkin 2021). Data from the North Delta were subsequently excluded because of lack of consistent long-term zooplankton sampling in the region.

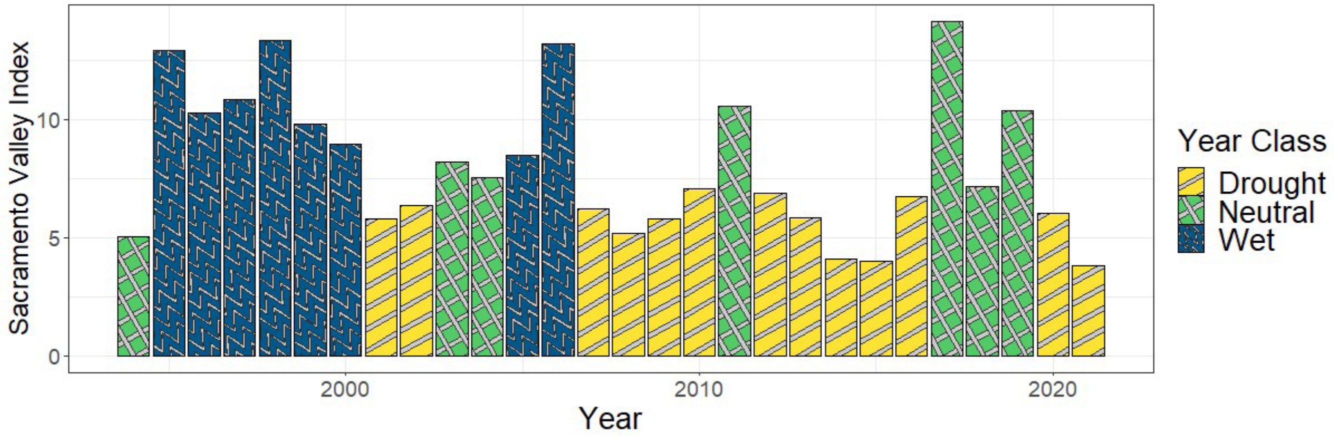

Figure 2 Water years classified as "Drought," "Normal," or "Wet" based on the Sacramento Valley Water Year Hydrologic Index (SVI). "Drought periods" are identified as having multiple years in a row with an SVI classification of Dry, Below Normal, or Critical; "wet periods" as having multiple years in a row with an SVI of Wet or Above Normal.

We downloaded SVI classifications from the California Department of Water Resources Data Exchange Center (*https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST*). We applied the term "drought periods" when multiple years in a row were classified as Dry, Below Normal, or Critical based on the SVI. We applied the term "wet periods" to multiple years in a row classified as Wet or Above Normal based on the SVI (Figure 2). For this paper, we only compared drought periods and wet periods. Years that did not fall into either category (i.e., "neutral" periods) did not have consecutive years of either type and were not included in analysis. It is important to note that drought indices are based on annual precipitation in the watershed, whereas the actual effects in the estuary are related to seasonal inflow. The link between inflow and precipitation is almost entirely human-managed since most of the Delta inflow originates from reservoir releases (Kimmerer 2004; Brown and Bauer 2010). Thus, the effects we may attribute to drought indices actually reflect the effects of drought management, rather than the result of natural variability.

Modeling

To analyze regional abundance differences between Drought and Wet years, we averaged biomass data for each of the four study taxa for each region and year. Because of the abundance of all taxa examined being highest during the warmer months (Barros 2021), our yearly averages only included samples collected from May through November of each year. Then, for each taxon and region combination, we conducted analysis of variance on the natural log-transformed yearly biomass averages for Drought years vs. Wet years.

To examine the effect of salinity on biomass, generalized additive models (GAMs) were fit for sample-level biomass and salinity data using the 'mgcv R' package (v1.8-34; Wood 2011). GAMs allow the use of smoothers that can model non-linear relationships ("splines") between a response and a predictor variable while making no assumptions about the shape of the curve. Splines are constructed from a number of component basis functions, and the number of component basis functions (k) controls the complexity of the smooth (the "wiggliness" of the curve). Thus, splines with higher basis dimensions are allowed to produce more wiggly curve shapes, while lower basis dimensions are constrained to smoother curve shapes. The number of basis functions was set to the default for salinity, and 5 for month, since each dataset contained data from 6 months.

Because of the high frequency of zero abundances in our dataset, we ran two different GAMs for each taxon. The first model for each taxon was a presence/absence binomial GAM, while the second model was a biomass negative-binomial GAM, using only samples that had the target taxon present. For all taxa, the binomial model was:

$$m1 : Presence \sim f(salinity) + f(year\ type) \qquad \text{Eq 1}$$

where the response variable is the presence of the target zooplankton taxon and the predictor variables are smooth functions of the salinity measured during sampling and the water year type (Drought or Wet). For all the taxa except *Daphnia* spp., the second model was:

$$m2 : \ln(BPUE) \sim f(salinity) + f(month) + f(year\ type) \qquad \text{Eq 2}$$

where the response variable was the natural log of the biomass and the predictor variables are smooth functions of the salinity, month, and year type. Month was included as a predictor variable because zooplankton biomass varies with seasonal cycles.

Because of regional differences in the abundance of *Daphnia* between the Sacramento and San Joaquin rivers (i.e., geographic variability unattributable to salinity), we included station as a random effect in its abundance model:

$$m2\ Daphnia\ \text{spp.} : \ln(BPUE)\, f(salinity) + f(month) + f(year\ type) + (1|station) \qquad \text{Eq 3}$$

For each taxon, we generated model predictions for each of the two models, multiplied together, and plotted with 95% confidence intervals to visualize trends. To visualize and check the dispersion and deviance of residuals, as well as the dispersion of response against fitted values, we generated diagnostic plots using the "*gam.check()*" call from the 'mgcv' package.

To determine how drought may affect zooplankton biomass, we first calculated each taxon's primary salinity zone, or the range of salinity values in which the taxon was most abundant. If significant changes in biomass occurred within that salinity range between Drought years and Wet years, we could conclude that something other than expansion or contraction of their primary salinity zone in the estuary was driving variation in biomass between year types. Using the 'hdrcde' R package (Hyndman et al. 2021) we calculated the highest-density regions, encompassing 80% of the predicted density under the model predictions for each taxa to determine their primary salinity zone. Since year type was included as a factor in the model, we calculated separate sets of primary salinity zones for drought and wet periods. To reconcile these into one primary salinity zone for each taxa, we averaged the salinity zone boundaries across Wet and Dry years.

We used an ANOVA to test for significant differences in mean monthly biomass within the taxon's primary salinity range between Drought and Wet years. Finally, we plotted the distribution of each taxon's primary salinity zone across the estuary during Dry and Wet years to further examine how these zones changed across the estuary. The geographic distribution of the primary salinity zone for each taxon is limited by the extent of the study, which extends from Carquinez Strait to just outside the Port of Stockton (Figure 1).

RESULTS

Regional Drought Effects

We found several regional differences in zooplankton biomass between Drought and Wet years (Figure 3), but not for all taxa and not across all regions. The abundance of *Daphnia* spp. decreased in Suisun Marsh (-89.7%) and Suisun Bay (-93.3%) during Drought years but did not change in the upstream regions. The abundance of *L. tetraspina* increased in Suisun Marsh (208.5%) and the confluence (102.8%), and the mysid *H. longirostris* also increased in biomass density in the confluence (110.1%) during Drought years. The calanoid copepod *P. forbesi* increased in abundance during Drought years in the upstream regions (South-Central = 64.2%) but decreased in the downstream regions (Suisun Marsh = -67.4%, Suisun Bay = -73.7%).

