

# Zooplankton ecology and trophic resources for rearing native fish on an agricultural floodplain in the Yolo Bypass California, USA

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**Abstract** Out-migrating juvenile Chinook Salmon *Oncorhynchus tshawytscha* in California's Central Valley lack frequent access to historical off-channel habitats such as floodplains. However, many regions have agricultural floodplains that may provide habitat value to young salmon. To determine the suitability of agricultural floodplain, this study tested whether winter-inundated rice fields in a historic flood basin in California's Central Valley could provide adequate food resources for rearing juvenile Chinook Salmon. We examined the suitability of flooded rice fields for three post-harvest habitat types: stubble, fallow, and disced. Soil emergent and pelagic zooplankton communities were compared to determine colonization sources. Winter-inundated rice fields had high densities of zooplankton, which increased over the course of the study. *Daphnia pulex*, a large-bodied cladoceran and an excellent forage species of juvenile Chinook Salmon, was abundant in our study. Cladocerans

colonized via source water while ostracods likely colonized from a soil egg bank. Overall, there was no discernable effect of habitat type on zooplankton community structure or density, except for *D. pulex*. Our results suggest that flooded agricultural rearing habitat can support juvenile Chinook Salmon based on high densities of zooplankton and other suitable habitat conditions have the potential to support a robust aquatic food web.

**Keywords** Floodplain · Zooplankton · *Daphnia* · Chinook Salmon · Colonization · Rice field

## Introduction

Floodplains are integral and ecologically important components of riverine ecosystems that provide habitat and trophic resources for aquatic and terrestrial animals (Junk et al. 1989; Tockner and Stanford 2002). Due to their unique topographical, hydrological, and chemical attributes that increase mixing, nutrient availability, and residence time compared to mainstem rivers, floodplains are sites of high productivity that support high biodiversity (Salo et al. 1986; Junk et al. 1989; Bayley 1995; Tockner and Stanford 2002; Schemel et al. 2004; Grosholz and Gallo 2006; Ahearn et al. 2006). The ecological importance of floodplain resources is apparent in the evolution of life history strategies of aquatic and terrestrial species that

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take advantage of floodplain productivity (Junk et al. 1989; Bayley 1995; Humphries et al. 1998). For example, many fish species use floodplains for spawning and rearing to capitalize on the productive ephemeral habitat.

Although floodplains are important components of functioning river and riparian ecosystems, 90% of Europe and North America's floodplains have been developed for human use, primarily for agricultural production (Tockner and Stanford 2002). The disconnection of floodplains from their associated rivers has led to a decrease in habitat for floodplain-adapted species. A lack of access to off-channel areas is potentially detrimental to fish populations and other species that depend on floodplains for nursery and spawning habitat (Sommer et al. 2007). Additionally, disconnection of floodplains from rivers may reduce river productivity. Floodplains in large lowland rivers increase ecosystem productivity through export of autochthonous organic matter to the main river channel and migration of river dwelling species to and from the floodplain (Junk et al. 1989). In California's Central Valley, only 5% of historic floodplains remain, with most existing as bypasses that divert water away from urban areas during high flow events (Opperman et al. 2010; Hanak et al. 2011).

Inundation in remnant floodplains, such as the Yolo Bypass in the Central Valley, does not occur at historic magnitudes due to management of upstream dams and levees (Opperman et al. 2010). Furthermore, California's bypasses are graded to allow for efficient drainage of floodwaters, which has decreased residence time compared to historic conditions (Sommer et al. 2001a). To regain the large-scale ecosystem benefits of floodplains to native fish and bird species, use of appropriate agricultural land can be considered as a surrogate to lost historic floodplains. The Yolo Bypass offers a major opportunity to seasonally utilize agricultural infrastructure as managed floodplains. Due to California's Mediterranean climate, crop cultivation occurs in spring through early autumn, whereas flooding typically occurs in winter; this timing could allow for use of agricultural lands as floodplains during the annual agricultural fallowing.

The flooding of agricultural lands may be particularly important for providing floodplain benefits to Chinook Salmon, *Oncorhynchus tshawytscha*, which exhibit increased growth and body condition in floodplain habitats (Sommer et al. 2001b; Jeffres

et al. 2008). Anadromous salmonids with greater mass or body condition at time of arrival to the ocean have increased survival and spawning return rates; thus, the growth benefits accrued in floodplains are germane to aiding native fish species (Unwin 1997; Satterthwaite et al. 2012).

Presently, the Yolo Bypass provides floodplain habitat for juvenile Chinook Salmon during natural inundation events, but these events are often brief or of low magnitude, which decreases the potential floodplain benefits accrued by juvenile salmon (Sommer et al. 2001a, b, 2005). However, floodable agricultural land in the Yolo Bypass, such as rice fields, could function as surrogate winter habitat for juvenile Chinook Salmon in the absence of natural flooding. For example, agricultural floodplain infrastructure could be used to increase residence time during natural inundation events. After taking advantage of floodplain productivity, fish would be able to return to the mainstem river via canals that drain the Yolo Bypass to the Sacramento River.

To potentially manage agricultural habitat for rearing juvenile Chinook Salmon, it is important to understand the availability of food resources. Prior to entering the ocean, the diet of young salmon is primarily composed of invertebrates (Healy 1991). In riverine habitats, juvenile Chinook Salmon feed on drifting macroinvertebrates (Healy 1991; Sommer et al. 2001b); however, salmon in lentic, slow water environments may feed heavily on zooplankton (Rondorf et al. 1990; Jeffres et al. 2008).

