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RESEARCH

Physical and Biological Responses to Flow in a Tidal Freshwater Slough Complex

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ABSTRACT

Although brackish marsh has been the subject of decades of research, tidal freshwater regions are still poorly understood. To provide insight into spatial and temporal dynamics of nutrients, physical conditions, and the plankton community in freshwater tidal habitat, we investigated from 2011 to 2014 a remnant freshwater tidal slough complex located in the Sacramento–San Joaquin Delta region of the San Francisco Estuary. Our results suggest that the tidal slough complex showed different seasonal nutrient, physical, and biological conditions when compared to a relatively homogenous adjacent large river channel, the Sacramento River. The tidal slough complex also showed substantial spatial variability in habitat conditions compared to nearby main river channels. Nutrient dynamics in the tidal slough complex appear to be driven by a complex suite of factors, including inflow from upstream tributaries and tidal flows from the downstream reach of the Sacramento River. Chlorophyll *a* in the tidal sloughs responded more strongly to upstream flow pulses than other environmental variables. The tidal slough complex generated significantly higher levels of chlorophyll *a* than other freshwater regions of the Delta. The 2011 and 2012 results were especially notable because unusually large flow pulses through the tidal slough complex appear to have contributed to rare phytoplankton blooms in downstream areas of the Delta during the fall months. Moreover, the 2012 flow pulse stimulated higher trophic levels, because significantly higher levels of zooplankton were in the tidal slough complex after the flow event. These results have important implications for our understanding of the functioning of freshwater tidal habitat, and for the design of potential restoration projects in these regions.

KEY WORDS

Sacramento–San Joaquin Delta, San Francisco Estuary, freshwater tidal wetlands, phytoplankton, zooplankton

INTRODUCTION

The high variability and complexity of estuaries are key drivers of overall high abundance of fish and other organisms in this habitat type (McClusky and Elliott 2004; Moyle et al. 2010). The merging of river systems and coastal oceans shape the unique attributes of estuaries, because tidal mixing of these fresh and salt water environments promotes variability in physical, chemical, and biological processes (Cebrian and Valiela 1999; Cloern 1996; Lucas et al. 2006). The distribution of tidal water over a complex landscape of marsh, channel, and floodplain habitats is also a key component of the enhanced productivity of estuarine ecosystems (Nixon 1988). Variability in abiotic and biotic conditions is strongly linked to fluctuations in seasonal and inter-annual freshwater flow (Skreslet 1986, 1997; Kimmerer 2002a, 2002b). Seasonal inflows mediate productivity through the transport of nutrients and by modifying the hydrologic properties of the water column, which alters water residence time, increases vertical mixing, and modifies salinity and turbidity (Paerl et al. 2006). Increased freshwater flow pulses can also lead to inundation of local floodplains habitats, which improve primary and secondary production by flushing nutrients and organic matter into adjacent main channel and downstream estuary habitat (Junk et al. 1989). Ecosystem complexity has also rendered estuaries vulnerable to anthropogenic changes. For example, urbanization has contributed to the depletion of over 65% of wetland habitat and over 90% of key species found in twelve of the world's most productive estuaries (Lotze et al. 2006).

Historically, the upper Sacramento–San Joaquin Delta (hereafter Delta) was a complex system of small dendritic channels, often exchanging water and its constituents with tidal marshes and floodplains (Whipple et al. 2012). This channel complexity allowed for greater spatial and temporal variation in water residence times, which likely enhanced food web productivity and exchange with larger downstream channel habitats (Robinson et al. 2014). Those channel networks contributed to increased variability in habitat and physical conditions that supported high productivity of biotic assemblages adapted to this unique ecosystem. However, the Delta has been radically altered, with the removal of most dendritic tidal channels producing a system with fewer, deeper, and wider channels, and a highly controlled flow regime. As a consequence of this and other human activities, the system has been identified as one of the most physically altered estuaries in the world (Nichols et al. 1986; Cloern 2007; Moyle et al. 2010). Exotic species have invaded numerous times, and the overall composition of the aquatic communities has been modified (Nichols et al. 1986; Grimaldo et al. 2004; Brown and Michniuk 2007; Cloern 2007). For example, the invasion of the bivalve Potamocorbula amurensis (Carlton et al. 1990) has led to dramatic declines in the biomass and overall composition of both the phytoplankton (Alpine and Cloern 1992; Cloern and Jassby 2012; Lucas and Thompson 2012) and zooplankton communities (Winder and Jassby 2011). In addition to these habitat changes, various other anthropogenic effects have occurred, such as the introduction of contaminants (Luoma and Cloern 1982), altered nutrient ratios (Wilkerson et al. 2006; Dugdale et al. 2007) and changes in sediment loads (Cloern and Jassby 2012). These habitat and food web effects have been linked to major declines in Delta fishes, including four key pelagic fishes: Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), Striped Bass (*Morone saxatilis*), and Threadfin Shad (*Dorosoma petenense*) (Feyrer et al. 2007; Sommer et al. 2007).

Although much of the historical tidal marsh has been lost from the Delta, some remnant freshwater tidal slough habitat still exists. The largest area is the Cache Slough Complex (CSC), a network of tidal channels and flooded islands. The CSC consists primarily of Cache Slough, Lindsey Slough, Liberty Island, the Sacramento Deep–Water Ship Channel, and the Yolo Bypass, the primary remaining floodplain of the estuary (Figure 1). This expansive region, located in the northern portion of the Delta, has more diverse habitat types (i.e., multiple channel sizes, broad shoals, tidal marsh, and dead-end sloughs) than other areas adjacent to the lower Sacramento River, and the CSC generates higher levels of both phytoplankton and zooplankton than the rest of the estuary (Lehman et al. 2010; Nelson et al. 2011; Sommer and Mejia 2013).

The Yolo Bypass floodplain is a main component of the CSC, and a major contributor to the local and downstream Delta food web during winter and spring high-flow events (Schemel et al. 2004; Sommer et al. 2004; Lehman et al. 2008). Local tributaries flood the Yolo Bypass in most years, and in 60% of years Sacramento River flows spill into Yolo Bypass at Fremont Weir and Sacramento Weir (Sommer et al. 2001a, 2004; Schemel et al. 2004). The Yolo Bypass

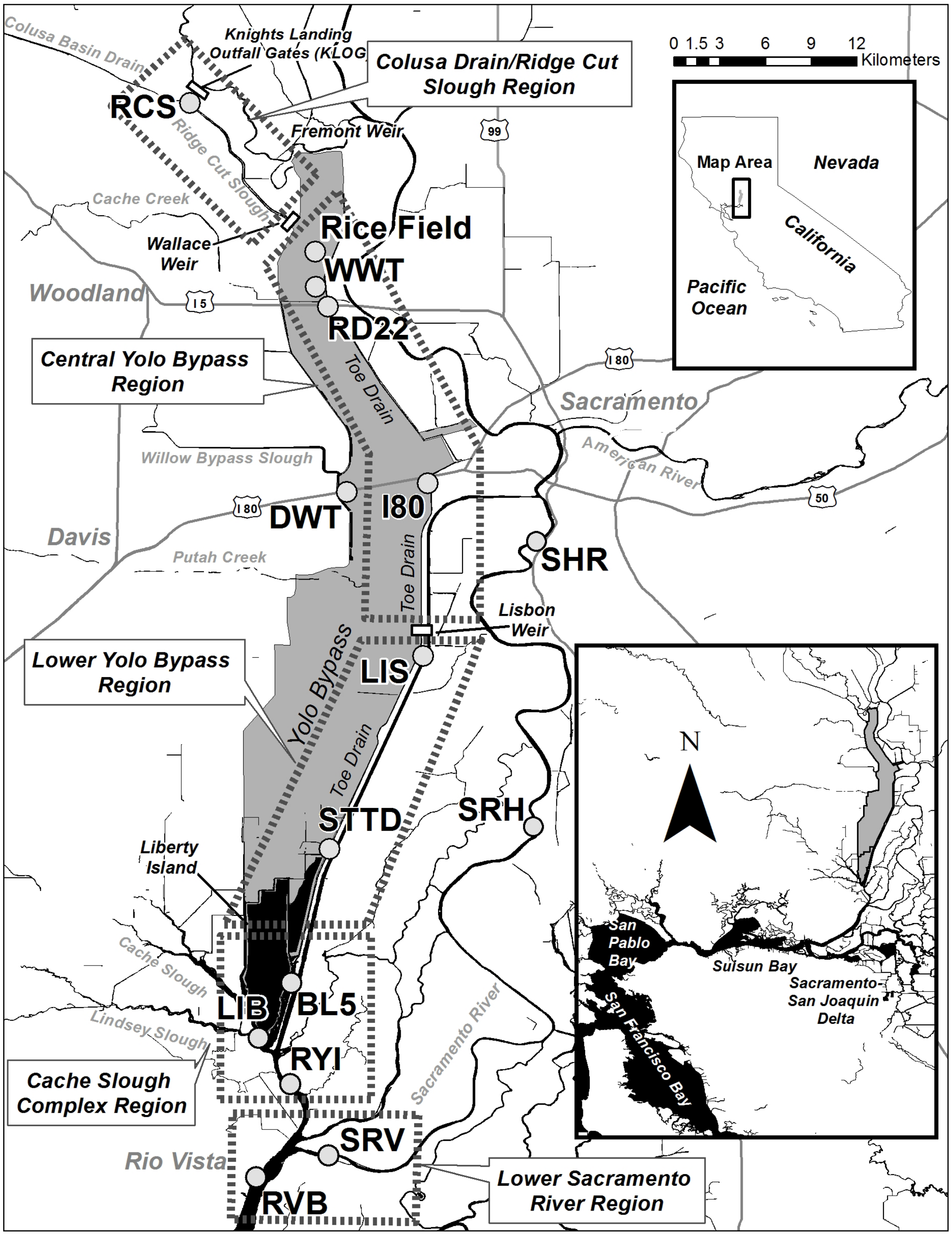

Figure 1 Map of the Yolo Bypass and Sacramento–San Joaquin Delta with water sampling stations, wastewater treatment discharge sampling locations, and the sampling locations with continuous water quality monitoring. Sites include Sherwood Harbor (SHR), Ridge Cut Slough at Hwy 113 (RCS), Toe Drain at Knaggs Ranch (KNA), Woodland Wastewater Treatment (WWT), Toe Drain at Road 22 (RD22), Davis Wastewater Treatment (DWT), Toe Drain at I80 (I80), Toe Drain below Lisbon Weir (LIS), Screw Trap at Toe Drain (STTD), Prospect Slough (BL5), Liberty Island (LIB), Cache Slough at Ryer Island (RYI), Sacramento River at Vieira's Marina (SRV), Sacramento River at Rio Vista (RVB), and Sacramento River at Hood (SRH). The five different sampling regions are outlined with a dashed line.

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shows higher chlorophyll *a* concentrations compared to the adjacent Sacramento River (Schemel et al. 2004; Sommer et al. 2004), likely a result of longer residence times, increased shallow water area, and warmer water temperatures (Sommer et al. 2004). Moreover, subsequent drainage of the floodplain can facilitate transport of production to the downstream food web (Jassby and Cloern 2000; Sommer et al. 2001a; Jassby et al. 2002; Schemel et al. 2004 Lehman et al. 2008). In addition, the Yolo Bypass is dominated by large spherical diatoms and green algal cells known to be good-quality food for higher trophic levels (Lehman et al. 2008). Despite the plethora of evidence for food web production during the wetter season, little is known about the role of Yolo Bypass and CSC food web production and downstream transport during the drier summer and fall months. This dearth of information is consistent with the tidal freshwater regions of other estuaries, which do not tend to be studied as well as brackish downstream regions (Odum 1988; Baldwin et al. 2009a).

The Yolo Bypass and the CSC have very different hydrology and channel geomorphology than the adjacent Sacramento River (Sommer et al. 2001a, 2004). During summer and fall, the Yolo Bypass and most other channels in the CSC region are shallow, narrow, light-limited, low-flow, and mostly riparian, rather than rip-rap-lined Sacramento River habitat. The exceptions are the broad open-water expanse of remnant tidal marsh habitat of Liberty Island, the deeper channel of lower Cache Slough, and the dredged Sacramento Deep-Water Ship Channel. This relatively complex region contrasts sharply with the large, leveed, deep, and higher-velocity Sacramento River. Both systems maintain temperatures in the summer and fall that favor phytoplankton growth and nutrient uptake (Lomas and Glibert 1999; Glibert et al. 2014); however, major differences in channel complexity can affect key physical processes such as tidal flows, residence time, salinity transport, and sediment transport and deposition (Robinson et al. 2014). These physical processes maintain a linkage to the biological community and influence plankton production (Kimmerer 2000b, 2002a; Paerl et al. 2006; Cloern 2007; Lucas et al. 2009). This connection between estuary aquatic ecosystems and the spatial complexity of adjacent landscapes is observed worldwide, especially in the aftermath of anthropogenic changes (Attrill et al. 1999; Meire et al. 2005; Shaffer et al. 2009). The loss of this complexity in the Sacramento River but the availability of heterogeneous landscape, wetland, and channel habitat in the CSC and Yolo Bypass are critical to the differences in how their trophic pathways and primary productivity function.

