Title

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Authors

Williamshen, Brian O

Luke, Kim

O'Rear, Teejay A

et al.

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The data associated with this publication are available upon request.

North Delta Arc Study 2022 Annual Report: Cache-Lindsey Slough Complex water quality, productivity, and fisheries

Prepared for Solano County Water Agency by:

Brian Williamshen*, Kim Luke, Teejay O'Rear, and John Durand*

Center for Watershed Sciences
University of California, Davis
One Shields Ave
Davis, CA 95616

*Contact information:
B. Williamshen
831-331-7848
bowilliamson@ucdavis.edu

J. Durand
530-601-3001
jrdurand@ucdavis.edu

Summary

The North Delta Arc – consisting of Suisun Marsh, the lower Sacramento River, the Cache-Lindsey Complex (CLC), and Yolo Bypass – offers numerous opportunities for wetlands fish restoration because of its vast intertidal area and surrounding uplands to accommodate sea-level rise, and connectivity to the upstream Yolo Bypass and downstream brackish bays. Although the CLC is currently the subject of numerous restoration efforts, it was once understudied relative to the main bays and rivers of the estuary, with only sparse, short-term data to gauge restoration success.

The UC Davis North Delta Arc Study began over a decade ago in 2012 to provide baseline data for restoration, elucidate mechanisms supporting native and desirable fishes, and document ecosystem responses to climate change and water management. The study has used a diverse, flexible array of research approaches that include water-quality, phytoplankton, zooplankton, and fish sampling. It has captured ecosystem responses to numerous environmental extremes: prolonged drought, record-high air and water temperatures, and record-high inflows. It has also documented dramatic changes in ecosystem function, and provided recommendations for water management, fish and wildlife management, and restoration design.

The study has documented major shifts in ecosystem composition. Low flows during the 2012-2016 drought promoted the spread of noxious aquatic weeds, accompanied by an increase in water clarity and a decline in suspended particles. The fish assemblage changed with water-quality conditions and aquatic-weed growth. Native, cool-water smelts declined while non-native, warm-water sunfishes increased. High flows and storm runoff in 2017 ended that drought and altered water quality but did not limit weeds and sunfishes, suggesting the CLC had passed a threshold. However, 2021 marked the first year that a decrease in aquatic weeds was observed, and was accompanied by an increase in some native species. Weeds remained depressed in 2022, the third consecutive drought year, and sunfish species abundance declined while other species increased, including three notable natives. Small sloughs with local inflows from streams, ponds, and agriculture drains, and high-to-variable water residence times in certain upstream reaches, have maintained relatively low water clarity, high plankton biomass, and relatively high native fish abundance during the 10-year study period.

Based on our findings we recommend that the Barker Slough Pumping Plant be moved out of the North Delta, connectivity with upland areas be increased in conjunction with managed pulse flows, tools to manage aquatic vegetation be explored, and that future restorations be designed to prevent colonization of aquatic vegetation.

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Introduction

The North Delta Arc ("Arc") forms a habitat corridor along the northern edge of the upper San Francisco Estuary that is the principle remaining refuge for many native species (Moyle et al. 2018). The Arc includes freshwater and brackish habitats extending from Suisun Marsh to the Yolo Bypass via the confluence of the Sacramento and San Joaquin rivers, the Sacramento River from the confluence to Steamboat Slough, Cache and Lindsey sloughs, Prospect and Shag sloughs and Liberty Island, the Toe Drain, and the Deep Water Ship Channel (Figure 1).