Previous studies of floodplain invertebrate colonization demonstrate that zooplankton colonize from both allochthonous and autochthonous sources (Tronstad et al. 2005, 2007). Autochthonous zooplankton emerge from quiescent resting stages in floodplain sediments and are adapted to cope with desiccation of ephemeral habitats (Havel et al. 2000; Tronstad et al. 2005; Benigno and Sommer 2008). Allochthonous invertebrates colonize from adjacent habitats by movement, oviposition, phoretic dispersal, or through floodwaters, either in water from the main river channel or from inundated water bodies within the floodplain (Havel et al. 2000; Tronstad et al. 2007).

Once floodwaters are colonized, abundances of zooplankton can easily increase to the tens of thousands of individuals per square meter and have 10–100 times the abundances found in the adjacent river habitats (Havel et al. 2000; Tronstad et al. 2005;

Grosholz and Gallo 2006; Tronstad et al. 2007). Previous studies in the Yolo Bypass have shown that zooplankton abundances were not significantly different between the Sacramento River and Yolo Bypass during peak flooding events but were higher during floodplain draining (Sommer et al. 2001b, 2004). Inundated agricultural lands (e.g., rice fields) in the Yolo Bypass, however, may have more abundant zooplankton resources than found in earlier studies due to differences in source communities and habitat conditions. Flooded rice fields in the Yolo Bypass are unique compared to natural flooding events as they receive inundation water from high productivity agricultural canals and are inundated in the summer and winter.

As part of a larger study of juvenile Chinook Salmon rearing in the Yolo Bypass, we sought to determine the effects of land use practices on zooplankton communities and colonization pathways. Understanding how the zooplankton community responds to the management of rice fields is a key issue in management of agricultural land for juvenile fish nursery habitat. Specifically, our hypotheses were as follows: (1) winter-inundated rice fields will provide abundant trophic resources for juvenile Chinook Salmon compared to the adjacent Sacramento River, (2) habitat type (post-harvest treatment of rice fields) affects the abundance of different zooplankton species, and (3) zooplankton community members have different colonization pathways (e.g., allochthonous vs. autochthonous sources).

## Methods

### Study site

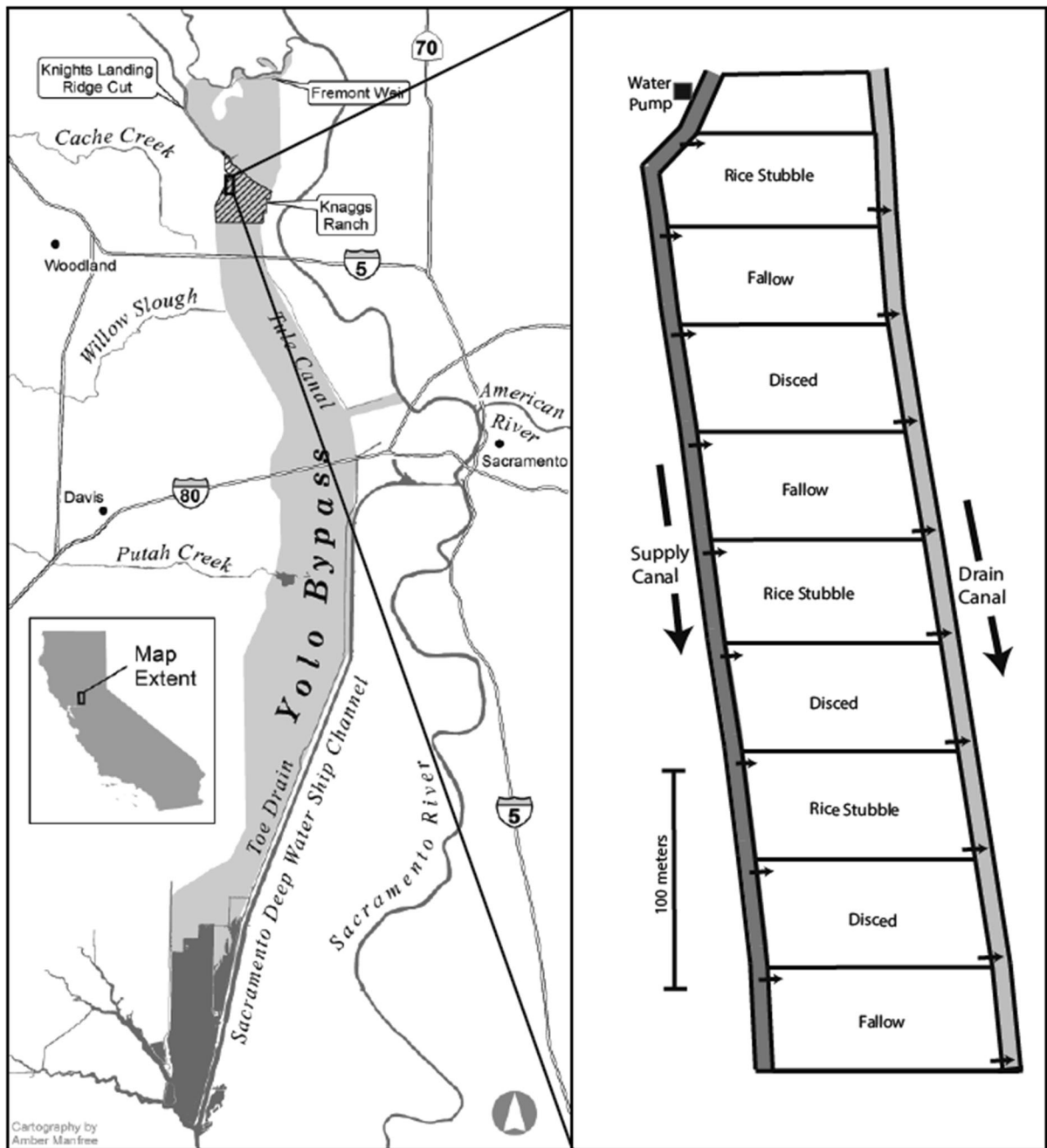
The Yolo Bypass is the largest and most frequently inundated relict floodplain in California covering 24,000 ha, experiencing some degree of flooding in about two out of every 3 years (Sommer et al. 2001a). Constructed in the 1930s, the Bypass acts as a flood control structure for the Sacramento Valley, shunting water away from important urban and agricultural infrastructure (Opperman et al. 2010). Inundation of the Bypass generally occurs between December and May; it receives floodwaters from the Sacramento River at the Fremont and Sacramento weirs, Knights Landing Ridge Cut, and local drainage water from

