Long-term trends in seasonality and abundance of three key zooplankters in the upper San Francisco Estuary

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Abstract (300 words)

Zooplankton provide critical food for threatened and endangered fish species in the San Francisco Estuary (estuary). Reduced food supply has been implicated in the Pelagic Organism Decline of the early 2000s and further changes in zooplankton abundance, seasonality, and distribution may continue to threaten declining fishes. While we have a wealth of monitoring data, we know little about the abundance trends of many estuary zooplankton species. To fill these gaps., we reviewed past research and then examined trends in seasonality and abundance from 1972 to present of three key but understudied zooplankton species (*Bosmina longirostris*, *Acanthocyclops* spp., and *Acartiella sinensis*) that play important roles in the estuary food web. All three species were found in the stomach contents of important estuarine fishes. We fit Bayesian generalized additive mixed models of each species' relationships with salinity, seasonality, year, and geography on an integrated database of zooplankton monitoring in the upper estuary. We found marked changes in the seasonality and overall abundance of each study species. *B. longirostris* no longer peaks in abundance in the fall months, *Acanthocyclops* spp. dramatically declined in all months and lost its strong relationship with salinity, and *A. sinensis* adult abundance has become increasingly driven by salinity while juveniles have developed wider seasonal abundance peaks. In this process, we have documented the relationship of each species with salinity and seasonality since the beginning of monitoring or their introduction, thus increasing our understanding of their ecology and importance in the estuary. These results can inform food web models, be paired with fish data to model the contributions of these species toward fish abundance trends, and be mirrored to elucidate other species' trends in future studies.

Keywords

Zooplankton, phenology, salinity, monitoring, generalized additive modeling, copepods, cladocerans, *Bosmina longirostris*, *Acanthocyclops*, *Acartiella sinensis*

Introduction

Zooplankton are critical components of aquatic food webs, connecting primary producers to upper trophic species such as fishes. Most fishes rely on zooplankton food in their larval stages when the starvation risk is highest (Hunter 1981). The seasonality of fish reproduction is often timed such that larvae coincide with peaks in the abundance of their zooplankton prey (Cushing 1969; Cushing 1990). However, when the seasonality of zooplankton abundance shifts due to climate change, species introductions, or other factors, larval starvation risk can increase as their peak abundance no longer coincides with peak food availability (Edwards and Richardson 2004; Durant et al. 2007). Thus, an understanding of the patterns in zooplankton abundance is critical to understanding the drivers of fish abundance.

The San Francisco Estuary (estuary) is home to several fish species listed under the United States Endangered Species Act and/or the California Endangered Species Act. Most depend on zooplankton prey for part or all of their life cycle. One of these species, Delta Smelt (*Hypomesus transpacificus)* is endemic to the estuary and relies on zooplankton for its full life cycle (Brown et al. 2016). Another fish, Longfin Smelt (*Spirinchus thaleichthys*), also relies on zooplankton throughout its life cycle (P. Chigbu and Sibley 1998; Paulinus Chigbu and Sibley 1998; Barros et al. 2022). A number of fish species, including Delta Smelt and Longfin Smelt, declined sharply in abundance in the early 2000s, during the "pelagic organism decline" (Feyrer et al. 2007; Sommer et al. 2007). This decline is thought to have been caused in part by reduced zooplankton food supply (Winder and Jassby 2011; Brown et al. 2016; Moyle et al. 2016).

Zooplankton research in the estuary to date has focused on a few key taxa, most notably the copepods *Pseudodiaptomus forbesi*, *Eurytemora affinis*, and *Limnoithona tetraspina*, as they are important food for threatened Delta Smelt and Longfin Smelt. (Bouley and Kimmerer 2006; Kimmerer et al. 2014; Kayfetz and Kimmerer 2017; Kimmerer et al. 2018). In floodplains adjacent to the Delta, some cladocerans have also received attention, particularly *Daphnia* spp., due to their importance in the diet of juvenile salmonids (Goertler et al. 2018; Corline et al. 2021).

One prior study has investigated changes in zooplankton phenology in the estuary. Merz et al. (2016) used a high-level approach to evaluate changes (from 1972-2014) to the date of maximum abundance of five zooplankton taxa: *E. affinis*, *Pseudodiaptomus* spp., other calanoids, cyclopoids, and non-copepods. They found that the peak abundances of all these zooplankton groups except the cyclopoids have shifted weeks to months earlier. However, analyses of the date of peak abundance can overlook the presence of multiple seasonal abundance peaks. Furthermore, the coarse taxonomic resolution of this study excluded analyses of some key species. Many members of the zooplankton community remain understudied, despite their role in the pelagic food web

In this study, we extensively review prior knowledge and derive new insights from monitoring data on three key but understudied zooplankton taxa. We chose to focus on *Bosmina longirostris*, *Acartiella sinensis*, and *Acanthocyclops* spp. (Fig. 1) due to their importance in estuarine ecology and fish diets as well as the paucity of prior studies on their dynamics in this estuary. We first review past studies from this estuary and other regions where these taxa occur, then describe the importance of each taxa in fish diets by tabulating their records in fish diets, and lastly examine their long-term trends in seasonality and abundance in the estuary by applying Bayesian generalized additive mixed models to an integrated database of zooplankton monitoring data (Bashevkin et al. 2020; Bashevkin et al. in review).

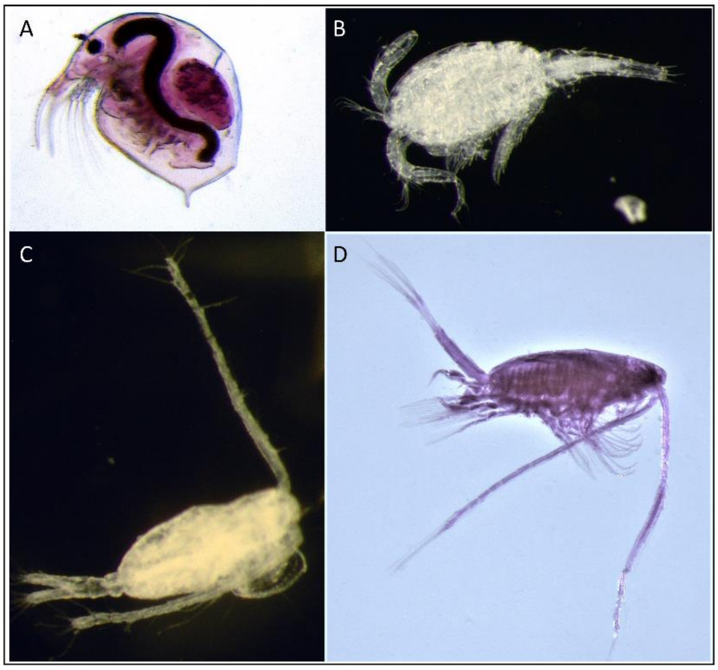


Figure 1. Photographs (not to scale) of our study species from the San Francisco Estuary. A) *Bosmina longirostris* adult (credit: CDFW Fish Restoration Program), B) *Acanthocyclops* spp. adult (credit: Tricia Bippus/CDFW), C) *Acartiella sinensis* juvenile (credit: Tricia Bippus/CDFW), D) *Acartiella sinensis* adult (credit: Michelle Avila/CDFW Fish Restoration Program).

Prior research on the study species

Bosmina longirostris

B. longirostris (Fig. 1A) is the most abundant cladoceran in the freshwater reaches of the Sacramento San Joaquin Delta (Bashevkin et al. 2020; Jeffres et al. 2020), where it has been a major component of the zooplankton community over the past 40 years (Ambler et al. 1985). Like *Daphnia* spp., it is abundant in off-channel habitat in the estuary (Corline et al. 2021), but unlike *Daphnia* spp. it is also abundant in the larger channels of the South Delta (Bashevkin et al. 2020; Jeffres et al. 2020). *Bosmina* spp. is consumed by fish in the estuary and elsewhere, including juvenile salmonids and Delta Smelt (Roegner et al. 2015; Goertler et al. 2018; Slater et al. 2019), but it rarely occurs in diets of larval Longfin Smelt (Jungbluth et al. 2021; Burris et al. in review), likely due to a mismatch in the salinity preferences of *Bosmina* spp. and Longfin Smelt. Its small size makes it generally less preferred than larger

Daphnia spp. in diets of juvenile salmon (Craddock et al. 1976; Holm and Møller 1984), and diets with high percentages of *Bosmina* spp. in juvenile perch result in low growth rates (Romare 2000). Both *Daphnia* spp. and *Bosmina* spp. tend to have lower nutritional quality (as measured by fatty acids) than copepods (Kratina and Winder 2015).

B. longirostris is a small, filter-feeding cladoceran found in lakes and rivers throughout the world, where it has received little attention due to its small body size (Adamczuk 2016). Despite its small size in comparison to members of the better-studied genus *Daphnia*, *B. longirostris* can still have a large impact on the food web. *B. longirostris* feeds broadly on phytoplankton, protists, and bacteria, ranging from 1-15 µm, and preferentially consumes algae over bacteria, when available (Balcer et al. 1984; Onandia et al. 2015)**.** *B. longirostris* is particularly effective in depressing biomass of small phytoplankton (Carpenter and Kitchell 1984) and is an efficient consumer of ciliates and bacteria (Jürgens et al. 1996), playing a key role in the microbial loop. It can also thrive on many types of cyanobacteria (Tõnno et al. 2016). *B. longirostris* is more tolerant of disturbance than many species of *Daphnia* (Hart 2004; Adamczuk 2016), with greater resistance to toxic cyanobacteria (Matveev and Balseiro 1990; Jiang et al. 2013; Jiang et al. 2014; Jiang et al. 2017), and a higher salinity tolerance than many other cladocerans (Adamczuk 2016). *Bosmina* spp. also has a higher thermal tolerance than many other freshwater zooplankton (Drenner et al. 1981; Jiang et al. 2014), leading to increasing dominance over other zooplankton as temperatures rise. *B. longirostris* typically lives 20-50 days and reproduces parthenogenically, producing 2-6 broods of 2-4 embryos each, though temperature, salinity, and predation pressure may impact life span and reproduction (Adamczuk and Mieczan 2019).

Acanthocyclops spp.

Acanthocyclops spp. (Fig. 1B) is a cyclopoid of unknown origin which occurs mostly in freshwater (Orsi and Mecum 1986). Previous studies in the estuary identified the species of *Acanthocyclops* in this region as *Acanthocyclops vernalis;* however, research in other areas discovered that *A. vernalis* is a species complex consisting of three cryptic species; *Acanthocyclops robustus*, *Acanthocyclops americanus*, and *A. vernalis* (Alekseev et al. 2002; Dodson et al. 2003; Miracle et al. 2013; Alekseev 2021). Due to possible morphological misidentifications, it is not known whether all three species in the *A. vernalis* complex are native to the estuary and were present in the past; however, Jungbluth et al. (2021) did find molecular evidence of all these species in larval Longfin Smelt diets recently collected in this region.

Before the introduction of the small cyclopoid *L. tetraspina* in 1993 (Orsi and Ohtsuka 1999), *Acanthocyclops* spp. was the most abundant cyclopoid in the estuary (Orsi and Mecum 1986). *Acanthocyclops* spp. is an important component of fish diets in this region, particularly Longfin Smelt (CDFW unpublished data; Hobbs et al. 2006; Burris et al. in review) and larval Pacific Herring (*Clupea pallasii*) (Jungbluth et al. 2021), with *Acanthocyclops* spp. being the most common cyclopoid consumed by larval Longfin Smelt (Jungbluth et al. 2021). *Acanthocyclops* spp. also has a higher nutritional value than *L. tetraspina*, and a similar fatty acid composition to that of the calanoid copepods *E. affinis* and *P. forbesi* (Kratina and Winder 2015).

While research on the ecology and biology of *Acanthocyclops* spp. is relatively limited in the estuary, the *A. vernalis* complex has been studied extensively in other regions including Europe, Russia, and the Great Lakes. Studies in these areas show that, despite the morphological similarities, *A. vernalis*, *A. robustus*, and *A. americanus* have different ecologies, life cycles, and environmental tolerances (Alekseev et al. 2002; Miracle et al.

2013; Alekseev 2021). *A. vernalis* and *A. robustus* inhabit littoral or near-benthic areas and *A. vernalis* has a benthic naupliar stage (Alekseev et al. 2002; Miracle et al. 2013) and vertically migrates at night (Evans and Stewart 1977). Both *A. vernalis* and *A. robustus* are also predatory, consuming copepod nauplii, cladocerans, rotifers, and occasionally larval fish (Anderson 1970; Kerfoot 1978; Gliwicz and Stibor 1993; Piasecki 2000). *A. americanus*, however, is pelagic throughout its lifecycle, found in varying salinities from the Mediterranean Sea (Alekseev 2021) to freshwater lakes (Alekseev et al. 2002), and is omnivorous. *A. americanus* nauplii consume primarily algae, with later life stages also consuming filamentous algae and cyanobacteria, in addition to cladocerans, nauplii, and rotifers (Enríquez-García et al. 2013; Sarma et al. 2019). All species can produce about 100 eggs per female, develop to sexual maturity in 10-14 days, and live 30-75 days depending on conditions, with *A. americanus* growing and reaching maturity faster than the others (Alekseev 2021). Species in the *A. vernalis* complex likely have different environmental tolerances, as has been shown by studies of their seasonal and spatial variation in abundance in other regions. *A. vernalis* may be more tolerant of colder temperatures than the other species, whereas *A. americanus* could have a higher temperature tolerance based on laboratory experiments and timing of peak abundance in areas outside the estuary (Alekseev 2021).

Acartiella sinensis

In the fall of 1993, the non-native calanoid copepod *A. sinensis* (Fig. 1C,D) was first detected in the estuary (Orsi and Ohtsuka 1999). Likely introduced via the ballast water of ships, the large (~1.2 – 1.5 mm in length) predatory calanoid is native to the estuaries and coasts of Southeast Asia (Shen and Lee 1963; Srinui and Ohtsuka 2015). The species has been recorded from estuaries along the East China Sea in salinities around 18-21 ppt (Shen and Lee 1963) to the brackish marshes of Thailand in salinities around 5 ppt (Srinui and

Ohtsuka 2015). In the Pearl River estuary of China, *A. sinensis* was the dominant copepod in brackish waters with salinities less than 15 ppt (Tan et al. 2004). Sampling in the Thale-Noi lake of Thailand showed changes in temperature and salinity were the main environmental variables impacting densities of *A. sinensis* in the region (Inpang 2008).