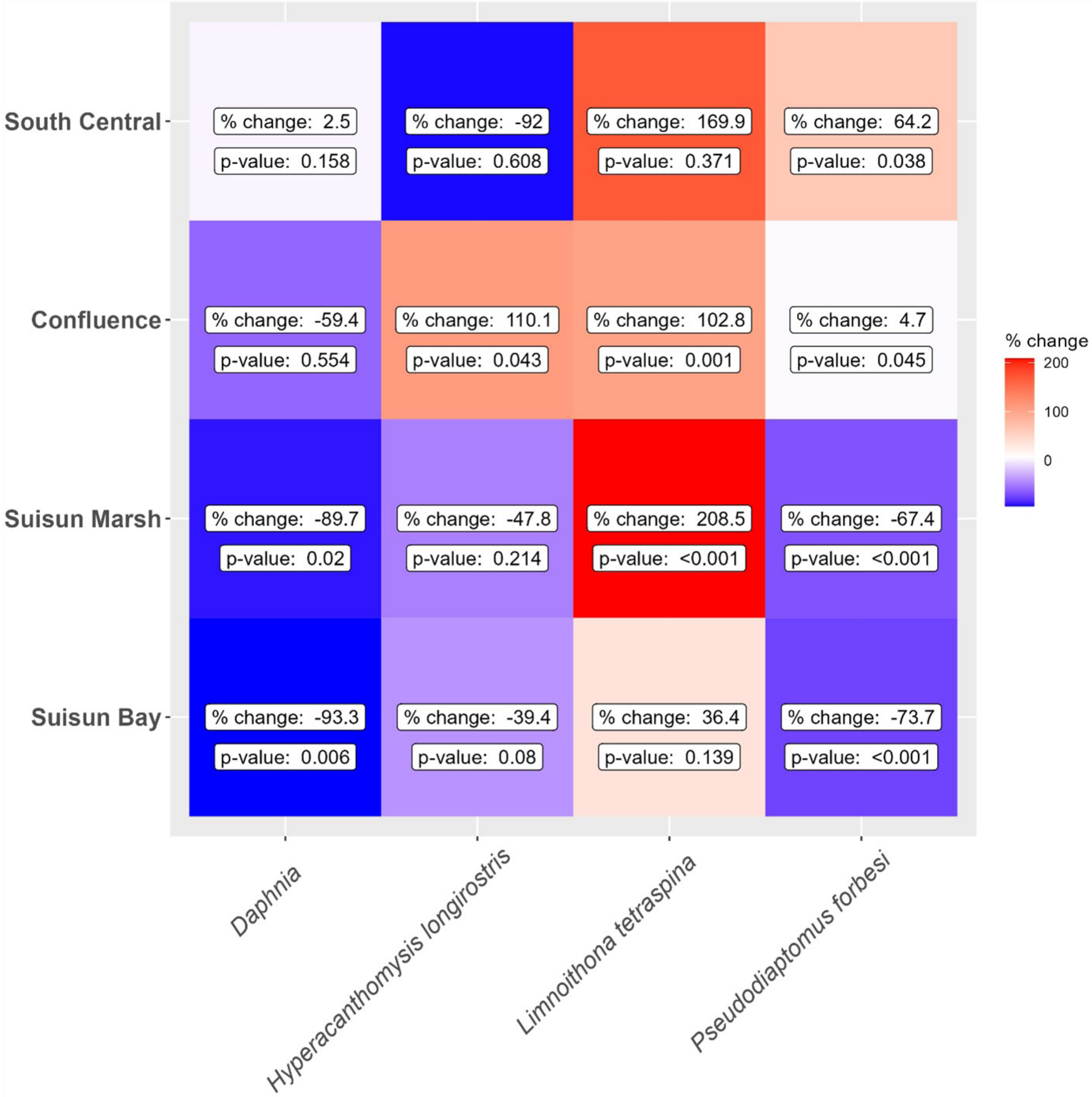

Figure 3 Changes in average annual biomass for target taxa and each analyzed region. Percent change shown represents the average change in biomass from Wet to Drought years. *Red shading* represents an increase, *blue shading* represents a decrease in abundance.

Salinity as a Driver

Salinity was an important factor in predicting the presence and abundance of all taxa in the study area, though it did not explain the majority of the variation (Table 1). For the studied taxa, salinity had the greatest effect on *Daphnia* spp. presence (adjusted $r^2 = 0.239$), likely because of *Daphnia*'s restriction to a narrow freshwater range (Figure 4). The presence of *P. forbesi* had a weaker correlation with salinity (adjusted $r^2 = 0.030$) and had a wider distribution from freshwater (<1 ppt) through the LSZ. However, its highest abundances were in the freshwater regions. Both *H. longirostris* and *L. tetraspina* had a wide salinity range correlated with higher abundances that stretched across the LSZ, with *L. tetraspina* having consistently high abundances up to 12.8 ppt.

Drought and Salinity Zones

Daphnia spp. had the smallest primary range of salinity, with the highest abundances in salinities below 0.9 ppt (Figure 5). *Pseudodiaptomus forbesi* was also most abundant in fresher water up to 3.5 ppt. Both *L. tetraspina* and *H. longirostris* had

Table 1 Model outputs for the relationship between biomass per unit effort (biomass), salinity, and year type for each taxon

H. longirostris	**Formula: presence ~ s(salinity) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.179	0.026
Salinity	<0.001	
H. longirostris	**Formula: biomass ~ s(salinity) + s(month, k = 5) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	<0.001	0.083
Salinity	<0.001	
Month	<0.001	
Daphnia	**Formula: presence ~ s(salinity) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	<0.001	0.239
Salinity	<0.001	
Daphnia	**Formula: biomass ~ s(salinity) + s(month, k = 5) + s(Station) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.214	0.184
Salinity	<0.001	
Month	<0.001	
Station	<0.001	
P. forbesi	**Formula: presence ~ s(salinity) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.01	0.03
Salinity	<0.001	
P. forbesi	**Formula: biomass ~ s(salinity) + s(month, k = 5) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.0985	0.188
Salinity	<0.001	
Month	<0.001	
L. tetraspina	**Formula: presence ~ s(salinity) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.008	0.0275
Salinity	<0.001	
L. tetraspina	**Formula: biomass ~ s(salinity) + s(month, k = 5) + s(Year Type)**	
Coefficient	P value	R-sq
Drought	0.145	0.343
Salinity	<0.001	
Month	<0.001	

their highest abundances in the brackish regions, while being found across a wide range of salinity values (*L. tetraspina* 1.4 to 12.6 ppt; *H. longirostris* 0.8 to 8.7 ppt).

Within their primary salinity zone, both *L. tetraspina* and *H. longirostris* were affected by drought, but in different ways. *L. tetraspina* increased in abundance an average of 62% during Drought years, while *H. longirostris* average biomass decreased by 30% (Table 2, Figure 6). Drought had no significant effect on the average annual biomass of the other two taxa within their primary salinity range.

The primary salinity zones of both *Daphnia* spp. and *P. forbesi* moved upriver during Drought years, shifting out of Suisun Bay and Marsh and into the confluence and South-Central Delta (Figure 6). *Limnoithona tetraspina* and *H. longirostris* had little change in their primary salinity zones, which stayed around the Suisun region during both Wet and Drought years.