Putah Creek, Cache Creek, and Willow Slough (Fig. 1). Flooding from the Fremont Weir typically occurs when flows in the Sacramento River exceed 2000 m<sup>3</sup>/s; initially, flows enter the Tule Canal and Toe Drain (Fig. 1), then move west as discharge exceeds the banks of the canal. When flows exceed 5000 m<sup>3</sup>/s, the Sacramento Weir may also overtop and flow into the Bypass from the east. Additional inflow from western tributaries can occur during storm events and create distinct water masses in the Yolo Bypass (Sommer et al. 2001a). Floodwaters drain out of the Bypass to the southeast, entering the Toe Drain and ultimately flow south into the Sacramento-San Joaquin Delta (Fig. 1).

Apart from flood protection, the Bypass provides agricultural and wildlife benefits. Two-thirds of the Bypass is privately owned agricultural land and is cultivated in the summer months with crops such as rice, wild rice, beets, tomato, corn and safflower (Sommer et al. 2001a; Opperman et al. 2010). Flooding and winter inundated rice fields are particularly important for waterfowl using the Pacific Flyway (Ackerman et al. 2006). Additionally, at least 42 species of fish use the Bypass including 15 native species (Sommer et al. 2001a). Native fish species include four runs of Chinook Salmon, green sturgeon *Acipenser medirostris*, white sturgeon *A. transmontanus* and Sacramento splittail *Pogonichthys macrolepidotus* (Sommer et al. 2001a, 2007; Schemel et al. 2004; Feyrer et al. 2006, 2007).

### Experimental fields

We constructed nine 0.79-ha experimental units on Knaggs Ranch in the north end of the Yolo Bypass (Fig. 1). Fields were inundated on February 5th 2013 with water from Knights Landing Ridge Cut, a channel that drains the Colusa Basin and supplies agricultural water to the Yolo Bypass, and were drained on March 27th 2013. Each field had an inlet at the northwestern corner supplied with water from a main canal and an outlet at the southwest, which ultimately drained into the Tule Canal. Inlet and outlet flow was controlled with a “rice box”, a 60 cm plastic culvert with a face-mounted slot that holds boards that manipulated inflow and outflow by elevation control. Experimental fields were continually connected to the inlet canal; however, flow into the fields was variable. Water elevations within the fields varied from 0.3 to 0.5 m depending on wind and



**Fig. 1** Map shows the location of the zooplankton study area and experimental treatment layout at Knaggs Ranch (cross hatched), Yolo Bypass (shaded), Yolo County, California, USA

flow conditions. Flow rates into the fields ranged from 0.0 to 0.06 cubic meters per second.

We randomly assigned a treatment that corresponded to a different habitat type. In this case, habitats were based on different post-harvest management options typically used in rice fields. The habitat

types were: rice stubble, disced, or 1-year fallow. Rice stubble refers to the management option where the remnant vegetation from the summer rice harvest is left to decompose while standing. Rice stubble, in this study, had an average stem density of 566 stems/m<sup>2</sup> and an average height of 0.3 m. Discing is a post-harvest

farming method where rice stubble is flooded and incorporated into the field to promote decomposition, eliminating much of the standing remnant vegetation. The fallow treatment had periodic inundation during the previous growing season, but was not cultivated or disced, remaining fallow for 1 year. Herbaceous plants colonized fallow fields with an average stem density of 390 stems/m<sup>2</sup> and an average height of 51 cm. In both disced and rice stubble treatment fields, rice was cultivated and harvested in the previous growing season. Each field was stocked with ~4500 juvenile Chinook Salmon from the Feather River Hatchery (Oroville, CA), which initially measured approximately  $53.6 \pm 0.15$  mm FL.

### Sampling

#### *Soil emergence*

We collected soil samples from November 9th to 16th, 2012 to assess the presence of autochthonous zooplankton and effects of different habitat treatments on the soil-resting invertebrates. We removed six soil samples from random points within each treatment field with a  $28 \times 40.6 \times 15.2$  cm metal form used to cut and remove the soil intact; samples were placed in  $28 \times 40.6 \times 35$  cm plastic containers fitted with mesh emergence trap lids to capture adult aquatic insects that emerged from the water. To simulate flooding, we re-hydrated each soil sample to a depth of 16 cm above the surface of the soil with well water at the Center for Land Based Learning in Winters, CA. Rehydrated samples were kept outdoors for the entire study period, which exposed soil invertebrate resting stages to ambient light and temperature conditions. During rain events, the samples were covered by a tarp to keep the sample containers from over-topping. The water column within each container was swept once a week for three weeks with a ~300 µm net for one minute to collect zooplankton and macroinvertebrates. Collected invertebrates were preserved in 70% ethyl alcohol.