Within a year after invasion, *A. sinensis* became the second most common calanoid copepod in the upper estuary, with its highest abundances in the lower salinity zone of Suisun and the West Delta during summer and fall (Hennessy 2018). The predatory *A. sinensis* has been shown to feed on the nauplii and copepodid life stages of other copepods in the estuary, primarily those of the abundant *L. tetraspina* and *P. forbesi* (York et al. 2014; Slaughter et al. 2016; Kayfetz and Kimmerer 2017). *A. sinensis* has also become a food item for the endangered Delta Smelt, appearing in their diets in summer and fall (Slater and Baxter 2014; Slater et al. 2019).

The invasion of *A. sinensis* was not without consequence. Since the invasion in 1993, the zooplankton assemblage in the low-salinity Suisun area has shifted in trophic composition. Once dominated by herbivorous cladocerans and copepods such as *E. affinis* and *P. forbesi*, the community has become more “top-heavy” with the spread of *A. sinensis* (Kratina et al. 2014; Kratina and Winder 2015). The sustainment of *A. sinensis* in the low-salinity zone and its high predation rate on the nauplii of *P. forbesi* is linked to a shift in the distribution of *P. forbesi* out of the low-salinity zone and upriver into more freshwater habitats (Kayfetz and Kimmerer 2017). This shift in the distribution of the important *P. forbesi* could have implications for the majority of planktivorous fishes that feed on the calanoid copepod populations.

Materials and Methods

Diet data

To investigate the occurrence of our study species in fish diets, we summarized data from the California Department of Fish and Wildlife (CDFW) Diet and Condition Study (“Diet Study”, https://wildlife.ca.gov/Conservation/Delta/Special-Studies). The CDFW Diet Study identifies and enumerates gut contents of young pelagic fishes in the estuary including Delta Smelt, Longfin Smelt, Striped Bass (*Morone saxatilis)*, Threadfin Shad (*Dorosoma petenense)*, American Shad (*Alosa sapidissima)*, and other species of interest collected by various Interagency Ecological Program monitoring surveys (Slater and Baxter 2014; Hammock et al. 2017; Slater et al. 2019). Fish were weighed, measured, the guts dissected, and prey items were identified to the lowest possible taxonomic level. In some cases, prey items were heavily digested and therefore could only be identified to higher taxonomic levels than our study taxa. Thus, these prey items were not included in our data. Fishes were chosen for processing based on other study needs, so relative sample size for each fish is not correlated to abundance in the estuary, but provides some information on relative rates of zooplankton consumption for each species.

The number of fish processed, number with food in their stomachs, fork length range, and number of fish that had eaten our focal taxa were extracted from the database. To maintain the same spatial coverage as the zooplankton datasets, only fish caught in San Pablo Bay and upstream were included in this analysis.

Zooplankton data

The data used for these analyses were obtained from an integrated database of five long-term zooplankton monitoring surveys in the upper estuary. These include the Environmental Monitoring Program (EMP), 20-mm Survey (20mm), Fall Midwater Trawl (FMWT), Summer Townet (STN), and Fish Restoration Program monitoring (FRP). These surveys are described in detail in Kayfetz et al. (2020) and Bashevkin et al. (in review). Briefly, EMP samples monthly year-round since 1972, 20mm samples every other week March through July since 1995, STN samples every other week June – August since 2005, FWMT samples monthly September through December since 2011, and FRP samples annually to monthly near tidal marshes (or areas soon to be restored to tidal marshes) March through December since 2015. Each survey samples at a set of fixed stations (Fig. 2). EMP also samples at a set of moving stations (entrapment zone, EZ) at locations where the bottom conductivity is 2 and 6 mS/cm. Many of these surveys collect other parameters such as fish abundance or water quality, but only the time period of zooplankton sampling is described above. Furthermore, sampling locations and frequency have changed over time (Kayfetz et al. 2020; Bashevkin et al. in review).

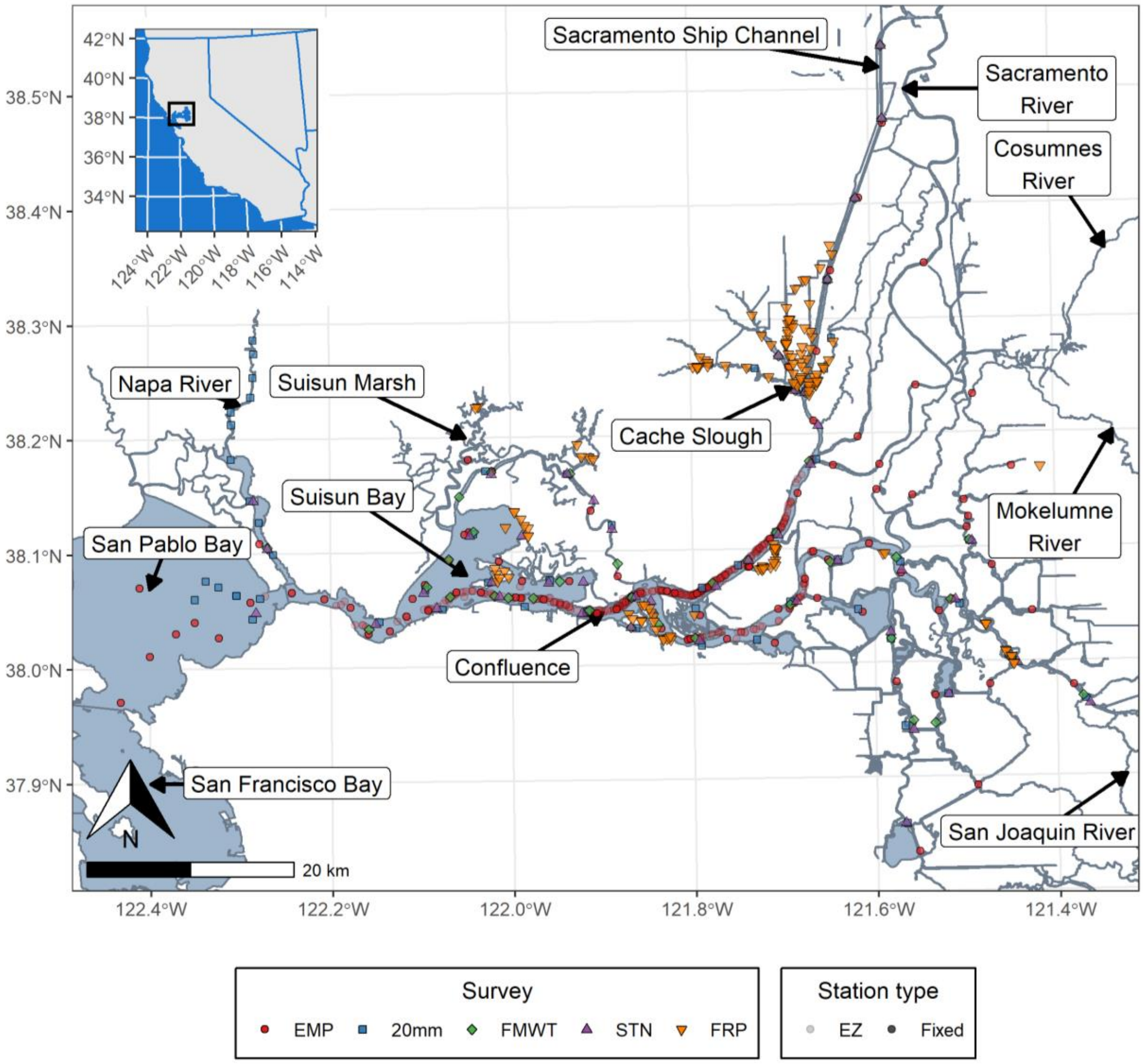


Figure 2. Map of the study area, depicting all sampling stations. Survey abbreviations are as follows: EMP = Environmental Monitoring Program, 20mm = 20-mm Survey, FMWT = Fall Midwater Trawl, STN = Summer Townet, FRP = Fish Restoration Program. The EMP survey has some non-fixed entrapment zone (EZ) stations that move with the salinity field and are depicted here with increased transparency.

The data from each survey are integrated by the R package zooper (Bashevkin 2021), which imports and standardizes the data from each survey. For the purposes of these analyses, we selected data from the mesozooplankton size-class, which corresponds to samples from the modified Clarke-Bumpus nets used by each survey, with mesh sizes of 150 – 160 µm. We selected all available data from each of our study species without missing values in our covariates. Adults and juveniles were analyzed separately since these distinct life stages have different behaviors and abundance drivers and play distinct demographic roles. *A. sinensis* was introduced to the estuary in 1993 (Orsi and Ohtsuka 1999), but adults were first counted in samples in 1994 and juveniles first counted in 2006. Thus, adult data were filtered to the start date of 1994 and juveniles to the start date of 2006. For the other species, only adult data were available at the taxonomic resolution of our analysis. The final dataset had 33,255 samples for *B. longirostris* adults, 32,026 samples for *Acanthocyclops* spp. adults, 17,189 samples for *A. sinensis* adults, and 11,224 samples for *A. sinensis* juveniles.

Exploratory data visualization revealed tighter relationships of each species' abundance with log-transformed salinity than raw salinity values. Thus, salinity was natural log-transformed for analyses. Furthermore, we centered all covariates (including log-transformed salinity) by their mean and standardized them by their standard deviation. Lastly, since many of the sampling stations from the different surveys were nearby one another (Fig. 2), we clustered all stations into groups within a 1 km radius.

Model structure

We fit Bayesian generalized additive mixed models with the R package brms (Bürkner 2017; Bürkner 2018), which uses the Bayesian modeling platform Stan (Stan Development Team 2021), as well as the R package mgcv (Wood 2011) to handle the smooth construction. Models were fit with a hurdle lognormal distribution, using the catch per unit effort (CPUE; organisms m^{-3}) of the specified taxa and life stage as the response variable. A hurdle model was used to account for the large number of 0s in the data.

Our overall approach was to model the probability of presence with a smoothed function of salinity, and the non-zero abundances with smooth functions of day of year, salinity, year, and their interactions, while accounting for space with a random intercept for each station. Our combination of a Bayesian method, which propagates uncertainty and handles unbalanced data, with a generalized additive model approach, which accounts for key covariates like salinity and seasonality, allowed us to resolve inconsistencies in the sampling designs, and incorporate both fixed stations and stations that move with the salinity field.

The hurdle probability (probability of 0 CPUE) was modeled with a cubic regression spline of salinity with a low basis dimension (k) of 5 since the relationship was expected to have a simple shape. The abundance of *Acartiella sinensis* was so strongly seasonal that we modified the hurdle component to also include seasonality. Thus, for *A. sinensis* we modeled the hurdle probability with a two-dimensional tensor product smooth of salinity (cubic regression spline, k=5) and day of year (cyclic cubic regression spline, k=4).

The non-zero CPUEs were modeled with a three-dimensional tensor product smooth of day of year (cyclic cubic regression spline, k=13), salinity (cubic regression spline, k=5), and year (cubic regression spline, k=5). The basis dimension for day of year was set to 13 to match the monthly nature of these sampling programs (since the smooth is cyclical, a basis dimension of 13 has 12 independent functions). The basis dimension for salinity was set to the low value of 5 because the relationship with salinity was expected to be a simple unimodal shape, and a basis dimension of 5 would still allow much greater complexity than that. The basis dimension for year was set to the low value of 5 because we were interested in evaluating broad long-term patterns, rather than fine-scaled year-to-year abundance trends. Thus, the results of this model represent broad long-term trends, not predicted abundances on specific years. For juvenile *A. sinensis*, the basis dimension for year was reduced to 3 since they have only been counted in samples since 2006 and thus the timeseries is shorter. We also included a random intercept for each station cluster.

We fit separate models on each species and life stage (4 total). Models were run on three chains, each for 5,000 iterations including 1,250 used for the warmup that were then discarded. We used weakly informative priors as recommended by the Stan authors (Stan Development Team 2021).

Each model was validated and checked prior to use. All models were inspected to ensure adequate sampling by verifying the posterior effective sample size (> 100 per chain) and Rhat values (< 1.05) (McElreath 2015). We further inspected visual plots comparing the model outputs to the raw data to ensure they matched. These plots included the proportion of zero values, the distribution of non-zero CPUE values, and the predicted non-zero CPUE values for each row in the dataset. We also inspected the spatiotemporal variograms for spatiotemporal autocorrelation using the R package gstat (Pebesma 2004; Gräler et al. 2016). We detected some residual autocorrelation, and thus used a conservative significance threshold of $p < 0.01$ to account for any potential impacts.

Model predictions

We visualized predicted values from the models to explore the abundance patterns of each species and life stage. Predicted values were generated over a range of covariates that included all combinations of 6 evenly spaced time-points per month (from 1972 to 2019) and a series of salinity values selected as quantiles from the raw data (every 0.05 from 0.05 to 0.95). Since there were some gaps in the timeseries (e.g., winters were not sampled some years in the 1970s and 1980s), those same gaps are preserved in the model predictions to avoid extrapolation. Model predictions were then plotted along with their 99% credible intervals. To visualize the multidimensional model outputs, we created three plots for each set of model predictions. Each plot had one of the covariates (salinity, day of year, or year) on the x-axis while the other two variables were illustrated with color or separate plots. For the two covariates included as color or separate plots, we chose a subset of the unique values used in generating model predictions in order to reduce plot complexity and aid interpretation. These values were chosen as an evenly spaced subset of the values available.

To explore spatial patterns in abundance, we extracted the mean estimated value from each station cluster random intercept. These values were then plotted over a map of the study region.

Results

Diet results

The CDFW Diet Study has processed 11,301 fish caught in San Pablo Bay and upstream through the Delta consisting of nine species; Delta Smelt, Longfin Smelt, age- 0 Striped Bass, Threadfin Shad, American Shad, Mississippi Silversides (*Menidia beryllina)*, Pacific Herring, Prickly Sculpin (C*ottus asper*), and *Tridentiger* spp. gobies (Table 1). A wide range of fork lengths was processed for all species, except for Pacific Herring, Prickly Sculpin, and *Tridentiger* spp. Gobies which only included larval fish. Time and seasonality of collection varied by fish species with year-round diet information only available for Delta Smelt and Longfin Smelt.

Our study zooplankton were eaten by at least one individual of each fish species, except Pacific Herring, which consumed none and is thus not discussed further here (Table 1). *Acanthocyclops* spp. were present in the most fish stomachs (n= 885) and *A. sinensis* juveniles were eaten the least (n= 88). Of the fish that consumed *Acanthocyclops* spp., Delta Smelt had the highest consumption (n= 800, 21% of fish with food present), and Striped Bass the least (n= 3 fish, 0.3%). Neither Prickly Sculpin nor *Tridentiger* spp. consumed *Acanthocyclops* spp.

