North Delta Food Subsidies Study: Monitoring Food Web Responses to the North Delta Flow Action

March 5, 2021

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Suggested Citation: Twardochleb L., Maguire A., Dixit L., Bedwell M., Orlando J., MacWilliams M., Bever A., and B. Davis. 2021. North Delta Food Subsidies Study: Monitoring Food Web Responses to the North Delta Flow Action, 2019 Report. Department of Water Resources, Division of Environmental Services.

Abstract

The North Delta is relatively rich in aquatic food resources compared to other regions of the San Francisco Estuary, but low or negative flows from water diversions during summer and fall limit the distribution of these resources downstream. The California Department of Water Resources has developed the North Delta Flow Action (NDFA), an adaptive management approach to increasing flow and distributing food resources downstream, thereby enhancing the quantity and quality of food for Delta Smelt and other species in the North Delta. The 2019 NDFA redirected agricultural drainage water into the Yolo Bypass region during fall to generate a managed flow pulse (i.e. an above-average flow) to increase food availability downstream. The North Delta Food Subsidies – Colusa Basin Drain Study monitored and evaluated the effects of the NDFA on the Delta food web. We found that the 2019 NDFA increased the quantity of plankton (fish food) in the Yolo Bypass, but not downstream in the Lower Sacramento River. In addition, more nutritious diatoms grew in the Yolo Bypass after the flow pulse than before, providing food for zooplankton. Collaborator studies provided evidence that the 2019 NDFA did not negatively affect growth or survival of Delta Smelt or Chinook salmon. Despite these benefits to the food web, increased contaminant loads and low nutrient availability in the flow pulse water could have affected the magnitude of food web responses. Moreover, the 2019 NDFA did not increase food availability downstream by as much as the 2016 NDFA using diversions of Sacramento River water. Future studies, including repeating the 2016 NDFA using Sacramento River water and an upcoming NDFA synthesis comparing the results of managed flow pulses on the North Delta food web from 2011-2019, will help us assess the effects of source water (agricultural return flows vs. Sacramento River), and other mediating factors such as hydrology, to adaptively manage the flow action to maximize food availability downstream.

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Introduction

The North Delta region of the San Francisco Estuary (SFE) (Fig. 1) is relatively rich in aquatic food resources compared to other regions, but low or negative flows from water diversions during summer and fall limit the distribution of these resources to downstream areas (Frantzich et al. 2018). With interagency support, the California Department of Water Resources (DWR) has developed the North Delta Flow Action (NDFA), an adaptive management strategy with the goal of increasing flows and distributing food resources downstream, thereby restoring more natural flow patterns and enhancing the quantity and quality of food for Delta Smelt and other species in the North Delta. The NDFA redirects agricultural drainage or Sacramento River water into the Yolo Bypass region for up to 2-4 weeks during summer or fall to generate a managed flow pulse (i.e. an above-average flow) of 25-30 mil m^3 (~20-25 TAF) to enhance food resources downstream. The North Delta Food Subsidies – Colusa Basin Drain Study monitors and evaluates the effects of the NDFA on the Delta food web. Here, we describe the motivations for conducting these managed flow pulses, and present results and implications of the North Delta Food Subsidies Study monitoring the effects of the 2019 NDFA.

Background

The SFE has low primary productivity and plankton biomass (Cloern and Jassby 2008) that have been declining since the mid-1970s (Jassby 2008, Cloern 2019). The decrease in primary productivity has affected other trophic levels in the SFE and is hypothesized to be a significant factor among others (e.g., water exports, invasive clams) contributing to the decline in zooplankton (i.e. fish prey) and pelagic fishes including Delta Smelt, Threadfin Shad, Longfin Smelt, and Age-0 Striped Bass since the early 2000s (Mac Nally et al. 2010, Hammock et al. 2019). The decline in pelagic fishes in the SFE is referred to as the Pelagic Organism Decline (Sommer et al. 2007, Baxter et al. 2008, 2010). Since the Yolo Bypass generates high levels of food resources, increased flow through the Yolo Bypass region may help increase lower trophic food web productivity in the SFE to benefit pelagic fishes such as Delta Smelt.

While overall productivity in the SFE is low, plankton production is relatively high in the Yolo Bypass; the region provides a significant source of phytoplankton biomass to the Delta during winter and spring when the floodplain is inundated (Lehman et al. 2008, Sommer et al. 2004). However, high diversion rates during summer and fall result in low or net negative flows (i.e. net flow is upstream after accounting for tidal effects) that likely inhibit transport of lower trophic level biomass to downstream areas of the estuary (Frantzich et al. 2018). Managed flow pulses during summer or fall through the Yolo Bypass can increase outflow, thereby transporting and increasing availability of plankton in the downstream regions of the estuary (Frantzich et al. 2018, 2019).

Recent observations provide insight into how managed flow pulses may influence lower trophic levels in the North Delta. In 2011, Fall Low Salinity Habitat (FLaSH; Brown et al. 2014) studies observed a phytoplankton bloom in the Lower Sacramento River shortly after a seasonal agricultural flow pulse passed through the Yolo Bypass. An agricultural flow pulse occurred again in 2012, followed by a downstream Delta phytoplankton bloom (Frantzich et al. 2018). These were the first fall blooms in over 20 years (ASC 2012). Delta phytoplankton blooms such as those resulting from the 2011 and 2012 flow pulses can indirectly benefit declining pelagic fish species by providing a food source for zooplankton (fish prey) (Sommer et al. 2007, Hammock et al. 2019). Monitoring by DWR has shown that the phytoplankton species composition during these fall flow pulses is dominated by diatoms (Frantzich et al. 2018), which are a primary food for copepods (Brown 2009, Lehman 1992, Orsi 1995). Copepods are an important component of the diet for many Delta larval and juvenile fishes, including Delta Smelt (Cloern et al. 1983, Obreski et al. 1992, IEP-MAST 2015).

Because of the potential benefits of summer-fall flow pulses through the Yolo Bypass to the Delta food web, the Delta Smelt Resiliency Strategy included managed flow pulses as a core strategy to benefit Delta Smelt (CNRA 2016). As a result, DWR together with interagency, landowner, and local district coordination, executed the first NDFA managed flow pulse during the summer of 2016 using diversions of Sacramento River water through the Yolo Bypass. The 2016 NDFA was followed by a significant increase in phytoplankton biomass downstream in the Cache Slough Complex (CSC) and Lower Sacramento River at Rio Vista (Frantzich et al. 2018, 2019). This downstream bloom was dominated by diatoms and cryptophytes that provide food for zooplankton (Frantzich et al. 2018, 2019). DWR found positive correlations between zooplankton growth and reproductive rates and phytoplankton biomass, demonstrating improved food web production and food quality (Frantzich et al. 2019). This successful managed flow pulse provided evidence that the NDFA could provide ecological benefits. Therefore, DWR and interagency collaborators repeated the NDFA in 2018 and 2019, but due to hydrology the action was conducted by redirecting agricultural return flows from rice field drainage instead of Sacramento River water through the Yolo Bypass. The NDFA has since been included as one of several adaptive management strategies of the Delta Smelt Summer-Fall Habitat Action, a new regulatory requirement in both the 2019 US Fish and Wildlife Service Biological Opinion (FWS BiOp) and 2020 Department of Fish and Wildlife Incidental Take Permit (DWF ITP) that aims to improve habitat conditions and food subsidies for Delta Smelt.

Study Goals and Objectives

The 2019 NDFA coordinated the release of agricultural return water during fall through the Yolo Bypass to achieve the following goals: 1) net positive outflow through the Yolo Bypass; 2) increased transport and/or production of plankton downstream; and 3) higher quantity and quality of food in the North Delta for Delta Smelt. The hypothesis for the 2019 North Delta Food Subsidies Study was that augmented flows resulting from the fall managed flow pulse increased food availability for juvenile and sub-adult Delta Smelt in the North Delta. Each year, the study monitors the lower trophic food web in the Yolo Bypass and downstream regions of CSC and the Lower Sacramento River, before, during, and after the managed flow pulse. We quantify changes in food availability through measurements of chlorophyll, phytoplankton biomass, zooplankton density, and plankton community composition. In addition, we monitor changes in flow, nutrients, and other water quality parameters to identify the mechanisms by which the managed flow pulse may affect the lower trophic food web. Lastly, contaminant concentrations and their food web consequences are evaluated (Orlando et al. 2020), because the 2018 North Delta Food Subsidies Study showed that phytoplankton productivity was low in that year and the phytoplankton community was completely void of nutritious diatoms observed in past blooms (2012 and 2016). It is therefore possible that the source water used to generate the flow pulse in 2018 (agricultural drainage) may have had higher pesticide loads than water used in 2016 (Sacramento River) and caused differences in phytoplankton composition and biomass between the two flow pulse types. Pesticides and contaminants in agricultural drainage water are of concern throughout the SFE as contributors to fish and food web declines (IEP-MAST 2015) and could have impacted diatom growth during the 2018 and 2019 agricultural return flow pulses. Thus, the 2019 study and future studies will monitor contaminant concentrations before, during, and after the flow pulse.

2019 Study Questions

1. How does the managed flow pulse alter hydrodynamics of the study region (Fig. 1), from the Colusa Basin Drain downstream to the Lower Sacramento River?
2. How do water quality and lower trophic levels of the food web change from north to south regions of the study area, before, during, and after the managed flow pulse?
3. Does contaminant loading increase during flow actions using the Colusa Basin agricultural water source?

Materials and Methods

Study Description

The 2019 NDFA redirected agricultural drainage water into Yolo Bypass from the Colusa Basin Drain between August 26 and September 21 and the duration of net positive flows measured at Lisbon Weir (Fig. 1) was 26 days. We targeted flows of 30 million m^3 (25 TAF) and a maximum average daily net flow of 19.8 m^3/s (700 cfs) at Lisbon Weir. Monitoring and analysis for the 2019 study were designed to assess the effects of the NDFA on hydrodynamics, water quality, nutrients, contaminants, chlorophyll-a, and components of the lower trophic food web, including phytoplankton and zooplankton, and was conducted with support from inter-agency collaborators (Table 1). With collaborators at San Francisco State University, we also monitored phytoplankton growth and nutrient uptake rates, but these results are not discussed in detail in this report. In addition, DWR monitored clam biomass and maximum filtration rates from the Yolo Bypass downstream to Rio Vista before the flow pulse, and Delta Smelt health in the region before and after the flow pulse as part of an ongoing enclosure study. Note, however, that the summer Yolo Bypass enclosure deployment was designed to test the temperature limits of Delta Smelt, rather than assess the effects of the flow action. California Department of Fish and Wildlife and the Yolo Bypass Habitat Restoration Section of DWR also monitored Fall Run Chinook Salmon catch, health, and survival at Wallace Weir in Yolo Bypass during and after the flow pulse. Although we only briefly discuss results of these fish monitoring efforts as they relate to the 2019 NDFA (see Discussion), results of these collaborative studies will be addressed comprehensively elsewhere (CDFW 2019, Kwan et al. 2020, Davis et al. 2021).

Time Period and Location

Monitoring for each abiotic and biotic parameter (Table 1) spanned from summer to fall across three periods before, during, and after the managed flow pulse. We classified the flow pulse periods as follows: *Before* - July 26 to August 25, 2019; *During* - August 26 to September 21, 2019; and *After* - September 22 to October 31, 2019. The overall sampling period for continuous water quality monitoring was July 26 to October 31, and for discrete water quality was August 7 to October 16, 2019.

The study area included 5 regions and 12 monitoring sites (Fig. 1, Table 2). Monitoring sites spanned from north to south within the 5 regions as follows: *Colusa Basin Drain/Ridge Cut Slough region*: 1) Rominger Bridge (RMB), 2) Ridge Cut Slough at Highway 113 (RCS); *Upper Yolo Bypass region*: 3) Woodland Wastewater Treatment Discharge (WWT), 4) Toe Drain at Road 22 (RD22), 5) Davis Wastewater Treatment Discharge (DWT), 6) Toe Drain at I80 (YBI80); *Lower Yolo Bypass region:* 7) Toe Drain below Lisbon Weir (LIS), 8) Screw Trap at Toe Drain (STTD); *Cache Slough Complex (CSC) region:* 9) Prospect Slough (BL5), 10) Base of Liberty Island (LIB); and *Lower Sacramento River Region:* 11) Cache Slough at Ryer Island (RYI) and 12) Sacramento River at Rio Vista Bridge (RVB). Although RYI is above the mainstem Sacramento River near CSC, we combined this site into the Lower Sacramento River region for two reasons: 1) Net flow conditions at RYI were similar to RVB in that they were heavily influenced by downstream tidal action, and 2) combining the sites ensured enough statistical power to test the effects of the managed flow pulse on each of the five regions (Table 2, Fig. 1). The WWT and DWT sites in Upper Yolo Bypass were monitored for a subset of abiotic parameters to assess sources of nutrient inputs from wastewater treatment plants. However, the focus of this report is on the food web response to the managed flow pulse, thus we present results for discrete water quality and lower trophic food web responses for sites where we monitored both abiotic and biotic parameters (sites excluding WWT and DWT; Table 1).

