

# Understanding community assembly rules in managed floodplain food webs

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**Abstract.** Community assembly has been an important topic in ecological research and theory for over a century. Recently, restoration ecologists have emphasized the use of community assembly rules, such as environmental filtering, to better inform management actions. Although there has been a strong call for the use of community assembly rules in terrestrial restoration ecology, few studies have examined their potential use in providing habitat benefits such as food resources to native species in large-scale managed aquatic ecosystems. In this study, we found evidence of deterministic community assembly mechanisms in zooplankton communities in floodplain and seasonally inundated off-channel habitats in California's Central Valley. Additionally, we found that all sampled off-channel floodplain habitat types had similar zooplankton communities and that assembly in floodplain habitats was governed by variables associated with increased water residence time. This study is the first to determine community assembly rules in floodplain-river ecosystems in order to assist managers in providing floodplain food-web benefits to native fish and wildlife species at the landscape scale.

**Key words:** deterministic community assembly; environmental filters; floodplain management; off-channel habitats; rice field; zooplankton.

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## INTRODUCTION

Community assembly rules—processes and conditions that control the presence and abundance of species in a community—have been a central topic in ecological research and theory for over a century (Clements 1916, Gleason 1927, Simberloff 1974, Diamond 1975, MacArthur and Wilson 2001). Restoration ecologists have emphasized the use of community assembly rules, such as environmental filtering, to better inform management actions (Keddy 1999, Laughlin 2014). For example, nuisance weed species in agricultural systems can be controlled by

management-related filtering, such as tilling (Smith 2006). Communities that assemble deterministically, through biotic and abiotic filters, can be predictably manipulated by habitat managers for species and ecosystem benefits. If communities assemble stochastically from random processes, then the results of management actions may not be predictable. Simply put, restoration and management actions can be futile if community assembly is due to mechanisms beyond the control or understanding of the practitioner.

Deterministic community assembly asserts that environmental conditions dictate species presence, and processes such as environmental

filtering or niche selection are the prevalent mechanisms dictating community membership (Chase and Myers 2011). Conversely, stochastic community assembly posits that species are functionally equivalent and community structure is highly influenced by random mechanisms such as dispersal limitation, ecological drift, and probabilistic dispersal that can lead to priority effects (Hubbell 2001, 2005). While both processes are active in forming communities, community assembly in harsh or dynamic environments is typically a product of deterministic environmental filtering where environmental conditions select for or against species traits (Arrington and Winemiller 2006, Chase and Myers 2011, Fernandes et al. 2014). Chase (2007) found that zooplankton communities in temporary ponds were more similar to each other than they were to those in perennial ponds due to frequent drying conditions, which selected for community members that could withstand desiccation or rapidly colonize ephemeral habitats. Communities in habitats characterized by strong environmental dynamics are likely to be deterministically assembled and therefore amenable to management actions resulting in predictable conservation outcomes.

Although there has been a strong call for the use of community assembly rules in terrestrial restoration ecology, few studies have examined their potential for improving restoration outcomes in large-scale aquatic ecosystems. Here, we look for evidence of deterministic or stochastic community assembly mechanisms in zooplankton communities in floodplain and seasonally inundated off-channel habitats in California's Central Valley. Floodplains are critical habitats for many of California's native fishes. Of particular importance are the abundant invertebrate communities typical of these off-channel ephemeral habitats which provide rich trophic resources for native fish (Sommer et al. 2001b, Grosholz and Gallo 2006, Jeffres et al. 2008). Despite their importance, it is estimated that 95% of historic floodplain habitats in the Central Valley have been lost due to hydrologic modification of rivers and urban and agricultural development of floodplains (Hanak et al. 2011).

In the Central Valley, urbanization and agricultural development adjacent to rivers limits the potential for floodplain restoration. However,

extensive winter inundation still occurs on river-adjacent agricultural lands, especially rice fields that occupy much of the formerly active floodplain. In addition, portions of historical floodplain now act as flood bypasses. During flood events, high flows are routed through these managed floodways in order to protect cities and key infrastructure (Katz et al. 2017). Previous studies in the Yolo Bypass have demonstrated that inundated bypass lands provide high-quality zooplankton food resources to native fishes such as Sacramento splittail (*Pogonichthys macrolepidotus*) and Chinook Salmon (*Oncorhynchus tshawytscha*; Sommer et al. 2001b, Feyrer et al. 2006, Corline et al. 2017). Chinook Salmon reared in floodplain and off-channel habitats experience greater growth rates than those in rivers due to the high abundance of zooplankton prey as well as increased water temperatures (Jeffres et al. 2008, Katz et al. 2017). For anadromous species such as Chinook Salmon improved growth during the juvenile stage can lead to greater survivorship as they migrate to the ocean. Due to the importance of floodplain zooplankton food resources for native fish that depend on these habitats, it is imperative that fisheries and land managers understand the environmental filters that control zooplankton community assembly.

We hypothesize that winter-inundated off-channel floodplain habitat types in California's Central Valley share environmental filters that lead to deterministically assembled zooplankton communities of similar species composition. To test this hypothesis, we compared zooplankton communities across a diversity of winter-inundated aquatic habitats, including riverine locations within leveed river channels, restored floodplains, inundated rice fields, inundated flood bypasses, and unintentionally inundated agricultural lands. This suite of habitats sampled encompasses the full breadth of off-channel floodplain habitat types in the Central Valley that could potentially provide floodplain benefits for native fish species during the winter inundation.