The sources and cycling of nutrients is another important driver of phytoplankton production within the Delta. Nutrient loading into the Delta from domestic, agricultural, and industrial discharge is high (Nichols et al. 1986), yet despite this high annual nitrogen loading there is minimal eutrophication (Cloern 2001). The responses by estuaries to nutrient enrichment can vary (Sharp 2001), but research in the Delta has provided evidence of negative effects on phytoplankton physiology (Wilkerson et al. 2006), and declines in primary productivity as a result of increased NH_4 effluent discharge into the Sacramento River from the Sacramento Regional Wastewater Treatment Plant (Yoshiyama and Sharp 2006; Dugdale et al. 2012; Parker et al. 2012). The reduction in primary productivity from increased anthropogenic NH_4 is not unique to the Delta, because this ecosystem response is observed in the Delaware (Yoshiyama and Sharp 2006) and Scheldt estuaries (Cox et al. 2009). Little is known about nutrient dynamics in the Yolo Bypass and the CSC for much of summer and fall when tidal flows from the Sacramento River drive the hydrodynamics (Morgan–King and Schoellhamer 2013), but evidence from the winter and spring shows that both regions have relatively high dissolved inorganic nitrogen concentrations non-limiting for primary production based on Redfield ratios (Schemel et al. 2004; Lehman et al. 2008, 2010). Measurements of NO_3 concentrations within the Yolo Bypass can account for over 90% of the dissolved inorganic nitrogen (DIN) concentration after floodplain inundation and drainage events (Schemel et al. 2004).

Our study sought to examine physical, chemical, and food web dynamics during summer–fall, a critical period for development in the early life stages of several declining pelagic fishes (e.g., Bennett 2005; Feyrer et al. 2007, 2011). For example, the physical habitat conditions within the estuary during the fall are significant in the density-dependent survival of Striped Bass from age-0 to age-3 (Kimmerer et al. 2000; Feyrer et al. 2007). These fall habitat conditions are likely even more important for short-lived pelagic fishes such as maturing Threadfin Shad and Delta Smelt (Feyrer et al. 2007; Rose et al. 2013). Additionally, the Yolo Bypass and the CSC have already been shown to support periodic higher densities of the endangered Delta Smelt than other regions of the Delta (Sommer and Mejia 2013). The Delta Smelt's local resiliency suggests that certain aspects of this region's habitat complexity better support this endemic fish, with bottom-up food-web productivity being one mechanism.

Our study is unique because it provides insight into the ecosystem function of a freshwater tidal slough habitat, a region under-represented in Bay–Delta research and in other estuaries. This study focused on expanding our understanding of the spatial and temporal trends in physical, chemical, and biological conditions in the summer and fall within the Yolo Bypass and the CSC. We hypothesized that the channel complexity of lower Yolo Bypass and the CSC would show substantially different physical and biological patterns than the adjacent Sacramento River and other regions of the Delta. Specific study questions included these three that follow:

1. Do abiotic and biotic conditions in the Yolo Bypass tidal slough habitat differ from those in the adjacent Sacramento River?
2. Are there regional differences in physical, chemical, and biological conditions across the Yolo Bypass/CSC tidal slough complex?
3. Do levels of chlorophyll *a* and zooplankton in the Yolo Bypass tidal slough habitat differ from those in other regions of the Delta?

METHODS

Site Description

The CSC is located in the upper freshwater tidal region of the Delta (Figure 1), and is described as having many of the characteristics of the historical unaltered Delta habitat (Grossinger and Whipple 2009, unreferenced, see "Notes"; Whipple et al. 2012). This region is composed of a myriad of tidal sloughs and channels (Figure 1) that surround the expansive open-water habitat of Liberty Island (21 km^2) (Lehman et al. 2010; Morgan–King and Schoellhamer 2013). The CSC provides perennial freshwater wetland habitat that influences both local invertebrate (Lehman et al. 2010; Sommer and Mejia 2013) and fish communities (Nobriga et al. 2005; Sommer et al. 2009, 2011; Sommer and Mejia 2013; Whitley and Bollens 2014). The relative complexity of the CSC is enhanced by its connection to the seasonal Yolo Bypass floodplain. The 24,000-ha Yolo Bypass is the primary remaining floodplain of the estuary. Though leveed and engineered as a flood-control system, the Yolo Bypass conveys up to 80% of Sacramento River basin flow during high-water events in the winter and spring, greatly expanding spawning and rearing habitat for several fishes consistent with Junk et al.'s (1989) flood pulse conceptual model (Sommer et al. 2001a, 2001b, 2004; Schemel et al. 2004; Feyrer et al. 2006). During the drier months of summer and early fall, a perennial riparian channel (Toe Drain) connects the Yolo Bypass to the tidal CSC and the greater estuary. The Toe Drain is narrow (≤ 50 m wide) and shallow (≤5 m deep), mostly linear, and flows along the east side of the leveed floodplain (Figure 1). In wet periods, the channel receives inflow from the Sacramento River as well as from smaller west-side tributaries. During the late-spring through fall, agriculture dominates the land use of the Yolo Bypass floodplain, with primary crops being rice, corn, tomatoes, and other grains (Sommer et al. 2001b). A large area of the Yolo Bypass is managed year-round as wildlife habitat. During drier months, the Toe Drain receives discharge from local and upstream irrigation uses as well as effluent from the Woodland, California and Davis, California wastewater treatment plants (sites WWT and DWT) (Figure 1). In addition, the lower reach of the Toe Drain is dominated by net-upstream tidal flows with source water mainly from the Sacramento River (Morgan–King and Schoellhamer 2013). The tidal excursion into the Toe Drain extends up to Sacramento, the northern edge of the Delta. The Lisbon Weir, a constructed rock barrier located approximately 21 km north of the terminus of the Toe Drain, is designed to trap water during flood tides, for use by the agricultural water users and the wildlife area (Figure 1). Consequently, the weir significantly affects the hydrology of the Toe Drain during low-flow periods.

Sample Collection

During 2011–2014, as part of the Yolo Bypass Fish Monitoring Program (Frantzich et al. 2013), we collected year-round lower trophic data every other week from the lower Yolo Bypass (STTD) and Sacramento River (SHR) (Figure 1). In 2013 and 2014, we collected additional water samples weekly during August to October along a north-to-south transect from the upper Yolo Bypass at Ridge Cut Slough (RCS) south to the Rio Vista Bridge (RVB) on the lower Sacramento River (Figure 1). For the purposes of this study, we divided the sampling transect into five distinct regions based on differences in key habitat attributes between sites. These regions included:

- Colusa Drain/Knights Landing Ridge Cut (RCS)
- Central Yolo Bypass (KNA, WWT, RD22, DWT, I80)
- Lower Yolo Bypass (LIS, STTD)
- Cache Slough Complex (BL5, LIB, RYI), and
- Sacramento River near Rio Vista (SRV, RVB).

Two separate crews sampled all stations on the same day.

Typically, we collected abiotic measurements and biological samples mid-morning, and sampled all sites within 24 hours of each other. At each site, we collected water temperature (°C), electrical conductivity ($\mu S\ cm^{-1}$), pH, and dissolved oxygen ($mg\,L^{-1}$) data using a Yellow Springs Instruments (YSI) 556 multi-parameter hand-held instrument. We measured turbidity (NTU) using a HACH 2100Q Portable Turbidity meter, and also collected additional Secchi depth measurements of water transparency (m). We collected water samples near the surface (≤ 1 m) to measure chlorophyll *a* and phaeophytin *a* as indicators of phytoplankton biomass—and to be comparable to long-term monitoring methods and sites. We stored water samples on wet ice (4° C) and filtered them for laboratory analyses the same day using Millipore 47-µm glass-fiber filters preserved with 1% magnesium carbonate. We collected zooplankton samples with a conical plankton net (0.50-m mouth, 2-m length, and 150-µm mesh) held just under the water surface for approximately 5 minutes during the mid- to late morning on an ebb tide. Our collection of zooplankton near surface could have underestimated the quantity and composition because of the known daytime (Kimmerer and Slaughter 2016) and tidal (Kimmerer et al. 2014) vertical migration of copepods, but we wanted to keep collection methods the same to be able to compare samples to long-term collection methods and previous years. We calculated the sample volume using General Oceanic's Model 2030R flow meters mounted in the mouth of the net. We concentrated and preserved zooplankton samples in 10% formalin and later transferred them to 95% ETOH so they could be identified taxonomically. We collected phytoplankton by filling a 50-mL amber glass vial with a portion of the water sample, and preserving it with 4% Lugol's solution to identify, enumerate, and measure cell dimension. We selected specific samples for analysis based on observed peak chlorophyll *a* values that provided evidence of where and when phytoplankton blooms were occurring. We collected water samples for soluble nitrate+nitrite (NO_3 + NO_2), ammonia (NH_4), orthophosphate (PO_4^{3-}), and silica ($Si\ (OH)_2$), and filtered them through Millipore HATF04700 0.45-µm filters and immediately froze them. We measured light irradiance (mole quanta $m^{-2} day^{-1}$) through vertical profiles at four depths determined by 75%, 50%, 25%, and 1% of surface irradiance, using a LICOR 193SA spherical quantum sensor to acquire an average depth-of-light measurement.

For all years, we obtained flow, velocity, and stage measurements in the Yolo Bypass from gauges operated by the California Department of Water Resources (CDWR) below Lisbon Weir (LIS) (*http://cdec.water.ca.gov/*), and we obtained Sacramento River flow measurements from the United States Geological Survey (USGS)-operated gauge at the Freeport Bridge (FPT) (*http://cdec.water.ca.gov/*). The CDWR used an acoustic Doppler current profiler (ADCP) and cross-sectional channel depth measurements to estimate the volume of fall discharge flows in the Yolo Bypass below LIS from August to October. In addition, we acquired continuous water-quality data from YSI 6600 multi-parameter water-quality sondes deployed and operated by the CDWR at SRH and RVB (*http://cdec.water.ca.gov/*) to determine changes in ambient water conditions downstream of the CSC and in the lower Sacramento River (Figure 1).

Analytical Procedures

We determined the concentrations of chlorophyll *a* and the degradation product phaeophytin *a* from the extraction of pigments on glass-fiber filters with 90% aqueous acetone and spectrophotometry (Standard Method 10200H, (APHA 2012). We analyzed the ambient nutrient concentrations using various established U.S. EPA and American Public Health Association (APHA) analysis methods: NO_3+NO_2 (Std. Method 4500-NO3-F Modified), NH_4 (EPA 350.1), PO_4 (EPA 365.1), and $Si(OH)_2$ (EPA 200.7D).

We determined and enumerated phytoplankton composition to at least the genus level using the Utermöhl microscope method (Utermöhl 1958) from samples collected at site LIS. Phytoplankton samples were counted for at least four hundred total algal units, with one hundred units of the dominant taxa. We recorded length measurements in micrometers (µm) on the first 25 units of major phytoplankton taxa and the first 5 units of minor taxa to calculate biovolume ($\mu m^3\ L^{-1}$) from formulas given for different algal shapes by Kellar et al. (1980). Additionally, we sub-sampled zooplankton samples to target up to a total count of 250 mesozooplankton and examined them under a compound microscope to at least the genus level, with taxonomic resolution dependent on species and life stage.

Statistical Analyses

Many of our analyses were simple graphical comparisons of different regions and time-periods. To address possible differences between the tidal slough complex and the Sacramento River (Study Question 1), we used a Mann–Whitney U test to compare the median concentrations of log-transformed chlorophyll *a* and zooplankton data between the Yolo Bypass (STTD) and Sacramento River (SHR). Because chlorophyll and zooplankton data have non-normal distribution with similar right-skewness, we used a non-parametric test. We evaluated the effect of flow on log-transformed chlorophyll *a* concentration and zooplankton densities at STTD and SHR by calculating Pearson correlation coefficients. We used a parametric test because we were comparing two measurable variables, and this test is not overly sensitive to non-normality (Edgell and Noon 1984).

To address variation in physical, chemical, and biological conditions in response to region and flow (Study Question 2), we used a Principal Component Analysis (PCA) for discrete data collected in 2013 and 2014. The PCA determines which physical, chemical, and biological variables explain the most variance between the upper and lower regions of the tidal slough complex before, during, and after the increased fall flows in the Yolo Bypass. All data was log (X+1)-transformed and normalized before PCA was run. The independent variables included: specific conductance (μScm^{-1}), dissolved oxygen (mgL^{-1}), pH, turbidity (NTU), water temperature (°C), chlorophyll *a* (μgL^{-1}), NH_4 (µM-N), NO_3 + NO_2 (µM–N), PO_4^{3-} (µM-P), and Si $(OH)_2$ (µM-Si). To further explain the significant differences in physical and chemical variables between regions, we used analysis of variance (ANOVA) and the Tukey Method to identify which regions grouped together by mean before, during, and after the flow pulse event.