A. sinensis adults were the second most consumed (n= 561), with at least one individual of each fish species eating adult *A. sinensis*, except Prickly Sculpin. American

Shad had the highest consumption of adult *A. sinensis (*n= 20 stomachs, 45%) followed by Delta Smelt (n= 437, 12%), Mississippi Silversides (n= 15, 8%), *Tridentiger* gobies (n= 23, 5%), Threadfin Shad (n= 17, 3%), Longfin Smelt (n= 48, 2%) and finally Striped Bass (n= 1, 0.1%) (Table 1). *A. sinensis* juveniles were consumed the least of our study species, with only 2% of Delta Smelt individuals (n= 74), and ≤ 1% of individuals from the other fish species (*Tridentiger*: n= 4, 0.9%; Threadfin Shad: n= 4, 0.7%; Mississippi Silversides: n= 1, 0.5%; Longfin Smelt: n= 5, 0.2%; Striped Bass and Prickly Sculpin: n= 0) with *A. sinensis* juveniles present in stomachs.

Bosmina was present in the guts of all fish species (n= 235) and was the third most consumed of our study zooplankton. Threadfin Shad ate *Bosmina* the most (n= 53, 9%), Delta Smelt the second most (n= 163, 4%), and Longfin Smelt ate the least (n= 1, 0.04%).

Table 1: Diet results for fish processed by the CDFW Diet and Condition Study and the number of fish that consumed each zooplankton species. "# fish" represents the number of fish of each species that were processed for stomach contents. "Season" indicates the seasons in which fish were collected, with "Sum" = summer and "Win" = winter. Fork lengths are given in mm. Zooplankton species are represented as follows: A = Acanthocyclops spp., AS = A. sinensis adults, AS juv = A. sinensis juveniles, and B = B. longirostris. Percentages represent the percent of fish with food present in their stomachs that consumed each prey species.

Fish species	# fish	Season	Fish with food present (%)	Min fork length	Max fork length	*A* (%)	*AS* (%)	*AS* juv (%)	*B* (%)
Delta Smelt	4317	All	3752 (87)	4.3	90	800 (21)	437 (12)	74 (2)	163 (4)
Longfin Smelt	3640	All	2558 (70)	4.4	124	69 (3)	48 (2)	5 (0.2)	1 (0.04)
Striped Bass	1187	Sum to Fall	966 (81)	5.1	142	3 (0.3)	1 (0.1)	0	9 (0.9)

Threadfin Shad	861	Sum to Fall	596 (69)	4.0	98	8 (1.3)	17 (3)	4 (0.7)	53 (9)
American Shad	47	Sum to Fall	44 (94)	19	90	0	20 (45)	2 (4.5)	0
Mississippi Silversides	192	Sum to Fall	189 (98)	16.5	95.8	5 (3)	15 (8)	1 (0.5)	6 (3)
Pacific Herring	389	Win	252 (65)	8.5	35.2	0	0	0	0
Prickly Sculpin	195	Win	82 (42)	5.3	11.2	0	0	0	2 (2)
Tridentiger spp. gobies	473	Sum	443 (93)	2.7	17	0	23 (5)	4 (0.9)	1 (0.2)

Bosmina longirostris adults

The abundance of adult *B. longirostris* has regularly peaked in the Spring between April and May. In earlier years, they had another large peak in the late summer to fall between August and October. In some years (1980 and 1985), this fall peak was as large as the spring peak. However, by 1990 the fall peak was greatly reduced to just a small increase, which has since continued to decrease in size, becoming non-existent by 2015 (Fig. 3).

B. longirostris adults are most abundant in freshwater, and abundance decreases as salinity increases (Fig. S1). In the moderate salinity of 1.113, the fall peak was larger than the spring peak in earlier years. However, as with the lower salinities, the fall peak was greatly reduced by 1995, shrinking smaller than the spring peak even as the overall abundance in this salinity continued to decrease over time (Fig. 3, S1).

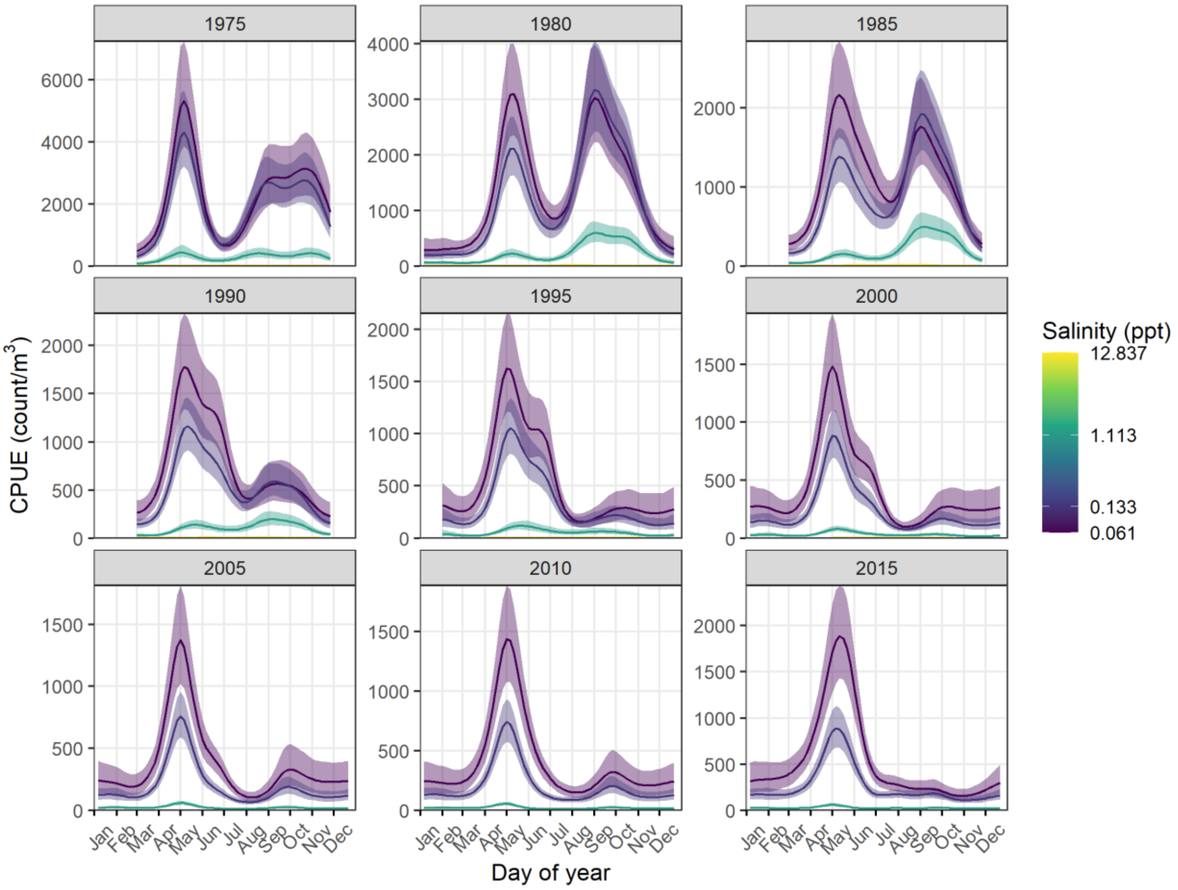


Figure 3. Seasonal patterns in Bosmina longirostris adult abundance with 99% credible intervals. Each plot represents predictions from different position on the smoothed yearly trend and may not represent exact conditions for that particular year. Predictions for different salinity values are represented by line and shading color, which is on the log scale. The y-axis limits differ among plots to facilitate comparison of seasonal trends. Absolute trends in abundance over time are represented in Fig. 4. Missing values (e.g., the months of Jan, Feb, and Dec in 1975) represent gaps in the raw data.

The abundance of adult *B. longirostris* has declined over time in most months. This is most apparent in August through November, corresponding to the loss of their former fall peak. In some months, their abundance has mostly decreased over time except in recent years which have a slight uptick. This recent uptick appears in January through March and May through July but is most significant in May through July (Fig. 4).

Controlling for all other factors (salinity, year, month), *B. longirostris* adults had the highest abundance in the Southeastern Delta. Other areas around the boundaries of the sampled area also had higher abundance such as San Pablo Bay, Napa River, and parts of the Cache Slough Complex and Sacramento Deep Water Ship Channel. The Sacramento River corridor between Cache Slough and Suisun Bay generally had low abundance, as did parts of the Northeastern Delta (Fig. 5).

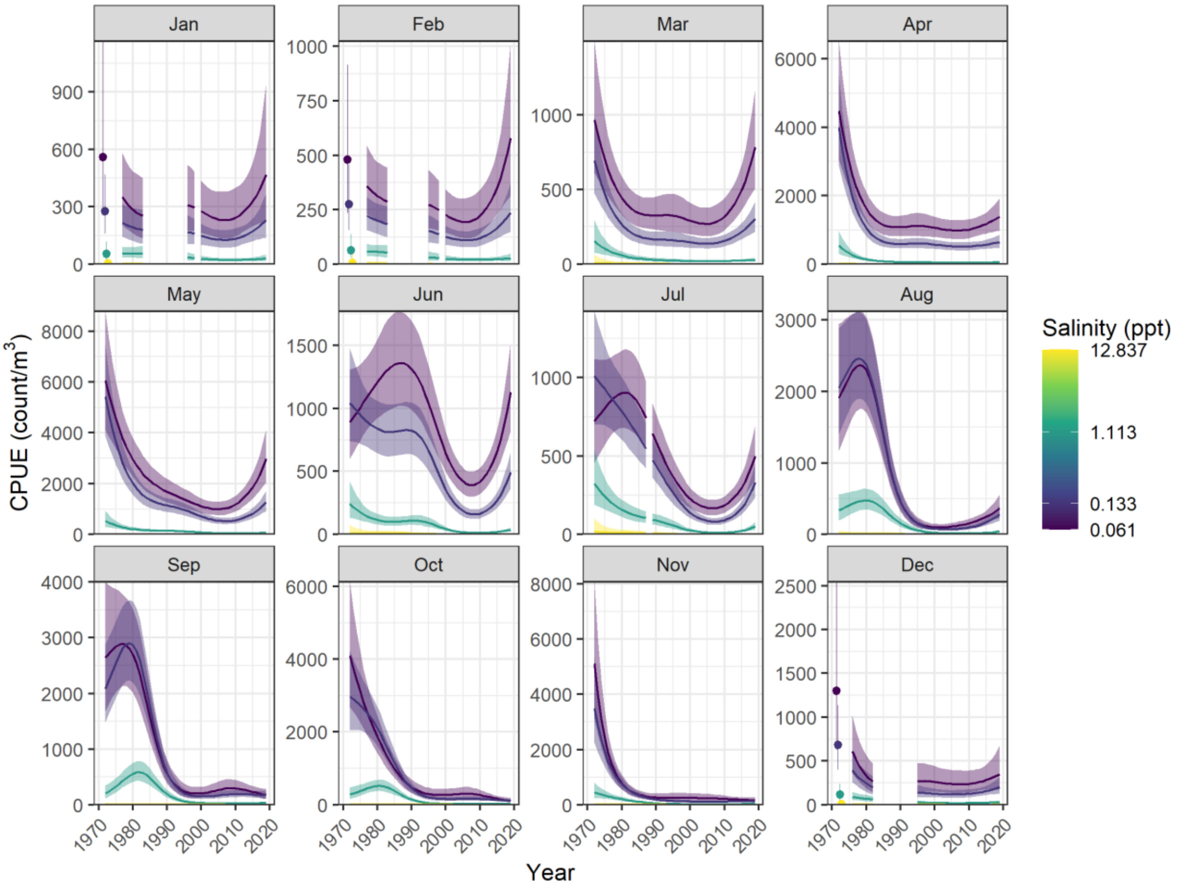


Figure 4. Yearly patterns in Bosmina longirostris adult abundance with 99% credible intervals. Each plot represents the pattern for a separate month. Predictions for different salinity values are represented by line and shading color, which is on the log scale. The y-axis limits differ among plots to facilitate comparison of long-term trends. Seasonal trends in abundance are represented in Fig. 3. Missing values represent gaps in the raw data.

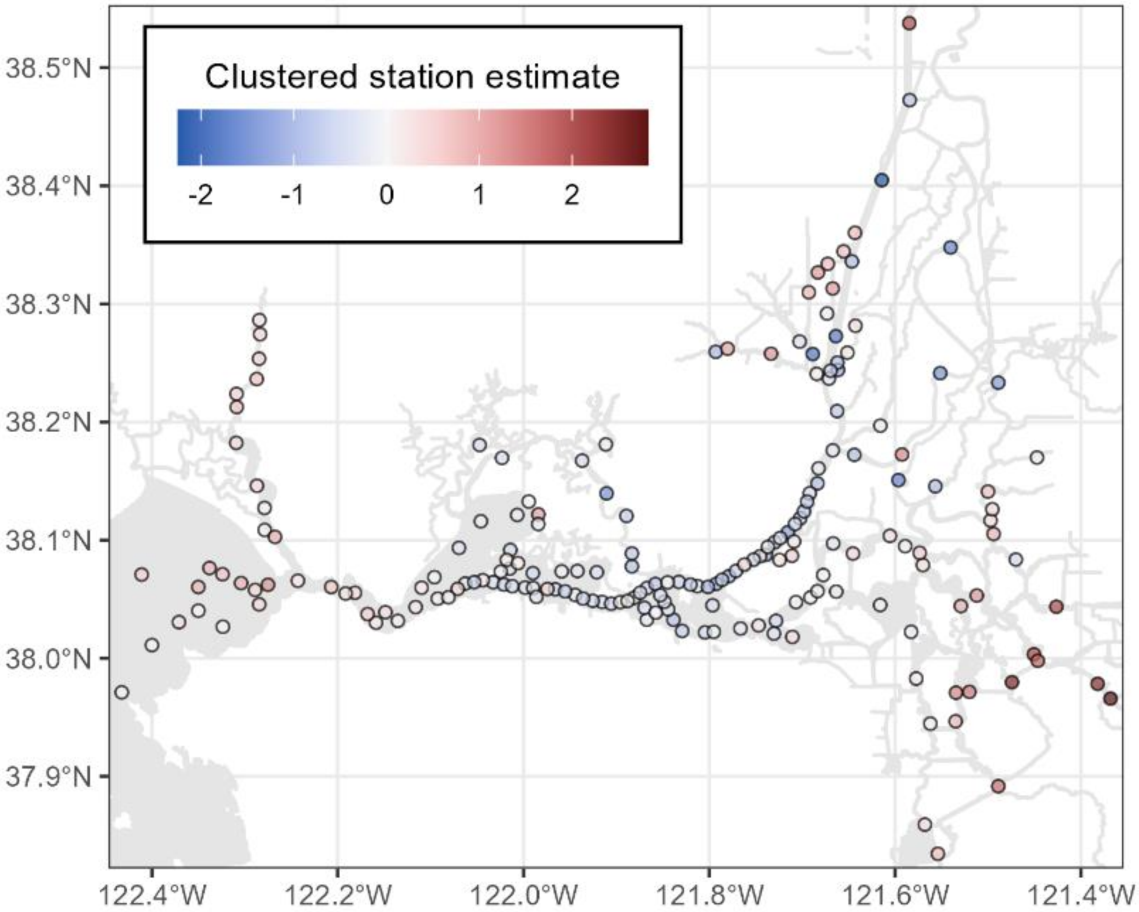


Figure 5. Estimated values of the clustered station random intercepts for *Bosmina longirostris* adults. Stations within 1 km were clustered into groups. Point color indicates whether each station cluster has higher or lower *B. longirostris* adult abundance, after controlling for the other covariates (day of year, salinity, and year).