## METHODS

### Study area

Historically, California's Central Valley had approximately 1.62 million hectares of wetland and floodplain habitat (Frayer et al. 1982).

Floodplains in the Central Valley typically inundate during winter and spring due to California's Mediterranean climate, with wet winters and dry summers. 95% of the historic floodplain habitats in the Central Valley have been lost due to reclamation for farming and urban development (Frayer et al. 1982, Dahl and Allord 1996, Hanak et al. 2011). However, winter inundation in the Central Valley still occurs in off-channel rice fields to aid in the decomposition of rice straw residue left after harvest, in flood bypasses for flood control, and naturally in restored floodplains. In addition to managed and restored floodplains, flood protection levees sometimes breach during flood events, inundating either agricultural or urban areas. Sampling for this study occurred in the Sacramento, Cosumnes, and Mokelumne rivers, rice fields, the Yolo Bypass, the Cosumnes River Floodplain, and an agricultural tract in the Delta unintentionally inundated due to levee failure (Fig. 1, Table 1).

#### Habitat types

*River habitats.*—The Sacramento River drains the north end of the Central Valley including tributaries from the Sierra Nevada mountains and the Coast Range mountains and drains approximately 6.9 million hectares. The Sacramento River and its tributaries are heavily regulated by large dams including Shasta Dam on the mainstem Sacramento River, Oroville Dam on the Feather River, and Folsom Dam on the American River. Extensive levees separate river channels from formerly activated floodplains. The Mokelumne River drains 550,000 ha from the west slope of the Sierra Nevada Mountains and is regulated by a series of upstream dams, with Camanche Dam being the most downstream regulating reservoir. The Cosumnes River drains 180,000 hectares and is the only large river that drains the Sierra Nevada mountains to the Central Valley without a major dam and as such has a relatively natural hydrograph. During the winter rainy season (December–March), the Cosumnes River generally contributes the majority of the flow into the heavily regulated lower Mokelumne River.

#### *Off-channel habitats.*—

*Flood bypass.*—The Yolo Bypass is a 24,000-ha flood control structure for the Sacramento Valley that diverts winter and spring floodwaters away

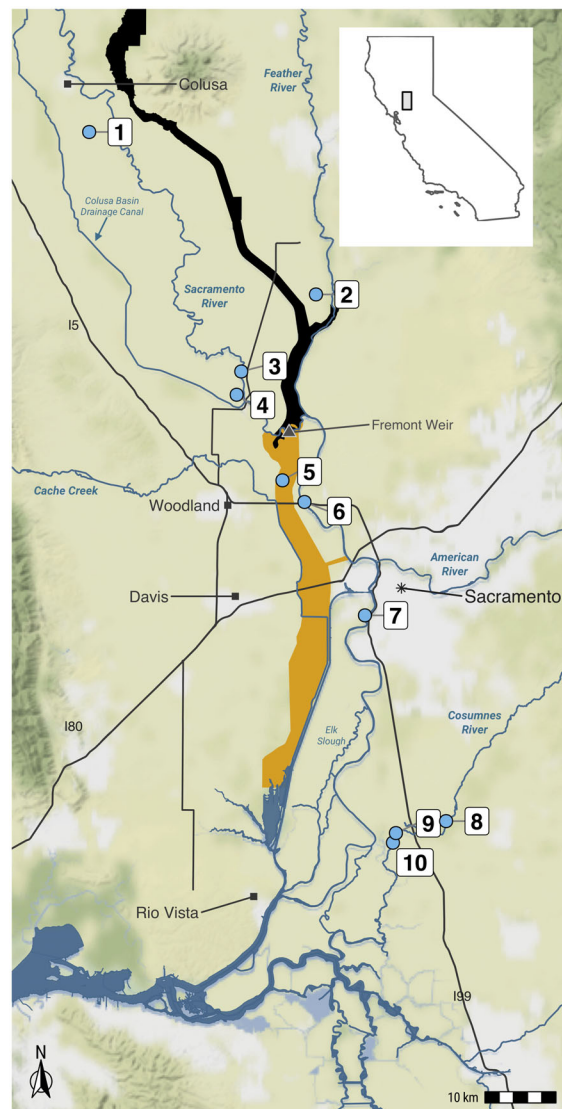


Fig. 1. Map of sampling localities from 2013 to 2018. See Table 1 for sampling localities and additional information.

from urban and agricultural infrastructure in the Sacramento area (Opperman et al. 2010). Two-thirds of the Yolo Bypass is privately owned and cultivated during the summer growing season with rice, wild rice, beets, tomato, corn and safflower (Sommer et al. 2001a, Opperman et al. 2010). The Sacramento River is the largest source of floodwater, and the Fremont Weir typically overtops when flows in the Sacramento River exceed 2000 m<sup>3</sup>/s. At 5000 m<sup>3</sup>/s, the Sacramento

Table 1. Sampling localities in decimal degrees.