DISCUSSION

To answer questions about how increasing severity and frequency of drought conditions may influence zooplankton species in the estuary, we examined how the distribution and abundance of four taxa changed during periods of drought. While initial analysis of the effects of drought on zooplankton abundance did not show changes at an estuary-wide level (IEP Drought Synthesis 2023), analysis at the regional level did show important effects. To further investigate the relationship between drought and zooplankton abundance, we narrowed our focus to specific key zooplankton taxa, their abundance correlation to salinity, and how that potentially fluctuated between Drought and Wet years.

Regional Changes to Abundance

We did not see a change in abundance for our examined taxa during Drought years on an estuary-wide scale (IEP Drought Synthesis 2023); however, all four taxa did have changes in abundance at the regional scale. *Daphnia* spp. saw decreases in abundance downstream in the

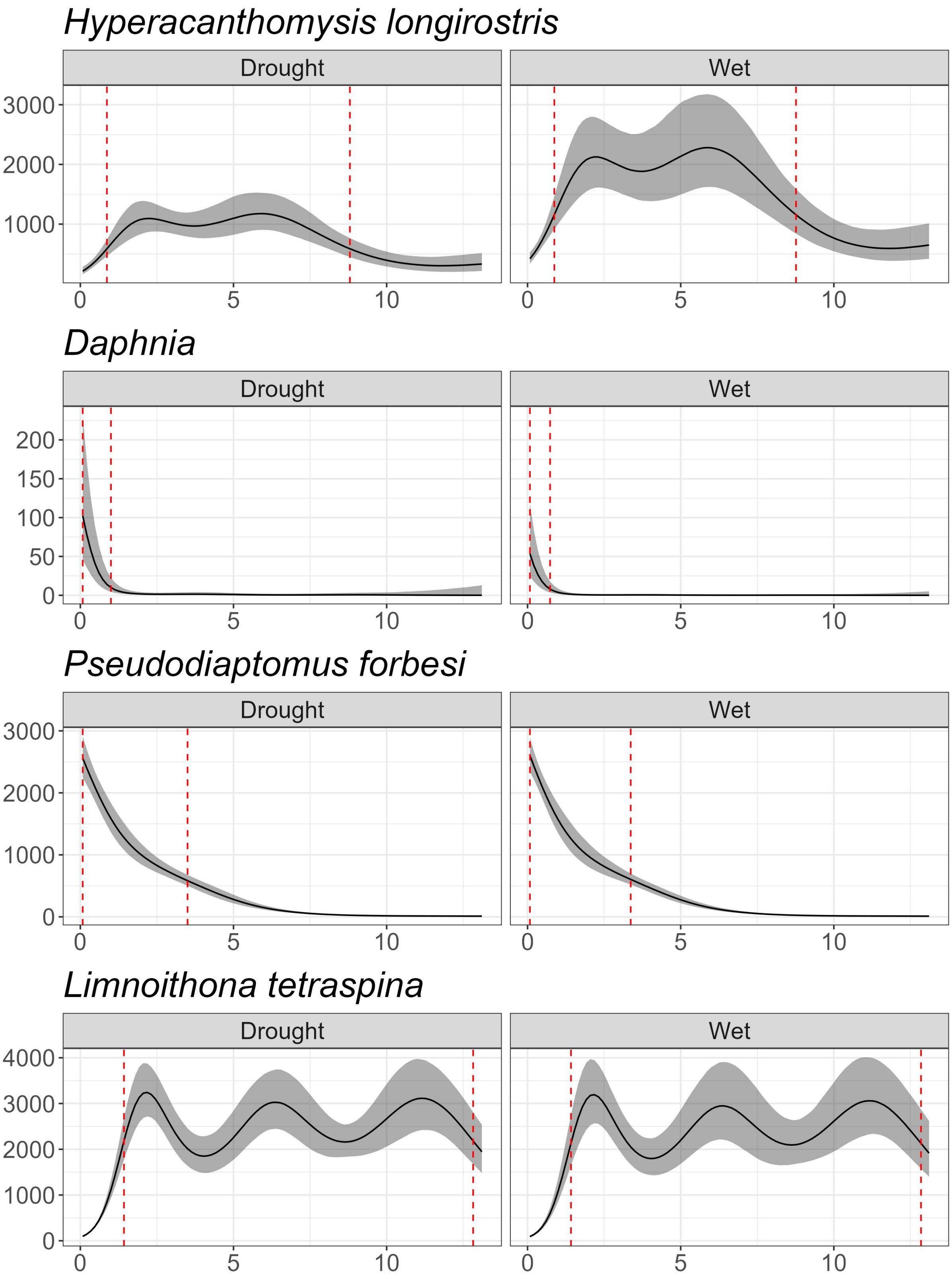

Figure 4 Model predictions for the effect of salinity on combined predictions from the presence/absence and abundance models (i.e., predicted probability of presence was multiplied by predicted abundance given presence) for all four taxa. *Vertical red dashed lines* indicate the minima and maxima of the highest-density region that encompassed 80% of the predicted density.

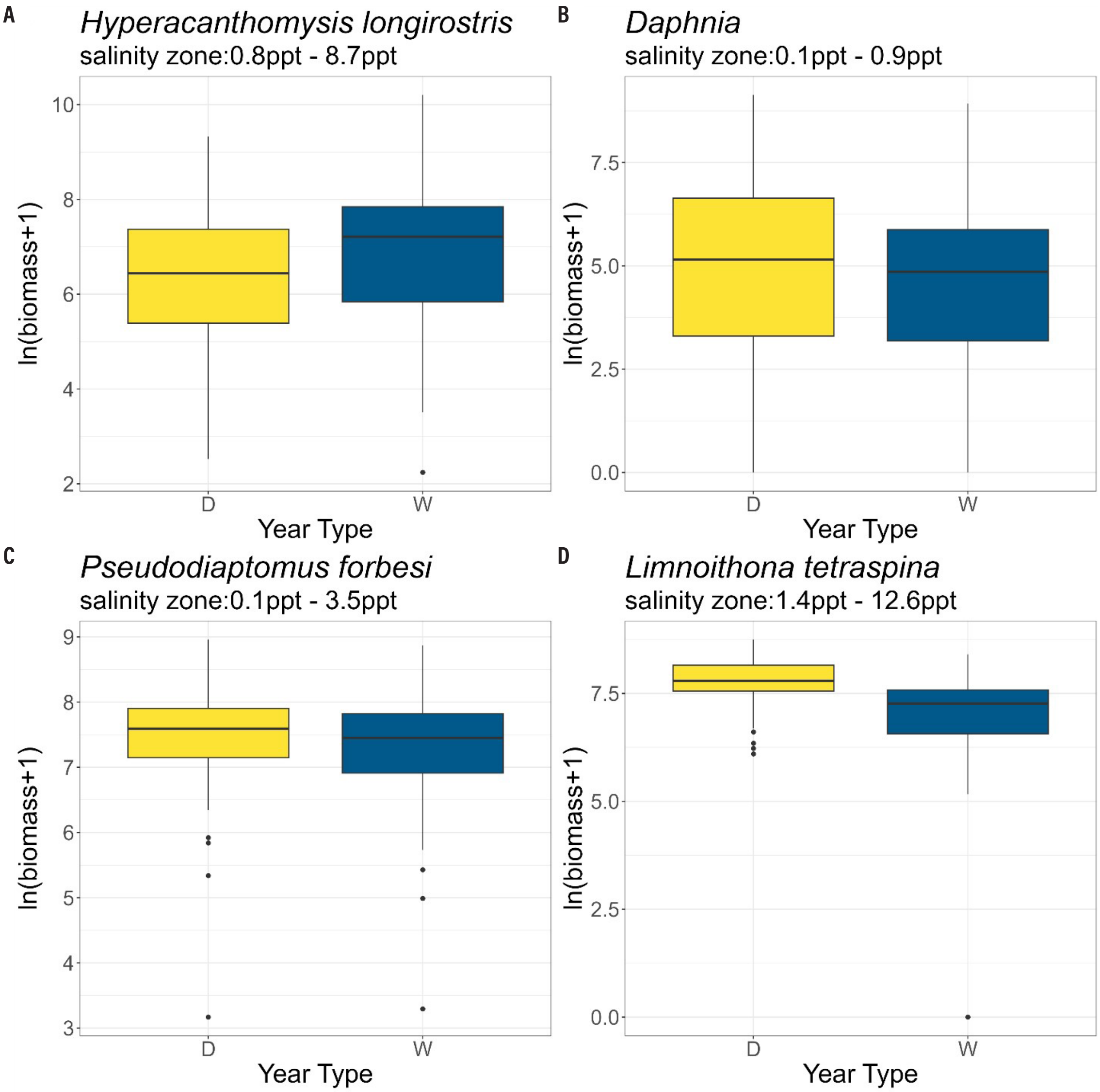

Figure 5 Boxplots of each taxon's average annual biomass within their primary salinity zone for Drought and Wet years