Table 1. Abiotic and biotic parameters that were monitored in response to the 2019 NDFA, and sampling locations, time period, data sources and/or collaborator agencies. The Yolo Bypass Fish Monitoring Program (YBFMP), Environmental Monitoring Program (EMP), Yolo Bypass Habitat Restoration Program, and Bryte Lab are groups at DWR. CBEC Eco Engineering (CBEC), Anchor QEA LLC. (Anchor QEA), and BSA Environmental Services, Inc. (BSA) are contractors/consultants with DWR, and U.S. Geological Survey (USGS) is a collaborator providing long-term multiparameter continuous water quality data and contaminants analysis. See Table 2 for abbreviations and descriptions of sampling locations.

Abiotic and Biotic Parameters	Data Source	Sampling Locations	Time Period
Habitat Conditions			
Average Daily Net Outflow	Continuous sensors – this study, USGS, Anchor QEA	RCS, Yolo Bypass near Woodland (near RD22), LIS, LIB, RYI, RVB, Sacramento River at Decker Island (SDI)	July - October
Temperature, Turbidity, Dissolved Oxygen, Conductivity, Chlorophyll	Continuous – this study, EMP, USGS Discrete – this study, EMP	Continuous: RMB, RCS, RD22, YBI80, LIS, STTD, BL5, LIB, RYI, RVB Discrete: RMB, RCS, WWT, RD22, DWT, YBI80, LIS, STTD, BL5, LIB, RYI, RVB	Continuous: July - October Discrete: August - October
Water Clarity (Secchi depth)	Discrete – this study	RMB, RCS, WWT, RD22, DWT, YBI80, LIS, STTD, BL5, LIB, RYI, RVB	August - October
Concentrations of Ammonium, Nitrate/Nitrite, Phosphorus	Continuous – this study Discrete – this study with DWR Bryte lab	RMB, RCS, WWT, RD22, DWT, YBI80, LIS, STTD, BL5, LIB, RYI, RVB	August - October
Contaminants	Discrete – this study with USGS Organic Chemistry Research Laboratory	RMB, RD22, LIS, STTD, BL5	August - October
Lower Trophic Food Web Responses			
Phytoplankton Biovolume, Community Composition	This study, YBFMP with BSA	RMB, RCS, RD22, YBI80, LIS, STTD, BL5, LIB, RYI, RVB	August - October
Productivity & Nutrient Uptake Rates	This study in collaboration with SFSU (results not reported in this report)	RMB, RCS, RD22, YBI80, LIS, STTD, LIB, RYI, RVB	August - October
Zooplankton Catch Per Unit Effort (CPUE), Community Composition	This study, YBFMP with BSA	RMB, RCS, RD22, YBI80, LIS, STTD, BL5, LIB, RYI, RVB	August - October
Fish Responses			
Smelt Cage Study	DWR	Yolo Bypass, Lower Sacramento River at Rio Vista	July - August (Before flow pulse) and October – November (After flow pulse)
Fall Run Chinook Salmon catch, health, survival	This study, Yolo Bypass Habitat Restoration Section, DFW	Wallace Weir, Yolo Bypass	September - December

Table 2. Regions and monitoring sites for the North Delta Food Subsidies Study.

Region	Monitoring Site Name	Site Code	Site Access	Latitude	Longitude
Colusa Basin Drain/Ridge Cut Slough	Colusa Basin Drain at Rominger Bridge	RMB	Land	38.842001°	-121.858371°
	Ridge Cut Slough at Hwy. 113	RCS	Land	38.793457°	-121.725447°
Central Yolo Bypass	Woodland Wastewater Discharge at Toe Drain	WWT	Land	38.681621°	-121.645775°
	Toe Drain at Rd. 22	RD22	Land	38.676367°	-121.643972°
	Davis Wastewater Discharge at Toe Drain	DWT	Land	38.567057°	-121.638239°
	Toe Drain at I80	I80	Land	38.573111°	-121.582958°
Lower Yolo Bypass	Toe Drain below Lisbon Weir	LIS	Land	38.474816°	-121.588584°
	Screw Trap at Toe Drain	STTD	Boat	38.353461°	-121.642975°
Cache Slough Complex (CSC)	Below Toe Drain in Prospect Slough	BL5	Boat	38.274460°	-121.665652°
	Base of Liberty Island	LIB	Boat	38.242100°	-121.684900°
Lower Sacramento River	Cache Slough at Ryer Island*	RYI	Boat	38.213167°	-121.668591°
	Sacramento River at Rio Vista Bridge	RVB	Boat	38.159737°	-121.686355°

*Ryer Island is included in the Lower Sacramento River region for similarities in flow conditions and statistical design.

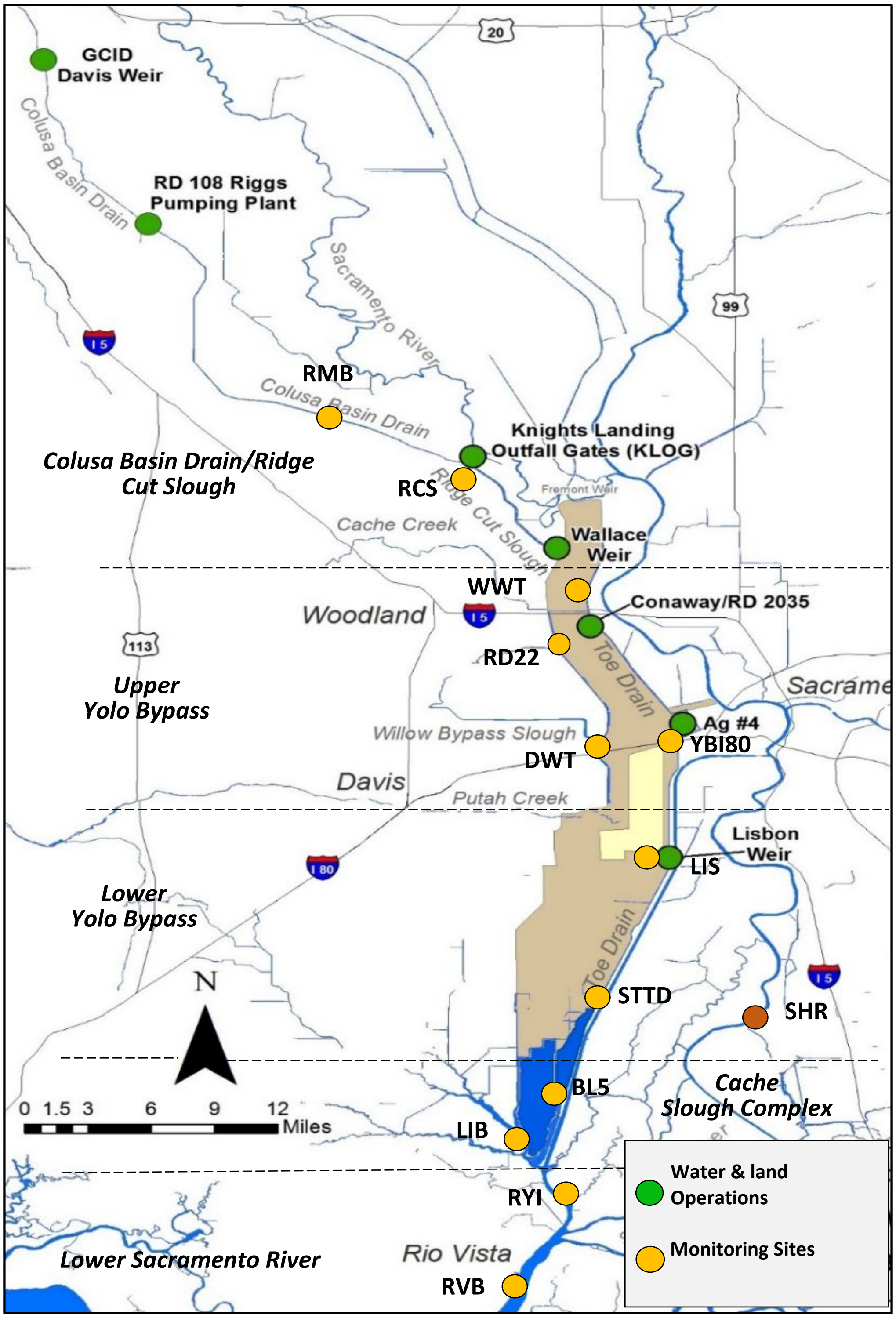

Figure 2. **Area map of the 2019 North Delta Food Subsidies Study.** Water and land operation sites are indicated in green circles and sites for monitoring continuous or discrete water quality and biological responses to the flow pulse are in yellow circles. The brown circle at Sacramento River at Sherwood Harbor (SHR) is a control site for biological monitoring. Monitoring sites are divided into the following regions from north to south: Colusa Basin Drain/Ridge Cut Slough, Upper Yolo Bypass, Lower Yolo Bypass, and Lower Sacramento River. Site abbreviations are as above (Table 2).

Hydrodynamics

In August 2019, DWR worked with landowners, reclamation and irrigation districts, and interagency collaborators to generate a managed flow pulse in the Yolo Bypass and downstream. These collaborators produced the managed flow pulse by re-directing agricultural return water from the Colusa Basin Drain, mainly from rice field drainage, through Knights Landing Ridge Cut (KLRC) and Wallace Weir into the Toe Drain of the Yolo Bypass and downstream regions. Water operations relied on existing infrastructure, including the Knights Landing Outfall Gates (KLOG), Wallace Weir, and agriculture crossings (Fig. 1). Operations of KLOG began August 27, increasing the water elevation to 27 ft until September 19 to divert Colusa Basin drainage water into KLRC, generating the flow pulse. In coordination with KLOG, Wallace Weir adjusted operations to convey drainage water at a target flow of 8.5 to 20 m^3/s (300-700 cfs), and modified culverts to allow additional flow through the Toe Drain.

We used the three-dimensional UnTRIM Bay-Delta model (MacWilliams et al. 2015, Anchor QEA 2020) to evaluate hydrodynamics of the 2019 managed flow pulse. The UnTRIM model predicts water flow and transport throughout the Bay-Delta and has been validated using time series of flow, stage, and specific conductance in the Yolo Bypass and CSC (MacWilliams et al. 2015). We previously used this model to evaluate 2011-2018 managed and non-managed flow pulses (Anchor QEA 2020). Simulations incorporated observed inflow (daily averaged), water temperature, and salinity in the Yolo Bypass. We simulated the movement, age and fate of water originating from the flow pulse and other water masses such as CSC to downstream stations, and the Lower Sacramento River at Rio Vista (Anchor QEA 2020). Our basic prediction was that the flow action would improve downstream transport through Cache Slough Complex. Hence, two simulations were evaluated for the 2019 flow pulse: 1) Action: including the managed flow pulse, and 2) No Action: with the managed flow pulse removed from the inflow hydrograph. For simulation 2, the No Action alternative, we removed the flow pulse by assuming a linear change in inflow past Lisbon Weir, from the observed flow immediately prior to the flow pulse to the observed flow immediately following the flow pulse. Thus, we simulated flows past Lisbon Weir during the flow pulse with measured flows from 2019 for simulation 1 and a close to constant upstream flow at Lisbon Weir for simulation 2, and we used identical observed flows at Lisbon Weir before and after the pulse for both simulations. It is important to note that simulation 2 had negative inflow during the flow pulse; that is, simulated flow through the Toe Drain was net negative (toward the north away from the CSC), because observed flow was net negative both before and after the 2019 managed flow pulse. Comparing simulation 1 and 2 allowed us to evaluate the effects of the flow pulse on water transport and age. We also performed tracer analysis to estimate the percentage of water originating from the flow pulse across locations and water age analysis to assess the average number of days required for the water originating from the flow pulse to reach locations within the study area.