Site code	Site name	Latitude	Longitude
1	Sycamore Family Trust	39.1441	−121.9746
2	Montna Farms	38.9383	−121.6071
3	Sacramento River at Knights Landing	38.8406	−121.7282
4	River Gardens Farm	38.8112	−121.7356
5	Yolo Bypass/Knaggs Ranch	38.7027	−121.6614
6	Sacramento River I5	38.6753	−121.6257
7	Sacramento River at Sherwood Harbor	38.5320	−121.5278
8	Cosumnes Floodplain	38.2713	−121.3962
9	McCormack-Williamson Tract	38.2562	−121.4775
10	Mokelumne River	38.2440	−121.4824

Weir's flash boards are removed and floodwaters flow into the Bypass from the east. Additional inflows from Knights Landing Ridge Cut, Cache Creek, Willow Slough, and Putah Creek can occur during storm events. Floodwaters drain out of the Yolo Bypass to the southeast and flow south into the Sacramento-San Joaquin Delta (Fig. 1, Table 1). Yolo Bypass samples used in our analysis are from when the bypass is inundated with water from the Fremont weir, not local inundation of rice fields.

**Rice field.**—Rice fields in the Sacramento Valley cover approximately 202,300 ha. These fields generally overlay clay-rich soils that were historically floodplain wetlands. Rice is planted in May and harvested in October. After harvest, approximately one third of these fields are inundated to aid in the decomposition of rice straw. Winter-inundated rice fields also provide habitat for migrating waterfowl and wading bird species using the Pacific Flyway (Ackerman et al. 2006). Sycamore Family Trust and River Garden Farms are adjacent to the Sacramento River, while Montna Farms sites are next to the Feather River. Knaggs Ranch rice fields are in the north end of the Yolo Bypass. Rice fields are inundated with water from agricultural drainage ditches, the Sacramento River, or the Feather River depending on location. North Valley rice fields and Knaggs Ranch are initially inundated with water from the Sacramento and Feather rivers and the Knights Landing Ridge Cut, respectively, to aid in rice straw decomposition.

**Cosumnes River floodplain.**—The Cosumnes River Preserve is a 16,000-ha preserve that conserves and restores agricultural, upland, and floodplain habitats along the Cosumnes River. Floodplains along the Cosumnes River consist of a mix of natural wooded floodplain, grassland, and wetlands as well as flooded rice fields. For this study, zooplankton were collected at the Triangle Floodplain. The site is located near the upstream extent of tidal influence and 5.7 km upstream of the confluence with the Mokelumne River. The Triangle Floodplain is approximately 40 ha and was previously annual row cropland. Levees were breached at the east and south sides of the agricultural parcel in 1997 and allowed for natural flooding of the site. The Triangle Floodplain is a complex habitat with various woody and herbaceous plant communities as well as geomorphic and topographic complexity. Inundation occurs when flows in the Cosumnes River exceed 25.7 m<sup>3</sup>/s, typically in winter and spring.

**McCormack-Williamson Tract.**—The McCormack-Williamson Tract (MWT) is a 602-hectare-leveed parcel of agricultural land located near Walnut Grove, California, in the North-East Delta (Fig. 1, Table 1). The MWT was first leveed in the 1920s and has been subject to periodic levee failure and flooding during high-water years since its reclamation. Since being reclaimed, MWT has been farmed with corn, tomatoes and other annual crops. MWT is currently slated for restoration into inter-tidal and floodplain habitat. During a high-water year in 2017, high winter flows in the Cosumnes River led to levee failures at the MWT that resulted in full inundation of the tract from 12 February 2017 to 30 May 2017.

### Zooplankton

**Sampling.**—Zooplankton samples were collected during the winter and spring months while habitats were flooded. Most sites were sampled either weekly, biweekly, or monthly, although the Cosumnes River floodplain was sampled as often as five times a week. A total of 365 samples were collected across all habitats (Appendix S1: Table S1). Sampling consisted of towing a 30-cm 150-μm mesh zooplankton net for one minute. Volume of water sampled during tows was quantified with a General Oceanics flow meter. Where tows were not possible, net



throws were used. Net throws were conducted with a 30 or 15 cm diameter 150- $\mu\text{m}$  zooplankton net attached to five meters of rope that was thrown the full five-meter distance and retrieved four times for a total sample volume of 1.41 and 0.35  $\text{m}^3$ , respectively. 15-cm zooplankton nets were used in rice fields when water levels were below 35 cm. The volume of water sampled was used to standardize zooplankton abundance and biomass calculations across methods. All samples were placed in Whirl-Pak bags (Madison, Wisconsin, USA) and preserved in a solution of 95% ethyl alcohol with rose bengal dye. Zooplankton samples from Sherwood Harbor on the Sacramento River were collected by the California Department of Water Resources using methods from Sommer et al. (2001b, 2004). Samples were collected with a 153- $\mu\text{m}$  mesh 0.5 m diameter Clark-Bumpus net equipped with a General Oceanics Flowmeter (Miami, Florida, USA) and preserved in 5% formalin.