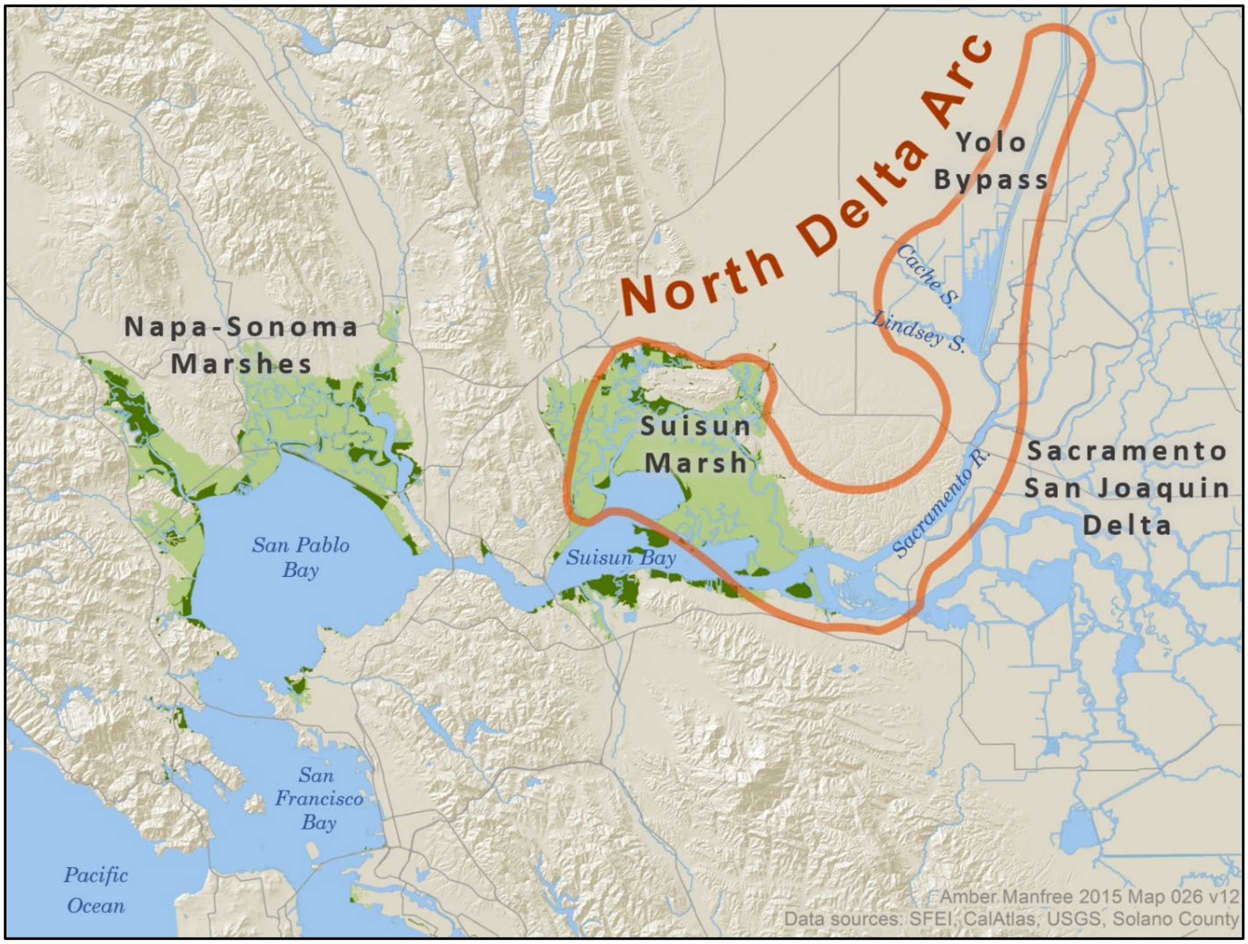

Figure 1. North Delta Arc, showing habitat corridor from Suisun Marsh to Yolo Bypass, including region of study at the Cache-Lindsey Slough Complex.