To determine differences in chlorophyll *a* and zooplankton (i.e., adult calanoid copepod adults) between the tidal slough complex and other tidal slough regions of the Delta (Study Question 3), we compared our results to data collected by the Interagency Ecological Program's (IEP) Environmental Monitoring Program (EMP), Zooplankton Study (*http://www.water.ca.gov/bdma/*). The EMP sampling stations were grouped into four geographical regions: Suisun, west Delta, central Delta, and south and east Delta, based on proximity and similar habitat type (Figure 2). We used the summer and fall monthly data collected at the three sites within each region to create a monthly regional mean chlorophyll *a* concentration and adult calanoid copepod densities for each year. We then log(X+1)-transformed and analyzed the data using analysis of similarities (ANOSIM) to determine the significant difference between fall and summer chlorophyll *a* levels and adult calanoid copepod densities to the Yolo Bypass (STTD). We used the non-parametric ANOSIM analysis as an alternative to a one-way ANOVA because of the non-normal distribution of the log(X+1)-transformed chlorophyll *a* and zooplankton

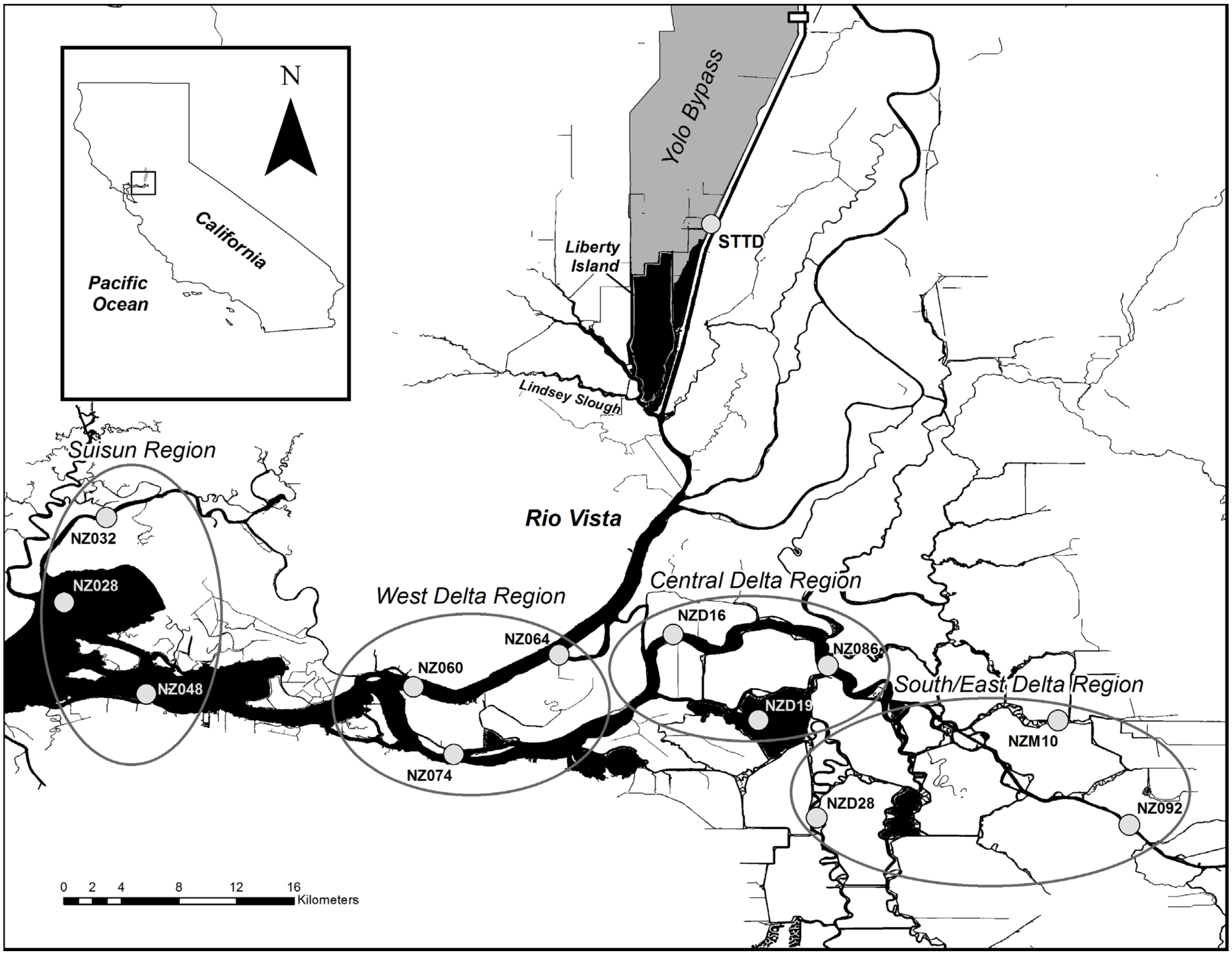

Figure 2 Map of IEP EMP Zooplankton Study sites in the Sacramento–San Joaquin Delta. The four different Delta regions are circled and those EMP sites within those regions were used to create representative mean summer and fall chlorophyll *a* and adult calanoid copepod densities to compare to the Yolo Bypass (site STTD).

data sets. We completed the univariate statistical analyses using Minitab 16 software (Minitab 16 Statistical Software 2010), and computed the multivariate analysis (PCA and ANOSIM) using PRIMER-E version 7 software (v7 2015).

RESULTS

Abiotic Conditions

Hydrograph

The measured flow conditions within the Sacramento River during the summer and fall followed typical seasonal trends, with flow conditions varying considerably among the years (Figure 3A). The general trend was a decrease in flow in each progressing year, as California experienced severe drought and record-low precipitation in 2013 and 2014. In 2011, a significant winter pulse flow in the Sacramento River and smaller west-side tributaries (i.e., Cache Creek and Putah Creek) resulted in the inundation of the Yolo Bypass floodplain (Figure 1). In 2012, 2013, and 2014, there were insufficient Sacramento River or tributary flows to provide considerable floodplain inundation. Flow pulses occurred in all years during the late summer and fall in the Toe Drain (Figure 3A and Figures 4A–4D). During July and August, the period of peak local water diversions, flows in the Toe Drain below Lisbon Weir were net negative (meaning flowing in an “upstream” direction after the tidal flow component was statistically removed; more precisely, the flood

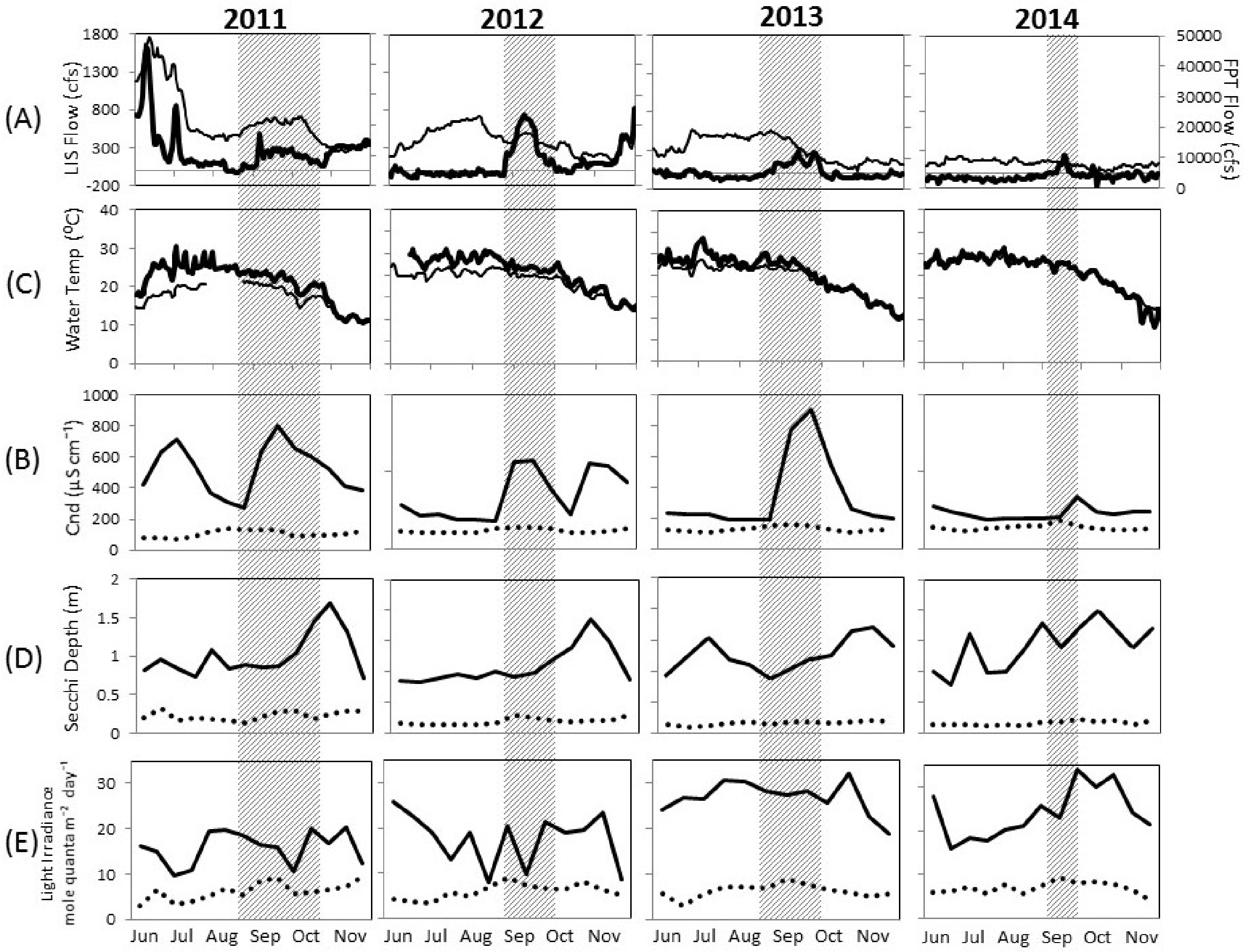

Figure 3 Physical conditions of Yolo Bypass (dark black line) and Sacramento River (fine black line and dotted line) during the months of June through November of: 2011, 2012, 2013, and 2014. The variables from top to bottom: (a) mean daily flow (cfs); (b) water temperature (°C); (c) electrical conductivity (μS cm^{-1}); (d) Secchi depth (m); (e) light irradiance (mole quanta m^{-2} day^{-1}) in the euphotic zone. Shaded area indicates increased flows in Yolo Bypass due to agricultural drainage.

tide was stronger than the ebb tide as a result of water withdrawal). With increased agricultural drainage flows in late August and early September, there was a subsequent switch to net positive flows (Figure 3A and Figures 4A–4D). The total estimated discharge volume in late summer and fall in 2011 (30 million m^3; 1.1 billion ft^3) and 2012 (33.6 million m^3; 1.2 billion ft^3) was substantially greater than any of the subsequent years measured because 2013 and 2014 discharge volumes were 14.1 and 3.1 million m^3 (5 and 1.1 million ft^3), respectively (Figures 4A–4D).

Water Quality in Sacramento River versus Yolo Bypass

In all years, the water temperatures for the Sacramento River (SHR) and Yolo Bypass (STTD) followed typical summer and fall seasonal trends and closely tracked one another. However, the Yolo Bypass (STTD) observed greater variability (standard deviaton 5.01 °C) and higher maximum water temperatures (up to 30.5 °C) in the high-flow year (2011) than in the drier 2012, 2013, and 2014 water years (Figure 3B). The Yolo Bypass consistently maintained a higher daily mean

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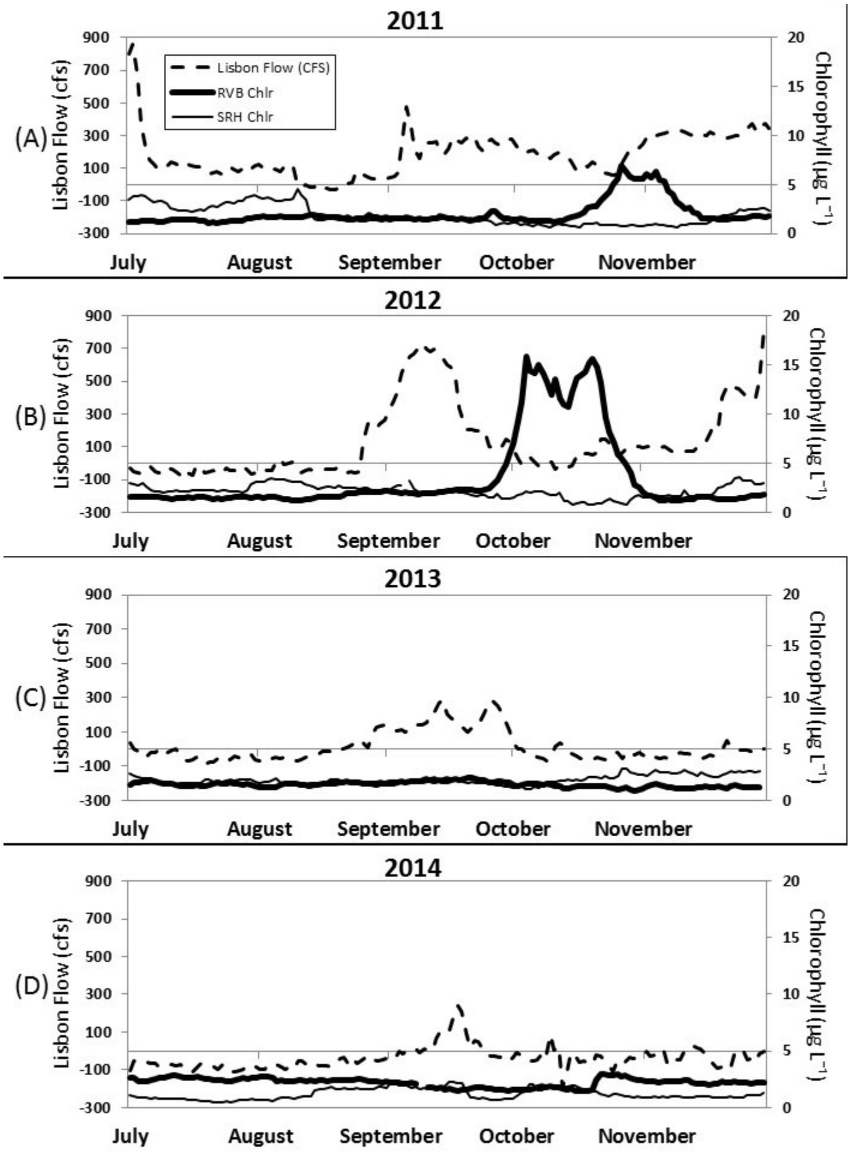

Figure 4 2011–2014 Daily average continuous chlorophyll (μg L^{-1}) from Sacramento River at Hood (SRH), Sacramento River at Rio Vista Bridge (RVB) and Lisbon (LIS) mean daily flow (cfs)

temperature of 20.8 °C compared to the Sacramento River at 19.1 °C in all years (Figure 3B). Electrical conductivity was also considerably higher in the Yolo Bypass throughout the summer and fall, with a mean of 364 μScm^{-1} compared to the Sacramento River at 123 μScm^{-1}. The electrical conductivity in the Yolo Bypass closely followed the changes in flow, and in most years reached maximum values > 800 μScm^{-1} in early September (Figures 3A, 3C). The mean Secchi depth of the Yolo Bypass was substantially lower in all years, at a mean depth of 0.19 m compared to the Sacramento River at 1.18 m (Figure 3D). In addition, mean total light irradiance in the euphotic zone for the Yolo Bypass was consistently lower than that in the Sacramento River, at a mean of 6.35 mole quanta m^{-2} day^{-1}, and maintained a low standard deviation of 1.64 mole quanta m^{-2} day^{-1} throughout the summer and fall. In comparison, the Sacramento River had a mean of 20.92 mole quanta m^{-2} day^{-1}, with a standard deviation of 6.55 mole quanta m^{-2} day^{-1} (Figure 3E). During September of each year, the mean total light

Table 1 Mean abiotic and biological measurements (2013 and 2014) for August–October from the following regions: Colusa Drain–Ridge Cut Slough (site RCS), central Yolo Bypass (sites KNA, I80, RD22), lower Yolo Bypass (sites LIS, STTD), Cache Slough Complex (sites BL5, LIB, RYI), and lower Sacramento River (sites SRV, RVB). Ranges and standard deviations of mean are in parentheses.