**Sorting.**—Due to the abundance of zooplankton within samples, a sub-sampling protocol was used. Samples were rinsed through a 150- $\mu\text{m}$  mesh screen and emptied into a beaker. The beaker was filled to the desired volume, depending on the density of zooplankton within the sample, and then sub-sampled with a 1- to 2-mL large bore pipette. If zooplankton densities were too great for enumeration, the sample was split using a Wildco Folsom Plankton Splitter (Wildco, Yulee, Florida, USA) prior to sub-sampling. Zooplankton samples were enumerated until greater than 100 individuals of the target species were counted. Target species were those which were most common in the samples. Invertebrates were identified to the lowest taxonomic level possible using keys from pertinent ecological literature (Thorp and Covich 2009). Copepods were also identified to the lowest taxonomic level possible (genus); however, because of the difficulties in identifying copepodids and nauplii, family-level assignment of Copepods was used for analysis except for *Acanthocyclops* sp. and *Pseudodiaptomus* sp, which were common in our samples. Rare zooplankton (less than five occurrences) that were found at low abundances were not used in our final analysis. Terrestrial invertebrates and macroinvertebrates were not included in final counts. Only zooplankton were used for analysis.

### Water quality

Discrete water quality data were collected for years 2014–2018 at each sampling site using a handheld YSI 6600 data sonde (YSI, Yellow Springs, Ohio, USA) equipped with probes for temperature, dissolved oxygen, pH, and electrical conductivity. Optical probes were used to measure chlorophyll *a* concentration; however, additional water grab samples were collected and analyzed for chlorophyll *a* to ensure that optical measurements were accurate. Grab sample chlorophyll *a* concentrations were measured using APHA standard techniques (Clesceri et al. 1998).

### Analysis

We used R version 3.6.2 (R Core Team 2019) for transformation and manipulation of zooplankton and water quality data using the packages *dplyr*, *readr*, *readxl*, *lubridate*, *reshape2*, and *tidyr* (Wickham 2012, Wickham et al. 2015, 2017, Wickham and Wickham 2016, Wickham and Bryan 2017). Visualizations were created using packages *ggplot2* and *ggforce* (Wickham 2011, Pedersen 2019).

**Community analysis.**—Bray-Curtis dissimilarity was used to test for community differences between sites and years. Average zooplankton abundance was used to counteract the variability of lag time from off-channel disconnection to ecosystem response and unpredictability of community resetting events. Floodplains and off-channel habitats are highly dynamic, with frequent connection and disconnection events. Disconnection from the river channel increases water residence time on floodplains that, after a temporal lag, result in high productivity and the establishment of zooplankton communities (Ahearn et al. 2006). However, frequent reconnection to the river results in flushing and resetting of these communities.

Although many authors log-transform their abundance data to highlight rare taxa before calculating Bray-Curtis dissimilarity, we believe that abundance is a key aspect to community composition in off-channel habitats and is an important consideration for assessing community similarity for trophic importance. Non-metric multidimensional scaling (NMDS) was used to assess community similarity. Groupings were tested for significance by ANOSIM (analysis of similarity),

a non-parametric permutation analysis that tests for differences between groups using dissimilarity data. All community analyses were conducted with the package *vegan* (Oksanen et al. 2013).

*Indicator species analysis.*—We used indicator species analysis to determine which species contributed to assemblage distinctiveness between groups. Indicator values are the product of relative frequency and relative abundance of each species; species that are good indicators are found exclusively and consistently within a group at high abundance. Permutation tests were used to determine indicator significance. Apart from determining which species were significant indicators, the analysis also has two metrics, specificity and fidelity. Fidelity refers to the probability of finding a species in a group, while specificity is how likely a group can be assigned if a species was found in a sample. Indicator species analysis was conducted with the package *indicspecies* (De Cáceres 2013).

*Bayesian modeling.*—To evaluate environmental predictors of zooplankton indicator species abundance, we used a probabilistic modeling framework to assess measured variables. Only off-channel environmental data from 2014 to 2018 were used to best estimate zooplankton indicators for floodplain communities. Data were log-scaled and Pearson correlation coefficients were calculated. All variables with correlations  $>0.7$  were removed from the model. We used a hierarchical mixed-effect model modified for Bayesian approximation and implemented in R 3.6.2 (R Core Team 2019) with *stan* (Stan Development Team 2016a) and the *brms* and *Rstan* packages (Stan Development Team 2016b, Bürkner 2018). Weak prior probability distributions (priors) were assigned to all parameter values to ensure model fit, fixed effects were assigned weakly informative Student's *t*-priors ( $df = 3$ , location = 0, scale = 2), and the standard deviations and residuals of random effects were assigned weakly informative normal priors (mean = 0, SD = 1). Final models were run with four chains for a minimum of 4000 iterations, and model performance was assessed using *rhat* values (a model diagnostic with expected value equal to 1) to ensure model convergence. The unit of observation in our model was the combined abundance off-channel indicator species

per sample (individuals per  $m^3$ ) by location and time.

## RESULTS

### Community comparisons

Community composition in off-channel habitats (natural floodplains, rice fields, flooded bypass, and inundated agricultural land from years spanning 2013–2018) was tightly clustered, indicative of more similar community composition between these sites (stress = 0.0038; Fig. 2). River sites were more dissimilar and had larger dispersion of similarity. Despite differences in dispersion, there was little overlap in clustering. Community similarity was significantly different between groups (ANOSIM,  $R = 0.8719$   $P = 0.001$ , permutation = 999). See Appendix S1: Fig. S1 for NMDS with site information.