Hydrodynamic, landscape, geochemical, and food-web processes in the Sacramento-San Joaquin Delta ("Delta"; Figure 1) have been greatly altered, affecting ecosystem function (Lund et al. 2007). In the late 1800s, hydraulic-mining sediment elevated river channel beds and increased flooding in the region (Thompson 1957). In response, Delta landowners dredged and leveed waterways to protect their farms. Large-scale flood control projects that straightened and widened main river channels were mostly completed by the early 1900s. Dendritic sloughs bordered by wetlands were replaced by deep, straightened channels buttressed by hardened levees, with most wetlands converted to farms (Thompson 1957). After state-wide droughts during the 1920s and 1930s, the federal government began building the Central Valley Project, followed by the construction of California's State Water Project several decades later. These form a system of reservoirs and aqueducts designed to store and transfer water for agricultural and municipal use (Lund et al. 2018). Dams, dikes, and diversions have separated aquatic and terrestrial processes, diminishing the influence of both floods and sediment transport on Delta landscapes.

These physical and biological changes have created novel environments, sometimes with feedback loops that amplify new conditions. Sediment loss combined with intensive farming of peat soils has caused deep and continuing subsidence in leveed Delta islands, increasingly compromising levee integrity (Mount and Twiss 2005). Flow reductions and sediment-trapping by dams have reduced turbidity, favoring proliferation of non-native submersed aquatic weeds, which then further slow and clear the water (Durand et al. 2016). Filter-feeding by invasive invertebrates, combined with increased water export, have reduced plankton abundance for pelagic crustaceans and fishes, leading to food limitation and population declines in many species (Kimmerer 1996; Moyle et al. 2016, Hammock et al. 2019).

Food-web, water-quality, and habitat degradation have reduced refuge and foraging opportunities for pelagic and native fishes (Grimaldo et al. 2004; Feyrer et al. 2007). Many once-common fishes are dwindling, such as striped bass (*Morone saxatilis*), and some are critically endangered, including delta smelt (*Hypomesus transpacificus*), winter-run Chinook salmon (*Oncorhynchus tshawytscha*), and green sturgeon (*Acipenser medirostris*). Major changes to the system are needed to aid the recovery of these species.

The CLC possesses considerable potential for successful restoration in the Delta (Durand 2017; Moyle et al. 2018). In contrast to other regions of the Delta, clay soils in the CLC have resisted subsidence in reclaimed lands, allowing potential re-creation of tidal marsh. Gradual upland slopes exist that can accommodate restoration and sea-level rise. Sediment transported from the Sacramento River, Yolo Bypass, and Ulatis Creek produces higher seasonal turbidity than in other Delta regions. Historic riparian vegetation and emergent marsh are common features in several reaches of the CLC. Until recently, submersed and floating aquatic weeds were less extensive in the CLC than in other areas of the Delta. The spatial complexity of the region; the connectivity to marshes, floodplains, and streams; and high food concentrations support seasonal and year-round habitats for migratory and resident native fishes (Simenstad et al. 2000). Thus, broad interest exists in restoring large tracts of tidal habitat in the CLC (ICF International 2013). Lindsey Slough Tidal Habitat Restoration Project was completed in 2015, Lower Yolo Ranch Tidal Habitat Restoration Project in 2020, and Lookout Slough Tidal Restoration Project is in progress with a completion date of 2024.

Because the CLC showed promise for restoration but was the subject of minimal study, the North Delta Arc Study began in 2012 to describe its aquatic ecosystem, to assess its response to environmental changes, and to update and inform restoration design and management. The study was updated in 2014 with grants from the State and Federal Contractors Water Agency, in 2016 with a California Department of Fish and Wildlife (CDFW) Proposition 1 grant, and in 2017 with a grant from Solano County Water Agency.

The study's chief objectives have been to:

(1) Understand temporal changes in water-quality conditions, plankton production, and invertebrate and fish assemblages in Cache and Lindsey sloughs resulting from tides, seasonal flow pulses, regional water diversion, and periods of drought and flood

(2) Understand spatial differences in ecosystem processes and composition between distinct slough networks within the CLC

(3) Compare water quality and fish assemblages across restored and adjacent sites, particularly the CDFW Lindsey Slough Tidal Habitat Restoration and the Wildlands North Liberty Island Mitigation Bank

(4) Develop a hydrodynamic model of water age and residence time to understand advection and dispersion in the North Delta, including the CLC