Table 2 ANOVA model (log (biomass + 1) ~ Drought) outputs and Tukey Honestly Significant Difference (HSD) comparisons of biomass between Drought and Wet years within the primary salinity zone for each taxon

Taxon	Primary salinity zone	ANOVA F value	W-D Tukey P value
H. longirostris	0.8–8.7 ppt	5.579	0.020
Daphnia	0.1–0.9 ppt	1.725	0.191
P. forbesi	0.1–3.5 ppt	2.145	0.145
L. tetraspina	1.4–12.6 ppt	22.120	<0.001

Suisun Marsh and Suisun Bay regions (Figure 3). The abundance of *P. forbesi* also decreased downstream, although it also increased in abundance upstream in the South-Central Delta during Drought years (Figure 3). *L. tetraspina* and *H. longirostris* only increased in abundance during Drought years, specifically in Suisun Marsh and the confluence (Figure 3). The increased density of *H. longirostris* during Drought years contrasts with the native *N. mercedis,* which decreased during Dry years (Siegfried et al. 1979). However, this relationship of *N. mercedis* with drought was quantified before the introduction

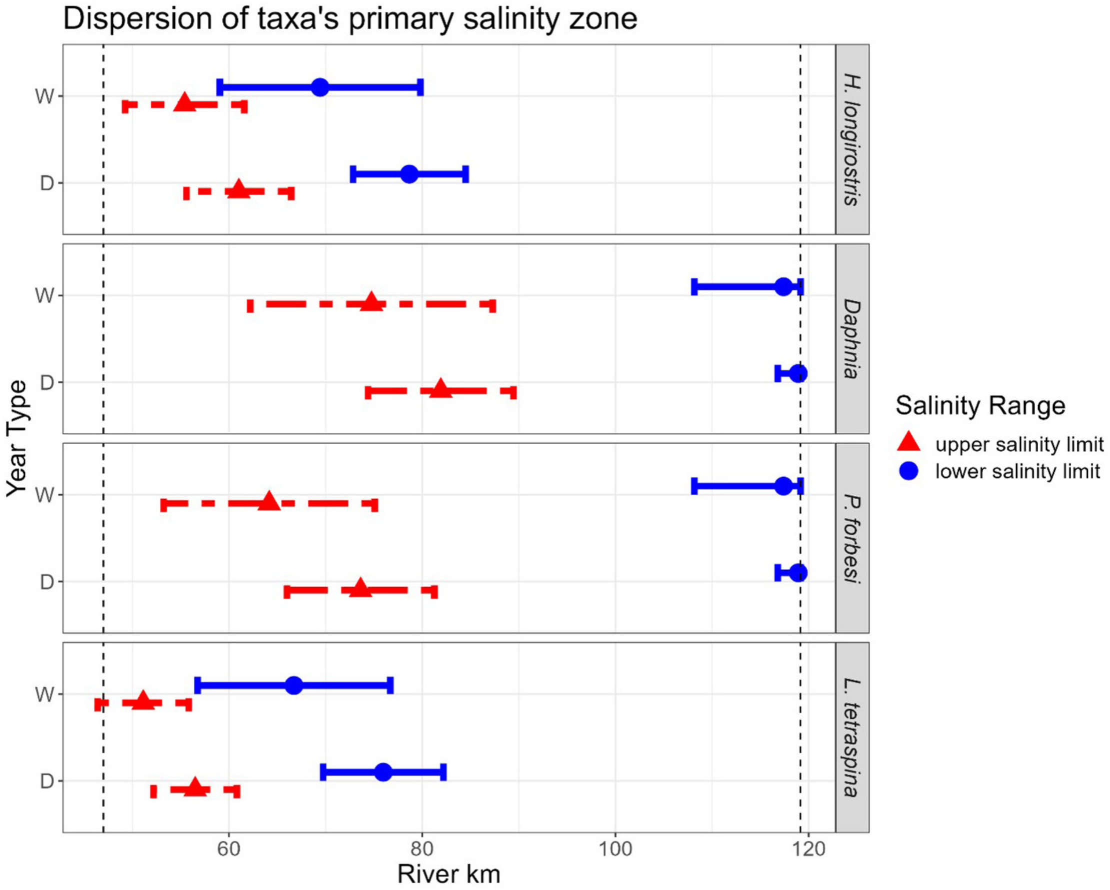

Figure 6 Spatial distribution of each taxon's *primary* salinity zone for Drought and Wet years. *Vertical dashed lines* represent the up- and down-stream extents of the study area. *X*-axis represents river kilometer (RKM) distance from the Golden Gate bridge. The *red dashed lines* represent the variable range of RKM distribution for that taxon's *upper* primary salinity limit (Figure 4) across years, and the *blue solid lines* represent the range of RKM distribution for that taxon's *lower* primary salinity limit across years. Refer to Figure 1 for geographic distribution based on RKM.

of *H. longirostris*, when *N. mercedis* was the most abundant mysid in the estuary (Siegfried et al. 1979).

Shifts with Salinity

Our modeling showed that salinity affected the presence and abundance of the four taxa we investigated (Figure 4). This is supported by prior research in the estuary that showed similar relationships between other zooplankton species and salinity (Ambler et al 1985; Orsi and Mecum 1986). Both *H. longirostris* and *L. tetraspina* had high probability of presence and high abundance within a wide range of salinity values that spanned the LSZ, while *Daphnia* spp. and *P. forbesi* were both limited to the upper, more freshwater reaches of the estuary. This aligns with previous research showing that *H. longirostris* and *L. tetraspina* are present across a broad range of salinity (Bouley and Kimmerer 2006; Avila and Hartman 2020), while *Daphnia* spp. is more restricted to freshwater (Gonçalves et al. 2007; Kayfetz and Kimmerer 2017).

During Drought years, when freshwater flows are low, the primary salinity zone of *P. forbesi* shifts upstream of Suisun Bay and Marsh (Figure 6). The lack of a change in biomass of *P. forbesi* within their primary salinity zone (Figure 6), coupled with the observed regional changes, suggests that the highest densities of this taxa shift up and down the estuary along with the salinity gradient. Kimmerer et al. (2018b) found a similar trend with a correlation between *P. forbesi* abundance and flow in Suisun during periods of high freshwater flow, but no correlation between flow and abundance in more consistently freshwater regions. While the upstream shift in the primary salinity zone of *P. forbesi* is correlated with its decreased abundance in Suisun Bay and Suisun Marsh and the confluence during Drought years, other factors may also have contributed. One potential mechanism for decreased abundance of *P. forbesi* and other zooplankton taxa in Suisun Bay and Suisun Marsh is the presence of the clam *P. amurensis* (Winder et al. 2011; Crauder et al. 2016), which both competes with the mesozooplankton for microplankton prey (Alpine and Cloern 1992), and also consumes the nauplius larvae of copepods (Kimmerer et al. 1994). Kimmerer et al. (2014) found that *P. forbesi* is food-limited in the LSZ in both Wet and Dry years, and both abundance and grazing rates of *P. amurensis* increase during Drought years (Hartman, Twardochleb et al., this issue), putting greater strain on the limited food supply for copepods.