Acanthocyclops spp. adults

The abundance of *Acanthocyclops* spp. adults has peaked regularly in the spring from April to May in all years. This peak is apparent in the two lower salinity levels (0.062 and 0.137) but generally not in the two higher salinities (1.402 and 13.017). In the second highest salinity of 1.402, abundance peaked in the winter from February through March in most years, although limited sampling in these months in some years may have masked the signal (Fig. 6).

Acanthocyclops spp. were most abundant in the lower salinities, peaking around 0.3. Abundance decreased on either side of that peak, but fell much lower in the highest salinities

(Fig. S2). Over time, the relationship of *Acanthocyclops* spp. with salinity leveled out such that they became equally abundant in all salinity levels in most months (Fig. S2).

The abundance of *Acanthocyclops* spp. has dramatically declined over time in all months. There was a slight uptick in the 1980s to 1990s in most months, but populations crashed again after this period (Fig. 7). Overall trends in January and February appear mostly flat with generally low abundance in all years but the missing data in those months may be obscuring patterns.

The highest *Acanthocyclops* spp. abundance after controlling for the other covariates was in Cache Slough, Suisun Marsh, the Southeastern Delta, Carquinez Strait, San Pablo Bay, and the Napa River. The lower Sacramento and San Joaquin rivers through Suisun Bay generally had lower abundances, as did most of the western-most areas (Fig. 8).

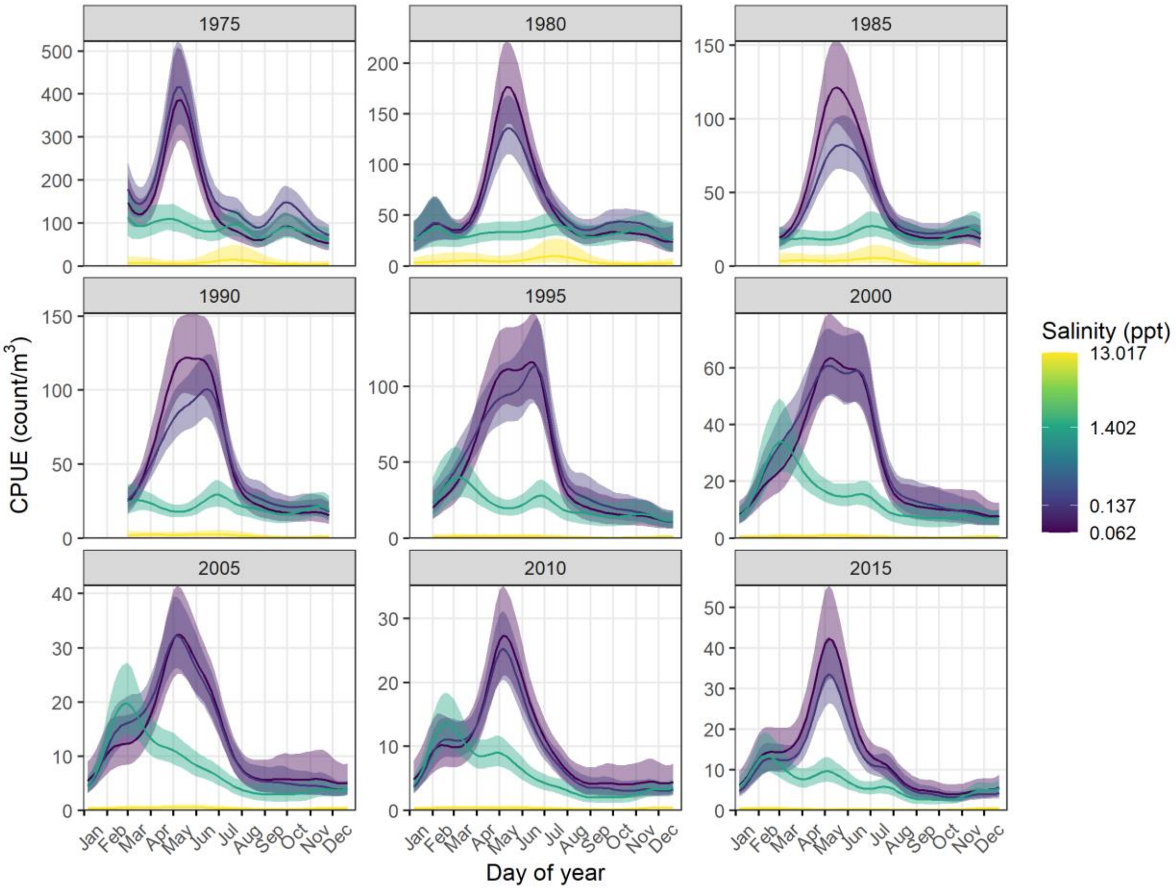
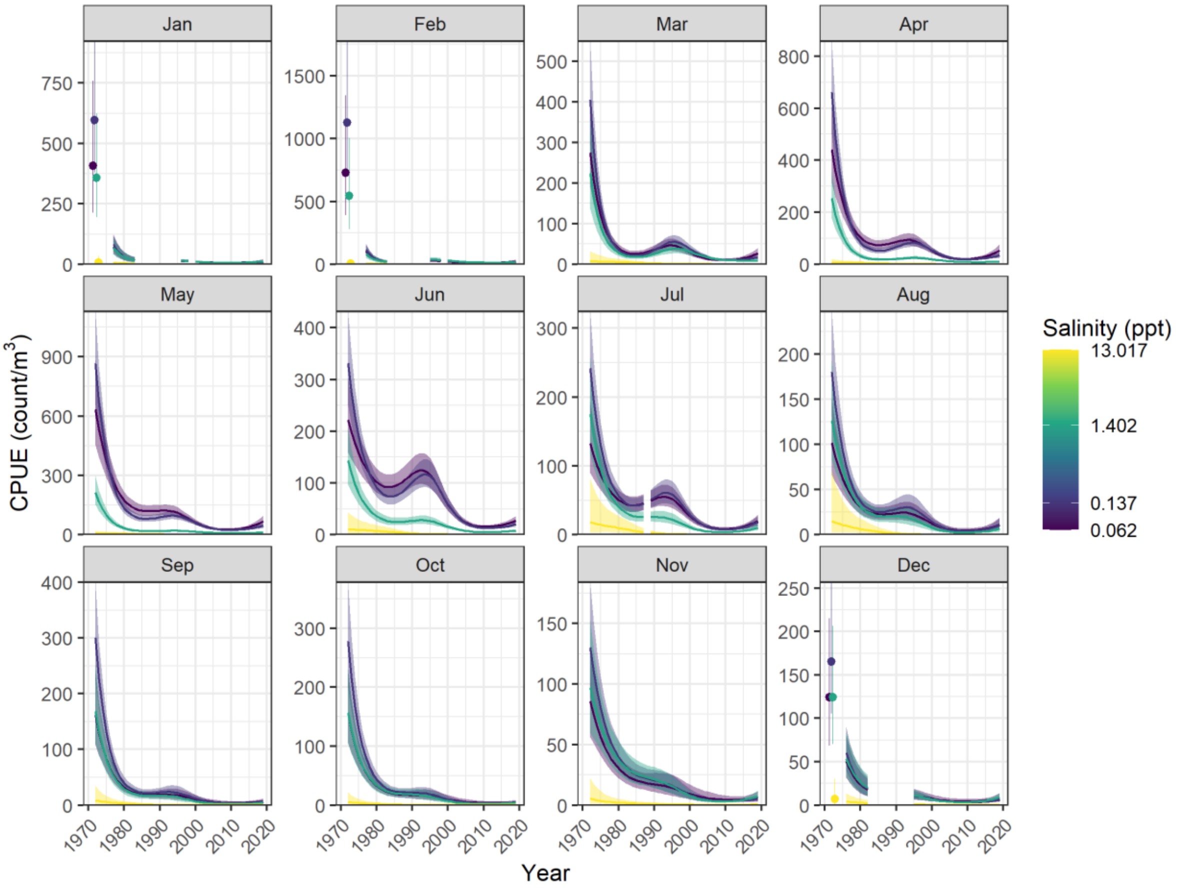


Figure 6. Seasonal patterns in Acanthocyclops spp. adult abundance with 99% credible intervals. See Fig. 3 for a full description.



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429 Figure 7. Yearly patterns in Acanthocyclops spp. adult abundance with 99% credible intervals. See Fig. 4 for a

430 full description.

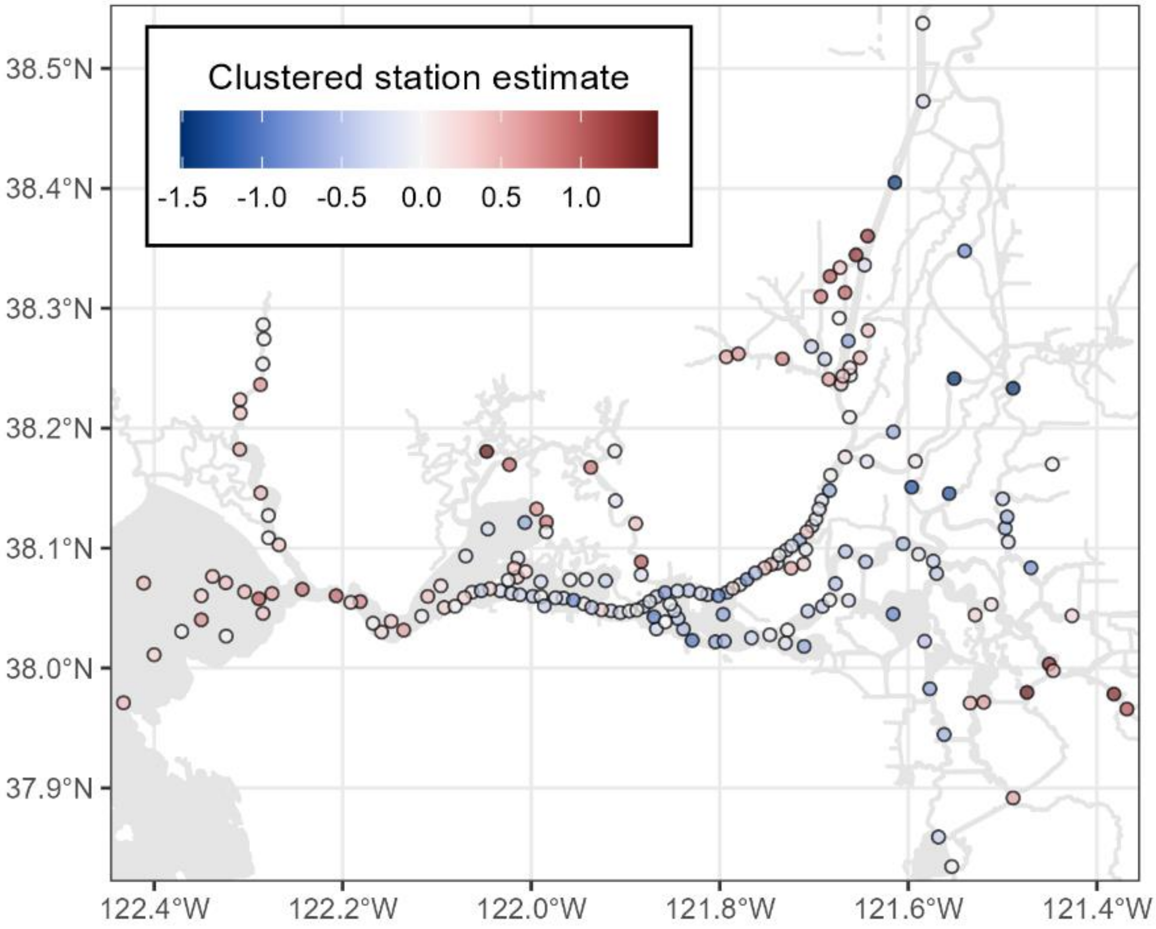


Figure 8. Estimated values of the clustered station random intercepts for *Acanthocyclops* spp. adults. See Fig. 5 for a full description.

Acartiella sinensis adults

A. sinensis had the strongest seasonality of the three species investigated. Adults peak in the fall from August through December with the highest levels in September and October. Abundances then dip close to zero from February through May (Fig. 9).

Adult *A. sinensis* were most abundant in moderate salinities between about 1 and 4. The effect of salinity on abundance has increased over time, especially in May through July where the peak was greatly reduced in earlier years (Fig. S3).

Unlike the other two species, *A. sinensis* adults did not exhibit any overall long-term decreases in abundance. However, the timeseries is shorter, only starting in 1994. In most months, the most recent abundance is similar to the earliest abundance level, but abundance did increase over time in March through July. The abundance peaked in the 2010s in most months and some months also had an earlier peak around 2000 (Fig. 10).

Spatially, *A. sinensis* adults had the highest abundance (controlling for all other covariates) along the corridor from the lower Sacramento River just below Cache Slough all the way through to Carquinez Strait. The Southeastern and Northern Delta had the lowest abundances (Fig. 11).