Water Quality

We monitored continuous water quality at sites in the Colusa Basin Drain to Lower Yolo Bypass at 15-minute intervals using YSI EXO2 multiparameter water quality sondes. Water quality parameters included temperature, specific conductance, turbidity, chlorophyll fluorescence, dissolved oxygen (DO), and pH. We calibrated EXO2 sondes using laboratory standards within 72 hours of field deployment using YSI KorEXO software version 2.2.0.5 and adhered to NCRO and DWR's Quality Assurance (QA) group supported methods (WQES 2019). Field site maintenance every three to four weeks included aquatic vegetation removal, PVC housing clean up, and exchange of a newly calibrated sonde with the used field sonde. Sonde data files were downloaded in the laboratory and each sonde parameter was checked for accuracy using laboratory standards. Continuous data for sites in the CSC and Lower Sacramento River were collected by USGS, DWR's Environmental Monitoring Program, and North Central Region Office. Some data points are missing during the study period for sites LIB and BL5 (Fig. 3) due to limited data availability during the study period from these other monitoring programs. We include only continuous chlorophyll fluorescence results in this report. Maguire et al. (2019) contains a complete report of other continuous water quality parameters for this study.

To monitor discrete physical and chemical water quality, we measured temperature, turbidity, dissolved oxygen, conductivity, and pH using a YSI ProDSS handheld sonde. While sampling discrete water quality, we also collected water samples to quantify concentrations of nutrients and chlorophyll-a. We collected water for land sites (DWT, WWT, I80, LIS, RMB, RCS, RD22) at < 1 m from the surface using a Nasco Swing Sampler and homogenized samples in the field with a homogenization bucket and samples from boat sites (STTD, BL5, RVB, LIB, RYI) using a Van Dorn water sampler. We validated nutrient and chlorophyll-a concentrations in water samples using field blanks and split replicates. On each sampling day, we collected a blank water sample to account for the effects of collection and lab procedures on measured nutrient concentrations, and a split replicate sample of chlorophyll-a at LIS and STTD to account for variability introduced by laboratory procedures. We collected replicate samples by homogenizing water samples in the field and then splitting them in the laboratory prior to filtering and analysis and created blank samples in the laboratory by following field collection procedures using deionized water.

Sample collection, storage, and analysis procedures followed methods of the US Environmental Protection Agency (U.S. EPA) and the Standard Methods for the Examination of Water and Waste Water (APHA 2005). We filtered nutrient and chlorophyll-a samples on the day of collection and sent samples to DWR Bryte Laboratory for analysis. Bryte Laboratory determined the concentrations of chlorophyll-a by extracting pigments on glass-fiber filters with 90% aqueous acetone and spectrophotometry (Standard Method 10200H; APHA 2012), and measured ambient nutrient concentrations using U.S. EPA and American Public Health Association (APHA) analysis methods: Nitrate/Nitrite (NO3+NO2; Std. Method 4500-NO3-F Modified), Ammonia (NH4; EPA 350.1), dissolved ortho-phosphate (PO4; EPA 365.1), and silica (Si(OH)2; EPA 200.7D). See Twardochleb et al. (2020) for more details about field and laboratory methods for discrete water quality.

Plankton

Concurrent with discrete water quality monitoring, we sampled the lower trophic food web at all sites, except for wastewater treatment sites (DWT and WWT). We collected phytoplankton samples using a subsample of homogenized water collected for nutrient sampling. We sampled zooplankton using 5-minute surface tows with a 150 µm mesh zooplankton net, with 0.5 m diameter mouth opening, attached to a 150 µm mesh cod end (Sea-Gear Corporation, Melbourne, FL, USA). The zooplankton net was affixed with a flow meter fitted with a low flow rotor (General Oceanics, Miami, FL, USA). Zooplankton tows were either from a boat or kayak, depending on site. We fixed zooplankton samples in 10% formalin with rose Bengal, and after a minimum of 2 weeks in fixative, transferred samples to 8% Lugol's solution.

We sent phytoplankton and zooplankton samples to BSA Environmental Inc., Beechwood, OH, for identification and quantification. There, phytoplankton were identified to at least the genus level using the Utermöhl method (Utermöhl 1958) and at least four hundred total algal units were counted in each sample, including one hundred units of the dominant taxa. Length (µm) was recorded for the first 25 units of major phytoplankton taxa and the first 5 units of minor taxa to calculate biovolume

(μm^3/mL), a surrogate for biomass, from formulas given for different algal shapes by Kellar et al. (1980). Zooplankton samples were sub-sampled, and 200 to 250 individuals were counted per sample for mesozooplankton and then identified to at least the order level, dependent on the taxon and life stage. Zooplankton count was calculated as follows: subsample count/[(subsample volume*number of subsamples)/total sample volume]. We then converted zooplankton counts to catch per unit effort (CPUE), a measure of density (Eq. 1), by dividing zooplankton counts by the volume of water sampled (m^3). Volume was determined by multiplying the net mouth area by the tow distance, where d is the net diameter and x = 57560 is the low flow rotor meter constant (Eq. 1).

$$\boldsymbol{CPUE = zooplankton\ count / \left(\left(\frac{3.14 * (d)^2}{4} \right) * \left(\frac{(EndMeter - StartMeter) * x}{999999} \right) \right)}$$

Equation 1. Calculation of catch per unit effort (CPUE) for zooplankton. Zooplankton count is divided by the volume of water sampled (m^3), which is calculated by multiplying the net mouth area by the distance, where d = diameter of the net and x=57560 is the low flow rotor constant.

Contaminants

To determine contaminants in water and sediment samples, we collected near surface water samples in 1 L amber glass bottles two times during each flow pulse period (before, during, and after), at 5 sites: 1) RMB, 2) RD22, 3) LIS, 4) STTD, and 5) BL5. We collected a total of 30 samples (6 from each site) during the study. We measured concentrations of a suite of 163 current-use pesticides in water and 128 pesticides on suspended sediments filtered from water samples at the USGS Organic Chemistry Research Laboratory (OCRL) within 24 hours of collection. Water samples were filtered through pre-weighed, baked 0.7 µm glass-fiber filters (Grade GF/F, Whatman, Piscataway, New Jersey) to remove suspended material, dried at room temperature overnight (in the dark), and then stored in a freezer at –20 °C until extraction. Following filtering, we extracted water samples and analyzed them using both liquid chromatography tandem mass spectrometry (LC/MS/MS) and gas chromatography/mass spectrometry (GC/MS). We analyzed water samples for 35 current-use pesticides by LC/MS/MS following the method described in detail in Hladik and Calhoun (2012), and an additional 127 current-use pesticides by GC/MS following the method described in Hladik et al. (2008, 2009). Suspended sediments were extracted and analyzed by GC/MS for 127 current-use pesticides following the method described in Hladik and McWayne (2012).

To validate pesticide concentrations in water samples, we used a suite of performance-based quality-control samples, including trip blanks, field replicates, laboratory matrix spikes, and matrix-spike replicates, and surrogate recoveries. Field crews collected two trip blanks consisting of 1 L amber glass bottles of organic-free blank water that were open to the atmosphere during the time of water sample collection. Following sample collection, we transported, processed, and analyzed trip blanks at the OCRL in the same manner as all environmental samples. No pesticides were detected in either of the trip blanks. We also analyzed filter papers used in the processing of the trip blank by GC/MS and detected no pesticides.

We analyzed three sequential field-replicate sample pairs (two by LC/MS/MS and one by GC/MS) to test the reproducibility of results. In addition, we analyzed suspended sediments trapped on filter papers that were used in the processing of the one replicate sample analyzed by GC/MS. In all cases, we found that the relative standard deviation between the replicate and its complementary environmental sample concentration was less than the control limit of 25%. The correlation of pesticide detections between the paired environmental and replicate samples was 100%.

In addition to field-replicates, we validated analytical results using two laboratory water matrix spikes (one each by GC/MS and LC/MS/MS), and one suspended-sediment matrix spike each paired with a matrix-spike-replicate, to assess pesticide recovery, degradation, sorption, and interferences caused by the sampling matrix. All samples met the data-quality objective of 70–130% matrix-spike recovery. The relative standard deviation between the matrix-spike samples and their complementary replicates was less than the 25% control limit in all cases. We also added surrogate compounds to each environmental and quality-control sample, as described in the method references listed earlier, to assess the efficiency of sample extraction for GC/MS and LC/MC/MS analytical methods. Recoveries of all surrogate compounds met the data-quality objective of 70–130% in every sample.

All data are available for public download via the U.S. Geological Survey National Water Information System database.

Data Analysis Methods

Statistical analyses were conducted in R (version 4.0.2). We performed a two-way analysis of variance (ANOVA) on discrete water quality (Table 3), phytoplankton, and zooplankton datasets. Only summary statistics are presented for nutrients due to unequal sample sizes and low replication for analyte concentrations below laboratory detection limits (Table 4). We log transformed dependent variables as needed to meet assumptions of normality and homogeneity of variance in model residuals. Dependent variables included physical water quality (all log transformed), discrete chlorophyll-a (log transformed), phytoplankton biomass as biovolume (log transformed), and zooplankton density as CPUE (log transformed). Independent fixed effect predictors were region (excluding SHR) and flow pulse period (before, during, and after the flow pulse). Monitoring site was included as a random effect to account for nesting of monitoring sites within regions. Models with significant terms were followed with Tukey post-hoc tests using the 'lsmeans' R package (version 2.30-0). We also evaluated changes in plankton community structure within each region across flow pulse periods, by quantifying the proportion of the total phytoplankton biomass or zooplankton density composed of each dominant taxon, where dominant taxa were those comprising ≥ 3% of the total biomass or density (Fig. 5).

For contaminants, we used a one-way ANOVA followed by Tukey's Honest Significant Difference (Tukey HSD) to test for differences in total pesticide concentrations across all sites (excluding the control site, SHR), before, during, and after the flow pulse. We log-transformed total pesticide concentrations prior to analyses to achieve normality and homoscedasticity in model residuals. For all analyses, we set the threshold for statistical significance to alpha=0.05.

Results

Hydrodynamics

The managed flow action that redirected agriculture drainage water into the Yolo Bypass resulted in a large flow pulse with a total estimated discharge volume of 38.9 million m^3 (31,600 AF) at Lisbon Weir. This discharge volume exceeded past managed (2016) and non-managed flow pulses (2011) and resembled the discharge volumes measured in 2012 (33.6 million m^3 [27 TAF]) and 2018 (24.4 million m^3 [19 TAF]). Net flow conditions were northward in the Yolo Bypass and CSC (negative inflow) before and after the managed flow pulse. The flow pulse resulted in changes to the hydrodynamics of the CSC; net flow through the Toe Drain and out of the CSC to Cache Slough reversed to southward (net positive) with increased flow out of the bypass (~20 m^3/s at LIS [750 cfs]) and CSC (~15 m^3/s [550 cfs]) (Fig. 2A,B). As predicted, the managed flow pulse resulted in southward transport of water originating in Little Holland Tract (LHT), Liberty Island, and the CSC channels towards Rio Vista. After the flow pulse ended, net flow reversed again to northward.

Our simulations made using the UnTRIM Bay-Delta model predicted that flow pulse water reached downstream locations quickly after the pulse began, as follows: the bottom of the Toe Drain in 2 days, Lower Liberty Island in 3 days, Cache Slough in 4 days, and Rio Vista after 5 days. By tracing water originating from the flow pulse, we also predicted that 100% of the water at the bottom of the Toe Drain originated from the flow pulse, whereas the percentage of the water mass originating from the flow pulse at downstream regions decreased from 20% to 2% from Liberty Island to Rio Vista, respectively (Fig. 2C).