Our examination showed that when flows are low in Drought years, the distribution of *Daphnia* spp. within the estuary is limited to upstream areas. Similar to *P. forbesi*, the primary salinity zone of *Daphnia* spp. narrowed within our study region during Drought years, resulting in a significant decrease in their abundance downstream. Orsi and Mecum (1986) found that *Daphnia* spp. abundance was positively correlated with chlorophyll, negatively correlated with salinity, and unrelated to flow. Chlorophyll in the South Delta increases during droughts, but the region is far enough upstream to see little change in salinity (Bosworth et al., this issue) so we expected increases in *Daphnia* spp. abundance. However, the expected increases in *Daphnia* spp. abundance did not occur in the South Delta during Drought years (Figure 3).

Unlike *P. forbesi* and *Daphnia* spp., *L. tetraspina* and *H. longirostris* abundance in the estuary did not significantly decrease during drought. *H. longirostris* did trend toward decreasing during droughts in three regions, but significantly increased during droughts in the confluence. *L. tetraspina* increased during droughts in all regions, but the change was only significant for the confluence and Suisun Marsh regions. When we examined changes in zooplankton abundance within only their primary salinity zones, *L. tetraspina* was the only one of our study taxa that showed an increase in abundance (~35% increase) during Drought years. *Hyperacanthomysis longirostris* saw the reverse effect, with abundance decreasing within its primary salinity zone during Drought years. Relatively little research has been conducted on *H. longirostris* to date, but they appear to have a greater temperature tolerance and smaller size at maturity than native mysids such as *N. mercedis*, resulting in an advantage over the native species (Avila and Hartman 2020). Like *L. tetraspina, H. longirostris* was more abundant in brackish water (Avila and Hartman 2020), compared to *P. forbesi* and *Daphnia* spp.

While prior research suggests salinity is one of the most important drivers of zooplankton distribution in the estuary, many other factors—including temperature, turbidity, food supply, and inter-specific interactions—may also influence zooplankton distribution and abundance (Kimmerer and Lougee 2015; Merz et al. 2016; Kayfetz and Kimmerer 2017). Although a full analysis of these factors is beyond the scope of this current study, future analyses may find other drought-driven changes in the ecosystem that alter zooplankton populations.

Ecological and Management Implications

The decline of many pelagic zooplankton species has resulted in the limitation of food resources for many fish species (Sommer et al. 2007). Management decisions that will increase zooplankton require a better understanding of the factors that affect low pelagic biomass in the estuary (Brown et al. 2016). Our study has shown that drought—and the related changes to the distribution of salinity—affects the abundance of key zooplankton resources in regions of the estuary that are important for native fishes.

Spatial overlap of predators and their prey—also known as the spatial match–mismatch hypothesis—is an important factor that drives recruitment strength, which can be affected by climate conditions and climate change (Durant et al. 2007). Changes in the abundance of zooplankton in specific regions of the estuary during Drought years could affect their availability to the fish that reside in those areas. Both *P. forbesi* and *Daphnia* spp. are important food items to age-0 Delta Smelt and juvenile salmon in the estuary (Slater and Baxter 2014; Sturrock et al. 2022)—fish which have historically utilized Suisun Bay and Suisun Marsh as rearing habitat (Merz et al. 2011). Drought conditions that result in the shifting of important prey such as *P. forbesi* and *Daphnia* spp. upriver, and into the South-Central Delta, where salmon and smelt are found less frequently (Buchanan et al. 2018; Merz et al. 2011), can result in a mismatch between the fish and the prey they need to be successful.

Even though the abundance of *L. tetraspina* increased in Suisun Marsh during Drought years (Figure 3), its high occurrence in the LSZ does not necessarily mean it can sustain fish populations. Because of its small size and therefore low nutritional value, fishes have to eat more of them to achieve the same biomass intake. Even though it now accounts for 95% of the adult copepod abundance and roughly 35% of copepod biomass in the LSZ (Merz et al. 2016; Barros 2021), it is not selected for by age-0 Delta Smelt (Slater and Baxter 2014; Slater et al. 2019), and appears to be selected against by larval Longfin Smelt (Jungbluth et al. 2021).

While both *L. tetraspina* and *H. longirostris* saw regional increases in abundance during Drought years, this may not correlate to an ability to replace other zooplankton prey that decline during drought. The varying importance and quality of different zooplankton taxa as food resources means that overall patterns of total zooplankton biomass in the estuary may not be as useful as taxon-specific patterns when considering how drought affects food abundance for fishes. The relationship between drought, salinity, and the regional abundance of ecologically important zooplankton taxa outlined in this research helps properly inform potential management actions.

Understanding how the abundance of these four zooplankton taxa interact with salinity and drought conditions can facilitate effective management efforts that aim to increase the abundance of food resources for fishes. When considering the release of hatchery and cultured fishes, it is important to have an understanding of the abundance patterns of zooplankton resources to ensure sufficient food supply (Beauchamp et al. 2004). If hatchery fish are released into Suisun Marsh or Suisun Bay during a Drought year, they will find a decreased abundance of important food items like *Daphnia* spp. and *P. forbesi*, which have shifted upstream with the distribution of freshwater. This is particularly important to keep in mind because salmonid release sites are frequently moved downstream during dry years (Sturrock et al. 2019), and Delta Smelt experimental releases are currently being planned at a variety of sites in the upper estuary (USFWS 2020). Of course moving the release of these fishes to the South-Central Delta during droughts, where prey are more abundant, may also be counter-productive because this region is typically hotter and can produce toxic algal blooms (Lehman et al. 2017). Managers can incorporate the findings of this paper to guide decision-making on the timing and location of fish releases to try and maximize the zooplankton prey available to the released fish.

CONCLUSIONS

Managed increases in freshwater outflow through the estuary are an important action that could improve ecosystem productivity and populations of listed fish species (Sommer 2020). When considering flow management as a method to try to increase food abundance for fish, it is important to account for how the flows will drive the distribution of salinity in the estuary. During drought conditions, will releases be enough to cause changes in the salinity field to increase abundance of important zooplankton taxa in target regions? If the flow actions *do* manage to shift salinity downstream, and increase target zooplankton abundance, do they correlate with a decrease in other potentially important upstream areas? Outcomes can be taxon- and region-specific, so it is necessary for managers to be specific about what results they are aiming to achieve—and where. Our study builds upon the knowledge of the relation between zooplankton and salinity distribution in the estuary (Orsi and Mecum 1986) by incorporating the changes in salinity distribution during Drought years and that distributions relationship to the regional abundance of zooplankton.