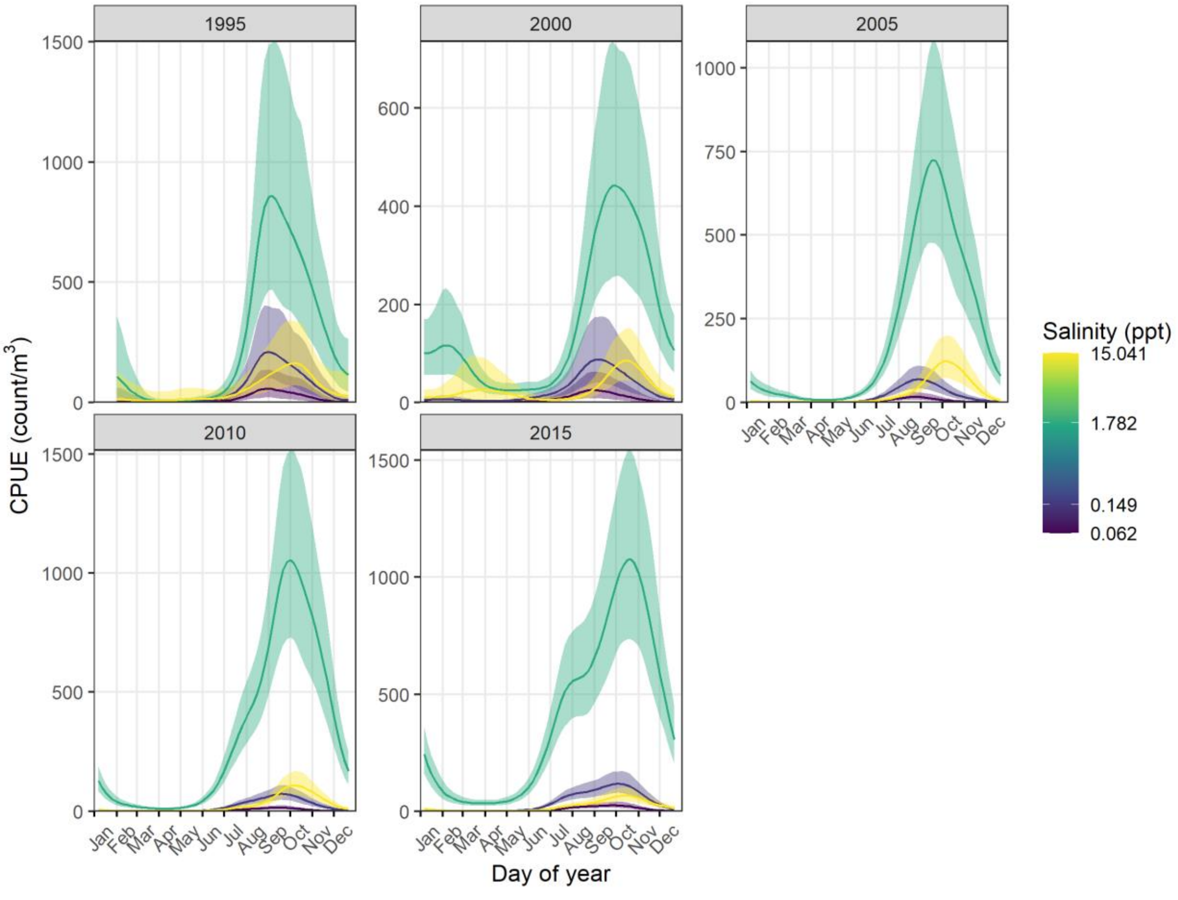
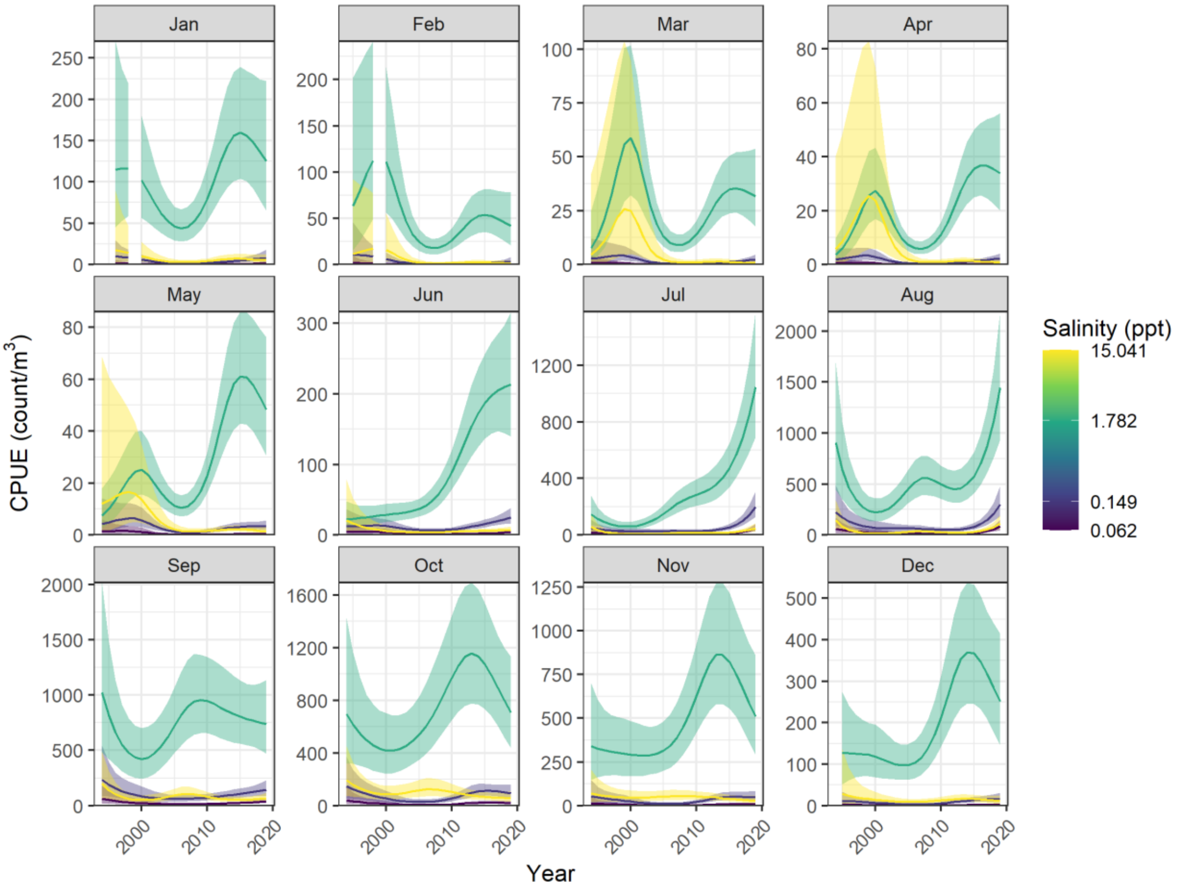


Figure 9. Seasonal patterns in Acartiella sinensis adult abundance with 99% credible intervals. See Fig. 3 for a full description.



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454 Figure 10. Yearly patterns in Acartiella sinensis adult abundance with 99% credible intervals. See Fig. 4 for a

455 full description.

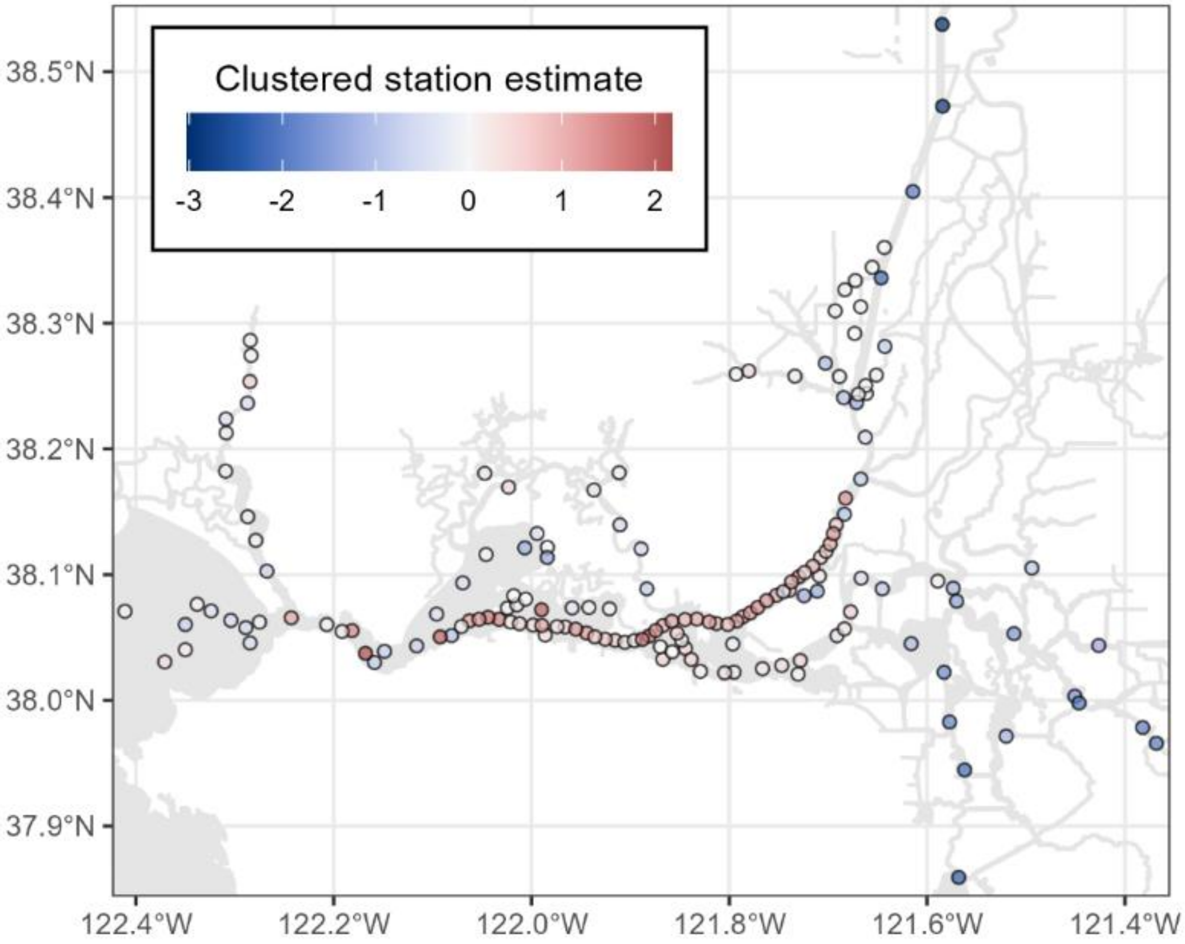

Figure 11. Estimated values of the clustered station random intercepts for *Acartiella sinensis* adults. See Fig. 5 for a full description.

Acartiella sinensis juveniles

Like the adults, juvenile *A. sinensis* also had strong seasonal abundance patterns, peaking over just a few months and then subsiding to close to zero abundance. Peaks occurred in the summer from July through September, but the width of the seasonal peak grew over time. In 2006 they were abundant for just 2 months (July and August) while in 2015 and 2018 they were abundant from April through November (Fig. 12).

A. sinensis juveniles were abundant in higher salinities > 4 but declined at the very highest salinities close to 16. Their abundance in lower salinities increased over time but always remained lower than the higher salinities (Fig. S4). In most years, the seasonal abundance peak was 1-2 months later at the highest salinity of ~16 than the other salinity levels (Fig. 12).

While the timeseries was much shorter (2006 – 2020) for *A. sinensis* juveniles than any of the other species and life stages investigated, we did detect some long-term trends in a few months. The trends were most apparent in the second highest salinity of 2.703 where they were most abundant. Abundance increased over time in April through June and decreased over time in August. This corresponds to the widening of the seasonal peak over time. The other months generally did not have any significant long-term trends (Fig. 13).

The spatial pattern of *A. sinensis* juveniles was less clear than the other species and life stages. However, they were generally most abundant along the San Joaquin River corridor in the Southern Delta and in some Suisun Bay stations. They were least abundant in the lower Sacramento River between Cache Slough and the Confluence, as well as in the Napa River and Eastern Suisun Marsh (Fig. 14).

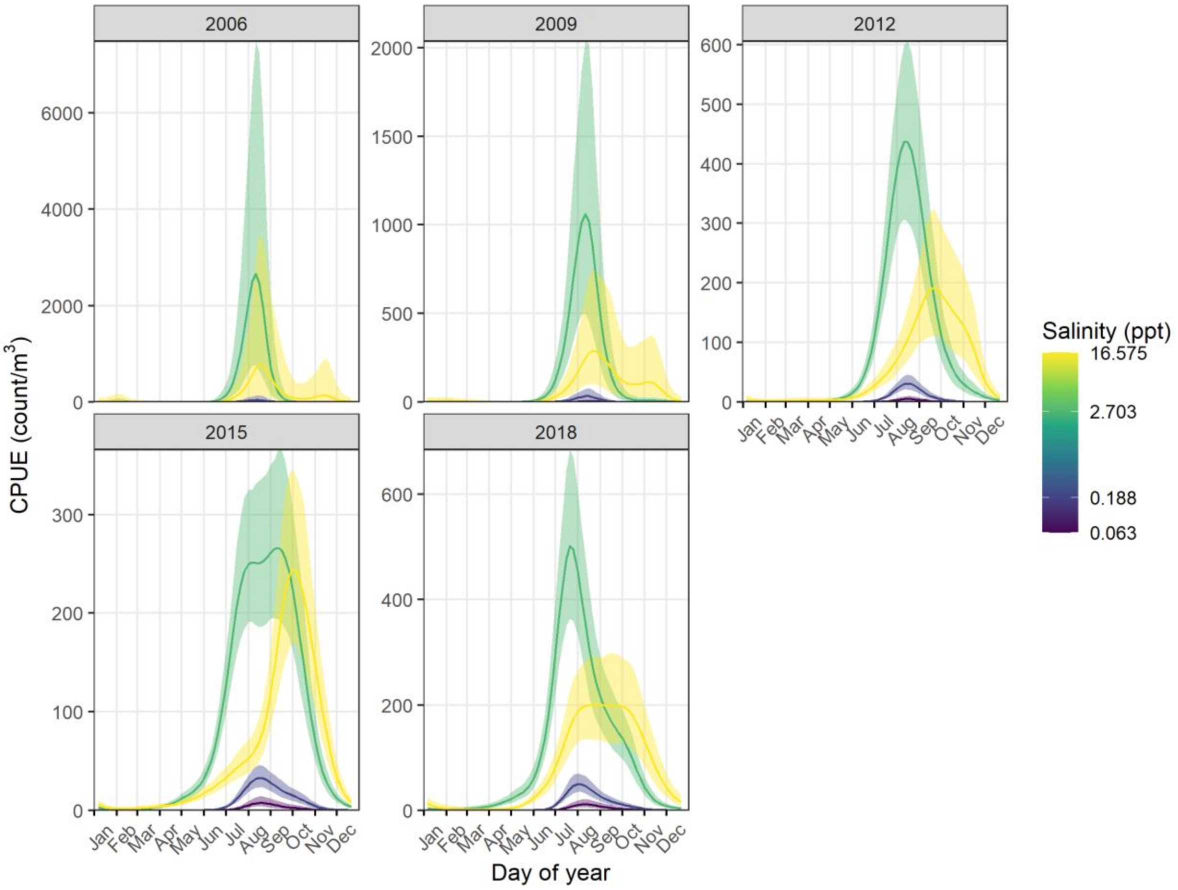

Figure 12. Seasonal patterns in Acartiella sinensis juvenile abundance with 99% credible intervals. See Fig. 3 for a full description.