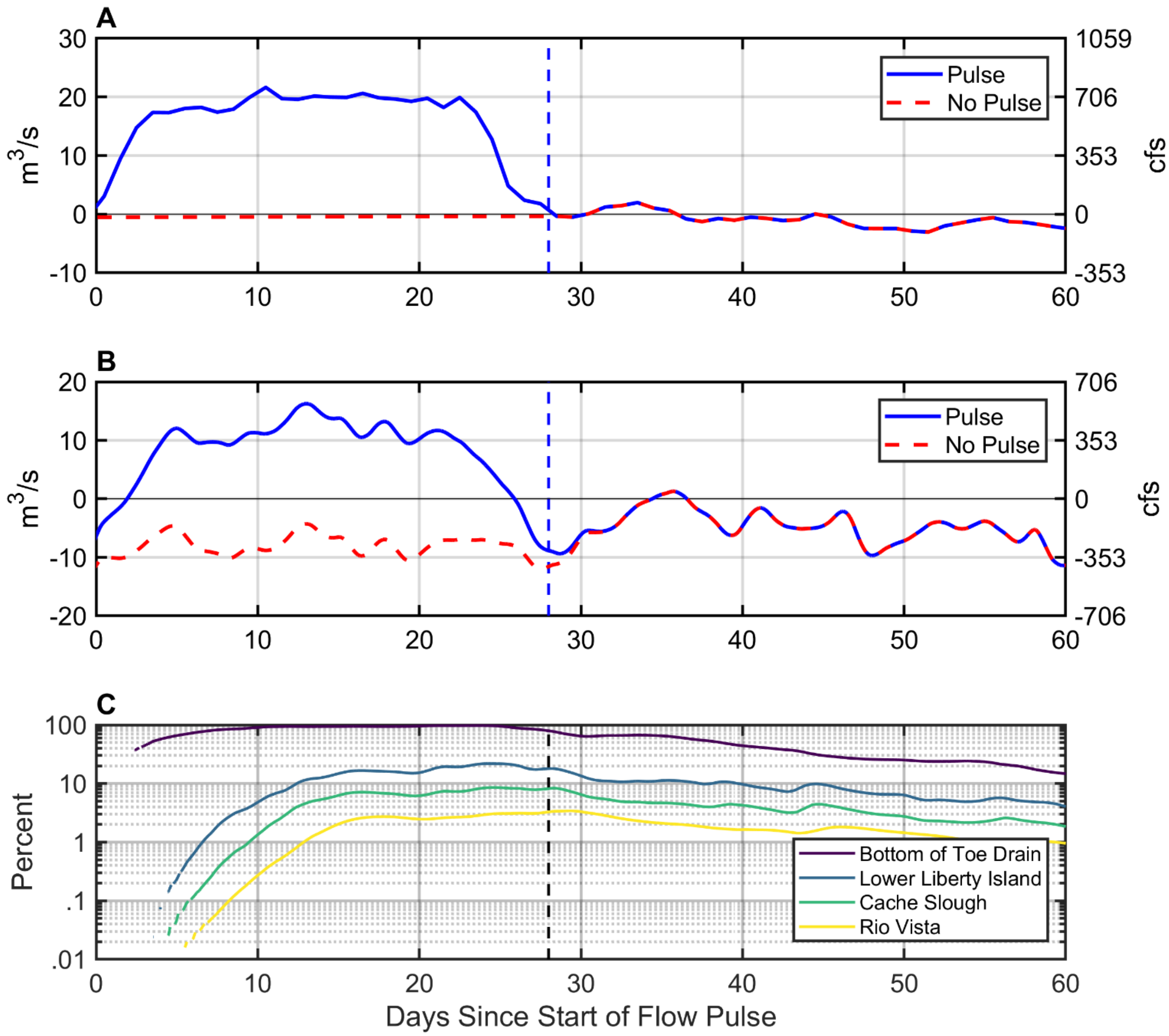

Figure 3. Hydrodynamics of the 2019 flow pulse. A) Daily-averaged water flow past Lisbon Weir in the Yolo Bypass during the 2019 managed flow pulse (blue) and simulated water flow without the managed flow pulse (red); B) 7-day running average of water flow from Cache Slough Complex with (blue) and without (red) the managed flow pulse; and C) predicted percentage of flow pulse water at key Yolo Bypass and downstream monitoring sites. The vertical dashed line in each panel represents the end of the managed flow pulse.

Water Quality

Water temperature (°C) differed only by flow pulse period (Table 3), decreasing after the flow pulse (Tukey; p<0.0001; Table 4). There was a significant interactive effect of flow pulse period and region on pH (Table 3). In Lower Yolo Bypass, pH was higher during the flow pulse than either before (Tukey; p<0.0001) or after (Tukey; p<0.001) and was higher after the flow pulse than before (Tukey; p<0.05). Specific conductivity (µS/cm at 25 °C) also differed by flow pulse period, depending on the region. Specific conductivity was higher during the flow pulse than either before (Tukey; p<0.0001) or after (Tukey; p<0.0001) in Lower Yolo Bypass and was higher during than before the flow pulse (Tukey; p<0.01) in CSC. Similarly, there were significant interactions between region and flow pulse period on turbidity (NTU) and dissolved oxygen (mg/L; Table 3). Turbidity decreased during and after the flow pulse in Upper Yolo Bypass (Tukey; p<0.01), and dissolved oxygen increased after the flow pulse in both Colusa Basin Drain/Ridge Cut Slough (Tukey after-before contrast; p<0.0001; Tukey after-during contrast; p<0.001) and Upper Yolo Bypass (Tukey after-before contrast; p<0.001; Tukey after-during contrast; p<0.0001). In Lower Yolo Bypass, dissolved oxygen was lower during the flow pulse than either before (Tukey; p<0.0001) or after (Tukey; p<0.0001).

Table 3. Results of two-way ANOVA testing for effects of region, flow pulse period (before, during, and after), and their interactions on physical water quality. df is degrees of freedom. Significant model terms are in bold.

Water Quality Measure	Model Term	F-statistic	df (term, residuals)	p-value
Water temperature (°C)	Region	1.911	4, 59	0.564
	Flow pulse period	**163.770**	**2, 59**	**<0.001**
	Interaction	1.405	8, 59	0.214
pH	Region	42.964	4, 59	0.114
	Flow pulse period	**17.493**	**2, 59**	**<0.001**
	Interaction	**5.261**	**8, 59**	**<0.001**
Specific conductivity (µS/cm at 25 °C)	**Region**	**364.606**	**4, 59**	**0.0393**
	Flow pulse period	**10.540**	**2, 59**	**<0.001**
	Interaction	**8.310**	**8, 59**	**<0.001**
Turbidity (NTU)	Region	37.041	4, 59	0.123
	Flow pulse period	**10.461**	**2, 59**	**<0.001**
	Interaction	**2.774**	**8, 59**	**0.011**
Dissolved oxygen (mg/L)	Region	6.724	4, 59	0.281
	Flow pulse period	**69.038**	**2, 59**	**<0.001**
	Interaction	**7.173**	**8, 59**	**<0.001**

Nutrient concentrations varied by region and flow pulse period (Table 4). Levels of nitrate/nitrite (mg/L) and dissolved organic phosphate (DOP, mg/L) were low in Colusa Basin Drain/Ridge Cut Slough, and the flow pulse transported low nutrient water into the Upper and Lower Yolo Bypass. By contrast, Silica concentrations (mg/L) increased during the flow pulse in Upper and Lower Yolo Bypass, and they decreased again slightly in the Colusa Basin Drain/Ridge Cut Slough and Yolo Bypass regions after the flow pulse. Concentrations of ammonia (mg/L) differed only among regions, not between flow pulse periods (Table 4). Ammonia levels were highest in the Cache Slough Complex and Lower Sacramento River across the pulse periods.

Table 4. Mean (±SD) discrete water quality by monitoring site for each flow pulse period (before, during, and after). Monitoring sites are arranged from north to south across the five study regions, except for SHR, which is a control site in the upper Sacramento River. The number of samples for physical water quality including temperature, Specific Conductivity (SPC), pH, dissolved oxygen (DO), and turbidity ranged from n=2-4 for each site and flow pulse period, whereas nutrient analytes, including ammonia, nitrate/nitrite, silica, dissolved ortho-phosphate (DOP) were n=1-3 due to limitations in laboratory reporting limits. N/A indicates no data to report because nutrient concentrations were below laboratory detection limits. *Limiting levels of nutrients for phytoplankton growth are 0.04 mg/L dissolved inorganic nitrogen (nitrate/nitrite + ammonia); 0.03 mg/L DOP; and 0.15 mg/L silica (Jassby 2005).

Region / ***Site*** / Flow Pulse Period	Temp (°C)	SPC (µS/cm at 25 °C)	pH	DO (mg/L)	Turbidity (NTU)	Ammonia* (mg/L)	Nitrate/* Nitrite (mg/L)	Silica (mg/L)*	DOP (mg/L)*
Sherwood Harbor									
SHR									
Before	20.9 (0.424)	113 (1.414)	7.63 (0.184)	8.685 (0.021)	8.65 (0.919)	N/A	0.062 (0.014)	15.6 (0.141)	N/A
During	19.433 (0.808)	122 (0)	7.42 (0.017)	8.98 (0.208)	8.9 (2.252)	0.021 (0.006)	N/A	16.9 (0.283)	N/A
After	14.967 (1.484)	112.667 (6.110)	7.417 (0.116)	9.583 (0.309)	6.467 (2.761)	0.005 (0.024)	0.086 (0.006)	15.25 (0.778)	N/A
Colusa Basin Drain/Ridge Cut Slough									
RMB									
Before	25.4 (1.697)	554.5 (23.335)	7.675 (0.050)	4.8 (0.453)	31.45 (4.313)	0.036 (0.002)	0.101 (0)	22.9 (0)	0.096 (0.023)
During	22.4 (1.414)	518 (9.899)	7.64 (0.113)	5.175 (0.177)	31.25 (11.526)	0.023 (0.005)	0.128 (0.041)	22.95 (1.061)	0.087 (0.041)
After	18 (2.078)	568 (12.124)	7.563 (0.046)	7.163 (0.162)	27.567 (8.718)	0.010 (0.004)	N/A	20.7 (1.556)	0.1 (0.005)
RCS									
Before	25.95 (1.344)	558.5 (27.577)	7.715 (0.035)	4.68 (0.283)	52.3 (21.213)	0.022 (0.008)	0.097 (0.011)	22.567 (1.305)	0.082 (0.015)
During	22.267 (1.155)	516 (6.928)	7.65 (0.017)	5.233 (0.237)	27.567 (3.580)	0.023 (0.002)	0.133 (0.042)	22.3 (0.866)	0.08 (0.038)
After	17.7 (2.687)	586.5 (16.263)	7.61 (0.042)	6.945 (0.460)	25.95 (3.323)	N/A	N/A	21.05 (1.287)	0.091 (0.004)
Upper Yolo Bypass									
RD22									
Before	25.633 (0.115)	776.333 (9.815)	8.1 (0.052)	6.247 (0.115)	45.867 (3.175)	0.051 (0.014)	2.49 (0.750)	18.05 (0.212)	0.972 (0.252)
During	22.6 (1.414)	520 (2.828)	7.655 (0.007)	4.715 (0.742)	29.9 (2.404)	0.017 (0.001)	0.1 (0.024)	23 (1.697)	0.078 (0.025)
After	17.95 (1.344)	734.5 (153.442)	7.625 (0.049)	6.825 (0.064)	35 (14.284)	0.050 (0)	1.922 (2.048)	23.15 (2.333)	0.484 (0.426)
I80									
Before	23.4 (0.866)	651 (38.105)	8.04 (0.069)	6.07 (0.450)	76.533 (2.656)	0.035 (0.018)	1.393 (0.274)	18.45 (1.061)	0.6 (0.054)
During	22.75 (1.909)	531.5 (2.121)	7.615 (0.318)	5.16 (0.523)	38.1 (5.798)	0.021 (0.010)	0.222 (0.072)	21.65 (0.778)	0.099 (0.011)
After	17.1 (0.283)	721.5 (4.950)	8.07 (0.424)	10.77 (4.865)	35.1 (4.525)	0.004 (0)	1.2 (0.170)	18.3 (0.566)	0.526 (0.217)
Lower Yolo Bypass									
LIS									
Before	24.6 (0.707)	492 (48.083)	8.145 (0.233)	6.585 (1.803)	48.85 (1.485)	0.014 (0.008)	0.166 (0)	12.5 (1.131)	0.225 (0.022)
During	23.467 (1.617)	560.333 (35.218)	7.747 (0.196)	4.753 (0.421)	35.6 (6.755)	0.024 (0.010)	0.296 (0.069)	21.9 (0.566)	0.127 (0.030)
After	16.8 (1.934)	408 (217.182)	7.928 (0.037)	7.77 (0.695)	33.225 (5.352)	0.012 (0)	0.312 (0.255)	17.2 (4.384)	0.147 (0)