#### *Pelagic zooplankton community*

A total of 69 pelagic samples were taken over the course of six weeks from February 13th 2013 to March 20th 2013 to measure differences in zooplankton community abundances among habitat treatments and

to determine allochthonous zooplankton inputs. Zooplankton samples were collected at initial flooding and once every week thereafter. The source water inlet canal was sampled prior to inundation and then during weeks three, four, five, and six. To assess invertebrate diversity and abundance on different habitat types and the inlet canal, a 153 µm zooplankton net attached to 5 m of rope was thrown the full 5-m distance and retrieved four times for a total volume of 1.92 cubic meters sampled per sample. Water velocity within the fields was negligible and therefore the volume that was calculated by length of rope and area of net was the actual volume sampled. Sampling locations were determined randomly within substrate habitat treatments via selection of random x and y distances from a random number table. All samples were placed in Whirlpak<sup>TM</sup> bags (Nasco, USA) and preserved in a solution of 95% ethyl alcohol.

#### *Sorting/identification*

Due to the abundance of invertebrates within samples, a sub-sampling protocol was used. Samples were rinsed through a 150-µm 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 mL large bore pipette. If invertebrate densities were too great for enumeration, the sample was split using a Wildco Folsom Sample Splitter (Wildco, Yulee, FL, USA) prior to sub-sampling. Zooplankton samples were enumerated until >300 *Daphnia pulex* were counted. *D. pulex* was the most important forage species for juvenile Chinook Salmon in this study (Katz, unpublished data) and thus a thorough sampling of this species was warranted to determine the suitability of rice fields in providing the food resources for salmon. The volume and number of aliquots removed was recorded and used to obtain total estimates of invertebrates per cubic meter. Due to the small number of invertebrates per collection in the soil emergent samples, these samples were not sub-sampled. Invertebrates were identified to the lowest taxonomic level possible using keys from pertinent ecological literature (Merritt et al. 2008; Thorp and Covich 2009; Mischke 2013). 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. Chironomids were only identified to family. Terrestrial invertebrates were not included in final counts.

### *Sacramento River Zooplankton*

Zooplankton samples were collected concurrently during the study period at Sherwood Harbor on the Sacramento River by the California Department of Water Resources using methods from Sommer et al. (2001a, b, 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, FL, USA) and preserved in 5% formalin. Flow meter distance and net dimensions were used to calculate zooplankton per cubic meter.

### *Water quality measurement*

Discrete water quality data was collected weekly using a handheld YSI 6600 data sonde (Yellow Springs, OH) equipped with probes for temperature, dissolved oxygen, pH and electrical conductivity. Weekly water samples were collected at the inlet and in the center of each field. Samples were analyzed for chlorophyll *a*, turbidity, nitrate, ammonia, total phosphorus, and orthophosphate. We were not able to process week one chlorophyll *a* samples due to excess silt encountered during collection. Wind speed data for the study period were downloaded from California Data Exchange Center (<http://cdec.water.ca.gov/index.html>) Woodland weather station (WLD). A wind event was classified as an average daily wind speed >6 mph.

### *Data analysis*

The six most abundant taxa, *D. pulex*, *Ceriodaphnia* sp., *Chydorus sphaericus*, *Simocephalus mixtus*, cyclopoid copepods, and ostracods, were used for comparisons among habitat treatments as well as the summed abundance of all taxa. Linear mixed effect models were fitted for taxa in both inundated rice field treatments and soil samples due to repeated measures and the randomized design of the experiments. The data were assumed normally distributed if the Shapiro–Wilkes test statistic was large ( $W > 0.94$ ) or the results insignificant ( $P > .05$ ). Abundances were log transformed  $\log(x + 1)$  to meet the

assumptions of the analysis. ANOVA was used to detect differences between the treatments and due to multiple comparison nature of the study a Bonferroni correct alpha was used to avoid false positives ( $0.05/27 = 0.0019$ ). Simple linear regressions were performed for each taxon per treatment to show changes in density associated with week. The inlet canal was a source of zooplankton colonists in our study; samples were used for qualitative comparisons, but were excluded from linear mixed effects model and ANOVA as it was not a treatment and was not sampled with the same consistency as the treatment fields. ANOVA was used to detect differences in water quality among habitat treatments. A Tukey's Honest Significant Difference test was performed to detect significant difference between habitat treatments. All calculations were performed in R Studio (Version 3.0.2).

## **Results**

### *Water quality*

#### *Physical and chemical*

All treatments had similar nutrient profiles with no significant difference among habitat treatments; ammonium ( $\text{NH}_4^+$ ) from 0.0408 to 0.0586 ppm (ANOVA,  $F = 0.4974$ ,  $df = 2,6$ ,  $P = 0.6311$ ), nitrate ( $\text{NO}_3$ ) ranged from 0.0049 to 0.0088 ppm (ANOVA,  $F = 1.2105$ ,  $df = 2,6$ ,  $P = 0.3617$ ), and soluble reactive phosphorous (SR- $\text{PO}_4$ ) from 0.0724 to 0.0818 ppm (ANOVA,  $F = 0.3524$ ,  $df = 2,6$ ,  $P = 0.7166$ ). Total phosphorous (P) was not different between the treatments (ANOVA,  $F = 2.8241$ ,  $df = 2,6$ ,  $P = 0.1367$ ). There was no significant difference between turbidity between treatments (ANOVA,  $F = 3.080$ ,  $df = 2,6$ ,  $P = 0.1201$ ), however, wind events raised turbidity (ANOVA,  $F = 6.5273$ ,  $df = 1,42$ ,  $P = 0.0143$ ). During wind events, the disced treatment had an average turbidity of 70 nephelometric turbidity units (NTUs), while the stubble and fallow treatments had an average turbidity of 36 NTUs and 26 NTUs, respectively. During non-wind events, the disced treatment had a slightly higher average turbidity at 27 NTUs while the stubble and fallow treatment had turbidity of 15 NTUs and 9 NTUs, respectively. Temperatures initially averaged



11 °C, but fell to 8 °C in the second week. Water temperature thereafter increased, with an average temperature of 17 °C in the fifth week. In week six temperatures decreased to 15 °C.