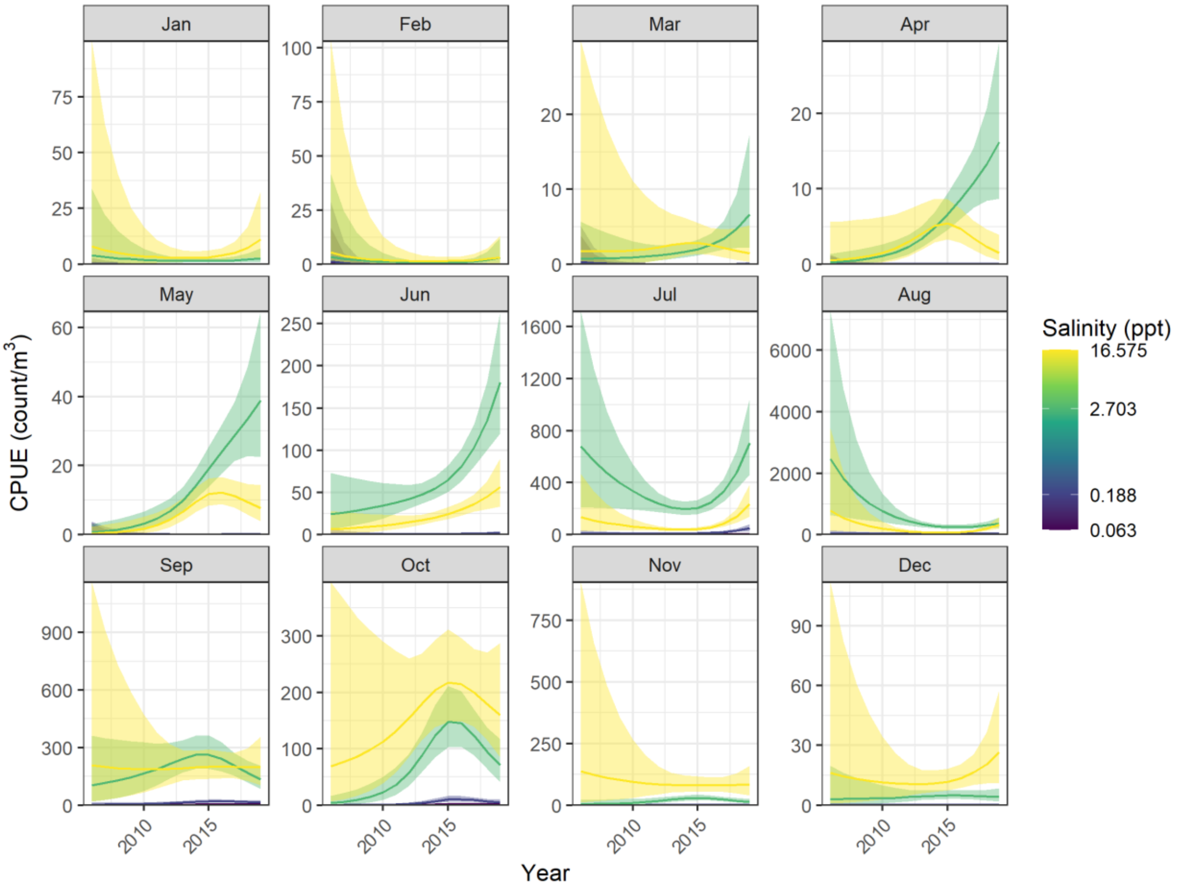

Figure 13. Yearly patterns in Acartiella sinensis juvenile abundance with 99% credible intervals. See Fig. 4 for a full description.

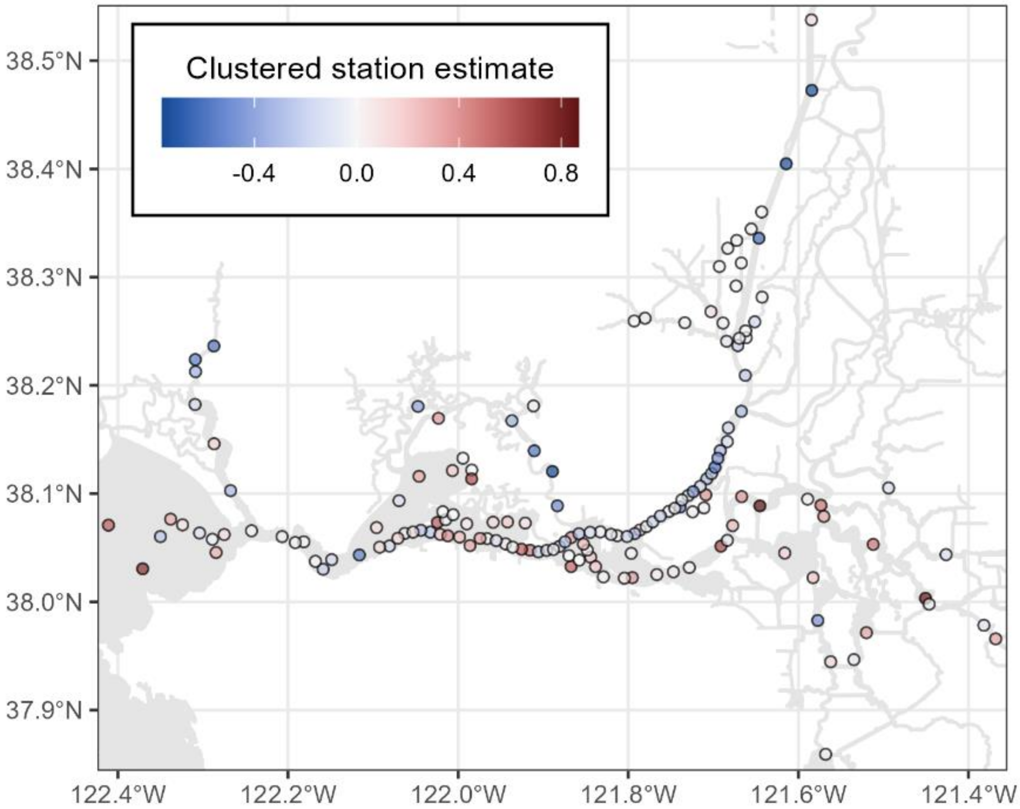

Figure 14. Estimated values of the clustered station random intercepts for *Acartiella sinensis* juveniles. See Fig. 5 for a full description.

Discussion

We found marked changes in the seasonality and overall abundance of three key zooplankton species in the upper estuary. *B. longirostris* no longer peaks in abundance in the fall months, *Acanthocyclops* spp. dramatically declined in all months and lost its strong relationship with salinity, and *A. sinensis* adult abundance has become increasingly driven by salinity while juveniles have developed wider abundance peaks. In this process, we have documented the relationship of each species with salinity and seasonality back to the beginning of monitoring or their introduction, increasing our understanding of their ecology and importance in the estuary.

Importance in fish diets

Of our study species, *Acanthocyclops* spp. was consumed by the most fish, particularly Delta Smelt and Longfin Smelt. This is consistent with other studies that show the importance of *Acanthocyclops* spp. in Longfin Smelt (Hobbs et al. 2006; Jungbluth et al. 2021), Delta Smelt (Lott 1998; Hammock et al. 2017), and larval Pacific Herring (Jungbluth et al. 2021) diets. *Acanthocyclops* spp. has a similar fatty acid composition to the calanoid copepod *E. affinis* (Kratina and Winder 2015), the preferred prey of Delta Smelt (Slater and Baxter 2014), and Longfin Smelt (Barros et al. 2022; Burris et al. in review), and presents an additional prey resource during the critical life stages of these fishes.

Adult *A. sinensis* were consumed the second most of our study species, but juveniles were consumed the least. Since its introduction, *A. sinensis* has become important prey for many fishes in the estuary during fall, especially Delta Smelt (Slater and Baxter 2014; Hammock et al. 2017; Slater et al. 2019). Because *A. sinensis* is predatory, it has a lower nutritional value (i.e. higher Carbon to Nitrogen ratio) than herbivorous copepods such as *P. forbesi* (Kratina and Winder 2015), another common prey of Delta Smelt. *A. sinensis* predates and limits the availability of *P. forbesi* in the low salinity zone (Kayfetz and Kimmerer 2017), replacing *P. forbesi* as a prey source for juvenile and young-of-year Delta Smelt. *A. sinensis* is not common in Longfin Smelt or Striped Bass diets, likely due to the peak seasonal abundance occurring when both fish species are larger and have transitioned to larger prey such as mysids and shrimp (Feyrer et al. 2003; Barros et al. 2022, CDFW unpublished data).

B. longirostris were consumed the second least of our study species. Threadfin Shad was the most frequent consumer of *B. longirostris* compared to the other fish species, although the amount was still low despite their spatial overlap. Unlike most of the other fishes examined, Threadfin Shad switch their feeding strategy from filter feeding to benthic organisms and detritus based on prey availability (Ingram and Ziebell 1983) and this could explain the low number of individuals that consumed *B. longirostris*. *B. longirostris*, and other cladocerans, have a lower nutritional value than copepods (Kratina and Winder 2015). However, cladocerans are still an important prey resource for fishes in the freshwater regions in the estuary such as salmonids (Goertler et al. 2018; Aha et al. 2021), Mississippi Silversides, and Threadfin Shad (Whitley and Bollens 2014), or during times when copepods are less abundant such as for Delta Smelt in winter and spring (Hammock et al. 2017; Slater et al. 2019).

Based on previous research (Lott 1998; Hobbs et al. 2006; Hammock et al. 2017; Jungbluth et al. 2021), it is likely that the presence of our study species in fish diets is higher than our data indicates. This could be due to damage during digestion hindering identification of prey to the taxonomic level of our study taxa, or that most fish samples were limited to specific seasons and may not have been collected at a time that our zooplankton species were present in the environment. Thus, our results likely represent undercounts of the actual abundance of our study taxa in fish diets.

Seasonal, salinity-related, and geographic abundance patterns

Currently, *B. longirostris* and *Acanthocyclops* spp. adults peak in the spring while *A. sinensis* adults peak in the fall and juveniles peak in the summer. The spring peaks line up with the spawning of Delta Smelt while summer and fall peaks provide critical food for Delta Smelt juveniles and young-of-the-year (Slater and Baxter 2014; Slater et al. 2019). The spring peaks also correspond to the outmigration of juvenile salmon and could provide important food necessary to increase growth rates and reduce oceanic predation risks (Herbold et al. 2018; Phillis et al. 2018; Zeug et al. 2019).

B. longirostris and *Acanthocyclops* spp. are also both most abundant in the lowest salinities, although *Acanthocyclops* spp. has a broader salinity range likely due to the different tolerances of the species in the complex. Freshwater habitat, especially in the spring, is where spawning for most native fish species occurs, including Delta Smelt and Sacramento Splittail (Moyle 2002). *A. sinensis* peaks in more saline water corresponding to the low salinity zone (generally defined as 0.5 to 6 ppt), which is a key habitat for rearing Delta Smelt (Sommer and Mejia 2013). The juveniles have a smaller salinity range and are abundant in more saline waters than the adults. The brackish and low salinity habitats are important rearing habitats for many native fishes that evolved in highly variable conditions, giving native fishes an advantage over non-native fishes (Moyle et al. 2010). Both *Acanthocyclops* spp. and *A. sinensis* are found in the diets of Longfin Smelt, which spawn and rear at slightly higher salinities than many other native fishes (Hobbs et al. 2006; Grimaldo et al. 2017; Jungbluth et al. 2021).

Adding to the pattern of similarity, *B. longirostris* and *Acanthocyclops* spp. had similar geographic patterns, with the highest abundance (controlling for other covariates) in the Cache Slough Complex and the southeastern and eastern boundaries of the study region. *B. longirostris* especially seemed to peak in areas of high residence time such as the northernmost location on the Sacramento Ship Channel and areas in the East Delta (Vroom et al. 2017; Lenoch et al. 2021). The Sacramento Ship channel is an important last refuge for Delta Smelt and other fishes (Young et al. 2021). *Acanthocyclops* spp. had very high geographic peaks in Suisun Marsh and Cache Slough, both areas with remnant and restored tidal wetlands that are important habitats for native fishes (Kimmerer et al. 2018; Colombano et al. 2020). They both also had generally low abundance from Suisun Bay upstream through the lower Sacramento and San Joaquin Rivers, which was the region of highest abundance for *A. sinensis* adults. *A. sinensis* adults had low abundance in the southeastern and northern regions. *A. sinensis* juveniles had some similarities to the adults but were much more abundant along the San Joaquin River corridor and had low abundance along the Sacramento River. They also had areas of high abundance in San Pablo Bay.

Long term changes

While *B. longirostris* and *Acanthocyclops* spp. have experienced overall declines in abundance over time, *A. sinensis* has mostly increased, although over a shorter time period. The declines of *B. longirostris* and *Acanthocyclops* correspond to noted regime shifts and overall plankton declines across many species (Winder and Jassby 2011). The increase of *A. sinensis* could be related to expansion following its recent invasion as it fills niches left by declining species.

The change to the seasonal pattern of *B. longirostris* abundance was puzzling. Prior to 1990, *Bosmina* experienced two peaks, one in the spring and a second peak in the fall. Something happened in the late 1980s to cause a crash in *B. longirostris* abundance during the fall. This fall peak may have been an important food source for juvenile Delta Smelt. While we may never be able to tell exactly why this peak disappeared, we discuss three theories here: changes to water management, invasive clams, and invasive copepods. Operation of the State Water Project and Central Valley project can significantly change flows in the San Joaquin River and the channels of the South Delta, where *Bosmina* is most abundant (Jassby et al. 2002; Jassby 2005). Exports from these water projects cause a decrease in residence time in the South Delta, particularly during the fall peak of *B. longirostris* (Hammock et al. 2019). Decreased residence time limits phytoplankton production, as well as directly exporting phytoplankton and zooplankton (Jassby et al. 2002; Hammock et al. 2019). However, this pattern first became apparent during increases to exports in the late 1970s (Hammock et al. 2019)**,** well before the disappearance of the fall peak of *B. longirostris*, so the export explanation is unlikely to be the main factor driving the decrease, though it could be part of the story.