Region *Site* Flow Pulse Period	Temp (°C)	SPC (µS/cm at 25 °C)	pH	DO (mg/L)	Turbidity (NTU)	Ammonia (mg/L)	Nitrate/ Nitrite (mg/L)	Silica (mg/L)	Phosphorus (mg/L)
STTD									
Before	24 (0.115)	193 (1.155)	8.585 (0.040)	7.97 (0.115)	21.7 (0.693)	0.009 (0.005)	N/A	13.05 (1.344)	0.229 (0.010)
During	23.35 (1.790)	576.5 (34.064)	7.8 (0.012)	5.88 (0.173)	27.1 (0.577)	0.019 (0.006)	0.273 (0.037)	21.7 (1.131)	0.137 (0.013)
After	16.46 (2.040)	265.2 (67.433)	8.36 (0.212)	8.962 (0.243)	17.38 (2.191)	0.009 (0)	N/A	12.85 (0.354)	0.124 (0.032)
Cache Slough Complex									
BL5									
Before	22.3 (0.990)	153.5 (6.364)	8.04 (0.283)	7.975 (0.163)	7.9 (0.849)	0.043 (0.029)	0.112 (0)	13 (0)	0.131 (0.023)
During	21.333 (1.270)	283 (50.229)	8.1 (0.052)	7.723 (0.150)	7.433 (2.194)	0.041 (0.006)	0.08 (0.010)	15.33 (0.115)	0.127 (0.011)
After	16.95 (0.778)	172 (11.314)	7.905 (0.205)	8.955 (0.502)	7.1 (2.121)	0.090 (0.018)	0.134 (0.004)	14.8 (0.141)	0.085 (0.007)
LIB									
Before	22.3 (0.520)	136.667 (4.619)	7.583 (0.248)	8.077 (0.462)	6.167 (0.404)	0.092 (0)	0.147 (0.098)	15.2 (1.273)	0.081 (0.016)
During	21.1 (1.556)	162 (21.213)	7.585 (0.021)	8 (0.212)	5.15 (1.485)	0.117 (0.030)	0.135 (0.030)	15.6 (0.566)	0.085 (0)
After	16.8 (0.990)	151 (5.657)	7.675 (0.035)	8.995 (0.290)	6.6 (1.131)	0.151 (0.042)	0.174 (0.042)	15.7 (0.566)	0.076 (0.002)
Lower Sacramento River									
RYI									
Before	22.15 (0.636)	132 (1.414)	7.525 (0.092)	7.96 (0.240)	5.9 (1.414)	0.164 (0.025)	0.171 (0.024)	15.25 (0.071)	0.071 (0.001)
During	21.333 (1.328)	148.333 (9.238)	7.503 (0.012)	7.93 (0.242)	4.8 (1.212)	0.152 (0.024)	0.145 (0.025)	16.25 (0.071)	0.074 (0.003)
After	16.75 (1.061)	139.5 (6.364)	7.5 (0.099)	8.78 (0.198)	6.25 (1.909)	0.228 (0.120)	0.199 (0.120)	16.2 (1.131)	0.073 (0.008)
RVB									
Before	22.3 (0.707)	132.5 (0.707)	7.505 (0.120)	7.86 (0.240)	6.5 (2.263)	0.144 (0.008)	0.196 (0.008)	15.45 (0.071)	0.076 (0.001)
During	21.15 (1.485)	148.5 (13.435)	7.39 (0.099)	7.96 (0.212)	5.5 (0.566)	0.152 (0.057)	0.166 (0.057)	16.4 (0.141)	0.072 (0.006)
After	17.233 (0.981)	136.333 (4.619)	7.31 (0.121)	8.57 (0.173)	6.967 (1.963)	0.21 (0.098)	0.221 (0.098)	16.25 (1.485)	0.072 (0)

Continuous chlorophyll fluorescence (µg/L) differed across regions before and after the flow pulse, with a general trend of low concentrations in southern regions and high concentrations in northern regions across all flow pulse periods (Fig. 3). The highest levels of chlorophyll fluorescence before the flow pulse were in the Upper Yolo Bypass and LIS in the Lower Yolo Bypass (Fig. 3B,C). High flows during the flow pulse reduced overall residence time and muted the diurnal and tidal fluctuations of chlorophyll fluorescence by transporting phytoplankton biomass out of the Yolo Bypass. In the Colusa Basin Drain/Ridge Cut Slough and Upper and Lower Yolo Bypass, chlorophyll fluorescence decreased during the flow pulse relative to before (Fig. 3A,B,C). The only site with a slight increase in chlorophyll fluorescence during the flow pulse was STTD in the Lower Yolo Bypass (Fig. 3C). Chlorophyll increased after the flow pulse in Colusa Basin Drain/Ridge Cut Slough, Upper Yolo Bypass, and at LIS in the Lower Yolo Bypass (Fig. 3A,B,C), indicating increased phytoplankton productivity in the northern regions. There was also a modest average increase in chlorophyll in the Lower Yolo Bypass region because of an increase at LIS and a decrease at STTD (Fig. 3A,B,C). No measurable changes were detected in CSC and the Lower Sacramento River during or after the flow pulse, during which chlorophyll fluorescence remained at levels less than 4.0 µg/L (Fig. 3D,E).

Discrete concentrations of chlorophyll-a (µg/L, Fig. 3) differed across regions (two-way ANOVA; $F_{4,45}$=10.35, p=0.01) and among the flow pulse periods ($F_{2,45}$=8.922, p<0.01), and there was a significant interaction between flow pulse period and region ($F_{8,45}$=4.804, p<0.01). Chlorophyll-a concentrations increased after the flow pulse relative to before (Tukey; p<0.05) and during the pulse (Tukey; p<0.001) in Colusa Basin Drain/Ridge Cut Slough (Table 3). In addition, concentrations were higher before (Tukey; p<0.001) and after (Tukey; p<0.001) than during the pulse in Upper Yolo Bypass.

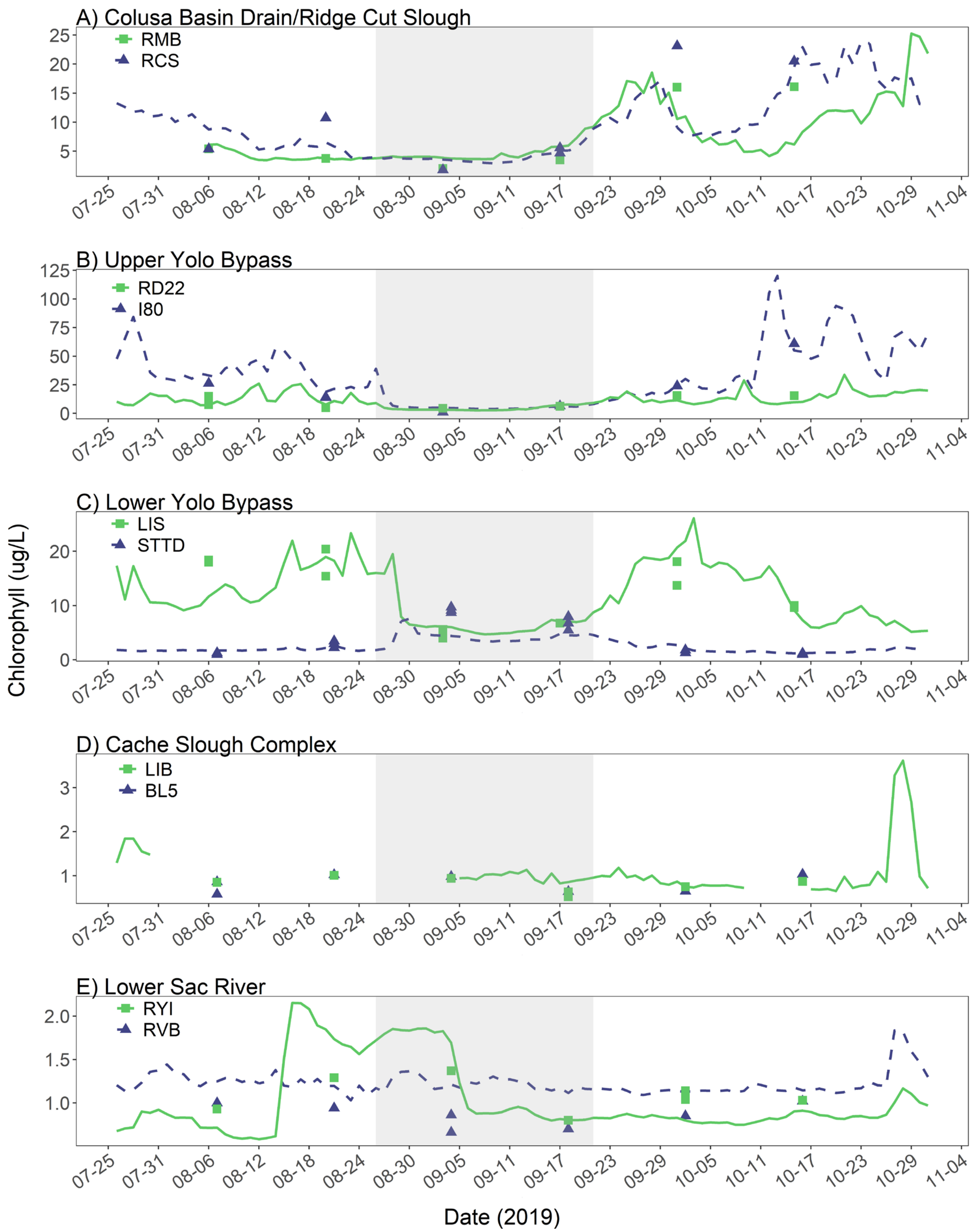

Figure 4. **Daily mean chlorophyll continuous (lines) and discrete data (points) for monitoring sites arranged vertically from north to south across regions.** Y-axis scales are adjusted to reflect each region's baseline variability in chlorophyll-a. The 'during' flow pulse period is identified by the gray shaded area. Note that continuous data were not recorded for BL5 and are missing for some time periods for LIB. Monitoring sites from top to bottom: Colusa Basin Drain at Rominger Bridge (RMB), Ridge Cut Slough at Hwy. 113 (RCS), Toe Drain at Rd. 22 (RD22), Toe Drain at I80 (I80), Toe Drain below Lisbon Weir (LIS), Screw Trap at Toe Drain (STTD), and Below Toe Drain in Prospect Slough (BL5), Base of Liberty Island (LIB), Cache Slough at Ryer Island (RYI), Sacramento River at Rio Vista Bridge (RVB).

Plankton

Total phytoplankton biovolume differed across regions (Fig. 4A; 2-way ANOVA; $F_{4,43}$=29.619, p=0.003), but there was no main effect of flow pulse period ($F_{2,43}$=2.068, p=0.14), or an interacting effect between the pulse period and region on biovolume ($F_{8,43}$=1.326, p=0.26). After the flow pulse, total phytoplankton biovolume increased in the Upper Yolo Bypass (Tukey, p<0.05), but remained similar in downstream regions. Cyanophytes (cyanobacteria) were the dominant taxon across all flow pulse periods; in particular, the cyanobacteria *Eucapsis* comprised >90% of the total biovolume (Fig. 5A). However, cryptophytes and flagellates increased after the action both in upstream regions and downstream in the CSC (Fig. 5A). In addition, the Upper and Lower Yolo Bypass regions underwent some changes in community structure across the flow pulse periods. For example, during the flow pulse we detected an increase in the centric diatom *Aulacoseira* to 10% of the total biovolume in the Upper Yolo Bypass, and after the action the centric diatom *Cyclotella* increased in the Upper and Lower Yolo Bypass to 35% and 30%, respectively, of the total phytoplankton biovolume (Fig. 5A). These changes were largely driven by increases in the proportion of diatoms relative to cyanobacteria at I80 and LIS.