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REFERENCES

Aha NM, Moyle PB, Fangue NA, Rypel AL, Durand JR. 2021. Managed wetlands can benefit juvenile Chinook Salmon in a tidal marsh. Estuaries Coasts. [accessed 2022 Oct 27];44:1440–1453. https://doi.org/10.1007/s12237-020-00880-4

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Estuarine Phytoplankton Dynamics. [accessed 2023 Jul 20];37:946–955. https://doi.org/10.4319/lo.1992.37.5.0946

Ambler JW, Cloern JE, Hutchinson A. 1985. Seasonal cycles of zooplankton from San Francisco Bay. Hydrobiologia. [accessed 2020 Mar 3];177–197. https://doi.org/10.1007/BF00048694

Avila M, Hartman R. 2020. San Francisco Estuary mysid abundance in the fall, and the potential for competitive advantage of *Hyperacanthomysis longirostris* over *Neomysis mercedis*. California Fish and Wildlife. [accessed 2020 Mar 3];106(1):19–38. https://doi.org/10.51492/cfwj.106.3

Barros A. 2021. Zooplankton trends in the upper SFE, 1974–2018. IEP Newsletter. [accessed 2022 May 17];40(1):5–14. Available from: https://cadwr.app.box.com/s/3fo2sh8hnyx5rv6btmu2ydsqif12zp4l

Barros A, Hobbs JA, Willmes M, Parker CM, Bisson M, Fangue NA, Rypel AL, Lewis LS. 2022. Spatial heterogeneity in prey availability, feeding success, and dietary selectivity for the threatened longfin melt. Estuaries Coasts. [accessed 2020 Mar 3]; 45:1766–1779. https://doi.org/10.1007/s12237-021-01024-y

Bashevkin SM. 2021. deltamapr: spatial data for the Bay–Delta. GitHub. [accessed 2022 May 17]. Available from: https://github.com/InteragencyEcologicalProgram/deltamapr

Bashevkin SM, Hartman R, Thomas M, Barros A, Burdi CE, Hennessy A, Tempel T, Kayfetz K. 2022. Five decades (1972–2020) of zooplankton monitoring in the upper San Francisco Estuary. PLoS ONE. [accessed 2022 May 17];17(3):e0265402. https://doi.org/10.1371/journal.pone.0265402

Beauchamp DA, Sergeant CJ, Mazur MM, Scheuerell JM, Schindler DE, Scheuerell MD, Fresh KL, Seiler DE, Quinn TP. 2004. Spatial–Temporal Dynamics of Early Feeding Demand and Food Supply for Sockeye Salmon Fry in Lake Washington. Trans Am Fish Soc. [accessed 2021 Mar 3];133:1014–1032. https://doi.org/10.1577/T03-093.1

Bollens SM, Breckenridge J, Cordell JR, Simenstad C, Kalata O. 2014. Zooplankton of tidal marsh channels in relation to environmental variables in the upper San Francisco Estuary. Aquat Biol. [accessed 2021 Sep 27];21:205–219. https://doi.org/10.3354/ab00589

Bollens SM, Breckenridge JK, Vanden Hooff RC, Cordell JR. 2011. Mesozooplankton of the lower San Francisco Estuary: spatio-temporal patterns, ENSO effects and the prevalence of non-indigenous species. J Plankt Res. [accessed 2021 Jul 30];33(9):1358–1377. https://doi.org/10.1093/plankt/fbr034

Bosworth DH, Bashevkin SM, Bouma-Gregson K, Hartman R, Stumpner EB. 2024. The anatomy of a drought in the upper San Francisco estuary: water quality and lower-trophic responses to multi-year droughts over a long-term record (1975–2021). San Franc Estuary Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art1*

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Mar Ecol Progr Ser. [accessed 2020 Mar 4];324:219–228. *https://doi.org/10.3354/meps324219*

Brown LR, Bauer ML. 2010. Effects of hydrologic infrastructure on flow regimes of California's Central Valley rivers: Implications for fish populations. River Res Appl. [accessed 2023 Jan 3];26(6):751–765. *https://doi.org/10.1002/rra.1293*

Brown LR, Kimmerer W, Conrad JL, Lesmeister S, Mueller–Solger A. 2016. Food webs of the Delta, Suisun Bay, and Suisun Marsh: an update on current understanding and possibilities for management. San Franc Estuary Watershed Sci. [accessed 2021 Jan 26];14(3). *https://doi.org/10.15447/sfews.2016v14iss3art4*

Buchanan RA, Brandes PL, Skalski JR. 2018. Survival of juvenile fall-run Chinook Salmon through the San Joaquin River Delta, California, 2010–2015. North Am J Fish Manage. [accessed 2020 Mar 16];38(3):663–679. *https://doi.org/10.1002/nafm.10063*

Burdi CE, Breining-Aday SM, 2022. SBS. 2022. Interagency Ecological Program: zooplankton and water quality data in the San Francisco Estuary collected by the Summer Townet and Fall Midwater Trawl monitoring programs. ver 2. Environmental Data Initiative. [accessed 2022 Nov 29]. *https://doi.org/10.6073/pasta/00db7da0265df448f167c823fb063a9a*

Carlton JT, Thompson JK, Schemel LE, Nichols FH. 1990. Remarkable invasion of San Francisco Bay (California USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. Mar Ecol Prog Ser. [accessed 2020 Feb 6];66:81–95. *https://doi.org/10.3354/meps066095*

[CDWR] California Department of Water Resources. 2020. California's most significant droughts: comparing historical and recent conditions. Sacramento (CA): California Department of Water Resources. [accessed 2023 Feb 6]. *https://cawaterlibrary.net/wp-content/uploads/2017/05/CalSignficantDroughts_v10_int.pdf*

Cloern JE. 2019. Patterns, pace, and processes of water-quality variability in a long-studied estuary. Limnol Oceanogr. [accessed 2022 Nov 28];64(S1):S192–S208. *https://doi.org/10.1002/lno.10958*

Cloern JE, Alpine AE, Cole BE, Wong RLJ, Arthur JF, Ball MD. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuarine Coastal Shelf Sci. [accessed 2018 Oct 7];16(4):415–429. *https://doi.org/10.1016/0272-7714(83)90103-8*

Corline NJ, Peek RA, Montgomery J, Katz JVE, Jeffres CA. 2021. Understanding community assembly rules in managed floodplain food webs. Ecosphere. [accessed 2020 Jan 27];12(2):e03330. *https://doi.org/10.1002/ecs2.3330*

Crauder JS, Thompson JK, Parchaso F, Anduaga RI, Pearson SA, Gehrts K, Fuller H, Wells E. 2016. Bivalve effects on the food web supporting Delta Smelt—a long-term study of bivalve recruitment, biomass, and grazing rate patterns with varying freshwater outflow. Reston (VA): US Geological Survey. [accessed 2021 Nov 28];216. *https://doi.org/10.3133/ofr20161005*

[CSWRCB] California State Water Resources Control Board. 2017. Scientific Basis report in support of new and modified requirements for inflows from the sacramento river and its tributaries and eastside tributaries to the Delta, Delta Outflows, Cold Water Habitat, and Interior Delta Flows. Sacramento (CA): CSWRCB. Available from: *https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/california_waterfix/exhibits/docs/PCFFA&IGFR/part2/pcffa_168.pdf*

Drought Synthesis Team. 2023. Ecological impacts of drought on Suisun Bay and the Sacramento–San Joaquin Delta. Interagency Ecological Program for the San Francisco Estuary. Technical Report 100. Sacramento (CA): California Department of Water Resources. 46 p. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=211225*

Durant JM, Hjermann DO, Ottersen G, Stenseth NC. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research. [accessed 2020 Mar 4];33(3):271–283. *https://doi.org/10.3354/cr033271*

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2020 Jan 27];348:33–46. *https://doi.org/10.3354/meps07003*

Goertler P, Jones K, Cordell J, Schreier B, Sommer T. 2018. Effects of extreme hydrologic regimes on juvenile Chinook Salmon prey resources and diet composition in a large river floodplain. Trans Am Fish Soc. [accessed 2021 Sep 7];147(2):287–299. *https://doi.org/10.1002/tafs.10028*