### Chlorophyll *a*

Chlorophyll *a* concentrations were extremely variable between habitat treatments and over time (Fig. 2) with no significant difference in chlorophyll *a* concentration among substrates (ANOVA,  $F = 0.3666$ ,  $df = 2,6$ ,  $P = 0.7076$ ) or week (ANOVA,  $F = 0.1363$ ,  $df = 1,33$ ,  $P = 0.7097$ ). Chlorophyll *a* was at its lowest level in most treatments during the 4th week of the study (0.68 ppb stubble, 0.673 ppb disced, and 0.81 ppb fallow).

### Zooplankton

#### Overall pelagic zooplankton abundance patterns

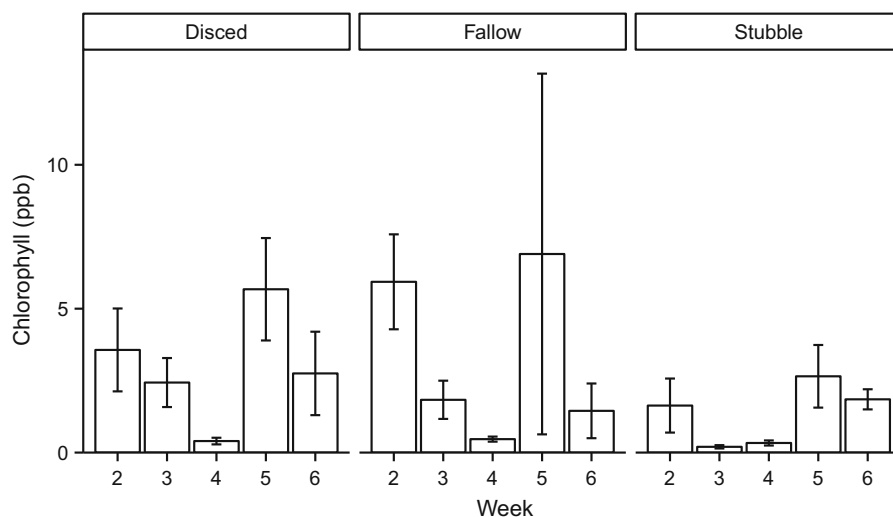
Average total zooplankton abundance increased for all habitat treatments throughout the study period except weeks four and five, when abundance either decreased (fallow and disced) or remained the same (stubble) (Fig. 3). There was only a trend toward a difference in total abundance between treatments (ANOVA,  $F = 4.57$ ,  $df = 2,6$ ,  $P = 0.0621$ ). However, zooplankton

abundance increased significantly (ANOVA,  $F = 56.06$ ,  $df = 1,42$ ,  $P < 0.0001$ ) as the study period progressed (Fig. 3). There was not a significant interaction between substrate and week (ANOVA,  $F = 0.253$ ,  $df = 2,42$ ,  $P = 0.7820$ ).

#### Responses of specific pelagic taxa

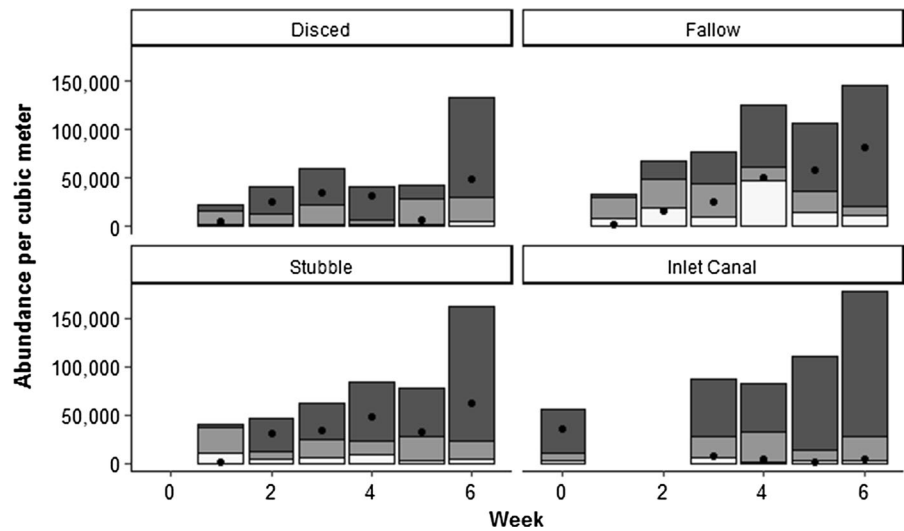
There was no distinguishable pattern to cyclopoid copepod abundance throughout the study. Neither time (ANOVA,  $F = 0.0163$ ,  $df = 1,42$ ,  $P = 0.33$ ) nor substrate (ANOVA,  $F = 0.4773$ ,  $df = 2,6$ ,  $P = 0.602$ ) predicted density of copepods in the experimental fields. Ostracods, in particular *Eucypris* sp., demonstrated a similar pattern to cyclopoid copepods, with variable mean densities over time. Substrate did not significantly affect ostracod abundance (ANOVA,  $F = 8.9615$ ,  $df = 2,6$ ,  $P = 0.015$ ) although lower abundances of ostracods were seen in the disced and stubble treatments than the fallow treatment (Fig. 3). Time did not significantly contribute to ostracod abundance (ANOVA,  $F = 0.9926$ ,  $df = 1,42$ ,  $P = 0.32$ ).