Zooplankton density (CPUE) varied across flow pulse periods and regions with a significant interacting effect (Fig. 4B; 2-way ANOVA; $F_{8,45}$=3.156, p=0.007); however, there was no main effect of region ($F_{4,45}$=0.543, p=0.713) or flow pulse period ($F_{2,45}$=2.190, p=0.488) on zooplankton. In upstream regions of Colusa Basin Drain and Upper Yolo Bypass, zooplankton CPUE consisted mainly of rotifers (microzooplankton), cyclopoid copepods, and cladocerans; however, the percentage of the zooplankton CPUE composed of rotifers increased from 10-30% to 60-80% after the flow pulse, depending on the region (Fig. 5B). In contrast, the community structure of downstream regions including the Lower Yolo Bypass, CSC, and the Lower Sacramento River were dominated by calanoid copepodids, ranging from 47% (Yolo Bypass) to 82% (CSC and Lower Sacramento River) of the zooplankton CPUE (Fig. 5B). *Pseudodiaptomus forbesi* adults (calanoid copepod) comprised 5-14% of the total CPUE in CSC and the Lower Sacramento River, and their density remained similar across flow pulse periods (Fig. 5B), whereas *Eurytemora affinis* adults (calanoid copepod) were detected only after the action and in the Lower Sacramento (Fig. 5B). Moreover, copepod nauplii increased to 17% of the total CPUE in downstream regions after the flow pulse.

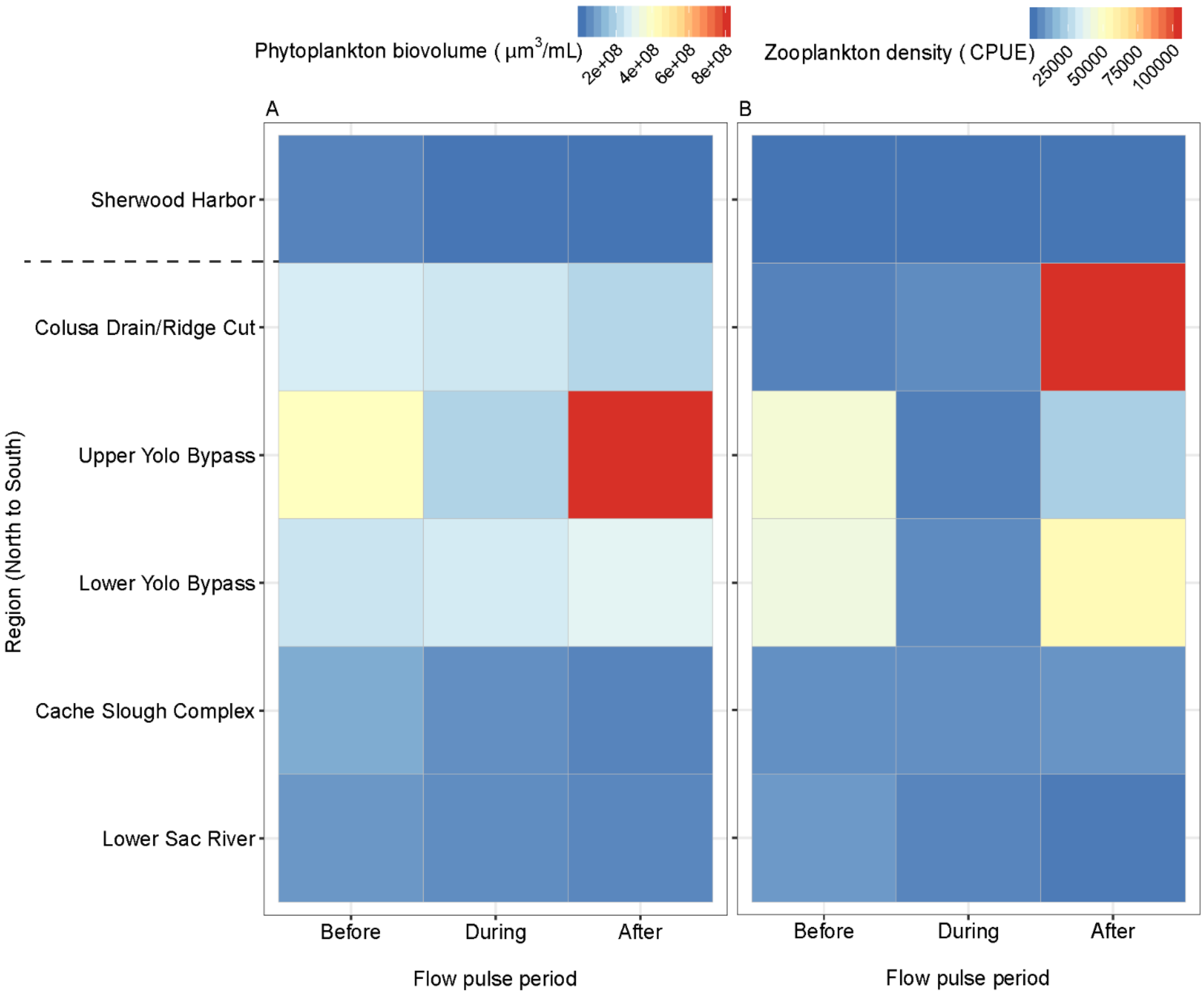

Figure 5. Plankton responses to the 2019 managed flow pulse. (A) Phytoplankton biovolume (µm^3/mL) and (B) Zooplankton densities (CPUE, catch per unit effort) collected before, during, and after the 2019 managed flow pulse. Phytoplankton and zooplankton are shown for Sherwood Harbor (a control site) and five regions of the study area, from north to south: Colusa Basin Drain/Ridge Cut Slough to Lower Sacramento River.

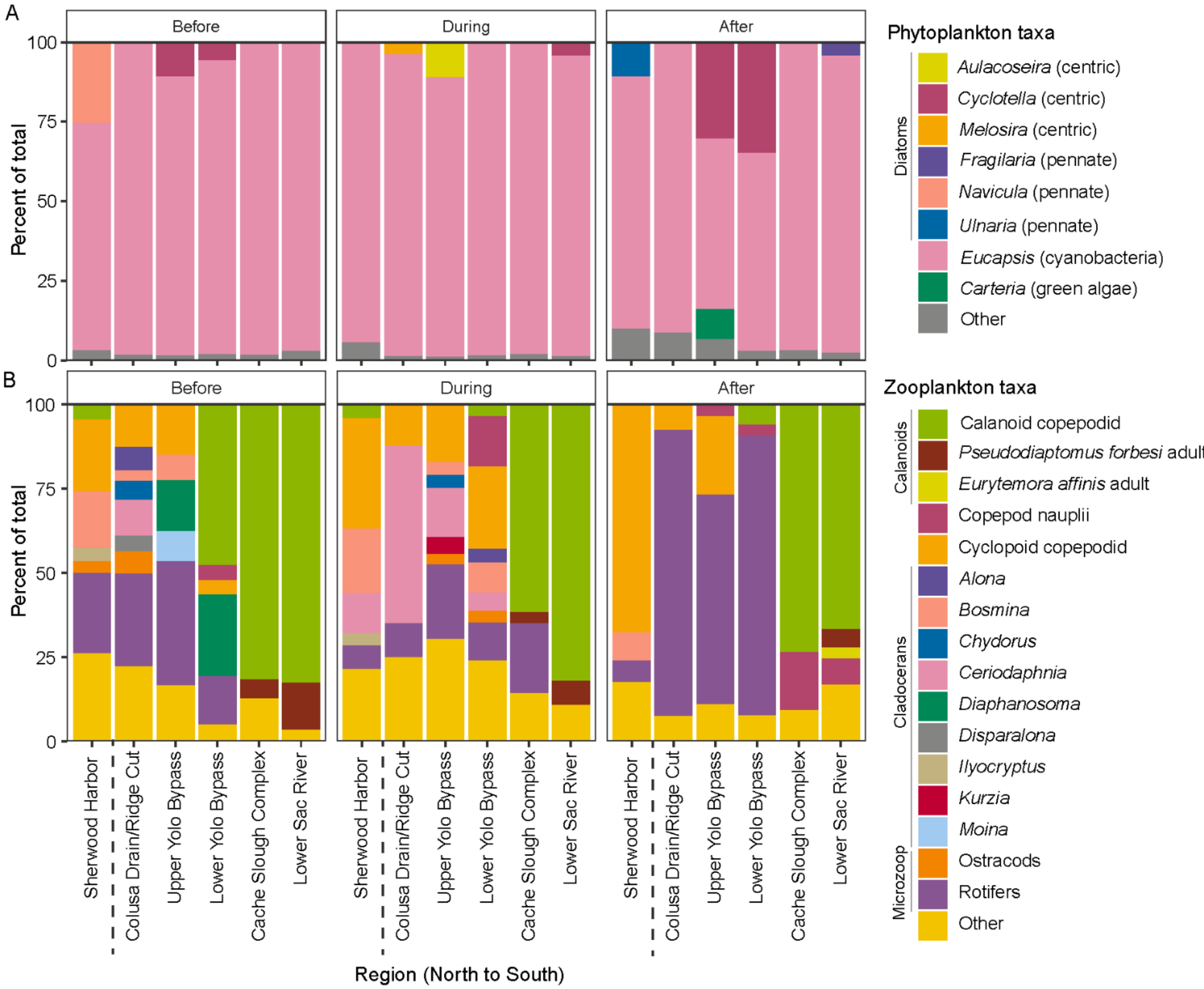

Figure 6. Community structure of (A) phytoplankton and (B) zooplankton before, during, and after the 2019 managed flow pulse. Dominant taxa shown here comprised ≥3% of the total phytoplankton biovolume or total zooplankton CPUE across flow pulse periods (before, during, after). Taxa comprising less than 3% of the total plankton biomass or CPUE were pooled in the 'Other' category. Phytoplankton and zooplankton are shown for Sherwood Harbor (a control site) and five regions of the study area, from north to south: Colusa Basin Drain/Ridge Cut Slough to Lower Sacramento River.

Contaminants

Total pesticide concentrations in water samples across all sites differed significantly among the flow pulse periods (Fig. 6; one-way ANOVA, $F_{2,27} = 4.769$, $p = 0.017$), and concentrations were significantly higher during than after the flow pulse (Fig. 6; Tukey HSD, p-adj = 0.014). We found no significant differences in total pesticide concentrations between before and during the flow pulse or before and after the flow pulse, which was largely driven by high pesticide concentrations at RMB before the pulse (Fig. 6).

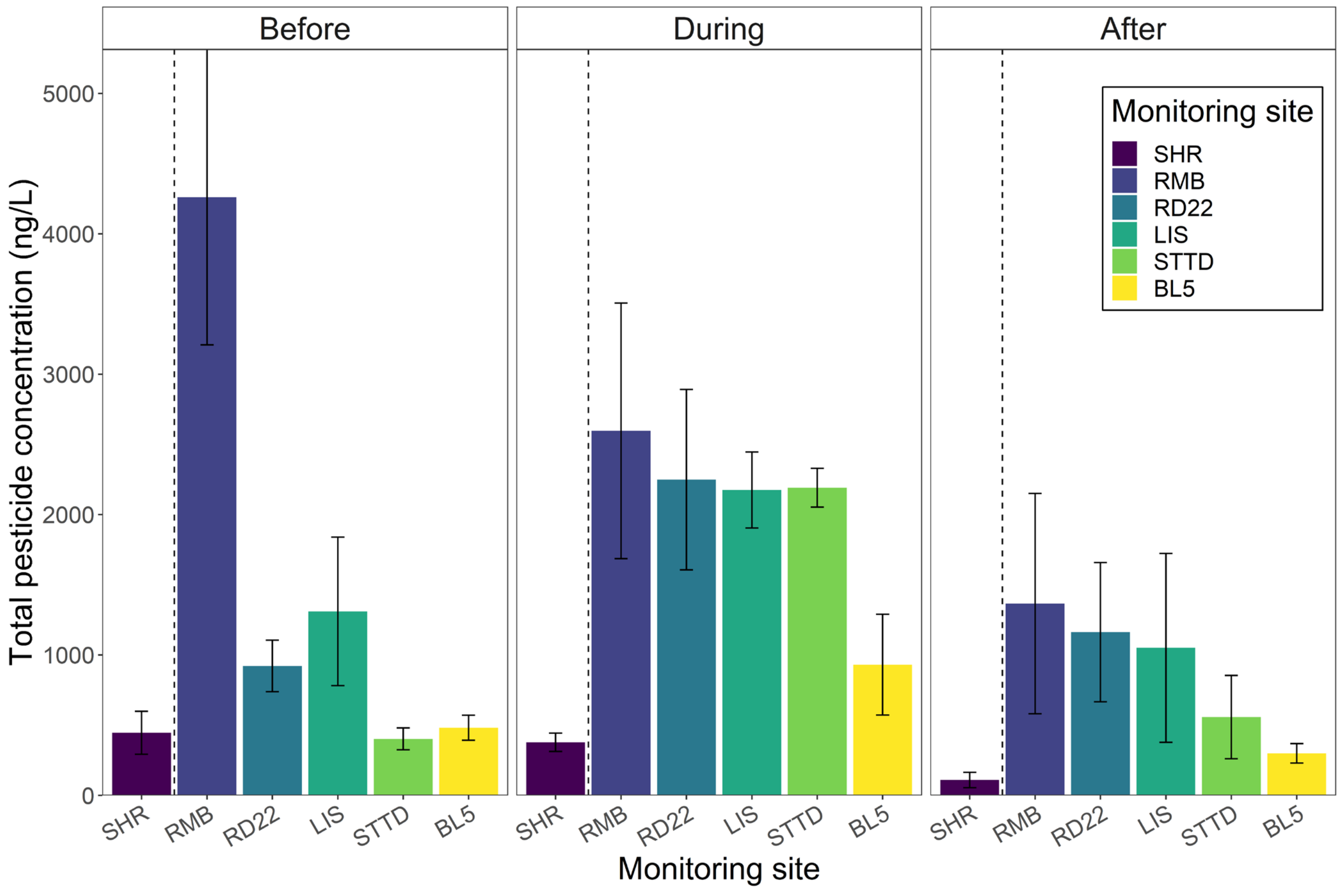

Figure 7. Total pesticide concentrations (Mean ± SD) in water samples by monitoring site before, during, and after the 2019 managed flow pulse. Monitoring sites are arranged from north to south across the study area starting with RMB, and SHR is a control site in the Sacramento River outside of the Yolo Bypass study area. From left to right: Sherwood Harbor (SHR), Colusa Basin Drain at Rominger Bridge (RMB), Toe Drain at Rd. 22 (RD22), Toe Drain below Lisbon Weir (LIS), Screw Trap at Toe Drain (STTD), and Below Toe Drain in Prospect Slough (BL5).