We completed interdisciplinary work that fulfilled or partially fulfilled several of the study's objectives and published our findings in a previous report (Durand *et al.* 2020). Partially fulfilling objective number one, an investigation of water quality and zooplankton in the CLC found that sites with higher conductivity generally supported higher chlorophyll-*a* concentrations and zooplankton densities, and that both primary and secondary productivity may have been tied to nutrient loading from upland agriculture runoff and treated urban wastewater (Jasper 2020). Current studies are experimentally comparing the rate of phytoplankton production and zooplankton concentration relative to environmental conditions and preliminary findings have been reported (Williamshen et *al.* 2022).

Fulfilling objective number two, we reported on a comparison between dead-end-slough and mainstem-river/slough sites within the Arc for 2013 and 2014 that determined that both chlorophyll-*a* concentration (proxy for phytoplankton) and zooplankton biomass were much higher at upstream sites (Montgomery 2017). A current study is expanding this analysis both spatially and temporally to better understand habitat function and zooplankton abundance in response to changing environmental conditions such as drought and flood. Partially fulfilling objective number three, a study comparing restoration and adjacent slough sites found lower abundance and a similar proportion of native fishes in the Lindsey Slough Restoration Project**,** and higher abundance and proportion of natives in the North Liberty Island Mitigation Bank (NLIMB) in 2015 and 2016 (Durand et *al.* 2020; Williamshen et *al.* 2022). Fulfilling objective number four, a hydrodynamic model identified that upper Cache Slough has higher water age (residence time) than downstream sites and that the Lindsey Network has a higher proportion of Sacramento River water compared to the upper Cache Network (Gross *et al.* 2019, Durand *et al.* 2020). Findings from these studies have enhanced our understanding of how the CLC functions and led to further research.

The following report details data collected throughout the duration of the Arc Study in pursuit of further fulfilling study objectives. Time-series data are presented from water-quality, aquatic vegetation, and fishes sampled from December 2012 through December 2022. These data show spatial and temporal patterns of ecosystem composition within the CLC and have led us to several conclusions and management recommendations.

Methods

Study Area

The CLC includes two distinct slough networks: (1) the Cache Network, which includes upper Cache Slough, Hass Slough, and Ulatis Creek; and (2) the Lindsey Network, which includes Lindsey Slough, Barker Slough, and Calhoun Cut. A combination of historical endeavors and water-management decisions have endowed each network with very different features despite their close geographic proximity. Both networks were historically connected to Maine and Jepson prairies, which drained much of Solano County east of the Vaca Mountains and north of the Montezuma Hills (along with Putah Creek to the north). Within and between the slough networks are differences in hydrodynamics, nutrient concentrations, and physical structure that affect water quality and fish assemblage.

The Cache Network is steeply leveed and subject to large seasonal flows from Ulatis Creek, receiving urban, flood, and agricultural runoff – including effluent from Vacaville's Easterly Wastewater Treatment Plant. Some upstream reaches, including Ulatis Creek and Cache Slough, exhibit high turbidity year-round, and have less submersed aquatic weeds than elsewhere in the Delta.

The Lindsey Network is mostly isolated from large flood flows but receives some water from local sources. Deep and leveed near the mouth, the slough expands into extensive intertidal and riparian habitats in the shallow upper reaches of the main tributaries, Barker Slough and Calhoun Cut. Water inputs come mostly from Jepson Prairie overland flow, the Big Ditch (Peterson Ranch), and the Barker Slough Watershed. Water quality in Barker Slough is largely affected by runoff from Campbell Lake, which accumulates salts and sediment, and by water exports for agriculture and the North Bay Aqueduct. Water export by the Barker Slough Pumping Plant for the North Bay Aqueduct is continuously measured and slowed or stopped under several conditions: when water quality declines due to runoff, when demand is low, or when facility maintenance is needed. Agricultural withdrawals occur mostly in summer and are largely unmonitored. The Lindsey Slough Tidal Habitat Restoration was implemented in Calhoun Cut in 2015, connecting the historic upper slough channel of Lindsey Slough to Calhoun Cut and Lindsey Slough.