*Indicators species analysis.*—Indicator species analysis was used to determine which species were found consistently and frequently within off-channel habitat in comparison with rivers. Off-channel habitats had ten indicator species which had significant *P*-values of  $<0.05$  (Table 2). Eight of the ten indicator species were cladocerans, three of which belonged to the genus *Daphnia*. *Acanthocyclops* sp. was the only cyclopoid copepod species. Specificity of off-channel indicators ranged from 0.8914 to 0.9984 signifying that their presence is largely restricted to off-channel habitats. Lower specificity for *Chydorus sphaericus* likely represents high periodic abundance in river habitats. *D. mendotea*, *D. pulex*, *S. mixtus*, *Acanthocyclops* sp., *Ceriodaphnia* sp., *Bosmina* sp., *Calanoid* sp., and *Chydorus sphaericus* all had fidelity measures of 1, indicating that these species always occurred in all off-channel sites and years. Lower fidelity for *Sida* sp. and *D. parvula* means that these species were not found in all off-channel habitats or years. High fidelity, specificity, and significance of off-channel indicator species demonstrate that they are consistent and dominant parts of the zooplankton community in these habitats.

Rivers had one significant indicator species (*P* value  $< 0.05$ ); copepod nauplii were largely restricted to riverine sites but were not found at all river sites. Copepod nauplii indicator values (fidelity, specificity, and *P*-values) may be an artifact of poor taxonomic resolution due to small

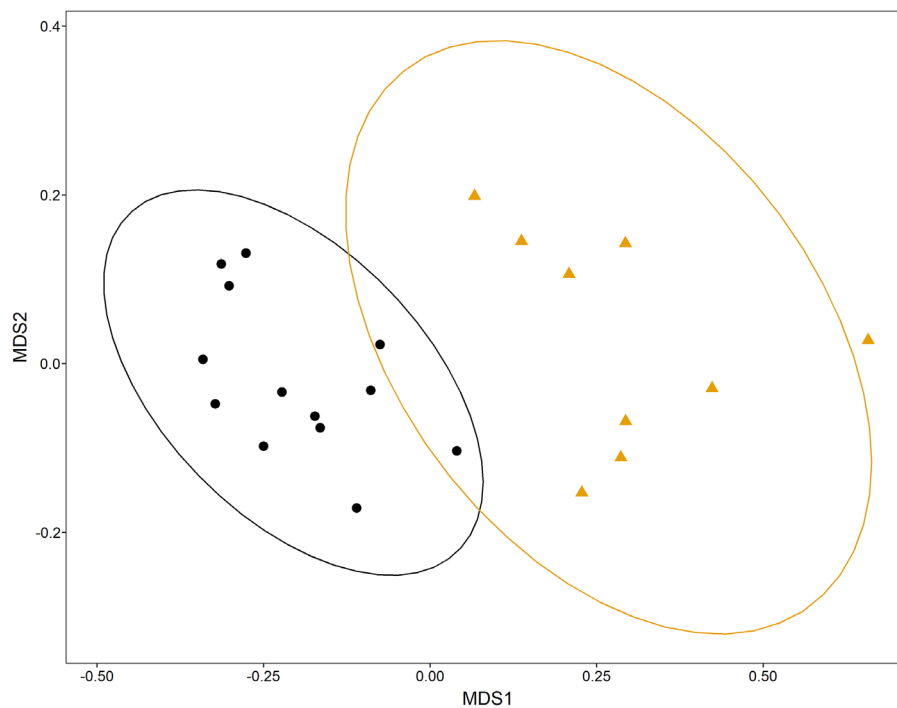


Fig. 2. NMDS of zooplankton community dissimilarity for river and off-channel sites from flood seasons 2013–2018.

Table 2. Indicator species, specificity, fidelity, and significance values for off-channel and river groups from flood seasons 2013–2018.

Taxa	Specificity	Fidelity	P
Off-channel			
<i>Daphnia mendotae</i>	0.998	1.000	0.0001
<i>Daphnia pulex</i>	0.998	1.000	0.0001
<i>Simocephalus mixtus</i>	0.986	1.000	0.0001
<i>Acanthocyclops</i> sp.	0.984	1.000	0.0001
<i>Ceriodaphnia</i> sp.	0.966	1.000	0.001
<i>Bosmina</i> sp.	0.922	1.000	0.0001
Calanoid sp.	0.901	1.000	0.001
<i>Chydorus sphaericus</i>	0.891	1.000	0.009
<i>Sida</i> sp.	0.973	0.615	0.045
<i>Daphnia parvula</i>	0.999	0.539	0.022
River			
Copepod nauplii	1.000	0.556	0.006

body size and should be interpreted with caution. Likewise, the 150- $\mu$ m mesh is biased toward zooplankton larger than most nauplii. River sites, in contrast to off-channel habitats, did not have a consistent distinct zooplankton community likely due to flushing conditions found in these

habitats (Pace et al. 1992) and potentially gear bias or poor taxonomic resolution of certain taxa.