We detected a total of 39 pesticides, including 11 fungicides, 15 herbicides, 12 insecticides, as well as the synergist piperonyl butoxide in water and sediment samples. Each water sample contained mixtures of between 13 and 25 pesticides. Nine pesticides were detected in every sample, and an additional six pesticides were detected in over half of the samples (Table 5). Pesticide concentrations ranged from 2,350 ng/L (azoxystrobin) to below method detection limits. Three water samples collected at RD22 (two pre-pulse and one post-pulse) contained the insecticide fipronil at concentrations above the U.S. Environmental Protection Agency aquatic life benchmark for chronic toxicity to invertebrates (11 ng/L), while a fourth sample collected at RMB during the pulse contained the pyrethroid insecticide bifenthrin at a concentration above the same benchmark for that pesticide (1.3 ng/L). We also detected four pesticides (azoxystrobin, bifenthrin, pendimethalin, and propiconazole) in sediment samples. Azoxystrobin was detected in three samples while the other compounds were detected in one sample each. The herbicide pendimethalin was only detected in suspended sediments.

Table 5. Detection frequencies of pesticides in water samples.

Pesticide	Detection Frequency
3,4-Dichloroaniline	100%
Azoxystrobin	100%
Chlorantraniliprole	100%
Fluopyram	100%
Fluxapyroxad	100%
Hexazinone	100%
Methoxyfenozide	100%
Metolachlor	100%
Propiconazole	100%
Boscalid	97%
Thiobencarb	83%
DCPMU	60%
DCPU	53%
Fluridone	53%
Penoxsulam	53%
Clomazone	47%
Diuron	43%
Carbendazim	40%
Diazinon	40%
Fipronil Desulfinyl	30%
Indaziflam	30%
Tebuconazole	23%
Fipronil	20%
Fipronil Sulfone	17%
Iprodione	17%
Chlorothalonil	13%
Fipronil Sulfide	13%
Simazine	13%
Diazinon oxon	10%
Fipronil Desulfinyl Amide	10%
PBO	7%
Tetraconazole	7%
Bifenthrin	3%
Dithiopyr	3%
Flupyradifurone	3%
Imidacloprid	3%
Napropamide	3%
Propyzamide	3%
Thiabendazole	3%

Discussion

Thanks to a successful partnership between agencies, landowners, and local irrigation and reclamation districts, the North Delta Flow Action generated a managed flow pulse using existing infrastructure to redirect agricultural return flows through the Yolo Bypass, producing measurable changes in water quality and the food web. The 2019 NDFA achieved net positive flows through the Yolo Bypass and exceeded flow pulse targets in discharge volume (25 TAF) and maximum average daily net flows (700 cfs) at Lisbon Weir. Hydrodynamic modeling of water sources during the pulse predicted up to 100% of the water at the bottom of the Toe Drain in the Yolo Bypass originated from the pulse, whereas 8 to 2% of the water downstream in Cache Slough and Rio Vista was traced from the pulse due to strong tidal influence and dilution from the Sacramento River. Hence, the flow pulse had the desired effect of improving transport to the Cache Slough Complex.

Consistent with results of hydrodynamic modeling, the flow action had stronger effects on water quality, nutrients, and the lower trophic food web in the Colusa Basin Drain/Ridge Cut Slough and Yolo Bypass regions compared to downstream. These food web changes included increases after the flow pulse in chlorophyll-a, phytoplankton biomass, and zooplankton density. We also observed changes in phytoplankton community composition, including an increase in the proportion of the community composed of centric diatoms, a nutritious food source for zooplankton (Brown 2009, Lehman 1992, Orsi 1995). These changes to the food web likely resulted from phytoplankton transport, resuspension, and local production. Despite the benefits of the managed flow pulse to the lower trophic food web in the Yolo Bypass, we found evidence suggesting that phytoplankton productivity may be been moderated by low nutrient levels in the agricultural inflow (e.g. Jassby 2005, Wilkerson et al. 2006, Glibert et al. 2014). In addition, the flow pulse coincided with increased pesticide concentrations in water, which can alter zooplankton behavior (Andrade et al. 2018), biomass, and community structure (van Wijngaarden et al. 2014; Hébert et al. 2020).

Hydrodynamics

The managed flow pulse significantly modified hydrodynamics in the Yolo Bypass by increasing transport of water from Colusa Basin Drain and Upper Yolo Bypass downstream relative to predicted flows in the absence of a managed flow pulse (Fig. 2A,B). The flow action also reversed typical fall outflow patterns for CSC from negative to positive. These hydrodynamic changes disturbed the habitat of the Yolo Bypass and CSC by redistributing water across sites where it is normally locked in by agricultural land and tidal activities. Thus, the effects of the flow pulse were consistent with the first goal of the project to improve transport to downstream areas.

Although hydrodynamics in the Yolo Bypass were strongly altered by the managed flow pulse, its effects in the Lower Sacramento River were less apparent due to differences in floodplain and river channel morphology among the regions. Upstream, the perennial Toe Drain is primarily influenced by water flowing from Colusa Basin Drain, local water use patterns, and other sources into the Yolo Bypass (Fig. 1). Downstream, the Toe Drain widens below BL5 and merges with the Sacramento River, meeting and mixing with a larger volume of water and becoming more tidally influenced. Therefore, sites downstream of where the Toe Drain meets the CSC, such as Rio Vista Bridge are more influenced by the Sacramento River, while upstream sites are influenced by the Yolo Bypass floodplain. As a result, the percentage of flow pulse water (1-4%) detected at Rio Vista is lower compared with the percentage (100%) in the Yolo Bypass, during years with managed flow actions. Regardless, this percentage of pulse water downstream originating from managed flow pulses is large compared to smaller flow pulses during summer and fall, for which as little as 0.01%-0.02% of the water at Rio Vista can be traced to the Yolo Bypass (e.g. 2017 and 2020 non-managed flow pulses; Anchor QEA 2020; USBR 2020). This indicates that dilution is inherent in the hydrology of the system downstream, but managed flow pulses nonetheless redistribute water and increase the percentage of water from Yolo Bypass (and other backwater channels) in the Lower Sacramento River (Anchor QEA 2020).

Water Quality

Because the 2019 NDFA had greater effects on hydrodynamics in Yolo Bypass than downstream, we observed larger changes in water quality during and after the flow pulse in the Yolo Bypass than in CSC and the Lower Sacramento River (Table 4). Water depleted in nutrients important for phytoplankton growth flowed from Colusa Basin Drain through the Yolo Bypass. As a result, concentrations of nitrate/nitrite and DOP decreased during the flow pulse in Upper and Lower Yolo Bypass, while concentrations of ammonia remained unchanged. In addition to changes in nutrients, changes in oxygen levels in the Yolo Bypass and CSC (Table 4) could potentially have affected food web responses during the pulse (see *Plankton*, below).

Plankton

Along with the transport of water, the flow pulse redistributed plankton downstream (Fig. 4) and likely resuspended centric diatoms (Fig. 5A). Together, these disturbances of the plankton community may have created opportunities within the Yolo Bypass for less dominant taxa, such as centric diatoms, to increase in abundance (Fig. 5A) (*intermediate disturbance hypothesis*; Connell 1978). Overall, phytoplankton biomass in the Yolo Bypass was dominated by cyanobacteria *Eucapsis*. However, the centric diatoms, *Aulacoseira* and *Cyclotella* increased compared to other taxa during and after the flow pulse. These taxa have resting life stages within the benthos that can be resuspended by high flows, which in turn increases their access to light and their growth rates (Kilham and Kilham 1975, McQuoid and Hobson 1996). These resting stages may have been resuspended into the water column through disturbance by the pulse water, enabling them to increase their biomass during and after the flow pulse (Fig. 5). However, we cannot confirm that centric diatoms were resuspended by disturbance of the benthos as we did not sample benthic phytoplankton during the study.

Although nutrient concentrations remained above levels thought to limit phytoplankton growth (Table 4; Jassby 2005), experiments showed that nutrient levels were limiting in the Yolo Bypass during the study (Wilkerson et al. 2020). Moreover, diatom growth proceeds most rapidly when concentrations of nitrate/nitrite are relatively high compared with ammonia (Wilkerson et al. 2006, Dugdale et al. 2007, Glibert et al. 2014), and thus diatoms were likely nutrient-limited in CSC and the Lower Sacramento River, where ammonia levels were high throughout the study (Table 4). Hence, while the flow pulse improved downstream transport of phytoplankton, additional primary production in CSC might have been moderated by low nutrient levels.

Despite reductions in nutrients in Yolo Bypass, concentrations of chlorophyll-a increased in Colusa Basin Drain and at one site (I80) in Upper Yolo Bypass after the flow pulse (Fig. 3). These changes likely resulted from local production, as evidenced by a slight decrease in concentrations of nitrate/nitrite and silica (Table 4), which suggests nutrient uptake by phytoplankton (Dugdale et al. 2007). Phytoplankton growth likely increased in upstream regions after the flow pulse due to seasonal changes in flow and turbidity (Table 4) increasing residence time and light availability (Lehman 1992, Jassby et al. 2002, Lucas et al. 2009). Chlorophyll-a normally increases as flow and turbidity decrease during fall in Colusa Basin Drain and at I80 in the Yolo Bypass, after the cessation of managed or non-managed flow pulses (Frantzich et al. 2018, 2019). Nutrients transported from wastewater treatment plants upstream of I80 during the flow pulse also may have contributed to the increase in chlorophyll-a (Frantzich et al. 2019). In contrast to 2019, the Sacramento River pulse of 2016 led to higher chlorophyll-a concentrations in upstream and downstream regions of Upper Yolo Bypass, CSC, and Lower Sacramento River (Frantzich et al. 2019). Replicating the 2016 NDFA using Sacramento River water, and comparisons of water quality and chlorophyll-a across years, will increase our understanding of these variable responses in lower trophic productivity to different types of managed flow pulses (see *Implications and Adaptive Management*, below).

Zooplankton density decreased during the flow pulse in the Upper and Lower Yolo Bypass (Fig. 4B), suggesting that zooplankton present before the pulse were transported downstream. Total zooplankton density then increased at upstream sites after the managed flow pulse (Fig. 4), with rotifers and cyclopoid copepods increasing to become the two dominant taxa, thereby reducing the community diversity after the flow pulse in the Yolo Bypass (Fig. 5B). Rotifers may have increased in abundance due to disturbance at upstream sites during the pulse, as zooplankton present before the flow pulse were transported downstream (Fig. 4B), creating an opportunity for rotifers to proliferate (Wetzel 2001). In addition, rotifers may have increased due to local food web production, as chlorophyll also increased after the flow pulse, providing additional food resources (Fig. 4A).