Cladocerans were the most abundant zooplankton group making up over 50% of all taxa in the infield samples with *D. pulex*, *C. sphaericus*, *Ceriodaphnia* sp., and *S. mixtus* making up the majority of the cladoceran assemblage (Fig. 3). Cladoceran density



**Fig. 2** Average chlorophyll *a* concentration per habitat treatment by week in parts per billion (ppb). Error bars are standard error. Week one data is not available due to excess silt encountered during collection

**Fig. 3** Average abundance of zooplankton in fallow, stubble, and disced treatments, as well as, the inlet canal. Cladocerans (dark grey), cyclopoida (grey), and ostracoda (white). Average *D. pulex* abundance (solid circles). Week zero corresponds to inlet sampling the week prior to inundation



increased over the course of the study period (ANOVA,  $F = 91.495$ ,  $df = 1,42$ ,  $P < 0.0001$ ), but did not differ among substrates (ANOVA,  $F = 1.299$ ,  $df = 2,6$ ,  $P = 0.3398$ ).

*D. pulex* abundance began at low densities across the treatments with an average abundance at inundation of 1493 individuals/m<sup>3</sup> (ind./m<sup>3</sup>) in the stubble, 4855 ind./m<sup>3</sup> in the disced treatment, and 2062 ind./m<sup>3</sup> in the fallow. By the end of the study, *D. pulex* density had risen to over 62,542 ind./m<sup>3</sup>, 48,934 ind./m<sup>3</sup>, and 81,925 ind./m<sup>3</sup> in stubble, disced, and fallow treatments respectively. Time (week) had the greatest effect on *D. pulex* abundance (ANOVA,  $F = 39.190$ ,  $df = 1,42$ ,  $P < 0.0001$ ), while treatment did not significantly affect *D. pulex* abundance (ANOVA,  $F = 2.135$ ,  $df = 2,6$ ,  $P = 0.1994$ ). There was no interaction between week and substrate for *D. pulex* (ANOVA,  $F = 5.184$ ,  $2,42$ ,  $P = 0.0097$ ).

*C. sphaericus* and *Ceriodaphnia* spp. were the two most abundant small-bodied cladocerans (body size typically <1 mm). Both *C. sphaericus* or *Ceriodaphnia* spp. increased in abundance over time (ANOVA,  $F = 91.803$ ,  $df = 1,42$ ,  $P < 0.0001$  *C. sphaericus*,  $F = 103.28$ ,  $df = 1,42$ ,  $P < 0.0001$  *Ceriodaphnia*), but were not affected by treatments (ANOVA,  $F = 4.1584$ ,  $df = 2,6$ ,  $P = 0.0736$ , *C. sphaericus*,  $F = 2.003$ ,  $df = 2,6$ ,  $P = 0.2157$  *Ceriodaphnia* spp.). *S. mixtus*, another large littoral daphniid, consistently made up a small fraction of the zooplankton community. *S. mixtus* densities increased over time (ANOVA,  $F = 80.598$ ,  $df = 1,42$ ,  $P < 0.0001$ ), but did not differ

significantly across treatments (ANOVA,  $F = 0.9733$ ,  $df = 2,6$ ,  $P = 0.43$ ).

#### Sources of zooplankton

##### Inlet water

The inlet canal served as a source for allochthonous zooplankton colonization and thus shared many of the same taxa such as the experimental fields including *D. pulex*, *S. mixtus*, *C. sphaericus*, *Ceriodaphnia* spp, cyclopoid copepods, rotifers, and *Eucypris* sp. ostracods. While *D. pulex* densities increased during the study period in the inundated rice fields, densities in the inlet canal declined over time (Fig. 3). Prior to inundation, the *D. pulex* abundance was high in the inlet canal at 35,625 ind./m<sup>3</sup>. After inundation, *D. pulex* densities declined while *S. mixtus* abundances increased in the inlet canal. Similarly, *C. sphaericus* densities remained higher in the inlet canal than the treatment fields during the study period.

##### Soil emergence

The dominant soil-emergent invertebrates were ostracods and cyclopoid copepods. Rotifers were periodically found in our samples, but due to our net mesh size their numbers could not be accurately assessed. Soils from the fallow field had a significantly higher number of emergent ostracods (ANOVA,  $F = 19.25$ ,  $df = 2$ ,  $P < 0.0001$ ) (Fig. 4). Copepod (ANOVA,



$F = 0.556$ ,  $df = 2$ ,  $P = 0.585$ ) abundances did not significantly differ among soils from different land uses. Snails, oligochaetes, odonates and chironomids were also present in the samples, but were intermittently observed or at low densities. No cladocerans or cladoceran resting stages were observed during our soil rehydration study.

#### Zooplankton resources in the Sacramento River

The Sacramento River had lower zooplankton densities in comparison to the inundated rice fields, with a maximum density of 196 ind./m<sup>3</sup> during the 1st week of the study and even lower thereafter (Fig. 5). Overall, cladoceran density did not exceed 81 ind./m<sup>3</sup>.

#### Discussion

Our results demonstrate that winter-inundated agricultural floodplains support much higher densities of zooplankton compared to the Sacramento River. Zooplankton abundance remained high throughout the study and cladoceran densities tended to increase over the six-week period, reflecting increasing temperatures and accumulation of individuals. Results for *D. pulex*, the main forage species for juvenile Chinook Salmon in our study, also suggest that remnant vegetation may affect bottom-up and top-down processes. Additionally, our comparison of the pelagic community and soil emergence results indicate