Region	**Water Temp (°C)**	**Elect. Cnd** ($\mu S\,cm^{-1}$)	**Turbidity (NTU)**	**DO** ($mg\,L^{-1}$)	**pH**	**Chl *a*** ($\mu g\,L^{-1}$)
Colusa Drain–Ridge Cut Slough	20.5 (15.6-25.6, 3.0)	534 (460-682, 53.2)	36.7 (24.2-62.1, 8.2)	6.91 (2.63-12.40, 2.1)	7.90 (7.20-8.58, 0.35)	20.1 (3.5-49.6, 12.8)
Central Yolo Bypass	20.3 (15.1-25.8, 2.7)	666 (453-1004, 132.6)	40.2 (10.5-70.3, 14.8)	6.51 (3.58-11.71, 1.7)	7.95 (7.21-8.55, 0.23)	20.4 (3.9-152.5, 23.7)
Lower Yolo Bypass	20.6 (15.9-23.8, 2.1)	442 (186-952, 267.4)	62.6 (34.1-203, 31.3)	7.52 (4.52-9.41, 1.2)	7.80 (6.49-8.64, 0.47)	13.4 (3.7-37.6, 7.2)
Cache Slough Complex	20.2 (16.1-23.5, 1.7)	182 (139-358, 34.0)	13.4 (0.73-50.5, 10.4)	8.90 (3.83-10.32, 0.9)	7.41 (6.49-8.91, 0.48)	3.5 (1.2-10.6, 2.1)
Sacramento River near Rio Vista	21.0 (16.6-24.2, 2.0)	184 (100-608, 72.5)	5.8 (1.63-17.30, 2.8)	8.63 (7.12-9.45, 0.5)	7.23 (6.38-8.02, 0.36)	2.2 (1.0-5.6, 1.0)

Table 2 Mean nutrient concentrations (2013 and 2014) for August–October by region. Ranges are in parentheses.

Region	**NH_4** (μM)	**$NO_3 + NO_2$** (μM)	**DIN** (μM)	**PO_4** (μM)	**$Si(OH)_2$** (μM)	**n : P**
Colusa Drain–Ridge Cut Slough	1.49 (0.55-6.87)	0.90 (0.09-2.94)	2.39 (0.65-7.47)	0.78 (0.42-1.16)	368 (284-445)	4 (1-9) [a]
Central Yolo Bypass	2.20 (0.55-15.02)	8.94 (0.09-35.27)	11.14 (0.75-35.83)	2.31 (0.22-6.21)	379 (203-487)	9 (1-22)
Lower Yolo Bypass	1.61 (0.09-8.07)	1.33 (0.55-7.37)	2.94 (0.65-10.99)	1.49 (0.32-4.20)	339 (256-482)	3 (<1-14) [a]
Cache Slough Complex	5.74 (0.55-14.52)	2.06 (0.09-4.58)	7.79 (0.65-18.01)	0.80 (0.59-1.48)	303 (263-335)	10 (1-19)
Sacramento River near Rio Vista	12.35 (4.82-36.59)	2.71 (0.69-5.03)	15.06 (7.32-39.93)	0.79 (0.58-1.08)	310 (117-413)	15 (9-25) [b]

a. Indicates regions of nitrogen limitation based on N : P ratio
b. Indicates regions of phosphorus limitation based on N : P ratio

irradiance for the Yolo Bypass increased by 1 to 2 mole quanta $m^{-2}\,day^{-1}$ with enhanced agricultural flows, increasing the depth of light availability in the photic zone.

Tidal Slough Regional Patterns

Discrete physical water measurements collected throughout the five distinct regions (Figure 1) during 2013 and 2014 showed that water temperatures during the study period of August–October ranged from 15.1 °C to –25.8 °C (Table 1). The mean water temperatures between regions before, during, and after the flow pulse were not significantly different (ANOVA $p > 0.05$) in both years. The warmest measured water temperatures occurred before the flow pulse in August of both years, with the upper regions of Colusa Drain Ridge/Cut and central Yolo Bypass experiencing the highest and lowest water temperatures (Table 1). Electrical conductivity and turbidity were both significantly different between regions (ANOVA $p > 0.05$) before, during, and after flow pulses. The central Yolo Bypass exhibited the highest measured values of electrical conductivity, with values decreasing in downstream regions (Table 1). In 2013, with higher agricultural discharge volumes, electrical conductivity subsequent increased, and turbidity in downstream regions decreased after the flow pulse, because mean values were not significantly different (Tukey test $p > 0.05$) between the regions above Lisbon Weir and the lower Yolo Bypass region (Figure 1). In addition, PCA results for PC axes 1 and 2, explaining the total variation of physical variables between regions for both years, found strong positive correlations with electrical conductivity (PC1: 0.429 and 0.434) and turbidity (PC1: 0.401 and 0.279) (PC2: 0.208 and 0.487) (Figure 5). The pH levels were highest in the central Yolo Bypass, with significant differences (Tukey test $p > 0.05$) observed between upper study regions and the downstream CSC and lower Sacramento River after flow pulses. The pH levels had a strong and positive correlation in both years for PC axes 1 (0.356 and 0.304). Dissolved oxygen concentrations were significantly different between regions (ANOVA $p > 0.05$), with the lowest mean concentrations and highest fluctuations in the uppermost regions of Colusa Drain–Ridge Cut Slough and the central Yolo Bypass before and during the flow pulses (Table 1).

Water samples collected and analyzed for chemical analyses throughout the five regions (Figure 1)

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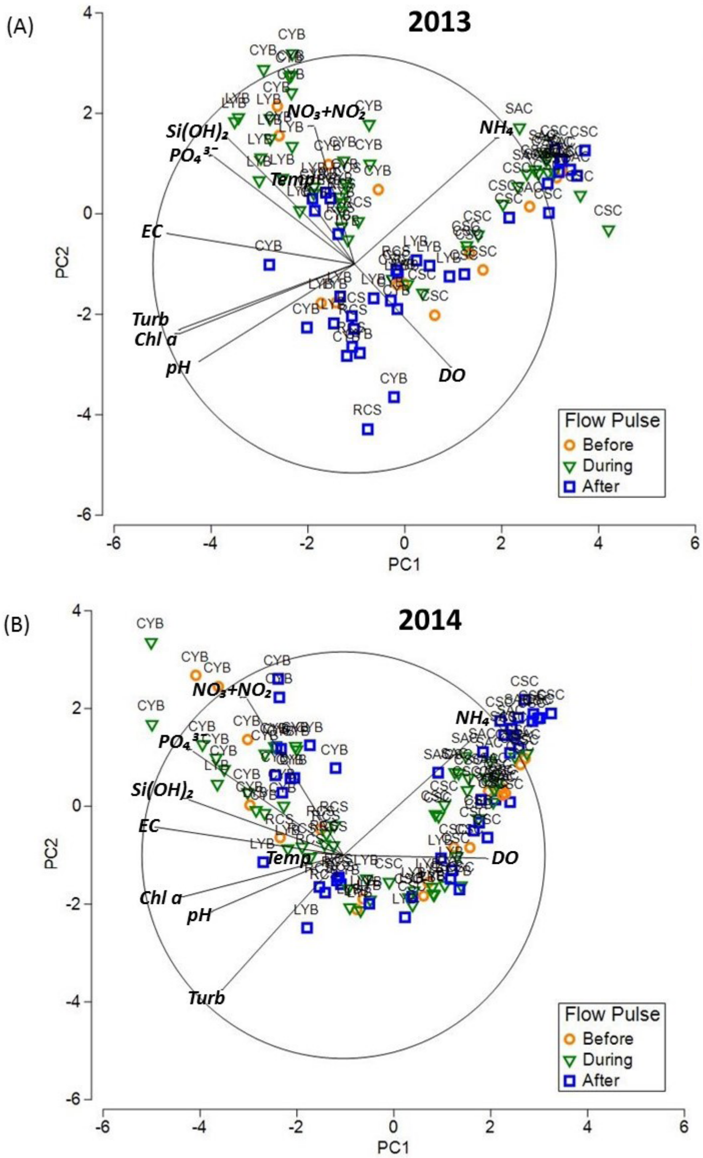

Figure 5 2013 and 2014 PCA ordination diagrams. Orange circles, green triangles, and blue circles represent water samples (2013, n = 95 and 2014, n = 117) collected before, during and after Yolo Bypass fall agricultural flow pulses. The vectors point in the direction of maximal variation between environmental variables by sampling region, and lengths are proportional to the total contribution in variance.

during 2013 and 2014 showed that DIN, PO_4, and $Si(OH)_4$ concentrations were significantly different among regions (ANOVA $p > 0.05$). The lowest nitrogen concentrations were in the uppermost Colusa Drain–Ridge Cut Slough region and the lower Yolo Bypass. Both regions had low N:P ratios, indicating nitrogen as a potential limiting nutrient for phytoplankton growth (Table 2, Figure 6). The highest concentrations of $NO_3 + NO_2$, PO_4, and $Si(OH)_2$ were in the central Yolo Bypass. This region had exceptionally high nitrogen inputs from wastewater treatment plant discharges, with $NO_3 + NO_2$ concentrations from site WWT at > 209 μM-N, and high mean NH_4 concentrations of 67.1 μM-N at site DWT. Both sites also had high levels of PO_4 with WWT values > 14.11 μM-P and DWT values >25.69 μM-P (Table 2; Figure 6). This region had a significant mean difference in both $NO_3 + NO_2$ and PO_4 concentrations from all other regions before, during, and after the flow pulse (Tukey test $p > 0.05$). The $NO_3 + NO_2$ and PO_4 concentrations for the lower Yolo Bypass elevated marginally during the rice-field drainage flows in September, with concentrations being much higher during the higher discharge flows in 2013 (Table 2, Figure 6). The CSC and lower Sacramento River regions had no significant difference (Tukey test < 0.05) in mean concentrations of DIN, PO_4, and $Si(OH)_2$. However, NH_4 concentrations and N : P ratios increased as sites within these regions progressed downstream (Table 2, Figure 6). The Sacramento River region had the highest mean N : P ratio, which indicated P may be a limiting nutrient. The PCA results for axes 1 and 2 that explain the total variation of chemical variables between regions before, during, and after the flow pulse for both years found strong positive correlation (0.323 and 0.349) with PO_4 in PC1, and strong negative correlation with $NO_3 + NO_2$ (-0.439, -0.569) and NH_4 (-0.400, -0.424) in PC2 (Figure 5).