Gonçalves AMM, Castro BB, Pardal MA, Gonçalves F. 2007. Salinity effects on survival and life history of two freshwater cladocerans (*Daphnia magna* and *Daphnia longispina*). *Annales de Limnologie* - Int J Limnol. [accessed 2021 Nov 28];43(1):13–20. *https://doi.org/10.1051/limn/2007022*

Gould AL, Kimmerer WJ. 2010. Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in the upper San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2020 Jan 27];412:163–177. *https://doi.org/10.3354/meps08650*

Greene VE, Sullivan LJ, Thompson JK, Kimmerer WJ. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Jan 4];431:183–193. *https://doi.org/10.3354/meps09099*

Hammock BG, Moose SP, Solis SS, Goharian E, Teh SJ. 2019. Hydrodynamic modeling coupled with long-term field data provide evidence for suppression of phytoplankton by invasive clams and freshwater exports in the San Francisco Estuary. Environ Manage. [accessed 2023 Jan 4];63:703–717. *https://doi.org/10.1007/s00267-019-01159-6*

Hartman R, Bashevkin SM, Barros A, Burdi CE, Patel C, Sommer T. 2021. Food for thought: connecting zooplankton science to management in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2022 Feb 18];19(3). *https://doi.org/10.15447/sfews.2021v19iss3art1*

Hartman R, Stumpner E, Burdi C, Bosworth D, Maguire A, IEP Drought Synthesis Team. 2024. Dry me a river: ecological effects of drought in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art5*

Hartman R, Twardochleb L, Burdi CE, Wells EH. 2024. Amazing graze: shifts in jellyfish and clam distributions during Dry years in the San Francisco Estuary. San Franc Estuary Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art4*

Hunter J. 1981. Feeding ecology and predation of marine fish larvae. In: Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries. Vol 1. Seattle (WA): University of Washington Press. p. 33–77.

Hutton PH, Rath JS, Roy SB. 2017. Freshwater flow to the San Francisco Bay–Delta estuary over nine decades. (Part 1): trend evaluation. Hydrological Processes. [accessed 2020 Apr 28]; 31(14):2500–2515. *https://doi.org/10.1002/hyp.11201*

Jassby A. 2008. Phytoplankton in the Upper San Francisco Estuary: Recent biomass trends, their causes and their trophic significance. San Franc Estuary Watershed Sci. [accessed 2020 Jan 27];(6)1. *https://doi.org/10.15447/sfews.2008v6iss1art2*

Jassby AD, Kimmerer WJ, Monismith SG, Armor C, Cloern JE, Powell TM, Schubel JR, Vendlinski TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecol Appl. [accessed 2020 Sep 25];5(1):272–289. *https://doi.org/10.2307/1942069.*

Jungbluth MJ, Burns J, Grimaldo L, Slaughter A, Katla A, Kimmerer W. 2021. Feeding habits and novel prey of larval fishes in the northern San Francisco Estuary. Environmental DNA. [accessed 2021 Oct 27];1–22. *https://doi.org/10.1002/edn3.226*

Kayfetz K, Kimmerer W. 2017. Abiotic and biotic controls on the copepod *Pseudodiaptomus forbesi* in the upper San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2021 Sep 7];581:85–101. *https://doi.org/10.3354/meps12294*

Kayfetz K, Bashevkin SM, Thomas M, Hartman R, Burdi CE, Hennessy A, Tempel T, Barros A. 2020. Zooplankton integrated dataset metadata report. IEP Technical Report 93. Sacramento (CA) California Department of Water Resources.

Kelley DW. 1965. Fish Bulletin 133: ecological studies of she Sacramento–San Joaquin Estuary. Part 1: zooplankton, zoobenthos, and fishes of San Pablo and Suisun bays, zooplankton and zoobenthos of the Delta. UC San Diego: Library – Scripps Digital Collection. p. 95-103. Available from: *https://escholarship.org/uc/item/7rb6b5xp*

Kimmerer W. 2004. Open water processes of the San Francisco Bay Estuary: from physical forcing to biological responses. San Franc Estuary Watershed Sci. [accessed 2023 Jan 6];2(1). *https://doi.org/10.15447/sfews.2004v2iss1art1*

Kimmerer W, Wilkerson F, Downing B, Dugdale R, Gross ES, Kayfetz K, Khanna S, Parker AE, Thompson JK. 2019. Effects of drought and the emergency drought barrier on the ecosystem of the California Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4]; 017(3). *https://doi.org/10.15447/sfews.2019v17iss3art2*

Kimmerer WJ. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser. [accessed 2021 Sep 27];243:39–55. *https://doi.org/10.3354/meps243039*

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Mar Ecol Prog Ser. [accessed 2022 Oct 23]; 324:207–218. *https://doi.org/10.3354/meps324207*

Kimmerer WJ, Burau JR, Bennett WA. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnol Oceanogr. [accessed 2019 June 30]; 43(7):1697–1709. *https://doi.org/10.4319/lo.1998.43.7.1697*

Kimmerer WJ, Gartside E, Orsi J. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Mar Ecol Prog Ser. [accessed 2022 Jun 1];13:81–93. *https://doi.org/10.3354/meps113081*

Kimmerer WJ, Gross ES, Slaughter AM, Durand JR. 2018a. Spatial Subsidies and Mortality of an Estuarine Copepod Revealed Using a Box Model. Estuaries Coasts. [accessed 2023 Jan 3];42(1):218–236. *https://doi.org/10.1007/s12237-018-0436-1*

Kimmerer WJ, Ignoffo TR, Kayfetz KR, Slaughter AM. 2018b. Effects of freshwater flow and phytoplankton biomass on growth, reproduction, and spatial subsidies of the estuarine copepod *Pseudodiaptomus forbesi*. Hydrobiologia. [accessed 2021 Sep 7];807(1):113–130. *https://doi.org/10.1007/s10750-017-3385-y*

Kimmerer WJ, Ignoffo TR, Slaughter AM, Gould AL. 2014. Food-limited reproduction and growth of three copepod species in the low-salinity zone of the San Francisco Estuary. J Plankt Res. [accessed 2021 July 7];36(3):722–735. *https://doi.org/10.1093/plankt/fbt128*

Kratina P, Winder M. 2015. Biotic invasions can alter nutritional composition of zooplankton communities. Oikos. [accessed 2020 Jan 27]; 124(10):1337–1345 *https://doi.org/10.1111/oik.02240*

Lehman PW, Kurobe T, Lesmeister S, Baxa D, Tung A, Teh SJ. 2017. Impacts of the 2014 severe drought on the *Microcystis* bloom in San Francisco Estuary. Harmful Algae. [accessed 2023 Jan 4];63(Suppl C):94–108. *https://doi.org/10.1016/j.hal.2017.01.011*

Lojkovic Burris ZP, Baxter RD, Burdi CE. 2022. Larval and juvenile Longfin Smelt diets as a function of fish size and prey density in the San Francisco Estuary. California Fish Wildlife Sci J. [accessed 2022 Nov 4];108:e11. *https://doi.org/10.51492/cfwj.108.11*

MacWilliams ML, Bever AJ, Gross ES, Ketefian GS, Kimmerer WJ, Franks SE, Lackey RT. 2015. Three-dimensional modeling of hydrodynamics and salinity in the San Francisco estuary: an evaluation of model accuracy, X2, and the low salinity zone. San Franc Estuary Watershed Sci. [accessed 2021 Mar 12];13(1). *https://doi.org/10.15447/sfews.2015v13iss1art2*