Due to data limitations from the study region, we cannot rule out seasonality as an additional cause of the rotifer increase (zooplankton data are not available for other seasons in the Yolo Bypass from IEP ZoopSynth), or potential interactive effects of pesticides on zooplankton taxa (as detailed in the next section). Furthermore, the appearance of *Eurytemora affinis*, an important species for Delta Smelt diets (Nobriga 2002, Slater and Baxter 2014), in the Lower Sacramento River after the flow pulse, may also have been due to seasonal change, as this species typically increases in abundance in the Delta during Fall (IEP ZoopSynth; accessed 12/9/2020). Seasonal fluctuations in zooplankton composition are a confounding factor that we plan to address with future studies.

While the North Delta can serve as a hot spot for plankton productivity, there is high variability in community composition and biomass in response to flow pulses (managed and non-managed) across years. The phytoplankton community in 2019 was dominated by cyanobacteria, with *Eucapsis* comprising more than 80% of the total biovolume across all regions and flow pulse periods (before, during, after); whereas diversity was greater in almost all previous years. In 2017 and 2018, a non-managed vs. managed pulse year, cyanobacteria composed less than 25% and 40% of the phytoplankton biovolume, respectively, as diatoms and green algae made up a greater proportion of the total biomass from June through October (Frantzich et al. 2019). Furthermore, cyanobacteria were hardly detected in the 2016 managed flow pulse, as the diatom *Aulacoseira* was dominant in downstream regions of CSC and Lower Sacramento River, opposite to the 2019 results.

As with phytoplankton, zooplankton responses in density and composition have also varied with each flow pulse. In 2016, there was an increase in Cladocera, particularly *Bosmina*, after the pulse in the Lower Yolo Bypass, as opposed to 2019 when Cladocera diversity decreased after the pulse. Densities of calanoid copepodites also increased in the Lower Yolo Bypass during 2016 and 2018, while in 2019 calanoid densities remained stable throughout the study (Frantzich et al. 2019). Variability in plankton responses across regions and years is likely influenced by factors such as plankton species composition and source water (Sacramento River vs. agricultural drainage), and the effects of these factors will be explored with subsequent studies.

Hydrology of the current and preceding year may also mediate plankton abundance and community composition in response to the flow pulse (e.g. Iriarte et al. 2017). Compared to other years, the 2019 NDFA had smaller effects on the downstream food web (Frantzich et al. 2018, 2019), despite that the timing, size, and duration (hereafter, “flow pulse metrics”) resembled other flow pulses (e.g. 2012 and 2018). While these years had comparable flow pulse metrics, there were overall differences in preceding hydrology (Frantzich et al. 2018, 2019) that could have affected lower trophic food web responses. Whereas 2019 was a wet year following a below normal year, 2012 and 2018 were both below normal years following wet years. More knowledge of how antecedent hydrology mediates the effects of the flow action will improve adaptive management, enabling fine tuning of flow pulse metrics for different hydrologic years.

Contaminants

Total pesticide concentrations were higher at all sites, except for the control site (SHR), during the flow pulse compared to before or after (Fig. 6). Total pesticide concentrations and the numbers of pesticides detected were highest at the furthest upstream sites in Colusa Basin Drain and Upper Yolo Bypass (RMB and RD22) closest to the agricultural source water, and lowest at the furthest downstream site in CSC (BL5). These patterns agree well with previously observed pesticide concentrations at these sites in the summer of 2018 under a similar managed flow pulse using agricultural return water (Orlando et al. 2020). The agricultural return water used in these managed flow pulses originated from rice field drainage, and pesticides primarily used in rice agriculture (azoxystrobin, clomazone, methoxyfenozide, penoxsulam, thiobencarb, and the propanil degradate 3,4-dichloroaniline) contributed more than half of the total pesticide burden per sample in 28 of the 30 samples analyzed in 2019. Finally, as in 2017 and 2018, three of the four EPA benchmark exceedances detected in 2019 (insecticide fipronil) occurred in samples from site RD22 which receives treated wastewater from the city of Woodland (Orlando et al. 2020).

More research is needed to understand what effects elevated pesticide concentrations during the managed flow pulse have on the lower trophic food web. For example, pesticide levels appear relatively high in both years with a flow action (e.g. 2018, 2019) and those without (e.g. 2017). It is therefore challenging to determine the relative contaminant effects of the flow pulse, versus the responses to local agricultural inputs in Yolo Bypass. In addition, we need more information about potential negative effects of different pesticides in the pulse water on plankton (van Wijngaarden et al. 2014); however, studies suggest that zooplankton exposure to pesticides (e.g., glyphosate, imidachloprid, azoxystrobin) can alter population dynamics, reduce biomass, and alter community structure (van Wijngaarden et al. 2014; Hébert et al. 2020). Across studies, copepods (calanoids, cyclopoids and nauplii) were most sensitive to pesticide exposures (van Wijngaarden et al. 2014; Hébert et al. 2020) including similar concentrations of azoxystrobin as measured in the 2019 flow pulse water (Table 5). By contrast, rotifer and cladoceran sensitivity may be pesticide specific. For example, rotifers are sensitive to glyphosate and imidachloprid (Hébert et al. 2020) but may be more tolerant to high levels of azoxystrobin (van Wijngaarden et al. 2014), and cladocerans display the opposite pattern.

With the multitude of various fungicides, herbicides, and insecticides detected in the current study, it is uncertain how their potential impacts on plankton could also affect their fish predators. Future years of the North Delta Food Subsidies Study could examine pesticide loads in zooplankton to evaluate the quality of food available for Delta Smelt and other native fishes. In addition, managed flow pulses using Sacramento River water may have different pesticide concentrations, including lower concentrations from agricultural sources and higher concentrations from urban sources, although we might expect overall greater dilution of contaminants with Sacramento River water. Repeating the 2016 flow action using diversions of Sacramento River water through Yolo Bypass would enable a comparison of the effects of different water sources on contaminant loads.

Effects on Fish

While the primary goal of the NDFA is to improve transport through the CSC, our hope is that this will result in increased food availability for Delta Smelt. However, it is challenging to evaluate the benefits of management actions on this species because it is rarely detected by monitoring surveys, and because there are numerous seasonal and ecological conditions that make it difficult to identify signals from individual actions. In the present study, we relied on indirect tools to evaluate management implications of the flow pulse for Delta Smelt: 1) monitoring changes in habitat quality and plankton, and 2) using hatchery Delta Smelt within enclosures to determine impacts on growth, diets, and survival in the study area before and after the management action. Delta Smelt enclosure studies in 2019 at Rio Vista showed 75% and 92.2% survival in August and October (before and after the flow pulse), respectively (Kwan et al. 2020). However, these results do not necessarily indicate that the managed flow pulse benefited Delta Smelt, because its effects were confounded by seasonal changes in temperature and dissolved oxygen (Table 4) that would have enhanced survival of Delta Smelt (IEP-MAST 2015). Delta Smelt growth, diets, and survival will be monitored in some years during future flow actions, dependent on timing and locations of Delta Smelt enclosure studies.

While the NDFA targets habitat improvements for Delta Smelt and other pelagic species, it is important to consider the effect of the flow pulse on migratory species such as fall-run Sacramento Chinook Salmon. Straying of salmon into Yolo Bypass during fall is a long-term issue, leading to stranding or fish taking longer to finish their migration (Sommer et al. 2013). Straying is enhanced by exceptionally high tidal flows at the mouth of Cache Slough Complex, which may increase movement of salmon towards Yolo Bypass. The effects of flow actions are therefore difficult to determine as tidal flows likely dominate overall straying patterns. Although there is some evidence that higher flow rates in the Toe Drain could help straying fish reach further upstream areas of Yolo Bypass, studies from 2012-2018 indicate that approximately 75% of fish successfully exit Yolo Bypass (Johnston et al. 2020).

CDFW monitored fish straying into the Yolo Bypass using gills nets, fyke trapping and the Wallace Weir Fish Rescue Facility during and after the 2019 managed flow pulse. Around the timing of the end of the pulse, salmonids were caught in the Rescue Facility; however, this overlapped with the normal occurrence of straying, beginning around October or November (Sommer et al. 2013). Of 363 salmonids caught and transported, there were only 11 mortalities (CDFW 2019; Davis et al. 2019). This suggests that the flow pulse had only minor effects on salmon and showed that the fish rescue facility can help to mitigate natural straying and mortalities. DWR and CDFW will continue monitoring salmon during subsequent managed flow pulses and are currently conducting a synthesis that suggests additional factors influence straying.

More information about the effects of the NDFA on salmon straying and Delta Smelt survival and growth is needed to adaptively manage the timing of the flow pulse. The highest catch of straying adult fall-run Chinook Salmon in Yolo Bypass occurs in October and November (Sommer et al. 2013). Thus, an earlier (summer) flow pulse may be better for survival of salmon. Additional data about the effects of the NDFA on these species would help determine optimal flow pulse timing.

Implications and Adaptive Management

When comparing the results of the 2019 North Delta Food Subsidies Study to the 2016 and 2018 studies, it is apparent that the managed flow pulse in 2016 using Sacramento River water produced stronger responses in plankton productivity in CSC and the Lower Sacramento River than the 2018 and 2019 actions using agricultural return water (Frantzich et al. 2019). Thus, a key management question is whether the NDFA using Sacramento River water is consistently better for food web productivity than agricultural return actions. This knowledge gap can only be addressed by repeating the Sacramento River action in future years and comparing food web responses to previous actions. These comparisons could identify the type of action most appropriate for achieving the NDFA goals of increasing food availability for Delta Smelt downstream of Yolo Bypass.

In addition to identifying the best water source for the flow pulse, it is important to understand the relative contributions of two mechanisms to increases in plankton productivity: 1) transport, and 2) local phytoplankton production. In 2019, concurrent increases in phytoplankton biomass and decreases in nutrients in Colusa Basin Drain and Upper Yolo Bypass, suggest that local food web production was partly responsible for phytoplankton growth (Table 4, Fig. 3). By contrast, transport of plankton and low nitrogen availability during the flow pulse suggest that upstream subsidies, rather local food web production, may have increased the biomass of centric diatoms in Yolo Bypass (Table 4, Fig. 4, 5). Local food web production and transport likely work together to increase plankton productivity after managed flows (Fig. 4, 5). For example, local production may depend on seeding from transport or resuspension of nutritious diatoms or zooplankton from upstream areas.

We plan to explore contributions of these mechanisms, along with the effects of antecedent hydrology and community composition, on the efficacy of the NDFA with a forthcoming synthesis comparing the effects of different types of non-managed and managed flow pulses (using Sacramento River water vs. agricultural return water), from 2011-2019 on the North Delta food web. In addition, we hope to replicate the 2016 NDFA using diversions of Sacramento River water during the summer of 2021, to examine the effects of non-agricultural source water on food web productivity. Repeating the NDFA in future years will also help us identify how hydrology (wet vs dry years) interacts with flow pulse metrics of timing, size, and duration, to achieve the greatest benefits in food web production. However, planning and implementation of NDFA will depend on the water year, as water supplies must also be available for other Delta requirements and water company obligations, and its use coordinated with other agencies and stakeholders. The goal of future studies and the upcoming synthesis are to provide recommendations for modifying future managed flow pulses to achieve the greatest increases in food availability for native fishes in the North Delta.

Conclusions

The 2019 NDFA redirected agricultural return flows through Yolo Bypass and increased the quantity of plankton (fish food) locally, but not downstream in the Lower Sacramento River. In addition, more diatoms grew in the Yolo Bypass after the flow pulse than before, providing food for zooplankton. Collaborator studies provided evidence that the 2019 NDFA did not negatively affect Chinook Salmon. Despite these benefits to the food web, high contaminant loads and low nutrient availability in the flow pulse water could have reduced potential food web responses. Moreover, the 2019 NDFA did not increase food availability downstream by as much as the 2016 NDFA using diversions of Sacramento River water. Yet, we are limited in our ability to recommend modifications to NDFA operations, because we have only conducted the NDFA using Sacramento River water in a single year (2016). To improve management recommendations, it is important to determine whether Sacramento River actions provide a better response. Future studies will help us assess the effects of source water (agricultural return flows vs. Sacramento River), and other mediating factors such as hydrology, to adaptively manage the flow action to maximize food availability downstream.

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