Biotic Conditions

Chlorophyll a

In all years, the chlorophyll *a* levels in the summer and fall were significantly higher ($p < 0.001$) in the Yolo Bypass (site STTD) than in the adjacent Sacramento River (site SHR) (Figure 7A, Table 3). The chlorophyll *a* levels in the Yolo Bypass

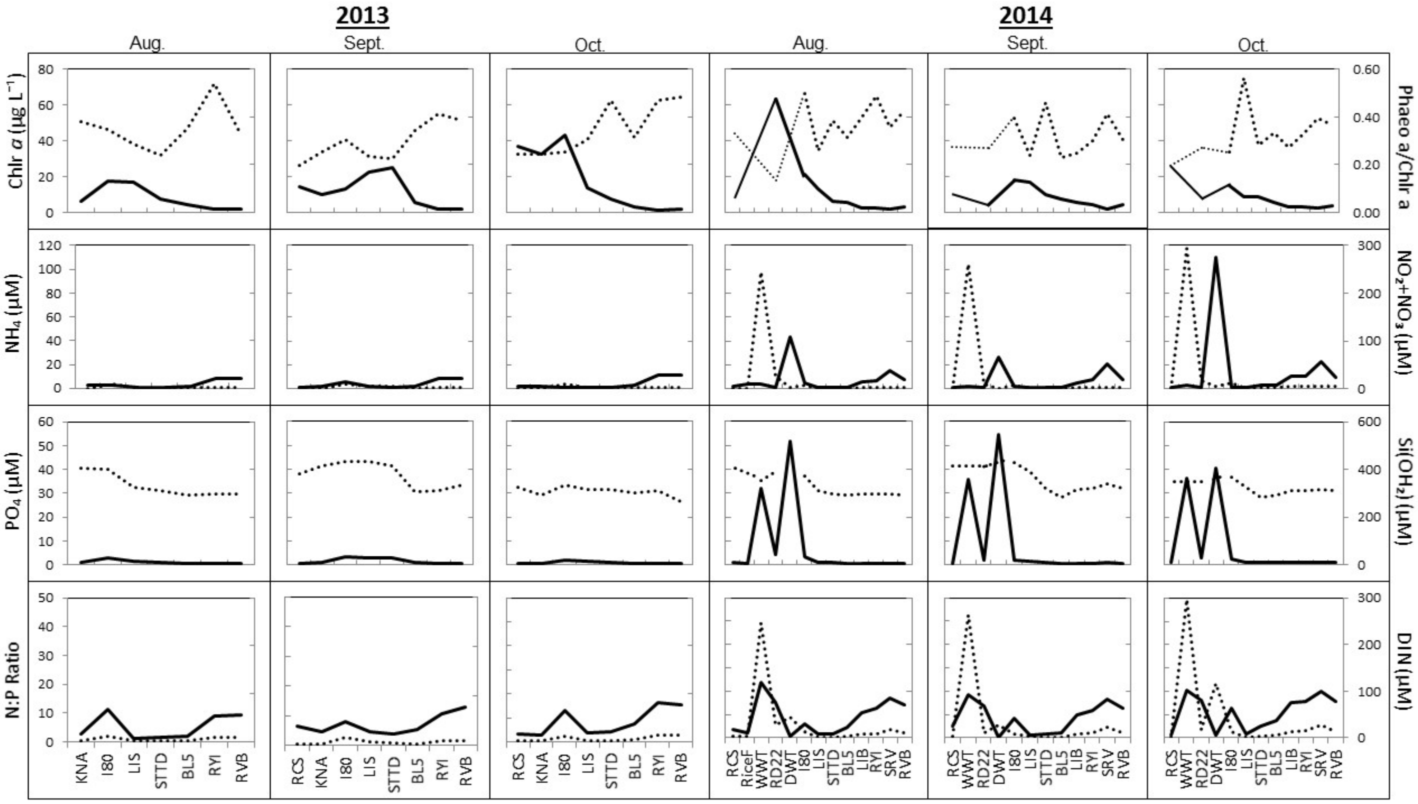

Figure 6 Monthly mean nutrient and chlorophyll *a* concentrations along a north to south transect of sampling sites from Yolo Bypass to lower Sacramento River at Rio Vista during August through October 2013 and 2014. The dark lines represent parameters aligned with the left (vertical) y-axis. The dotted lines represent parameters aligned with the right (vertical) y-axis.

increased each year during the month of September (Figure 7A). There was a significant ($p<0.001$) relationship between flow and chlorophyll *a* for the Sacramento River in the summer and fall; Yolo Bypass chlorophyll *a* showed a positive relationship with flow but was not statistically significant (Table 4). In 2011 and 2012, major increases in chlorophyll *a* during late summer–fall in the Yolo Bypass (Figure 7A) were followed several weeks later by increased chlorophyll *a* in the downstream reach of the Sacramento River at Rio Vista (Figures 4A, 4B). Of the years studied, these 2 years had the highest seasonal flow pulses through the region (Figures 4A–4D).

Zooplankton Community

In all years, *Bosmina* (89% of the cladoceran in number m^{-3}), *Pseudodiaptomus forbesi* (57% of calanoid copepod adults), and *Sinocalanus doerrii* (42% of calanoid copepod adults) dominated the Yolo Bypass zooplankton community. In the Sacramento River, calanoid copepod adults were composed predominately of *Diaptomidae* spp. (32%), *Osphranticum labronectum* (29%), and *Sinocalanus doerrii* (19%). The Sacramento River cladoceran composition was more diverse than that of the Yolo Bypass, with *Bosmina* (39%), *Ceriodaphnia* (25%), *Daphnia* (18%), and *Chydorus* (15%) as the dominant species. There were significant differences in the densities of both calanoid copepod adults ($p<0.001$) and cladocerans ($p=0.0013$) between the Yolo Bypass and Sacramento River, with the Sacramento River having lower densities (Table 3, Figures 7A, 7B). Summer and fall flows were significantly correlated ($p=0.001$) with adult calanoid copepod abundance in the Yolo Bypass, but, in the Sacramento River for the same period, flow did not correlate with adult

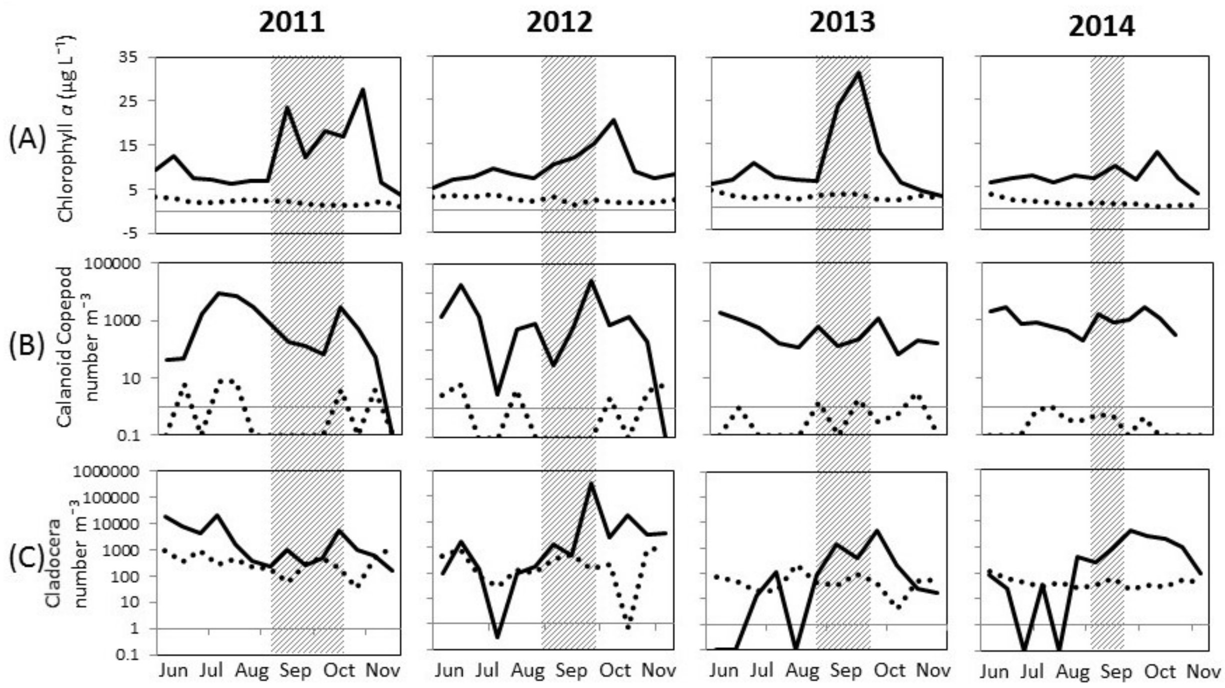

Figure 7 Trends in lower trophic levels in the Yolo Bypass (solid black symbols) and Sacramento River (clear black symbols) during May through November of 2011, 2012, 2013, and 2014. The variables from top to bottom are: (a) chlorophyll *a* ($\mu g\ L^{-1}$); (b) density of calanoid copepod adults (number m^{-3}); (c) density of cladocerans (number m^{-3}). Note that 0.1 = 0 density for copepods and cladocerans. The highlighted portions of the flow graphs represent the summer and fall increased rice field drainage flows in the Yolo Bypass.

Table 3 Results of Mann–Whitney sign tests ($P > 0.05$) comparing levels of different organisms in the Yolo Bypass (STTD) and Sacramento River (SHR) for all years combined (June–November 2011–2014)

Biological data	Z	N	P
Chloropyll *a*	−8.48	50	<0.0001
Calanoid copepod adults	−8.15	50	<0.0001
Cladocera	−3.21	50	0.0013

calanoid copepod abundance (Table 4). For each year, the densities of both cladocerans and calanoid copepod adults in the Yolo Bypass increased during October. We observed the increased zooplankton densities after increases in Yolo Bypass agricultural flows and increased chlorophyll *a* concentrations (Figures 7B, 7C). Specifically, in October 2012, we saw exceptional densities of both cladocerans and copepods adults, with *Bosmina* (301,067 m^{-3}) and *Pseudodiaptomus forbesi* (17,369 m^{-3}) as the dominant taxa.

Tidal Slough Regional Patterns

In 2013 and 2014, biological conditions within the ecosystem from north to south varied much like the abiotic conditions. The chlorophyll *a* concentrations between all regions in both years before, during, and after flow pulses were significantly different (ANOVA $p > 0.05$). In addition, PCA results for PC axes 1 and 2 (Figure 5) – representing the total variation of physical, chemical, and biological conditions between regions for both years – showed strong positive correlations with chlorophyll *a* on PC1 (0.402, 0.370) and moderate correlations on PC 2 (0.223, 0.150). The mean phaeophytin *a*:chlorophyll *a* ratios were lower in the upper regions and increased with distance downstream.

The Colusa Drain/Knights Landing Ridge Cut region had high mean chlorophyll *a* concentrations, but concentrations were lower before the agricultural drainage flows ($\leq 11\ \mu g\ L^{-1}$) and elevated after flow pulses, because October mean concentrations were $40\ \mu g\ L^{-1}$ (Figure 6). The central Yolo Bypass

Table 4 Correlations between flow and biological data in the Yolo Bypass and Sacramento River for all years (June–November 2011–2014). Pearson correlation coefficients are shown with the number of observations and P-values in parentheses.

Biological data	Sacramento River (SHR)	Yolo Bypass (STTD)
Chloropyll *a*	0.506 (n = 50, < 0.001)	0.235 (n = 50, 0.097)
Calanoid copepod adults	0.244 (n=50, 0.087)	−0.443 (n=50, 0.001)
Cladocera	0.429 (n = 50, 0.002)	0.170 (n = 50, 0.233)

Table 5 Organism counts of dominant phytoplankton in samples collected during elevated flows and chlorophyll *a* in Yolo Bypass on September 8, 2013, and September 18, 2014. The collection periods were selected based on high chlorophyll *a* values in lab-analyzed samples.

Year	Station	Species	Organisms mL^{-1}
2013	LIS	*Thalassiosira* spp. (diatom)	2,577
		Aulacoseira spp. (diatom)	463
		Trachelomonas spp. (flagellate)	152
		Assorted other diatoms (*Nitzschia, Synedra, Cocconeis, Cyclotella*)	18–205
		Assorted other greens (*Crucigeniella, Scenedesmus, Chlamydomas*)	53–71
		Assorted other flagellates (*Kephyrion, Stromobomonas, Pseudokephyrion*)	4–36
2104	LIS	*Thalassiosira* spp. (diatom)	7,311
		Aulacoseira spp. (diatom)	1,711
		Rhodomonas spp. (green)	817
		Assorted other diatoms (*Cyclotella, Nitzschia, Amphora, Cocconeis*)	78–233
		Assorted other greens (*Chlorella, Crucigeniella, Scenedesmus*)	411–583

mean chlorophyll *a* concentrations were the highest compared to all other regions, but concentrations were highly variable at the sites directly below the wastewater treatment discharge (Figure 1, Figure 6). The lower Yolo Bypass chlorophyll *a* concentration was moderate, elevating in both years during increased agricultural discharge flows in September (Figure 6). In 2013, with higher agricultural discharge volumes, the mean concentrations of chlorophyll *a* substantially increased in the lower Yolo Bypass region compared to the central Yolo Bypass, resulting in a significant mean difference between regions. We analyzed samples from the lower Yolo Bypass for phytoplankton composition and densities during elevated chlorophyll *a* and high discharge flows at LIS below Lisbon Weir. In both years, the centric diatom *Thalassiosira* spp. dominated the phytoplankton community (Table 5). The composition in both years was predominantly diatoms, with 88% in 2013 and 80% in 2014. Flagellates made up a very small amount of the overall biomass in both years, with only 5% in 2013 and 0.6% in 2014.

The lower CSC and Sacramento River regions were characterized by low chlorophyll *a* concentrations and did not have a significant mean difference (Tukey test $p < 0.05$) before, during, or after the flow pulse. The highest chlorophyll *a* concentrations in both years were measured in late September in Prospect Slough (site BL5) after the LIS flow gage (Figure 6) measured peak flows. In 2014, the CSC region had no significant mean difference (Tukey test $p < 0.05$) from the lower Yolo Bypass region during the flow pulse. The elevated mean chlorophyll *a* concentration in both the lower Yolo Bypass and the upper site in the CSC region suggests that the fall flows observed in 2013 and 2014 transported phytoplankton and may have stimulated local phytoplankton production downstream of the Toe Drain.