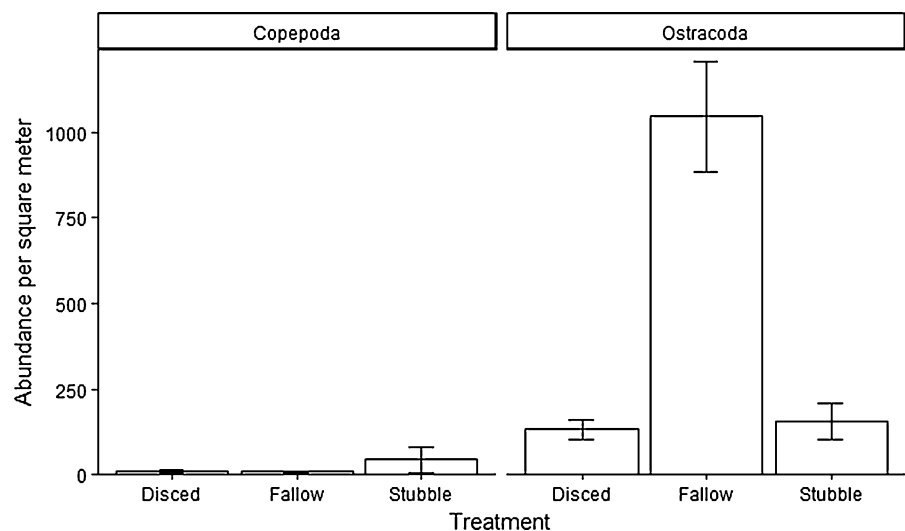
different community members colonize from allochthonous (inlet) and autochthonous (soil) pathways.

#### Trophic resources for rearing salmon

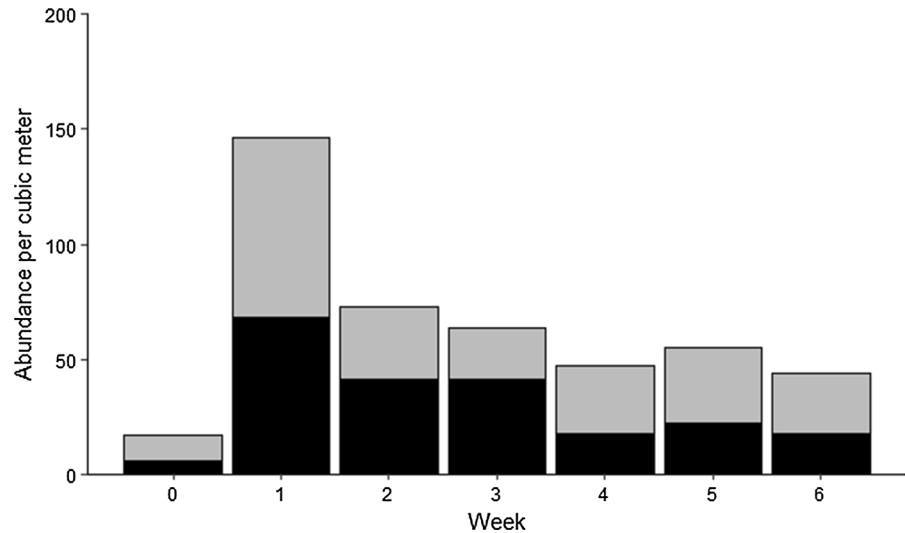
In comparison to the Sacramento River, the experimental fields had 150 times or greater zooplankton and cladoceran densities during the study period. Moreover, zooplankton densities observed in experimental fields were relatively high as compared to previous observations in the Yolo Bypass during flood events and Sacramento River in other years (Sommer et al. 2001b, 2004).

The high abundances of *D. pulex* found throughout the study period support the idea that an agricultural floodplain can provide food resources needed for rapid juvenile Chinook Salmon growth. Diet analyses of juvenile Chinook Salmon from a concurrent study in the same experimental fields indicate that *D. pulex* was the main food resource in the inundated rice fields (Katz et al. in review). Similarly, gut contents of Chinook Salmon in agricultural floodplain (rice fields) in the Yolo Bypass in 2012 contained >85% daphniids and had some of the highest growth rates recorded for Chinook Salmon in the Central Valley (Katz, unpublished data). Studies of juvenile Chinook Salmon (50–218 mm FL) in other lentic water bodies found that salmon selectively fed on large *Daphnia* spp. (Craddock et al. 1976; Merz 2002; Koehler et al. 2006; Jeffres et al. 2008). *D. pulex* found in our experimental

**Fig. 4** Average abundance of soil emergent zooplankton per square meter for stubble, fallow, and disced habitat treatments. Error bars are standard error



**Fig. 5** Abundances of copepods (gray), and cladocerans (black) in the Sacramento River from February 8th 2013 to March 20th 2013. Week corresponds to week of study period



fields were likely a highly suitable forage species for juvenile Chinook Salmon due to their pelagic nature, slow movement, and large size ( $1.211 \pm 0.49$  mm).

A previous study of juvenile Chinook Salmon reared on the Yolo Bypass found that salmon primarily fed on chironomids (Diptera) (Sommer et al. 2001b). The difference in diets between our study and the previous study may be a reflection of differing conditions during high flow versus low flow events. Specifically, high flow events result in higher velocities, and are based on Sacramento River water sources rather than the local tributary sources used in our investigation. For example, Sommer et al. (2004) found that flow was significantly associated with chironomid abundance in drift samples taken during high flow events. This may be due in part to the ability of higher flows to entrain chironomids from the benthos, and the inundation of large areas of soil, the primary source of these invertebrates (Benigno and Sommer 2008).

#### Habitat effects on zooplankton community

We did not find a consistent effect of habitat type on most members of the zooplankton community. However, *D. pulex* population densities in the disced treatment during the fifth week of the experiment had lower average abundance in comparison to the fallow and stubble treatment, which may have highlighted the effect of vegetation in providing detrital food pathways and refuge from predators.

The drop in *D. pulex* density in the disced habitat treatment followed a fall in chlorophyll *a* concentrations in all treatments in week four, which is likely a result of over-grazing by the zooplankton community. Similar results have been observed in the Cosumnes River floodplain where zooplankton populations depleted their food resources and subsequently declined in density (Grosholz and Gallo 2006). Vegetated fields may have been able to provide an alternative detrital based food web that *D. pulex* could have utilized to maintain high population densities. Submerged dead vegetation, like that found in our experimental fields, can provide detrital resource that cladocerans can take advantage of (Mladenov et al. 2005).