Physical and hydrodynamic differences between the Lindsey Network and Cache Network provide an opportunity to study mechanisms that drive biological differences. Water withdrawals and inputs affect hydrodynamics, water quality, food-web production, and species composition of the CLC. Locally, elements that affect the system are (1) Ulatis Creek inflows; (2) agriculture runoff (for example, Hass Slough and the Big Ditch system); (3) overland flow (for example, at upper Lindsey/Calhoun and Barker sloughs); (4) municipal and agricultural withdrawals, including the Barker Slough Pumping Plant; and (5) restoration projects. Regionally, elements with potential to affect the CLC are (1) winter/spring Yolo Bypass flows during flood years; (2) autumn Yolo Bypass planned releases from rice fields to support the Delta Smelt Resiliency Strategy; and (3) Sacramento River flows and changes in water quality (for example, the Sacramento Regional Wastewater Treatment Plant upgrade in 2021).

Climatic Conditions

We used the Net Delta Outflow Index ("Delta outflow") as an indicator of water conditions across the study period and watershed (Kimmerer 2004, Feyrer *et al.* 2015). Delta outflow was calculated by summing river flows entering the Delta; channel depletions; in-Delta diversions; and State

Water Project, Central Valley Project, and Contra Costa Water District exports. Delta outflow was obtained from the California Department of Water Resources (DWR 2023).

Sampling

Sampling has been conducted monthly since December 2012 across the Arc, with a focus on the CLC, which includes Cache and Lindsey sloughs and their smaller tributaries (Barker Slough, Calhoun Cut, Hass Slough, and Ulatis Creek; Figure 2). Originally, otter trawls were conducted around Liberty Island, but these were discontinued due to floods in 2017 that introduced bottom hazards to the region; biannual electrofishing sites and monthly water-quality transects were continued, however. The study area encompasses numerous planned and implemented restoration sites, including the Lindsey Slough