Comparisons to Other Tidal Regions of the Delta

From 2011 to 2014, the Yolo Bypass (site STTD) showed significantly higher average chlorophyll *a* concentrations in the summer and fall compared with the Suisun, west Delta, central Delta, and south and east Delta regions (ANOSIM $p < 0.05$) (Figures 2, 8). The chlorophyll *a* concentrations ranged from 31.40 $\mu g\,L^{-1}$ to 2.56 $\mu g\,L^{-1}$ in the Yolo Bypass, 44.32 $\mu g\,L^{-1}$ to 1.03 $\mu g\,L^{-1}$ in Suisun, 61.30 $\mu g\,L^{-1}$ to 0.77 $\mu g\,L^{-1}$ in the west Delta, 11.11 $\mu g\,L^{-1}$ to 0.74 $\mu g\,L^{-1}$ in the central Delta, and 18.20 $\mu g\,L^{-1}$ to 0.88 in the south and east Delta. The west Delta region (site NZ064, Figure 2) showed an exceptionally high chlorophyll *a* concentration ($>60\,\mu g\,L^{-1}$) on October 8, 2012 after the Yolo Bypass high agricultural discharge flows. The

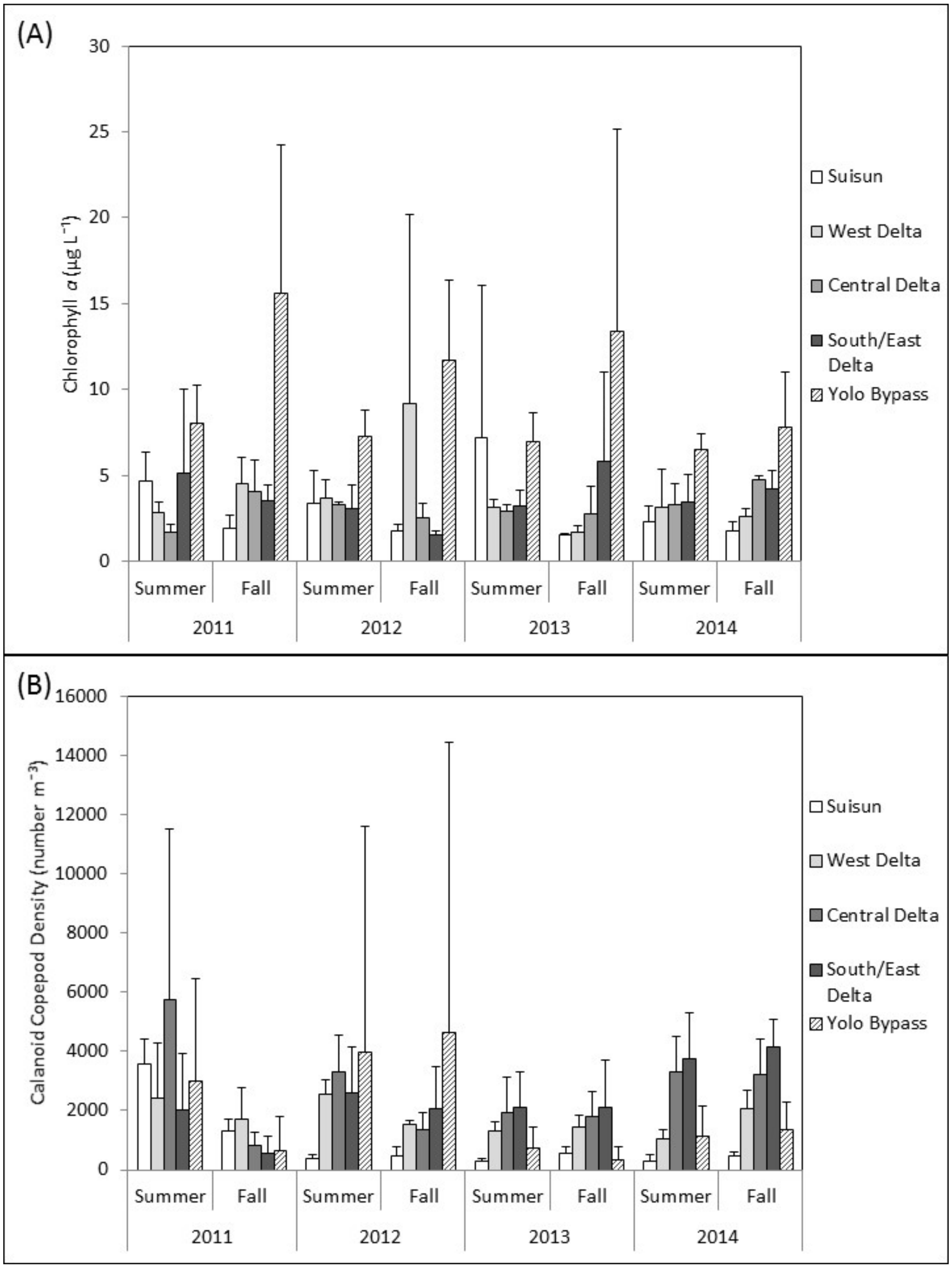

Figure 8 Summer and fall mean chlorophyll *a* ($\mu g\ L^{-1}$) and adult calanoid copepod density (number m^{-3}) for different Delta regions and Yolo Bypass (site STTD). Error bars show one standard deviation.

summer and fall mean densities of adult calanoid copepods in the Yolo Bypass were significantly different compared to other tidal regions in the Delta (ANOSIM $p < 0.05$). The adult calanoid copepod densities showed more variability than chlorophyll *a* among all years, and average densities were lower than all regions except Suisun during the lower-flow years of 2013 and 2014 (Figure 8). The October 2012 mean fall adult calanoid copepod densities were higher in the Yolo Bypass than in all other regions after the unprecedented fall agricultural discharge flows, with densities >24,000 m^{-3}. Comparable fall 2012 samples from Suisun ranged from 397 m^{-3} to 1,275 m^{-3}, in the west Delta from 607 m^{-3} to 2,297 m^{-3}, in the central Delta from 850 m^{-3} to 2,920 m^{-3}, and in the south and east Delta from 1,457 m^{-3} to 4,944 m^{-3}.

DISCUSSION

Our study was designed to characterize regional variability within CSC (Study Question 2), and to examine potential differences between the CSC and Sacramento River (Study Question 1) and other parts of the Delta (Study Question 3). Our results suggest that the habitat variability in the CSC allows it to retain many positive attributes of a freshwater tidal slough complex despite its substantial channel alterations. For example, the region showed different physical and biological conditions than the large, relatively homogenous Sacramento River channel (Study Question 1). The CSC also had complex regional nutrient dynamics that were influenced by local effluent discharge, tidal mixing, and flow (Study Question 2). Chlorophyll *a* and zooplankton in the tidal sloughs we studied responded strongly to return flow inputs. The tidal slough complex generated higher levels of food web organisms (e.g., chlorophyll *a*, zooplankton) than some other regions of the Delta (Study Question 3). The 2012 results were especially notable, because an unusually large flow pulse through the tidal slough complex appears to have contributed to a rare fall phytoplankton bloom in the lower Sacramento River and western Delta. These results have important implications for our understanding of the functioning of freshwater tidal habitat, its potential to contribute production to adjacent open-water areas, and for the development of management actions to improve estuarine food webs.

Physical Conditions

The physical characteristics within the uppermost reaches of the study area (Colusa Drain–Ridge Cut Slough region and upper regions of the Yolo Bypass Toe Drain) fit many of the key attributes found in other productive shallow-water and predominantly autotrophic habitats (Cloern 2007; Robinson et al. 2014). There was substantial regional variability, with higher water temperature, conductance, turbidity, and pH in the upper regions compared to the lower regions. The upper reaches of our study area also had periodically low dissolved oxygen values during morning hours, which could be attributed to a combination of increased phytoplankton respiration at night, higher water temperatures, and slower water movement. The lower regions of the Yolo Bypass, below Lisbon Weir, differed in various physical characteristics, predominantly from strong tidal exchange with downstream water sources from flooded islands and channel habitats in the CSC and the lower Sacramento River.

The high turbidity we observed in the Yolo Bypass and the CSC is consistent with previous studies of the region (Morgan–King and Schoellhamer 2013) that have determined that this region has a landward flux of high-sediment concentrations locally during low-outflow periods. Moreover, turbidity determines the depth of the euphotic zone, an important factor controlling estuarine primary production (Cloern 1987, 1991; Wilkerson et al. 2006; Dugdale et al. 2007). For phytoplankton growth, the Yolo Bypass and the CSC appear to be a light-limited system throughout the summer and fall, a finding consistent with previous studies in other seasons (Lehman et al. 2008).

Nutrient Dynamics

We saw strong regional variation in nutrients along our sampling transect from Colusa Drain downstream through the tidal slough complex (Table 2, Figure 6). Overall, the data for the season we studied suggest that nutrient patterns in the region are driven by a complex interaction between inputs from agriculture and wastewater treatment plants, and tidal inputs from downstream areas.

Role of Agricultural Inputs

Since the upper part of the study area has substantial agricultural land use, we expected that our northernmost sites would have high levels of nutrients associated with agricultural practices. However, nutrient levels in the northern region were not substantially different from those in other regions. For example, PO_4 did not show a strong longitudinal gradient. Note, however, that PO_4 was not limiting throughout any of the sampling sites, with concentrations >0.32 µm-P (Jassby 2005; Lehman et al. 2008). A more surprising result was that nitrogen concentrations were low in the Colusa Drain–Ridge Cut Slough region, and at the Upper Yolo Bypass rice field outflow (site Rice Field), compared to the rest of the study area. Before increased rice field discharge flows, nitrogen concentrations in the upper sampling sites (RCS, KNA, and Rice Field) near Colusa Drain were frequently near or below the limiting value of 0.65 µm-N (Jassby 2005; Lehman et al. 2008) for DIN. Consequently, the low concentrations of N within the uppermost region of the Yolo Bypass suggest that demand by local primary productivity surpasses the N supply during much of the summer. These results do not, however, mean that upstream agricultural flow inputs have no effect on nutrient dynamics. We observed subsequent increases in $NO_3 + NO_2$ and PO_4 concentrations at lower tidal slough sites (LIS, STTD, and BL5) after increased rice-drainage flows. These flows redistribute nutrients along the tidal gradient of the region, therefore providing improved conditions for increased local and downstream primary production.

Role of Wastewater Treatment Inputs

The nitrogen concentrations in the central Yolo Bypass region were higher below the Woodland (site WWT) and Davis (site DWT) wastewater treatment discharge points, compared with the Colusa Drain–Ridge Cut Slough region (Table 2; Figure 6). Therefore, we hypothesize that urban wastewater treatment inputs influence nutrient dynamics in the tidal channel network more strongly than agricultural sources. Nutrient conditions throughout the Delta have been considered non-limiting to phytoplankton based on relatively high levels of NO_3 (Schemel and Hager 1986; Kimmerer 2002a; Wilkerson et al. 2006), and studies have only extremely rarely observed nutrient limitation in the Delta as a result of prevalent effluent and agricultural discharges (Jassby et al. 2002). The substantial nutrient loading by the Woodland and Davis plants (sites WWT and DWT) appears to highly influence the timing and magnitude of local primary production. Specifically, these effluent water sources alter the availability of nutrients for phytoplankton to assimilate, which in turn affects the overall growth rate (Reynolds 1999; Glibert et al. 2011).

Role of Tidal Inputs

For much of summer and fall, the hydrodynamics of the CSC are driven by tidal flows from the Sacramento River (Morgan–King and Schoellhamer 2013). The influence of these tidal flows appears also to be reflected in the nutrient data. For example, the southernmost sites had much higher concentrations of NH_4, suggesting dispersal from the Sacramento River (Table 2; Figure 6). This NH_4 likely originates near the City of Sacramento, where NH_4 is the primary form of nitrogen the Sacramento Regional Wastewater Treatment Plant discharges (Jassby et al. 2002). The Sacramento River water enriched in NH_4 flows downstream to the confluence with Cache Slough and is then tidally dispersed into the CSC and other regions of the estuary (Dugdale et al. 2012; Parker et al. 2012).

Lower Trophic Levels

Chlorophyll *a*

A key finding from our study was that seasonal chlorophyll *a* concentrations in the CSC and the lower Yolo Bypass were significantly higher than those in the adjacent Sacramento River and other regions of the Delta. In addition, chlorophyll *a* levels increased in association with enhanced agricultural return flows in fall. These observations are consistent with relatively higher Yolo Bypass chlorophyll *a* levels during the winter and spring (Sommer et al. 2004). Note, however, that chlorophyll *a* was negatively correlated to flow during winter flood events, and that phytoplankton blooms occurred as the Yolo Bypass drained. Sommer et al. (2004)

concluded that lower water velocities, higher temperature, and higher residence time within the inundated floodplain improved physical habitat conditions within the Yolo Bypass, aiding in phytoplankton production. The habitat conditions observed in the summer and fall in the tidal channel of the Yolo Bypass also have similar characteristics of long residence time, higher water temperatures, and low water velocities. The shallow channel bathymetry and lower flow rate in our study area therefore fits the "Slower is Greener" and "Shallower is Greener" model (Lucas and Thompson 2012), which has been observed in the San Francisco Estuary (Jassby 2005; Ahearn et al. 2006) and in other estuaries (Howarth et al. 2000; Paerl and Huisman 2008; Bukaveckas et al. 2011). Moreover, there appears to be some potential for this productivity to subsidize downstream habitats as suggested by up to 5-fold increases in Rio Vista total chlorophyll after the fall 2011 and 2012 flow pulses through the Yolo Bypass and the CSC (Figures 4A, 4B). Hence, the CSC intermittently serves as a donor habitat for the downstream food web (Polis et al. 1997; Cloern 2007) during both flood recession (Sommer et al. 2004; Lehman et al. 2008) and, at times, during increased summer and fall outflow conditions.

Nutrients also play a strong role in phytoplankton production in the tidal slough complex. During summer and fall, the key inputs include agricultural flows, wastewater discharge, and tidal flows. This pattern is consistent with results during winter and spring flood periods, when a strong relationship was observed between local discharges of nutrients from tributaries and phytoplankton production (Schemel et al. 2004). Most of the primary sources of nutrient inputs to the Toe Drain are located upstream of Lisbon Weir, and the export of those nutrients requires adequate net downstream flow to reach the downstream extent of the CSC. The Lisbon Weir may create a partial nutrient barrier and is likely the cause of periods of lower phytoplankton production at lower sites (LIS, STTD, and BL5) during late summer (July–August), especially in below normal water years. This becomes evident during the extended periods of net negative outflow in the lower Yolo Bypass, when this region experiences minimal nutrient input and high residence time, causing nitrogen concentrations to reach growth-limiting levels for local phytoplankton. The extent of nutrient exchange and phytoplankton production in the CSC during fall therefore depends on tidal inputs of nutrients from the Sacramento River, and the intensity and duration of tributary flows. Our findings comport with Wilkerson et al. (2015) that chlorophyll *a* accumulation is improved with a combination of optimal freshwater flow, improved light, and faster nitrogen uptake with NO_3.