Furthermore, vegetation in the fallow and stubble treatments may have offered physical protection from predation. Vegetation has been shown to offer cladocerans physical refuge from visual predators such as fish (Manatunge et al. 2000; Meerhoff et al. 2007). *D. pulex* was the main forage for juvenile Chinook Salmon in the concurrent study (Katz unpublished data) and thus likely experienced the greatest predation pressure in comparison to other zooplankton species. The use of submerged vegetation as a refuge may explain why *D. pulex* had higher abundances in the fallow and stubble treatments. We could not definitively determine the effect of fish grazing versus other environmental effects on the zooplankton community because all treatments in our study contained juvenile Chinook salmon at 0.5 fish per square meter

and fish grazing rate per treatment was unknown. This density of fish is observed during natural flooding events in the Yolo Bypass (Sommer et al. 2001b).

#### Time and cladoceran abundance

Cladocerans were not significantly affected by field treatment overall; however, the cladoceran densities increased each week. Water residence time has been shown to be the main factor in governing zooplankton diversity and biomass allowing populations to grow and more species to colonize and complete their life cycles (Baranyi et al. 2002; Serrano and Fahd 2005; Tavernini et al. 2005). Given that cladocerans have high intrinsic growth rates and that temperatures in our experimental fields were high enough for most cladocerans to mature from egg to adult in less than a week, sufficient time elapsed to account for the large populations of cladocerans seen in our experimental fields (Frank et al. 1957; Allan 1976). Furthermore, temperature increased over the course of the study, likely leading to increased growth and reproductive rates of cladocerans over time. Despite the initial decrease in temperature during the first week of the study, temperatures were mostly in the optimal range for *Daphnia* spp. population growth: 15–20 degrees Celsius (Goss and Bunting 1983).

#### Colonization

A major objective of our study was to determine the relative importance of allochthonous versus autochthonous sources of zooplankton, our results suggest that both pathways are important routes of colonization. These inputs are highlighted by the differing results for two key species groups: ostracods and cladocerans.

#### Ostracods

Although ostracods may have been affected by habitat treatment during inundation, it is unclear what these mechanisms are. It is most likely that, due to their life history characteristics, ostracods were affected by treatment while still in the dormant soil phase. In the soil rehydration experiment, the fallow treatment had significantly higher numbers of ostracods than either the stubble or disced treatment. It is likely that the

fallow fields had higher ostracod abundances due to decreased soil disturbance and increased detritus.

Agricultural processes such as disking can decrease soil invertebrate emergence thus acting in a manner similar to sedimentation by altering dissolved oxygen, temperature, and light emergence cues (Gleason et al. 2003). This is especially pertinent for ostracods which deposit their eggs on the soil surface. It is possible that the fallow treatments had greater detritus on the soil surface. Greater detritus in the fallow fields could have contributed to high ostracod abundance by increasing the available surface area for ostracod egg oviposition; substrate surface area has been shown to be a significant factor in ostracod abundance (Aguilar-Alberola and Mesquita-Joanes 2011). It is unlikely that ostracod eggs would have been damaged during disking activities due to their small size and recalcitrant shells. Furthermore, the direct mirroring of ostracod populations between treatments from soil emergent communities indicates the soil propagule bank is the most important pathway for ostracod colonization.

#### Cladocerans

The Knights Landing Ridge Cut was the only colonization pathway observed for cladocerans. This is surprising as cyclical parthenogenic populations of daphniids that inhabit temporary waters are known to colonize via propagules from sediment. Although male *D. pulex* were recorded in our study and females with ephippia were observed, soil samples lacked emergent *Daphnia* spp. Furthermore, no ephippia were found in the rehydrated samples. This may be due to fields, in the previous inundation period, being drained before ephippia were produced. Additionally, the act of draining the fields may have washed ephippia out of rice fields decreasing or eliminating their abundance in the soil propagule bank. This may be especially true as *D. pulex* ephippia were observed floating on the surface of the inundated fields (Corline pers. obs.). Conversely, our rehydration study may have not provided the appropriate environment cues for cladoceran emergence. This is unlikely as the samples were rehydrated outdoors and exposed to ambient temperatures close to that of the study site, and other soil taxa with similar emergence cues were able to emerge.

Source floodwater led to the establishment of the *D. pulex* populations. Using densities of *D. pulex* in the inlet canal prior to field inundation, a low estimate for *D. pulex* density at inoculation is 1849 ind./m<sup>3</sup>. We observed that the *D. pulex* population from time of flooding continued to grow throughout the study period reflecting warm temperatures and abundant food. However, the inlet canal population declined with time indicating that the initial drift of *D. pulex* into the fields was the founding population. Colonization from the inlet canal was likely low after the initial inundation of the experimental fields. This dynamic is likely a result of the high volume of water flushed into the fields and the low volume that moved through the fields during inundation. At inundation, the fields were flooded with approximately 3210 m<sup>3</sup> of water; however, flows into the fields from the inlet canal after that time period remained low at an average of 0.02 m<sup>3</sup>/s.

### Management implications

This study suggests that agricultural floodplain can produce high primary and secondary productivity. These conditions in turn may be useful for young fishes such as juvenile Chinook Salmon that historically used floodplains. The suitability of these habitats for rearing fish stems from the high abundances of zooplankton in comparison to the Sacramento River. Abundances of zooplankton did not significantly differ between treatments and *D. pulex* densities remained high in all treatments, which suggests that there is some flexibility in the selection of agricultural habitats intended for juvenile Chinook Salmon rearing. Another important management consideration is the source of water for initial flooding because the invertebrates available as food will differ depending on tributary source.

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