*Influence of environmental variables based on Bayesian analysis.*—We compared four models and selected the best model using leave-one-out posterior comparisons (loo; Yao et al. 2018). The final model had the lowest loo score and when controlling for year, site, and month group effects, indicated increasing electrical conductivity (EC) and water temperature had a positive influence on abundance of the indicator species (Fig. 3, Table 3). Model estimates for pH indicated the opposite, and pH was the only environmental variable tested that showed a negative relationship with indicator species abundance. In Bayesian inference, an effect is not present when a distribution simply differs from zero; thus, to assess the effect strength of each variable, we used a test of practical equivalence which combines HDI (highest density interval) and ROPE (a region of practical equivalence; Kruschke 2018). This test evaluates what proportion of samples within a predictor's distribution (the HDI) fall inside or outside a region of practical equivalence

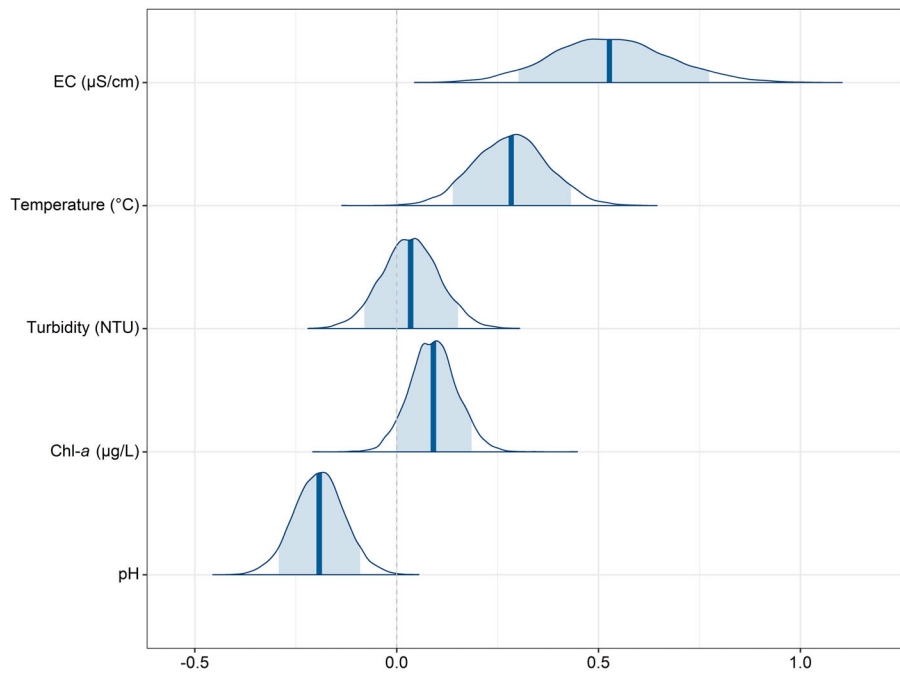


Fig. 3. Standardized coefficient estimates from posterior distributions on effect size for indicator species abundance, marked with 89% HDI.

Table 3. Mean, standard deviation (SD), and range of environmental variable measure at each site and year.

Site	Temperature (°C)		EC (mS/cm)		pH		Turbidity (NTU)		Chlorophyll <i>a</i> (µg/L)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
McCormack-Williamson Tract 2017	16.2 (3.0)	11.6–25.1	54.4 (6.6)	35.6–66.7	7.62 (0.19)	7.21–8.03	14.2 (12.5)	0.9–57.2	2.0 (1.1)	0.4–4.24
Cosumnes Floodplain 2018	16.1 (3.6)	10.4–21.9	101.4 (30.5)	57.6–158.8	8.00 (0.35)	7.15–8.82	8.1 (5.0)	2.4–25.3	2.4 (1.5)	0.7–6.1
Flooded Bypass 2017	12.1 (3.7)	7.9–20.6	239.1 (179.6)	52–539.1	8.08 (0.35)	7.54–8.89	46.4 (35.1)	11.1–156.2	4.6 (4.3)	0.8–14.4
Sutter Bypass Rice 2017	11.1 (3.2)	4.7–16.9	211.5 (73.6)	135.5–361.3	7.62 (0.29)	7.17–7.99	139.0 (142.7)	11.0–462.3	7.5 (6.2)	1.9–19.8
River Garden Rice 2017	6.8 (3.1)	3.7–11.4	93.4 (14.7)	77.8–121.1	7.79 (0.55)	6.84–8.28	32.8 (35.0)	2.2–81.9	2.7 (0.9)	1.7–4.2
River Garden Rice 2018	10.1 (3.3)	4.0–19.0	112.4 (20.6)	89.3–161.8	7.94 (0.27)	7.45–8.34	89.0 (126.0)	1.6–443.9	5.0 (4.1)	1.5–14.0
Sutter Bypass Rice 2018	12.3 (3.7)	6.9–19.2	283.4 (63.1)	231.6–436.3	7.77 (0.33)	7.27–8.26	34.8 (32.4)	6.1–135.5	3.5 (1.5)	1.9–7.1
Sycamore Family Trust 2017	8.4 (2.5)	4.4–11.8	275.5 (34.9)	222.4–335.7	7.68 (0.23)	7.24–7.97	101.8 (48.4)	10.1–186.0	6.1 (3.1)	2.2–13.6
Sycamore Family Trust 2018	9.7 (2.9)	6.5–16.2	259.1 (39.3)	199.8–373.4	8.04 (0.29)	7.58–8.46	854.4 (455.5)	9.6–1514.0	22.8 (24.2)	7.8–93.1
Yolo Bypass Rice 2015	14.7 (1.2)	13.9–17.3	670.9 (29.8)	619.2–721.5	8.37 (0.16)	8.18–8.59	25.9 (18.1)	12.1–61.3	5.2 (2.9)	1.0–9.9
Yolo Bypass Rice 2016	12.2 (3.1)	6.7–20.1	531.8 (115.7)	334.1–750.2	8.13 (0.23)	7.58–8.66	14.5 (18.4)	3.0–107.0	4.9 (2.3)	2.3–10.2



(ROPE). If the HDI of a model predictor lies inside, or only partially outside of a ROPE, the parameters may be considered to have little or no effect on the response. If the entire distribution falls outside of a ROPE, then the null hypothesis (that the parameter has no effect on the response) may be rejected.