The abundance of diatoms in the CSC is an important observation because phytoplankton communities in the upper estuary have shifted from diatoms to higher proportions of flagellates, cyanobacteria, and chlorophytes (Winder and Jassby 2011). Diatoms are rich in highly unsaturated fatty acids (HUFA), a critical biological compound that is important in maintaining high growth and high reproductive and survival rates for a myriad of aquatic organisms (Brett et al. 1997).

Zooplankton

A notable result was that zooplankton densities for adult calanoid copepods and cladocerans in the Yolo Bypass tidal channels were significantly higher than in the adjacent Sacramento River and other regions of the Delta. These elevated densities were not surprising, because zooplankton are more abundant in areas of the estuary with relatively low flows, high temperatures, and elevated chlorophyll *a* concentrations (Lopez et al. 2006). Moreover, the relatively low densities of zooplankton in the Sacramento River and other parts of the Delta are well documented (Orsi and Mecum 1986,; Sommer et al. 2001b). Hence, our results suggest that the tidal slough complex has at least regional benefits for higher trophic levels. For example, the relatively high levels of *Pseudodiaptomus forbesi* in the CSC is significant, because this copepod has been identified as a dominant summertime food item for Delta Smelt (Nobriga 2002; Slater and Baxter 2014). Our results, therefore, help to support the finding of Hammock et al. (2015) that Delta Smelt growth and nutritional status were higher in the complex freshwater tidal habitats of the CCS than in the downstream Sacramento River or Suisun Bay.

Management Implications

One of the most serious resource-management issues in the San Francisco Estuary is the long-term decline in lower tropic level productivity (Jassby 2008; Winder and Jassby 2011; Cloern and Jassby 2012). The depleted food web has contributed strongly to a long-term collapse of the pelagic ecosystem (Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010). In addition, the declines in several fishes have created a resource-management issue of national significance since the Delta represents a major part of the habitat of the endangered Delta Smelt, while also providing the water supply for 8% of the population of the United States (Service 2007). Conflicts between water supply and species management have therefore led to major efforts to improve the status of state- and federally-listed Delta fishes. The restoration of tidal wetlands has become a major focus of resource managers (Baldwin et al. 2009b), based on an extreme long-term loss of tidal wetland habitat (Nichols et al. 1986; Cloern and Jassby 2012; Whipple et al. 2012). Our study provides insight into both the potential benefits of freshwater tidal sloughs, as well as the importance of flow and nutrient inputs.

Habitat Diversity

The modern Delta supports only 3% of the historical freshwater emergent wetland area, which consisted of a complex network of hundreds of thousands of acres of tidal freshwater wetlands and over a thousand kilometers of tidal sloughs (Whipple et al. 2012). Our results from one of the last remaining freshwater tidal wetland and slough habitats indicate that these regions support some of the ecosystem benefits of the historical Delta landscape. Hence, this study supports the concept that improving habitat diversity through restoration can have regional benefits. Our findings are therefore consistent with the proposal that future landscape restoration and water management will provide the spatial and temporal variability that can help improve ecosystem function and biodiversity (Moyle et al. 2010). It is important to note, however, that restoration of tidal sloughs in the upper estuary will not guarantee enhanced local or regional increases in fish production. There may be scenarios where food web benefits could be undermined by invasive species or contaminants. The San Francisco Estuary, including the Delta, is one of the most invaded estuaries on the planet, with major issues from introduced bivalves, aquatic weeds, and harmful algal blooms (Lucas et al. 2002; Lopez et al. 2006; Brown and Michniuk 2007; Lehman et al. 2010, 2013). At the very least, our work suggests that increasing variation in bathymetry (e.g., by creating a mosaic of shallow water areas like the Yolo Bypass and the CSC), creates a greater potential for improved plankton production (Jassby et al. 2002; Lucas et al. 2002; Lopez et al. 2006; Cloern 2007), improving food web support for the estuary.

Flow and Nutrient Effects

An additional issue for the design of restoration projects is that phytoplankton production appears to rely on complex interactions between different nutrient inputs and flow, which include both upstream and tidal sources. The specific conditions that facilitate algal blooms in complex tidal channels such as our study area are unclear, and require focused field studies and modeling. However, it is likely that a key requirement will be sustained net positive ("downstream") flows in the region. At present, summer and fall flow periods are dominated by net low to negative flows as a result of water diversions in the CSC and the Yolo Bypass (e.g., Figure 3A; Morgan–King and Schoellhamer (2013). Our study provides evidence that enhanced flows could improve the food web contribution of this region. Specifically, a notable finding of our research was that high seasonal flows through the tidal slough complex in 2011 and 2012 aided in a downstream Delta phytoplankton bloom (Figures 4A, 4B). This region of the Delta had not seen fall chlorophyll *a* levels greater than 10 μgL^{-1} for at least 2 decades (Baxter et al. 2015). Hence, these results indicate that restoration actions that include improved channel diversity and flows in freshwater tidal sloughs can provide food web subsidies to adjacent regions of the estuary.

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REFERENCES

Ahearn DS, Viers JH, Mount JF, Dahlgren RA. 2006. Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. Freshwater Biol 51(8):1417-1433. *https://doi.org/10.1111/j.1365-2427.2006.01580.x*

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37(5):946-955. *https://doi.org/10.4319/lo.1992.37.5.0946*

[APHA] American Public Health Association. 2012. Standard methods for the examination of water and wastewater. Washington, D.C.: American Public Health Association.

Attrill MJ, Bilton DT, Rowden AA, Rundle SD, Thomas RM. 1999. The impact of encroachment and bankside development on the habitat complexity and supralittoral invertebrate communities of the Thames Estuary foreshore. Aquat Conserv-Mar Freshw Ecosyst 9(2):237-247. *https://doi.org/10.1002/(sici)1099-0755(199903/04)9:2<237::aid-aqc344>3.0.co;2-s*

Baldwin AH, Barendregt A, Whigham DF. 2009a. Tidal freshwater wetlands—an introduction to the ecosystem. Weikersheim, Germany: Margraf Publishers. p. 2-10.

Baldwin AH, Hammerschlag RS, Cahoon DR. 2009b. Evaluation of restored tidal freshwater wetlands. Amsterdam: Elsevier Science. p. 801-832.

Baxter R, Brown L, Castillo G, Conrad JL, Stevenson JC, Dekar M, Dekar M, Feyrer F, Hunt T, Jones K, et al. 2015. An updated conceptual model of Delta Smelt biology: our evolving understanding of estuarine fish. Interagency Ecological Program, Management, Analysis, and Synthesis Team. Available from: *http://www.water.ca.gov/iep/docs/Delta_Smelt_MAST_Synthesis_Report_January%202015.pdf*

Bennett WA. 2005. Critical assessment of the Delta Smelt population in the San Francisco Estuary, California. San Franc Estuary Watershed Sci 3(2). *https://doi.org/10.15447/sfews.2005v3iss2art1*

Brown LR, Michniuk D. 2007. Littoral fish assemblages of the alien-dominated Sacramento-San Joaquin Delta, California, 1980-1983 and 2001-2003. Estuaries Coasts 30(1):186-200. *https://doi.org/10.1007/BF02782979*

Bukaveckas PA, Barry LE, Beckwith MJ, David V, Lederer B. 2011. Factors determining the location of the chlorophyll maximum and the fate of algal production within the tidal freshwater James River. Estuaries Coasts 34(3):569-582. *https://doi.org/10.1007/s12237-010-9372-4*

Carlton JT, Thompson JK, Schemel LE, Nichols FH. 1990. Remarkable invasion of San-Francisco Bay, (California, USA) by the Asian clam *Potamocorbula amurensis*. 1. Introduction and Dispersal. Mar Ecol-Prog Ser 66(1-2):81-94. *https://doi.org/10.3354/meps066081*

Cebrian J, Valiela I. 1999. Seasonal patterns in phytoplankton biomass in coastal ecosystems. J Plankton Res 21(3):429-444. *https://doi.org/10.1093/plankt/21.3.429*

Cloern JE. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont Shelf Res 7(11-12):1367-1381. *https://doi.org/10.1016/0278-4343(87)90042-2*

Cloern JE. 2001. Annual variations in river flow and primary production in south San-Francisco Bay Estuary (USA). In: Elliott M, Ducrotoy JP, editors. 2001. Estuaries and coasts: spatial and temporal intercomparisons. Proceeding of the 19th Symposium of the Estuarine & Coastal Sciences Association; 1991; University Caen Normandy, Caen France. Olsen & Olsen. p. 91-96. Available from: *https://sfbay.wr.usgs.gov/publications/pdf/cloern_1991_flow.pdf*

Cloern JE. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. Rev Geophys 34(2):127-168. *https://doi.org/10.1029/96rg00986*

Cloern JE. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar Ecol-Prog Ser 210:223-253. *https://doi.org/10.3354/meps210223*

Cloern JE. 2007. Habitat connectivity and ecosystem productivity: implications from a simple model. Am Nat 169(1):E21-E33. *https://doi.org/10.1086/510258*

Cloern JE, Jassby AD. 2012. Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. Rev Geophys 50(RG4001):1-33. *https://doi.org/10.1029/2012RG000397*

Cox TJS, Maris T, Soetaert K, Conley DJ, Van Damme S, Meire P, Middelburg JJ, Vos M, Struyf E. 2009. A macro-tidal freshwater ecosystem recovering from hypereutrophication: the Schelde case study. Biogeosciences 6(12):2935-2948. *https://doi.org/10.5194/bg-6-2935-2009*

Dugdale RC, Wilkerson F, Parker AE, Marchi A, Taberski K. 2012. River flow and ammonium discharge determine spring phytoplankton blooms in an urbanized estuary. Estuar Coast Shelf Sci 115:187-199. *https://doi.org/10.1016/j.ecss.2012.08.025*

Dugdale RC, Wilkerson FP, Hogue VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuar Coast Shelf Sci 73(1-2):17-29. *https://doi.org/10.1016/j.ecss.2006.12.008*

Edgell SE, Noon SM. 1984. Effect of violation of normality on the t–test of the correlation coefficient. Psychological Bull 95:576-583. *https://doi.org/10.1037/0033-2909.95.3.576*

Feyrer F, Newman K, Nobriga M, Sommer T. 2011. Modeling the effects of future outflow on the abiotic habitat of an imperiled estuarine fish. Estuaries Coasts 34(1):120-128 *https://doi.org/10.1007/s12237-010-9343-9*

Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci 64:723-734. *https://doi.org/10.1139/F07-048*

Feyrer F, Sommer T, Harrell W. 2006. Managing floodplain inundation for native fish: production dynamics of age-0 splittail (*Pogonichthys macrolepidotus*) in California's Yolo Bypass. Hydrobiologia 573:213-226. *https://doi.org/10.1007/s10750-006-0273-2*

Frantzich J, Ikemiyagi N, Conrad JL. 2013. 2010-2011 Yolo bypass fisheries monitoring status and trends report. IEP Newsletter [cited 2016 Mar 16]; 26(1):45-52. Available from: *http://www.water.ca.gov/iep/docs/IEP_Vol26_1.pdf*

Glibert PM, Dugdale RC, Wilkerson F, Parker AE, Alexander J, Antell E, Blaser S, Johnson A, Lee J, Lee T, et al. 2014. Major - but rare - spring blooms in 2014 in San Francisco Bay Delta, California, a result of the long-term drought, increased residence time, and altered nutrient loads and forms. J Exper Mar Biol Ecol 460:8-18. *https://doi.org/10.1016/j.jembe.2014.06.001*

Glibert PM, Fullerton D, Burkholder JM, Cornwell JC, Kana TM. 2011. Ecological Stoichiometry, Biogeochemical Cycling, Invasive Species, and Aquatic Food Webs: San Francisco Estuary and Comparative Systems. Rev Fish Sci 19(4):358-417. *https://doi.org/10.1080/10641262.2011.611916*

Grimaldo LF, Miller RE, Peregrin CM, Hymanson ZP. 2004. Spatial and temporal distribution of native and alien ichthyoplankton in three habitat types of the Sacramento-San Joaquin Delta. In: Feyrer F, Brown LR, Brown RL, Orsi JJ, editors. Early life history of fishes in the San Francisco Estuary and watershed. Bethesda, MD: American Fisheries Society. p. 81-96.

Hammock BG, Hobbs JA, Slater SB, Acuna S, Teh SJ. 2015. Contaminant and food limitation stress in an endangered estuarine fish. Sci Total Environ 532:316-326. *https://doi.org/10.1016/j.scitotenv.2015.06.018*

Howarth RW, Swaney DP, Butler TJ, Marino R. 2000. Climatic control on eutrophication of the Hudson River estuary. Ecosystems. 3(2):210-215. *https://doi.org/10.1007/s100210000020*

Jassby AD. 2005. Phytoplankton Regulation in a Eutrophic Tidal River (San Joaquin River, California). San Franc Estuary Watershed Sci 3(1). *https://doi.org/10.15447/sfews.2005v3iss1art5*

Jassby A. 2008. Phytoplankton in the upper San Francisco Estuary: recent biomass trends, their causes, and their trophic significance. San Franc Estuary Watershed Sci 6(1). *https://doi.org/10.15447/sfews.2008v6iss1art2*

Jassby AD, Cloern JE. 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). Aquat Conserv-Mar Freshw Ecosyst 10(5):323-352. *https://doi.org/10.1002/1099-0755(200009/10)10:5<323::aid-aqc417>3.0.co;2-j*

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

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river floodplain systems. In: Dodge DP, editor. Proceeding of the International Large River Symposium; 1989: Canadian Special Publication of Fisheries and Aquatic Sciences. p. 110-127.