Mahardja B, Tobias V, Khanna S, Mitchell L, Lehman P, Sommer T, Brown L, Culberson S, Conrad JL. 2021. Resistance and resilience of pelagic and littoral fishes to drought in the San Francisco Estuary. Ecol Appl. [accessed 2023 Nov 28];31(2):1–16. *https://doi.org/10.1002/eap.2243*

Merz JE, Bergman PS, Simonis JL, Delaney D, Pierson J, Anders P. 2016. Long-term seasonal trends in the prey community of Delta Smelt (*Hypomesus transpacificus*) within the Sacramento–San Joaquin Delta, California. Estuaries Coasts. [accessed 2021 Sep 7]; 39(5):1526–1536. *https://doi.org/10.1007/s12237-016-0097-x*

Merz JE, Hamilton S, Bergman PS, Cavallo B. 2011. Spatial perspective for delta smelt: a summary of contemporary survey data. California Fish and Game. [accessed 2020 Jan 27];97(4):164–189. Available from: *https://www.baydeltalive.com/assets/06942155460a79991fdf1b57f641b1b4/application/pdf/CFG_097-4_2011-2-DeltaSmelt1.pdf*

Modlin RF, Orsi. JJ. 1997. Acanthomysis bowmani, a new species, and *A. aspera* Ii, Mysidacea newly reported from the Sacramento–San Joaquin Estuary, California (Crustacea: Mysidae). Proceedings of the Biological Society of Washington. 10(3):439–446.

Moyle PB, Brown LR, Durand JR, Hobbs JA. 2016. Delta Smelt: life history and decline of a once-abundant species in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Jan 3];14(2). *https://doi.org/10.15447/sfews.2016v14iss2art6*

Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of delta smelt in the Sacramento–San Joaquin Estuary, California. Trans Am Fish Soc. [accessed 2018 Oct 7];121(1):67–77. *https://doi.org/10.1080/1548-8659*

Nichols FH. 1985. Increased benthic grazing: and alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976–1977 drought. Estuarine Coastal Shelf Sci. [accessed 2020 Jan 27];21:379–388. *https://doi.org/10.1016/0272-7714(85)90018-6*

Orsi JJ, Mecum WL. 1986. Zooplankton distribution and abundance in the Sacramento–San Joaquin Delta in relation to certain environmental factors. Estuaries. [accessed 2020 Jan 27];9(4B):326–339. *https://doi.org/10.2307/1351412*

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankt Biol Ecol. [accessed 2020 Jan 27];46(2):128–131.

Reis GJ, Howard JK, Rosenfield JA. 2019. Clarifying effects of environmental protections on freshwater flows to–and water exports from–the San Francisco Bay estuary. San Franc Estuary Watershed Sci. [accessed 2023 Mar 1];17(1). *https://doi.org/10.15447/sfews.2019v17iss1art1*

Rollwagen-Bollens G, Gifford S, Bollens SM. 2011. The role of protistan microzooplankton in the upper San Francisco Estuary planktonic food web: source or sink? Estuaries Coasts. [accessed 2022 Jan 27];34(5):1026–1038. *https://doi.org/10.1007/s12237-011-9374-x*

Siegfried CA, Kopache ME, Knight AW. 1979. The Distribution and Abundance of *Neomysis mercedis* in Relation to the Entrapment Zone in the Western Sacramento–San Joaquin Delta. Trans Am Fish Soc. [accessed 2020 Jan 27];108(3):262–270. *https://doi.org/10.1577/1548-8659(1979)108<262:tdaaon>2.0.co;2*

Slater SB, Baxter RD. 2014. Diet, prey selection and body condition of age-0 Delta Smelt, *Hypomesus transpacificus*, in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2021 Sep 7];14(4). *http://doi.org/10.15447/sfews.2014v12iss3art1*

Slater SB, Schultz A, Hammock BG, Hennessy A, Burdi C. 2019. Patterns of Zooplankton Consumption by Juvenile and Adult Delta Smelt (*Hypomesus transpacificus*). In: Schultz AA, editor. Directed Outflow Project: Technical Report 1. Sacramento (CA): US Bureau of Reclamation, Bay–Delta Office, Mid-Pacific Region. p. 9–54.

Slaughter A, Ignoffo TR, Kimmerer W. 2016. Predation impact of Acartiella sinensis, an introduced predatory copepod in the San Francisco Estuary, USA. Mar Ecol Prog Ser. [accessed 2020 Nov 19];547. *https://doi.org/10.3354/meps11640*

Sommer T. 2020. How to respond? An introduction to current Bay–Delta natural resources management options. San Franc Estuary Watershed Sci. [accessed 2020 Jan 27];18(3). *https://doi.org/10.15447/sfews.2020v18iss3art1*

Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, et al. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries. [accessed 2023 Jan 3];32(6):270–277. *https://doi.org/10.1577/1548-8446(2007)32[270:TCOPFI]2.0.CO;2*

Sturrock AM, Ogaz M, Neal K, Corline NJ, Peek R, Myers D, Schluep S, Levinson M, Johnson RC, Jeffres CA. 2022. Floodplain trophic subsidies in a modified river network: managed foodscapes of the future? Landscape Ecology. [accessed 2022 Nov 3];44(9):433–444. *https://doi.org/10.1007/s10980-022-01526-5*

Sturrock AM, Satterthaite WH, Cervantes-Yoshida KM, Huber ER, Sturrock HJW, Nusslé S, Carlson SM. 2019. Eight decades of hatchery salmon releases in the California Central Valley: Factors influencing straying and resilience. Fisheries. [accessed 2023 Sep 12];37:2991–3009. *https://doi.org/10.1002/fsh.10267*

Sullivan LJ, Ignoffo TR, Baskerville-Bridges B, Ostrach DJ, Kimmerer WJ. 2016. Prey selection of larval and juvenile planktivorous fish: impacts of introduced prey. Environ Biol Fish. [accessed 2021 Sep 7];99(8):633–646. *https://doi.org/10.1007/s10641-016-0505-x*

Suzuki KW, Nakayama K, Tanaka M. 2009. Horizontal distribution and population dynamics of the dominant mysid *Hyperacanthomysis longirostris* along a temperate macrotidal estuary (Chikugo River estuary, Japan). Estuarine, Coastal and Shelf Science. [accessed 2022 Jun 22];83(4):516–528. *https://doi.org/10.1016/j.ecss.2009.04.023*

Tiffan KF, Erhardt JM, St. John SJ. 2014. Prey Availability, Consumption, and Quality Contribute to Variation in Growth of Subyearling Chinook Salmon Rearing in Riverine and Reservoir Habitats. Trans Am Fish Soc. [accessed 2020 Mar 16];143(1):219–229. *http://doi.org/10.1080/00028487.2013.839958*

[USFWS] US Fish and Wildlife Service. 2020. Delta Smelt supplementation strategy. US Fish and Wildlife Service, San Francisco Bay–Delta Fish and Wildlife Office. Available from: *https://www.fws.gov/project/delta-smelt-supplementation*

Winder M, Jassby AD. 2011. Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. Estuaries Coasts. [accessed 2021 Sep 27];34(4):675–690. *https://doi.org/10.1007/s12237-010-9342-x*

Winder M, Jassby AD, Mac Nally R. 2011. Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. Ecology Letters. [accessed 2019 Jun 30];14(8):749–757. *https://doi.org/10.1111/j.1461-0248.2011.01635.x*

Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology). [accessed 2022 Nov 3];73(1):3–36. *https://doi.org/10.1111/j.1467-9868.2010.00749.x*