EC and water temperature were the only variables that had zero samples fall inside the ROPE, with 89% HDI ranges of 0.32–0.76 and 0.15–0.44, respectively. There is 10% probability that the effect size of pH is practically equivalent to zero, while there is 0% probability that the effect size is zero for EC and for water temperature (Fig 4).

## DISCUSSION

### Community assembly

We found that zooplankton communities in winter-inundated off-channel floodplain habitats

in California's Central Valley assemble deterministically. Although many authors have promoted the use of community assembly mechanisms for ecological management and restoration, their application to large-scale managed aquatic ecosystems has previously been untested. Community assembly in inundated floodplain habitats has frequently been attributed to deterministic processes due to non-random patterns in species assemblages (Miranda and Lucas 2004, Arrington and Winemiller 2006, Lewis et al. 2006, Fernandes et al. 2014). However, these findings have not been universal and studies of phytoplankton and floristic colonization have shown that stochastic factors can be important components of community assembly in these habitats (Trowbridge 2010, Devercelli et al. 2016).

Non-random clustering of community similarity is indicative of deterministic community assembly (Chase 2007). The tight clustering of

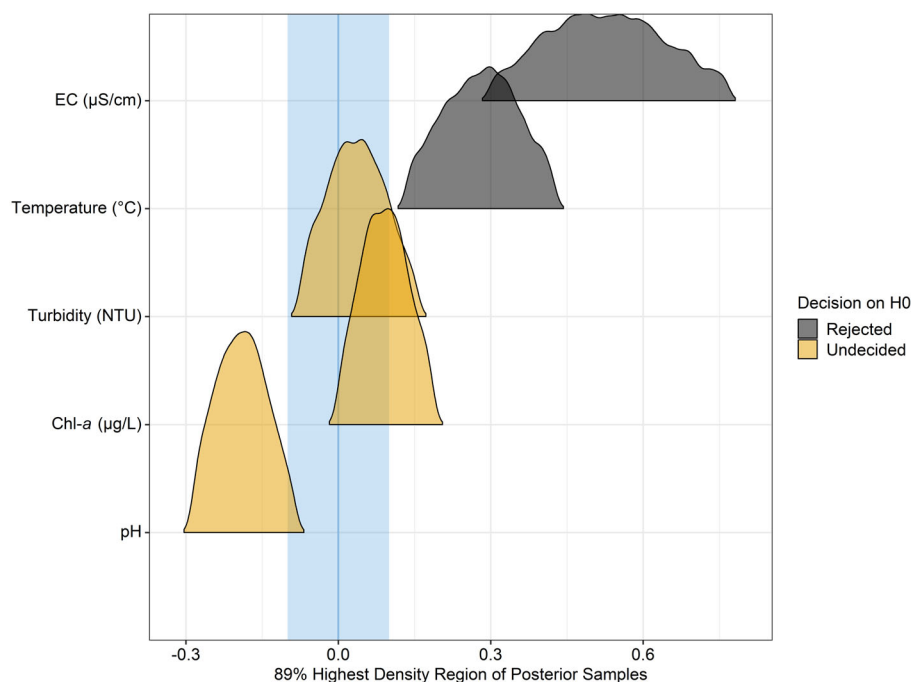


Fig. 4. Equivalence test using HDI and ROPE (region of practical equivalence; see Kruschke 2018), the null value of 0 is marked by a vertical line, annotated with the ROPE limits (blue shaded regions around zero). Each model parameter estimate shows the posterior distribution, and how much of the distribution that falls below, within, and above the ROPE. Notice that the 89% HDI falls entirely outside the ROPE for EC and water temperature, thus these parameters can be credibly rejected from a null model (as having no effect). There is a 10% probability that the effect size is practically equivalent to zero for pH, while there is 0% probability that the effect size is zero for EC and water temperature.

off-channel zooplankton communities in our NMDS analysis indicates that these communities were spatio-temporally similar. These results are striking given the broad variety of off-channel habitat and management types surveyed across two independent river drainages in this multi-year study, which included both flood and drought conditions. Such a large spatio-temporal span is likely to highlight stochastic processes such as dispersal limitation and priority effects (via probabilistic dispersal) should they be present (Hubbell 2001, 2005). However, we did not find evidence for either of these stochastic processes. Based on our results, environmental conditions in floodplains and off-channel habitats create similar environmentally determined niches which select for the same species from the regional species pool.