Kellar PE, Paulson SA, Paulson LJ. 1980. Methods for biological, chemical, and physical analyses in reservoirs. Lake Mead Limological Research Center, University of Nevada Las Vegas. Tech. Report 5. Available from: *https://digitalscholarship.unlv.edu/cgi/viewcontent.cgi?article=1086&context=water_pubs*

Kimmerer W, Cowan J, JH, Miller L, Rose K. 2000. Analysis of an estuarine striped bass (*Morone saxatilis*) population: influence of density-dependent mortality between metamorphosis and recruitment. Can J Fisheries Aquat Sci 57(2):478-486. *https://doi.org/10.1139/cjfas-57-2-478*

Kimmerer WJ. 2002a. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol-Prog Ser 243:39-55. *https://doi.org/10.3354/meps243039*

Kimmerer WJ. 2002b. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries. 25(6B):1275-1290. *https://doi.org/10.1007/BF02692224*

Kimmerer WJ, Gross ES, MacWilliams ML. 2014. Tidal migration and retention of estuarine zooplankton investigated using a particle-tracking model. Limnol Oceanogr 59(3):901-916. *https://doi.org/10.4319/lo.2014.59.3.0901*

Kimmerer W, Slaughter A. 2016. Fine-scale distributions of zooplankton in the northern San Francisco Estuary. San Franc Estuary Watershed Sci 14(3). *https://doi.org/10.15447/sfews.2016v14iss3art2*

Lehman PW, Marr K, Boyer GL, Acuna S, Teh SJ. 2013. Long-term trends and causal factors associated with *Microcystis* abundance and toxicity in San Francisco Estuary and implications for climate change impacts. Hydrobiologia 718(1):141-158. *https://doi.org/10.1007/s10750-013-1612-8*

Lehman PW, Mayr S, Mecum L, Enright C. 2010. The freshwater tidal wetland Liberty Island, CA was both a source and sink of inorganic and organic material to the San Francisco Estuary. Aquat Ecol 44(2):359-372. *https://doi.org/10.1007/s10452-009-9295-y*

Lehman PW, Sommer T, Rivard L. 2008. The influence of floodplain habitat on the quantity and quality of riverine phytoplankton carbon produced during the flood season in San Francisco Estuary. Aquat Ecol 42(3):363-378. *https://doi.org/10.1007/s10452-007-9102-6*

Lomas MW, Glibert PM. 1999. Temperature regulation of nitrate uptake: A novel hypothesis about nitrate uptake and reduction in cool-water diatoms. Limnol Oceanogr 44(3):556-572. *https://doi.org/10.4319/lo.1999.44.3.0556*

Lopez CB, Cloern JE, Schraga TS, Little AJ, Lucas LV, Thompson JK, Burau JR. 2006. Ecological values of shallow-water habitats: Implications for the restoration of disturbed ecosystems. Ecosystems 9(3):422-440. *https://doi.org/10.1007/s10021-005-0113-7*

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312(5781):1806-1809. *https://doi.org/10.1126/science.1128035*

Lucas LV, Cloern JE, Thompson JK, Monsen NE. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: Restoration implications. Ecol Appl 12(5):1528-1547. *https://doi.org/10.2307/3099989*

Lucas LV, Sereno DM, Burau JR, Schraga TS, Lopez CB, Stacey MT, Parchevsky KV, Parchevsky VP. 2006. Intradaily variability of water quality in a shallow tidal lagoon: mechanisms and implications. Estuaries Coasts 29(5):711-730. *https://doi.org/10.1007/BF02786523*

Lucas LV, Thompson JK. 2012. Changing restoration rules: Exotic bivalves interact with residence time and depth to control phytoplankton productivity. Ecosphere 3(12). *https://doi.org/10.1890/ES12-00251.1*

Lucas LV, Thompson JK, Brown LR. 2009. Why are diverse relationships observed between phytoplankton biomass and transport time? Limnol Oceanogr 54(1):381-390. *https://doi.org/10.4319/lo.2009.54.1.0381*

Luoma SN, Cloern JE. 1982. The impact of waste-water discharge on biological communities in San Francisco Bay. In: Kockelman WJ, Conomos TJ, Leviton AE, editors. San Francisco Bay: use and protection. p. 137-160.

Mac Nally R, Thomson JR, Kimmerer WJ, Feyrer F, Newman KB, Sih A, Bennett WA, Brown L, Fleishman E, Culberson SD, et al. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol Appl 20(5):1417-1430. *https://doi.org/10.1890/09-1724.1*

McClusky DD, Elliott M. 2004. The estuarine ecosystem: ecology, threats, and management. Oxford, UK: Oxford University Press. p. 1-209.

Meire P, Ysebaert T, Van Damme S, Van den Bergh E, Maris T, Struyf E. 2005. The Scheldt Estuary: a description of a changing ecosystem. Hydrobiologia. 540:1-11. *https://doi.org/10.1007/s10750-005-0896-8*

Minitab 16 statistical software. 2010. [computer software]. State College, PA: Minitab, Inc.

Morgan-King TL, Schoellhamer DH. 2013. Suspended-sediment flux and retention in a backwater tidal slough complex near the landward boundary of an estuary. Estuaries Coasts 36(2):300-318. *https://doi.org/10.1007/s12237-012-9574-z*

Moyle PB, Lund JR, Bennett WA, Fleenor WE. 2010. Habitat variability and complexity in the upper San Francisco Estuary. San Franc Estuary Watershed Sci 8(3). *https://doi.org/10.15447/sfews.2010v8iss3*

Nelson C, Benigno G, Conrad L. 2011. Mysid abundance in a restored freshwater wetland. IEP Newsletter [cited 2016 Apr 14]; 24(3):16-22. Available from: *http://www.water.ca.gov/iep/products/newsletter.cfm*

Nichols FH, Cloern JE, Luoma SN, Peterson DH. 1986. The modification of an estuary. Science 231:567-573. *https://doi.org/10.1126/science.231.4738.567*

Nixon SW. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnol Oceanogr 33(4):1005-1025. *https://doi.org/10.4319/lo.1988.33.4_part_2.1005*

Nobriga ML. 2002. Larval Delta Smelt diet composition and feeding incidence: environmental and ontogenetic influences. California Fish Game 88(4):149-164.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28(5):776-785. *https://doi.org/10.1007/BF02732915*

Odum WE. 1988. Comparative ecology of tidal freshwater and salt marshes. Ann Rev Ecol System 19:147-176.

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

Paerl HW, Huisman J. 2008. Climate - blooms like it hot. Science 320(5872):57-58. *https://doi.org/10.1126/science.1155398*

Paerl HW, Valdes LM, Peierls BL, Adolf JE, Harding LW. 2006. Anthropogenic and climatic influences on the eutrophication of large estuarine ecosystems. Limnol Oceanogr 51(1):448-462. *https://doi.org/10.4319/lo.2006.51.1_part_2.0448*

Parker AE, Dugdale RC, Wilkerson FP. 2012. Elevated ammonium concentrations from wastewater discharge depress primary productivity in the Sacramento River and the northern San Francisco Estuary. Mar Pollut Bull 64(3):574-586. *https://doi.org/10.1016/j.marpolbul.2011.12.016*

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Ann Rev Ecol System 28:289-316. *https://doi.org/10.1146/annurev.ecolsys.28.1.289*

Reynolds CS. 1999. Non-determinism to probability, or N:P in the community ecology of phytoplankton. Archiv Fur Hydrobiologie 146(1):23-35.

Robinson AH SS, Beagle J, Grossinger RM, Grenier JL, Askevold RA. 2014. A delta transformed ecological functions, spatial metrics, and landscape change in the Sacramento-San Joaquin Delta. Richmond, CA: San Francisco Estuary Institute-Aquatic Science Center. Available from: *http://www.sfei.org/documents/delta-transformed-ecological-functions-spatial-metrics-and-landscape-change-sacramento-san*

Rose KA, Kimmerer WJ, Edwards KP, Bennett WA. 2013. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: II. Alternative baselines and good versus bad years. Trans Am Fish Soc 142(5):1260-1272. *https://doi.org/10.1080/00028487.2013.799519*

Schemel LE, Hager SW. 1986. Chemical variability in the Sacramento River and in northern San Francisco Bay. Estuaries 9(4A):270-283. *https://doi.org/10.2307/1352099*

Schemel LE, Sommer TR, Muller-Solger AB, Harrell WC. 2004. Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, USA. Hydrobiologia 513(1-3):129-139. *https://doi.org/10.1023/B:hydr.0000018178.85404.1c*

Service RF. 2007. Delta blues, California style. Science 317(5837):442-445. *https://doi.org/10.1126/science.317.5837.442*

Shaffer JA, Beirne M, Ritchie T, Paradis R, Barry D, Crain P. 2009. Fish habitat use response to anthropogenic induced changes of physical processes in the Elwha Estuary, Washington, USA. Hydrobiologia 636(1):179-190. *https://doi.org/10.1007/s10750-009-9947-x*

Sharp JH. 2001. Marine and communities, stress from eutrophication. Encyclopedia of biodiversity. New York, NY: Academic Press. p. 1-11.

Skreslet S. 1986. The role of freshwater outflow in coastal marine ecosystems. New York, NY: Springer-Verlag. p. 3-12.

Skreslet S. 1997. A conceptual model of the trophodynamical response to river discharge in a large marine ecosystem. J Marine Systems 12(1-4):187-198. *https://doi.org/10.1016/s0924-7963(96)00097-8*

Slater SB, Baxter RD. 2014. Diet, prey selection, and body condition of age-0 Delta Smelt, *Hypomesus transpacificus*, in the upper San Francisco Estuary. San Franc Estuary Watershed Sci 12(3). *https://doi.org/10.15447/sfews.2014v12iss3art1*

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

Sommer T, Harrell WC, Nobriga M, Brown R, Moyle P, Kimmerer W, Schemel L. 2001a. California's Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. Fisheries 26(8):6-16. *https://doi.org/10.1577/1548-8446(2001)026<0006:cyb>2.0.co;2*

Sommer TR, Harrell WC, Solger AM, Tom B, Kimmerer W. 2004. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. Aquat Conserv-Mar Freshw Ecosyst 14(3):247-261. *https://doi.org/10.1002/aqc.620*

Sommer T, Mejia F. 2013. A place to call home: a synthesis of Delta Smelt habitat in the upper San Francisco Estuary. San Franc Estuary Watershed Sci 11(2). *https://doi.org/10.15447/sfews.2013v11iss2art4*

Sommer T, Mejia FH, Nobriga ML, Feyrer F, Grimaldo L. 2011. The spawning migration of Delta Smelt in the upper San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2016 Feb 10]; 9(2). *https://doi.org/10.15447/sfews.2014v9iss2art2*

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001b. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Can J Fish Aquat Sci 58:325-333. *https://doi.org/10.1139/cjfas-58-2-325*

Sommer T, Reece K, Meija F. 2009. Delta smelt life-history contingents: a possible upstream rearing strategy? IEP Newsletter [cited 2016 Jan 04]; 22(1):11-13. Available from: *http://www.water.ca.gov/iep/products/newsletter.cfm*

Thomson JR, Kimmerer WJ, Brown LR, Newman KB, Mac Nally R, Bennett WA, Feyrer F, Fleishman E. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecol App 20(5):1431-1448. *https://doi.org/10.1890/09-0998.1*

Utermöhl H. 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik. Mitteilung Internationale Vereinigung fuer Theoretische und Amgewandte Limnologie. 9:1-38. v7. 2015. PRIMER v7. In: Clarke KRaRNG, editor. 2015. User manual/tutorial. Plymouth: PRIMER-E.

Whipple AA, Grossinger RM, Rankin D, Standford B, Askevold RA. 2012. Sacramento-San Joaquin Delta historical ecology investigation: exploring pattern and process. Prepared for the California Department of Fish and Game and Ecosystem Restoration Program. Richmond, CA: San Francisco Estuary Institute-Aquatic Science Center. Available from: *http://www.sfei.org/documents/sacramento-san-joaquin-delta-historical-ecology-investigation-exploring-pattern-and-proces*

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

Wilkerson FP, Dugdale RC, Hogue VE, Marchi A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. Estuaries Coasts 29(3):401-416. *https://doi.org/10.1007/BF02784989*

Wilkerson FP, Dugdale RC, Parker AE, Blaser SB, Pimenta A. 2015. Nutrient uptake and primary productivity in an urban estuary: using rate measurements to evaluate phytoplankton response to different hydrological and nutrient conditions. Aquat Ecol 49(2):211-233. *https://doi.org/10.1007/s10452-015-9516-5*

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

Yoshiyama K, Sharp JH. 2006. Phytoplankton response to nutrient enrichment in an urbanized estuary: apparent inhibition of primary production by overeutrophication. Limnol Oceanogr 51(1):424-434. *https://doi.org/10.4319/lo.2006.51.1_part_2.0424*

NOTES

Grossinger RM, Whipple AA. 2009. Historical ecology of the California Delta: emerging concepts of a complex and dynamic system. Paper presented at: CALFED Science Program workshop: Ecosystem Restoration of the Landscape Scale; Sacramento, CA.