Invasive species may be a more likely explanation for the change in the seasonal peaks of *B. longirostris*. The entire zooplankton community experienced a decline in abundance in the western portions of the estuary due, in part, to the introduction of the overbite clam (*Potamocorbula amurensis*) in 1986 (Kimmerer and Orsi 1996). The overbite clam has an extremely high filtration rate, greater than any native benthic grazer, and caused a crash in chlorophyll-a in Suisun Marsh and Suisun Bay. Zooplankton suffered from loss of food resources as well as directly through grazing on zooplankton nauplii (Kimmerer and Thompson 2014; Kimmerer and Lougee 2015). Grazing rates of overbite clams peak in summer and fall as biomass increases and higher water temperatures cause increases in metabolic rates (Crauder et al. 2016), so they would be well positioned to reduce the *B. longirostris* fall peak without impacting the spring peak. Could this have caused a reduction in fall *B. longirostris*? We feel this is unlikely to be the main cause, because *B. longirostris* chiefly occurs in the freshwater reaches of the Delta, whereas the overbite clam occurs mainly in areas with salinity > 2ppt (Crauder et al. 2016). While clams may not be the obvious answer, there was another important species introduction in the late 1980s with greater potential to directly impact *B. longirostris*. The calanoid copepod *P. forbesi* was introduced in 1987 and quickly became the most abundant calanoid in the system (Orsi and Walter 1991). *P. forbesi* peaks in abundance from July through October, overlapping with the historic peak in *B. longirostris* abundance, and they occur in high abundances in the South Delta where *B. longirostris* is common (Kayfetz and Kimmerer 2017). *P. forbesi* may be competing with *B. longirostris* for food resources during the fall when previously most other zooplankton peaked earlier in the year.

The dramatic decline of *Acanthocyclops* spp. abundance may be related to the invasion of the cyclopoid *Limnoithona tetraspina* in 1993 (Orsi and Ohtsuka 1999). Before this invasion, *Acanthocyclops* spp. was the most abundant cyclopoid in the region (Orsi and Mecum 1986). After 1994, *L. tetraspina* quickly dominated the copepod community (Hennessy 2018) with *Acanthocyclops* spp. averaging ~1% of the abundance of *L. tetraspina* (Bashevkin et al. 2020). The invasion of *L. tetraspina* could have facilitated the decline of *Acanthocyclops* spp. either through direct competition or through facilitation of a common predator, *A. sinensis*, as it likely did for *P. forbesi* (Kayfetz and Kimmerer 2017).

Acanthocyclops spp. also exhibited a reduction in their relationship to salinity over time. This is likely due to the differing salinity tolerances of the species within the complex and changes in the relative abundances of those species over time. Unfortunately, we do not have data on the abundances of each species in the complex so we cannot untangle the individual patterns. *A. vernalis* has been described as native to the estuary (Orsi and Mecum 1986; Kratina and Winder 2015). However, since the presence of the *A. vernalis* species complex in the estuary has only recently been confirmed (Jungbluth et al 2021), it is unknown which species could be native, or if some were introduced during the study period. The strong relationship with salinity in early years (Fig. S2) may be indicative of one or more species with lower salinity tolerances initially dominating, then later an invasion and expansion of the higher salinity species such as *A. americanus* which has been found in high salinity areas including the Mediterranean Sea (Alekseev 2021). The invasion of the predatory *A. sinensis* in more saline areas, as well as the shift in phytoplankton communities caused by invasion of *Potamocorbula amurensis* (Lucas et al. 2016), could also have contributed to this shift by taking over from salinity as the prime limiting abundance factor.

Adult *A. sinensis* were increasingly driven by salinity over time. In the earlier years, they were present in all salinities in our study and even equally abundant in high salinities of

15 and low salinities of 0.15. The also exhibited a unique winter-spring abundance peak in the two highest salinities that disappeared by 2005. They invaded in 1993 (Orsi and Ohtsuka 1999), thus this pattern could reflect them settling into their ecological niche over time. Another predatory copepod, *Tortanus dextrilobatus,* was introduced in 1994 and is found in higher salinities around 13- 19 ppt (Orsi and Ohtsuka 1999; Bollens et al. 2002). *T. dextrilobatus* typically peaks in summer (Bollens et al. 2014); however, when first introduced it also peaked in March and April (Hooff and Bollens 2004). Potential competition from *T. dextrilobatus* could thus have contributed to adult *A. sinensis* losing its spring peak in those higher salinities.

Interestingly, *A. sinensis* juveniles had increasingly wide seasonal abundance peaks over time, driven in part by differing timing of the two highest salinity bins. Abundance peaks were regularly 1-2 months later in the highest salinity (16.575) than in any of the lower salinities, which all peaked around the same time. The abundance peak of the highest salinity also grew relatively larger compared to the lower salinities over time, which led to an overall widening of the seasonal abundance peak for *A. sinensis* juveniles. However, the width of the abundance peak in each lower salinity level also seemed to widen over time. This demonstrates shifting phenology of *A. sinensis,* which could be caused by changes in the timing and location of reproduction, predation, or feeding. The zooplankton community has undergone many shifts over the history of this dataset (Orsi and Ohtsuka 1999; Winder and Jassby 2011), with *A. sinensis* potentially having its own impacts on lower trophic level zooplankton (Kayfetz and Kimmerer 2017). Since *A. sinensis* is predatory it could be following the abundance shifts of other species, resulting in changes to the location and timing of reproduction, thus impacting both adult and juvenile abundances. Alternatively, this shifted phenology could be caused by changes to the salinity field in recent years which have resulted in higher salinity intrusions further into the estuary due to increased and persisting droughts (Ghalambor et al. 2021).

Conclusions

Many of the fishes in the estuary rely on zooplankton for at least part of their life cycle. Changes in prey resources can affect higher trophic levels by reducing the amount of available food or shifting the timing of peak abundance, thereby creating a mismatch between critical fish life stages and their prey. We found long-term shifts in all three of our study species. These shifts included changes in seasonality, salinity preference, and long-term abundance. Further studies investigating these patterns in additional species would be important to understand the past dynamics of zooplankton in the estuary. These results increase our understanding of the zooplankton community, which could inform the development of food web models and be matched to trends in fish abundance to examine the direct influence of declining zooplankton species on managed species.

References

Adamczuk M. 2016. Past, present, and future roles of small cladoceran *Bosmina longirostris* (O. F. Müller, 1785) in aquatic ecosystems. Hydrobiologia. 767(1):1–11. doi:10.1007/s10750-015-2495-7.

Adamczuk M, Mieczan T. 2019. Within-species phenotypic diversity enhances resistance to stress - A case study using the polymorphic species *Bosmina longirostris*. International Review of Hydrobiology. 104(5–6):137–146. doi:10.1002/iroh.201901985.

Aha NM, Moyle PB, Fangue NA, Rypel AL, Durand JR. 2021. Managed Wetlands Can Benefit Juvenile Chinook Salmon in a Tidal Marsh. Estuaries and Coasts. doi:10.1007/s12237-020-00880-4. [accessed 2021 Jan 25]. https://doi.org/10.1007/s12237-020-00880-4.

Alekseev V, Fefilova E, Dumont H. 2002. Some noteworthy free-living copepods from surface freshwater in Belgium. Belgian Journal of Zoology. 132(2):133–139.

Alekseev VR. 2021. Confusing Invader: *Acanthocyclops americanus* (Copepoda: Cyclopoida) and Its Biological, Anthropogenic and Climate-Dependent Mechanisms of Rapid Distribution in Eurasia. Water. 13(10):1423. doi:10.3390/w13101423.

Ambler JW, Cloern JE, Hutchinson A. 1985. Seasonal cycles of zooplankton from San Francisco Bay. In: Cloern JE, Nichols FH, editors. Temporal Dynamics of an Estuary: San Francisco Bay. Dordrecht: Springer Netherlands. (Developments in Hydrobiology). p. 177–197. [accessed 2020 May 18]. https://doi.org/10.1007/978-94-009-5528-8_11.

Anderson RS. 1970. Predator–prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can J Zool. 48(6):1229–1240. doi:10.1139/z70-212.

Balcer MD, Korda NL, Dodson SI. 1984. Zooplankton of the Great Lakes: A Guide to the Identification and Ecology of the Common Crustacean Species. Univ of Wisconsin Press.

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 Smelt. Estuaries and Coasts. doi:10.1007/s12237-021-01024-y. [accessed 2022 Jan 12]. https://doi.org/10.1007/s12237-021-01024-y.

Bashevkin SM. 2021. zooper: an R package to download and integrate zooplankton datasets from the Upper San Francisco Estuary. v2.2.0. Zenodo. doi:10.5281/zenodo.4923868. [accessed 2021 Jun 10]. https://zenodo.org/record/4923868.

Bashevkin SM, Hartman R, Thomas M, Barros A, Burdi C, Hennessy A, Tempel T, Kayfetz K. 2020. Interagency Ecological Program: Zooplankton abundance in the Upper San Francisco Estuary from 1972-2018, an integration of 5 long-term monitoring programs. Environmental Data Initiative. doi:10.6073/PASTA/0C400C670830E4C8F7FD45C187EFDCB9. [accessed 2020 Jun 10]. https://portal.edirepository.org/nis/mapbrowse?packageid=edi.539.1.

Bashevkin SM, Hartman R, Thomas M, Barros A, Burdi CE, Hennessy A, Tempel T, Kayfetz K. in review. Five decades (1972-2020) of zooplankton monitoring in the upper San Francisco Estuary.

Bollens SM, Breckenridge JK, Cordell JR, Simenstad CA, Kalata O. 2014. Zooplankton of tidal marsh channels in relation to environmental variables in the upper San Francisco Estuary. Aquatic Biology. 21(3):205–219. doi:10.3354/ab00589.

Bollens SM, Cordell JR, Avent S, Hooff R. 2002. Zooplankton invasions: a brief review, plus two case studies from the northeast Pacific Ocean. Hydrobiologia. 480(1):87–110. doi:10.1023/A:1021233018533.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series. 324:219–228. doi:10.3354/meps324219.

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 Francisco Estuary and Watershed Science. 14(3). [accessed 2019 Aug 6]. https://escholarship.org/uc/item/4mk5326r.

Bürkner P-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software. 80(1):1–28. doi:10.18637/jss.v080.i01.

Bürkner P-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. The R Journal. 10(1):395–411.

Burris ZP, Baxter RD, Burdi CE. in review. Larval and juvenile Longfin Smelt diets as a function of fish size and prey density in the San Francisco Estuary. California Fish and Wildlife Journal.

Carpenter SR, Kitchell JF. 1984. Plankton Community Structure and Limnetic Primary Production. The American Naturalist. 124(2):159–172. doi:10.1086/284261.

Chigbu P., Sibley TH. 1998. Predation by longfin smelt (Spirinchus thaleichthys) on the mysid Neomysis mercedis in Lake Washington. Freshwater Biology. 40(2):295–304. doi:10.1046/j.1365-2427.1998.00354.x.

Chigbu Paulinus, Sibley TH. 1998. Feeding ecology of longfin smelt (Spirinchus thaleichthys Ayres) in Lake Washington. Fisheries Research. 38(2):109–119. doi:10.1016/S0165-7836(98)00156-8.

Colombano DD, Manfree AD, O’ Rear TA, Durand JR, Moyle PB. 2020. Estuarine-terrestrial habitat gradients enhance nursery function for resident and transient fishes in the San Francisco Estuary. Marine Ecology Progress Series. 637:141–157. doi:10.3354/meps13238.

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

Craddock DR, Blahm TH, Parente WD. 1976. Occurrence and Utilization of Zooplankton by Juvenile Chinook Salmon in the Lower Columbia River. Transactions of the American Fisheries Society. 105(1):72–76. doi:10.1577/1548-8659(1976)105<72:OAUOZB>2.0.CO;2.

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: U.S. Geological Survey Open-File Report Report No.: 2016–1005. [accessed 2019 Oct 4]. http://pubs.er.usgs.gov/publication/ofr20161005.

Cushing DH. 1969. The Regularity of the Spawning Season of Some Fishes. ICES Journal of Marine Science. 33(1):81–92. doi:10.1093/icesjms/33.1.81.

Cushing DH. 1990. Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. In: Blaxter JHS, Southward AJ, editors. Advances in Marine Biology. Vol. 26. Academic Press. p. 249–293. [accessed 2020 Jul 6]. http://www.sciencedirect.com/science/article/pii/S0065288108602023.

Dodson SI, Grishanin AndreyK, Gross K, Wyngaard GA. 2003. Morphological analysis of some cryptic species in the *Acanthocyclops vernalis* species complex from North America. Hydrobiologia. 500(1):131–143. doi:10.1023/A:1024678018090.

Drenner RW, Vinyard GL, O’Brien WJ, Triplett JR, Wagner J. 1981. The Zooplankton Community of Lacygne Lake: A Cooling Pond in Kansas. The Southwestern Naturalist. 26(3):243–249. doi:10.2307/3670904.

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research. 33(3):271–283. doi:10.3354/cr033271.

Edwards M, Richardson AJ. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature. 430(7002):881–884. doi:10.1038/nature02808.

Enríquez-García C, Nandini S, Sarma SSS. 2013. Feeding behaviour of *Acanthocyclops americanus* (Marsh) (Copepoda: Cyclopoida). Journal of Natural History. 47(5–12):853–862. doi:10.1080/00222933.2012.747637.

Evans MS, Stewart JA. 1977. Epibenthic and benthic microcrustaceans (copepods, cladocerans, ostracods) from a nearshore area in southeastern Lake Michigan1. Limnology and Oceanography. 22(6):1059–1066. doi:10.4319/lo.1977.22.6.1059.

Feyrer F, Herbold B, Matern SA, Moyle PB. 2003. Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes. 67(3):277–288. doi:10.1023/A:1025839132274.

Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci. 64(4):723–734. doi:10.1139/f07-048.

Ghalambor CK, Gross ES, Grosholtz ED, Jeffries KM, Largier JK, McCormick SD, Sommer T, Velotta J, Whitehead A. 2021. Ecological Effects of Climate-Driven Salinity Variation in the San Francisco Estuary: Can We Anticipate and Manage the Coming Changes? San Francisco Estuary and Watershed Science. 19(2). doi:10.15447/sfews.2021v19iss2art3. [accessed 2021 Jun 9]. https://escholarship.org/uc/item/5271t1bd.

Gliwicz ZM, Stibor H. 1993. Egg predation by copepods in *Daphnia* brood cavities. Oecologia. 95(2):295–298. doi:10.1007/BF00323503.

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. Transactions of the American Fisheries Society. 147(2):287–299. doi:10.1002/tafs.10028.

Gräler B, Pebesma E, Heuvelink G. 2016. Spatio-temporal interpolation using gstat. RFID Journal. 8(1):204–218.

Grimaldo L, Feyrer F, Burns J, Maniscalco D. 2017. Sampling Uncharted Waters: Examining Rearing Habitat of Larval Longfin Smelt (*Spirinchus thaleichthys*) in the Upper San Francisco Estuary. Estuaries and Coasts. 40(6):1771–1784. doi:10.1007/s12237-017-0255-9.

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. Environmental Management. 63(6):703–717. doi:10.1007/s00267-019-01159-6.