Off-channel zooplankton communities were dominated by cladoceran and cyclopoid copepod species. Indicator analysis demonstrated that the zooplankton community primarily consisted of cladocerans, with some of the best indicators being large bodied cladocerans such as *D. pulex*, *D. mendotae*, and *Simocephalus* sp. which are high-quality forage for juvenile fish (Katz et al. 2017). Indicator species are those which are found frequently, consistently, and at high abundance in their chosen group, and thus, our results indicate that high-quality zooplankton food resources for fish are found at all off-channel floodplain study sites and at high abundances. This is consistent with studies of other floodplain and off-channel habitats in California's Central Valley where cladocerans dominate the zooplankton community assemblage (Grosholz and Gallo 2006, Corline et al. 2017). Additionally, reliable off-channel indicator species further confirms our hypothesis of deterministic zooplankton community assembly in off-channel habitats in the Central Valley, as these species were found in off-channel habitats regardless of management type or location.

Indicator species abundance was strongly influenced by increases in electrical conductivity (EC) and water temperature, and somewhat associated with decreases in pH. EC increases through time in inundated low-velocity off-channel habitats due to both evaporation and leaching of ions from underlying sediments. High EC associated with salinity can negatively impact zooplankton, especially cladocerans (Anton-

Pardo and Armengol 2012). Most studies have focused on the role of NaCl on zooplankton communities and physiology in high salinity environments such as coastal lakes, lagoons, and road salt-impacted ponds (Van Meter et al. 2011, Anton-Pardo and Armengol 2012, Paturej and Gutkowska 2015). Given the positive relationship between zooplankton abundance and EC in our study, it is likely that increased conductivity was due to ions that did not negatively impact off-channel zooplankton. Additionally, zooplankton abundance was associated with changes in EC regardless of initial concentration (Appendix S1: Fig. S2). This result implies that zooplankton were not responding to changes in EC, but rather to increased residence time in floodplain and off-channel habitats.

In California's Mediterranean climate, floodplain inundation occurs in winter and early spring when day length, sun angle, and the total amount of solar radiation absorbed by floodwaters is increasing, all of which tend to lead to steady seasonal increases in water temperature (Ahearn et al. 2006). Temperature can strongly effect zooplankton metabolic rates, size, and fecundity, with temperatures between 12° and 15°C leading to maximum growth and reproductive rates for cladocerans given suitable trophic resources (Masclaux et al. 2009, Arendt 2011). The positive relationship between temperature and indicator zooplankton abundance suggests that food resources were not limiting at most of our study sites.

pH increases and decreases due to photosynthesis and bicarbonate buffering processes. Decreased pH can also be due to CO<sub>2</sub> released from microbial respiration decomposing organic matter and from the release of organic acids from sediments. The relationship between pH and zooplankton morbidity and mortality is well studied with the majority of impacts associated with low pH (Ivanova 1987, Havens 1992), while high pH greater than 9 can have detrimental effects on zooplankton reproduction (Vijverberg et al. 1996). pH in our study ranged from 6.8 to 8.9 and was negatively associated with indicator zooplankton abundance. It is possible that higher pHs may have contributed to decreased reproductive success and mortality of zooplankton; however, it was unlikely as we observed high zooplankton densities at all pH levels sampled.

The relationship between pH and zooplankton abundance warrants further study in floodplain and off-channel habitats.

Although zooplankton species in our study could have been directly responding to changes in EC and temperature, these chemical and physical changes reflect common qualities of off-channel habitats: increased residence time of floodwaters. Previous studies of floodplain zooplankton communities have found that residence time is the overall determinant of assembly and abundance, with higher residence time habitats having higher diversity and density of cladocerans and copepods (Baranyi et al. 2002, Ahearn et al. 2006). Increased residence time in off-channel habitats is indicative of the fundamental floodplain process of inundation and disconnection from the main river channel that creates relatively warm water temperatures, low-velocity, and abundant basal food resources in comparison with deeper and higher velocity habitats (Junk et al. 1989, Tockner and Stanford 2002, Ahearn et al. 2006). Although water residence time is likely the most important variable determining zooplankton species assemblage in off-channel habitats in our study, we do not know what species trait residence time selects for. All species found in our study are associated with pond-like conditions, but further study of species functional traits may help explain what aspects of increased residence time leads to their proliferation.

#### *Management implications*

California's Central Valley was historically a habitat mosaic of rivers, lakes, wetlands, and floodplains. Although much of this habitat has been lost, large areas of winter-inundated farmland, flood bypasses, and restored and pre-restoration floodplains still exist. These novel habitats provide a unique opportunity to create a multi-use landscape where winter inundation on low-lying agricultural lands, managed wetlands, and flood protection infrastructure could provide trophic resources to native species. Since zooplankton communities in these diverse floodplain habitats are consistent across years and land use types, there is considerable opportunity to use this information to inform conservation management actions. Community assembly rules have been used in weed abatement (Smith 2006)

and grassland restoration management strategies (Hulvey and Aigner 2014), but never before in large-scale aquatic ecosystem management.

Deterministic assembly of off-channel zooplankton communities suggests that flooding of off-channel lands capable of sustaining long residence times could consistently provide abundant, high-quality food-web resources for native fish populations that have access to these critical trophic resources. Our data also indicate that newly restored floodplain habitat can immediately provide food benefits similar to mature floodplain restoration sites. Residence time appears to be the most important factor for zooplankton community assembly in off-channel habitats, and floodplain restoration design and management of infrastructure must take water residence time into account in order to provide floodplain food-web benefits to native fish species.

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