Hammock BG, Slater SB, Baxter RD, Fangue NA, Cocherell D, Hennessy A, Kurobe T, Tai CY, Teh SJ. 2017. Foraging and metabolic consequences of semi-anadromy for an endangered estuarine fish. Plos ONE. 12(3):e0173497. doi:10.1371/journal.pone.0173497.

Hart RC. 2004. Cladoceran Periodicity Patterns in Relation to Selected Environmental Factors in Two Cascading Warm-Water Reservoirs Over a Decade. Hydrobiologia. 526(1):99–117. doi:10.1023/B:HYDR.0000041610.56021.63.

Hennessy A. 2018. Zooplankton Monitoring 2017. Interagency Ecological Program Newsletter. 32(1):21–32.

Herbold B, Carlson SM, Henery R, Johnson RC, Mantua N, McClure M, Moyle PB, Sommer T. 2018. Managing for Salmon Resilience in California's Variable and Changing Climate. San Francisco Estuary and Watershed Science. 16(2). doi:10.15447/sfews.2018v16iss2art3. [accessed 2022 Jan 12]. https://escholarship.org/uc/item/8rb3z3nj.

Hobbs JA, Bennett WA, Burton JE. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Francisco estuary. Journal of Fish Biology. 69(3):907–922. doi:10.1111/j.1095-8649.2006.01176.x.

Holm JChr, Møller D. 1984. Growth and prey selection by Atlantic salmon yearlings reared on live freshwater zooplankton. Aquaculture. 43(4):401–412. doi:10.1016/0044-8486(84)90248-5.

Hooff RC, Bollens SM. 2004. Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary. Marine Ecology Progress Series. 277:167–179. doi:10.3354/meps277167.

Hunter JR. 1981. Feeding Ecology and predation of marine fish larvae. In: Lasker R, editor. Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries. Vol. 1. Seattle: University of Washington Press. p. 33–77.

Ingram W, Ziebell CD. 1983. Diet Shifts to Benthic Feeding by Threadfin Shad. Transactions of the American Fisheries Society. 112(4):554–556. doi:10.1577/1548-8659(1983)112<554:DSTBFB>2.0.CO;2.

Inpang R. 2008. Annual changes of zooplankton communities of different size fractions in Thale-Noi, Phatthalung Province [M.Sc Thesis]. Prince of Songkla University.

Jassby AD. 2005. Phytoplankton Regulation in a Eutrophic Tidal River (San Joaquin River, California). San Francisco Estuary and Watershed Science. 3(1). doi:10.15447/sfews.2005v3iss1art5. [accessed 2021 Sep 2]. https://escholarship.org/uc/item/9jb2t96d.

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnology and Oceanography. 47(3):698–712. doi:10.4319/lo.2002.47.3.0698.

Jeffres CA, Holmes EJ, Sommer TR, Katz JVE. 2020. Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. PLOS ONE. 15(9):e0216019. doi:10.1371/journal.pone.0216019.

Jiang X, Li Q, Liang H, Zhao S, Zhang L, Zhao Y, Chen L, Yang W, Xiang X. 2013. Clonal Variation in Growth Plasticity within a *Bosmina longirostris* Population: The Potential for Resistance to Toxic Cyanobacteria. PLOS ONE. 8(9):e73540. doi:10.1371/journal.pone.0073540.

Jiang X, Xie J, Xu Y, Zhong W, Zhu X, Zhu C. 2017. Increasing dominance of small zooplankton with toxic cyanobacteria. Freshwater Biology. 62(2):429–443. doi:10.1111/fwb.12877.

Jiang X, Yang W, Xiang X, Niu Y, Chen L, Zhang J. 2014. Cyanobacteria alter competitive outcomes between *Daphnia* and *Bosmina* in dependence on environmental conditions. Fundamental and Applied Limnology. 184(1):11–22.

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. 3(6):1059–1080. doi:10.1002/edn3.226.

Jürgens K, Wickham SA, Rothhaupt KO, Santer B. 1996. Feeding rates of macro- and microzooplankton on heterotrophic nanoflagellates. Limnology and Oceanography. 41(8):1833–1839. doi:10.4319/lo.1996.41.8.1833.

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.

Kayfetz K, Kimmerer W. 2017. Abiotic and biotic controls on the copepod *Pseudodiaptomus forbesi* in the upper San Francisco Estuary. Marine Ecology Progress Series. 581:85–101. doi:10.3354/meps12294.

Kerfoot WC. 1978. Combat between predatory copepods and their prey: *Cyclops*, *Epischura*, and *Bosmina*. Limnology and Oceanography. 23(6):1089–1102. doi:10.4319/lo.1978.23.6.1089.

Kimmerer W, Ignoffo TR, Bemowski B, Modéran J, Holmes A, Bergamaschi B. 2018. Zooplankton Dynamics in the Cache Slough Complex of the Upper San Francisco Estuary. San Francisco Estuary and Watershed Science. 16(3). doi:10.15447/sfews.2018v16iss3art4. [accessed 2020 May 21]. https://escholarship.org/uc/item/63k1z819.

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 Plankton Res. 36(3):722–735. doi:10.1093/plankt/fbt128.

Kimmerer WJ, Lougee L. 2015. Bivalve grazing causes substantial mortality to an estuarine copepod population. Journal of Experimental Marine Biology and Ecology. 473:53–63. doi:10.1016/j.jembe.2015.08.005.

Kimmerer WJ, Orsi JJ. 1996. Changes in the zooplankton of the San Francisco Bay Estuary since the introduction of the clam *Potamocorbula amurensis*. In: Hollibaugh JT, editor. San Francisco Bay: The Ecosystem. San Francisco, CA: Pacific Division of the American Association for the Advancement of Science. p. 403–424.

Kimmerer WJ, Thompson JK. 2014. Phytoplankton Growth Balanced by Clam and Zooplankton Grazing and Net Transport into the Low-Salinity Zone of the San Francisco Estuary. Estuaries and Coasts. 37(5):1202–1218. doi:10.1007/s12237-013-9753-6.

Kratina P, Nally RM, Kimmerer WJ, Thomson JR, Winder M. 2014. Human-induced biotic invasions and changes in plankton interaction networks. Journal of Applied Ecology. 51(4):1066–1074. doi:10.1111/1365-2664.12266.

Kratina P, Winder M. 2015. Biotic invasions can alter nutritional composition of zooplankton communities. Oikos. 124(10):1337–1345. doi:10.1111/oik.02240.

Lenoch LK, Stumpner PR, Burau JR, Loken LC, Sadro S. 2021. Dispersion and Stratification Dynamics in the Upper Sacramento River Deep Water Ship Channel. San Francisco Estuary and Watershed Science. 19(4). doi:10.15447/sfews.2021v19iss4art5. [accessed 2021 Dec 16]. https://escholarship.org/uc/item/6741j5k3.

Lott J. 1998. Feeding Habits of Juvenile and Adult Delta Smelt from the Sacramento-San Joaquin River Estuary. IEP Newsletter. 11(1):14–19.

Lucas LV, Cloern JE, Thompson JK, Stacey MT, Koseff JR. 2016. Bivalve Grazing Can Shape Phytoplankton Communities. Frontiers in Marine Science. 3:14. doi:10.3389/fmars.2016.00014.

Matveev VF, Balseiro EG. 1990. Contrasting responses of two cladocerans to changes in the nutritional value of nannoplankton. Freshwater Biology. 23(2):197–204.

McElreath R. 2015. Statistical rethinking: A Bayesian course with examples in R and Stan. Boca Raton, FL: CRC Press.

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 and Coasts. 39(5):1526–1536. doi:10.1007/s12237-016-0097-x.

Miracle MR, Alekseev V, Monchenko V, Sentandreu V, Vicente E. 2013. Molecular-genetic-based contribution to the taxonomy of the *Acanthocyclops robustus* group. Journal of Natural History. 47(5–12):863–888. doi:10.1080/00222933.2012.744432.

Moyle PB. 2002. Inland Fishes of California: Revised and Expanded. University of California Press.

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 Francisco Estuary and Watershed Science. 14(2). doi:10.15447/sfews.2016v14iss2art6. [accessed 2019 Aug 6]. https://escholarship.org/uc/item/09k9f76s.

Moyle PB, Lund JR, Bennett WA, Fleenor WE. 2010. Habitat Variability and Complexity in the Upper San Francisco Estuary. San Francisco Estuary and Watershed Science. 8(3). doi:https://doi.org/10.15447/sfews.2010v8iss3art1. [accessed 2021 Feb 2]. https://escholarship.org/uc/item/0kf0d32x.

Onandia G, Dias JD, Miracle MR. 2015. Zooplankton grazing on natural algae and bacteria under hypertrophic conditions. Limnetica. 34(2):541–560.

Orsi JJ, Mecum WL. 1986. Zooplankton distribution and abundance in the Sacramento-San Joaquin delta in relation to certain environmental factors. Estuaries. 9(4):326–339. doi: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. Plankton Biology and Ecology. 46(2):128–131.

Orsi JJ, Walter TE. 1991. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin Estuary. In: Uye SI, Nishida S, Ho J-S, editors. Proc. Fourth Internl. Conf. on Copepoda. Hiroshima: Bull. Plankton Soc. Jpn. p. 553–562.

Pebesma EJ. 2004. Multivariable geostatistics in S: the gstat package. Computers & Geosciences. 30(7):683–691. doi:10.1016/j.cageo.2004.03.012.

Phillis CC, Sturrock AM, Johnson RC, Weber PK. 2018. Endangered winter-run Chinook salmon rely on diverse rearing habitats in a highly altered landscape. Biological Conservation. 217:358–362. doi:10.1016/j.biocon.2017.10.023.

Piasecki WG. 2000. Attacks of cyclopoid *Acanthocyclops robustus* [Sars] on newly hatched cyprinids. Electronic Journal of Polish Agricultural Universities Series Fisheries. 1(03). [accessed 2021 Sep 3]. https://www.infona.pl//resource/bwmeta1.element.agro-article-c69d1cf5-d408-436f-9b5e-810f38f00c59.

Roegner C, Bottom D, Baptista A, Campbell L, Goertler P, Hinton S, McNatt R, Simenstad C, Teel D, Fresh K. 2015. Salmon Habitat Use of Tidal-fluvial Habitats of the Columbia River Estuary, 2010-2013. Final Report. Report of research by NOAA Fisheries, Northwest Fisheries Science Center to US Army Corps of Engineers, Portland District.

Romare P. 2000. Growth of larval and juvenile perch: the importance of diet and fish density. Journal of Fish Biology. 56(4):876–889. doi:10.1111/j.1095-8649.2000.tb00878.x.

Sarma SSS, Miracle MR, Nandini S, Vicente E. 2019. Predation by *Acanthocyclops americanus* (Copepoda: Cyclopoida) in the hypertrophic shallow waterbody, Lake Albufera (Spain): field and laboratory observations. Hydrobiologia. 829(1):5–17. doi:10.1007/s10750-018-3546-7.

Shen C-J, Lee F. 1963. The estuarine copepoda of Chiekong and Zaikong rivers, Kwangtung Province China. Acta Zool Sin. 15:571–596.

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 Francisco Estuary and Watershed Science. 12(3). [accessed 2020 Jan 24]. https://escholarship.org/uc/item/52k878sb.

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

Slaughter AM, Ignoffo TR, Kimmerer W. 2016. Predation impact of *Acartiella sinensis*, an introduced predatory copepod in the San Francisco Estuary, USA. Marine Ecology Progress Series. 547:47–60. doi:10.3354/meps11640.

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: El Colapso de los Peces Pelagicos en La Cabecera Del Estuario San Francisco. Fisheries. 32(6):270–277. doi:10.1577/1548-8446(2007)32[270:TCOPFI]2.0.CO;2.

Sommer T, Mejia F. 2013. A Place to Call Home: A Synthesis of Delta Smelt Habitat in the Upper San Francisco Estuary. San Francisco Estuary and Watershed Science. 11(2). doi:10.15447/sfews.2013v11iss2art4. [accessed 2021 May 13]. https://escholarship.org/uc/item/32c8t244.

Srinui K, Ohtsuka S. 2015. Supplementary Description of Three *Acartiella* Species (Crustacea: Copepoda: Calanoida) from Estuarine Waters in Thailand. Species Diversity. 20(2):167–181. doi:10.12782/sd.20.2.167.

Stan Development Team. 2021. Stan User’s Guide. Version 2.27. [accessed 2020 Oct 14]. https://mc-stan.org/docs/2_24/stan-users-guide/index.html.

Tan Y, Huang L, Chen Q, Huang X. 2004. Seasonal variation in zooplankton composition and grazing impact on phytoplankton standing stock in the Pearl River Estuary, China. Continental Shelf Research. 24(16):1949–1968. doi:10.1016/j.csr.2004.06.018.

Tõnno I, Agasild H, Kõiv T, Freiberg R, Nõges P, Nõges T. 2016. Algal Diet of Small-Bodied Crustacean Zooplankton in a Cyanobacteria-Dominated Eutrophic Lake. PLOS ONE. 11(4):e0154526. doi:10.1371/journal.pone.0154526.

Vroom J, Wegen M van der, Martyr-Koller RC, Lucas LV. 2017. What Determines Water Temperature Dynamics in the San Francisco Bay-Delta System? Water Resources Research. 53(11):9901–9921. doi:10.1002/2016WR020062.

Whitley SN, Bollens SM. 2014. Fish assemblages across a vegetation gradient in a restoring tidal freshwater wetland: diets and potential for resource competition. Environ Biol Fish. 97(6):659–674. doi:10.1007/s10641-013-0168-9.

Winder M, Jassby AD. 2011. Shifts in Zooplankton Community Structure: Implications for Food Web Processes in the Upper San Francisco Estuary. Estuaries and Coasts. 34(4):675–690. doi:10.1007/s12237-010-9342-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). 73(1):3–36. doi:https://doi.org/10.1111/j.1467-9868.2010.00749.x.

York JK, McManus GB, Kimmerer WJ, Slaughter AM, Ignoffo TR. 2014. Trophic Links in the Plankton in the Low Salinity Zone of a Large Temperate Estuary: Top-down Effects of Introduced Copepods. Estuaries and Coasts. 37(3):576–588. doi:10.1007/s12237-013-9698-9.

Young MJ, Feyrer F, Stumpner PR, Larwood V, Patton O, Brown LR. 2021. Hydrodynamics drive pelagic communities and food web structure in a tidal environment. International Review of Hydrobiology. 106(2):69–85. doi:https://doi.org/10.1002/iroh.202002063.

Zeug SC, Wiesenfeld J, Sellheim K, Brodsky A, Merz JE. 2019. Assessment of Juvenile Chinook Salmon Rearing Habitat Potential Prior to Species Reintroduction. North American Journal of Fisheries Management. 39(4):762–777. doi:10.1002/nafm.10309.