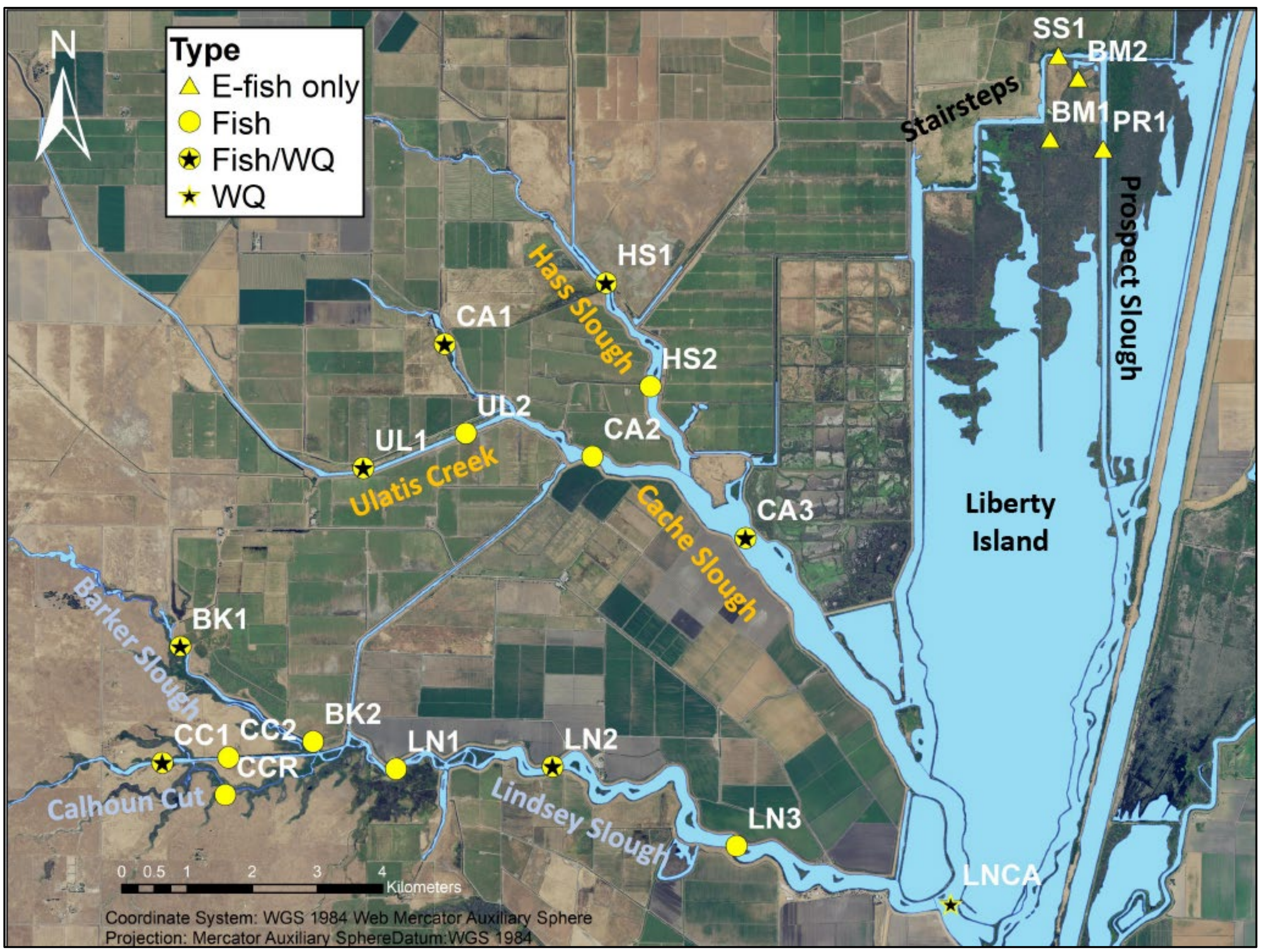

Figure 2. Current sample sites in the Cache-Lindsey Slough Complex. Yellow triangles indicate electrofishing only sites, circles indicate trawl and electrofishing sites (fish), and black stars indicate water-quality and zooplankton collection sites (WQ). Cache Network sites are labeled in light orange; Lindsey Network sites are labeled in light blue.

Restoration Project (for which the study has pre- and post-implementation data), the North Liberty Island Mitigation Bank, the Beaver Ponds (post-implementation data), the Lower Yolo Ranch Tidal Restoration (pre- and post-implementation data), and the proposed Lookout Slough restoration (pre-implementation data). Since early 2015, electrofishing, water-quality, and zooplankton surveys have included several sites beyond the CLC, including those in Prospect sloughs and in the Stairsteps. Sites in the Toe Drain of Yolo Bypass were sampled only rarely during exploratory surveys. Due to the COVID-19 pandemic, electrofishing did not occur in 2020; otter-trawling did not occur April, May, and June 2020; and water-quality/zooplankton sampling did not occur in April and May 2020.

In this report, the following sites are associated with the Cache Network (including Ulatis Creek and Hass Slough): UL1, UL2, CA1, CA2, CA3, HS1, and HS2. The following sites are associated with the Lindsey Network (including Calhoun Cut and Barker Slough): CC1, CC2, BK1, BK2, LN1, and LN2, and LN3. Site numbers indicate location of site along slough, with "1" being furthest upstream and "3" being furthest downstream. A single water-quality/zooplankton sampling site was located at the confluence of Cache and Lindsey sloughs (LNCA). Discrete water quality was sampled in all upper reaches (UL1, CA1, HS1, CC1, BK1), two mid-slough reaches (CA3, LN2), and a site at the confluence of the two slough networks (LNCA). In addition, biannual electrofishing surveys were conducted at each of these sites, plus sites around Liberty Island, and included SG1, SG2, BP1, BP2, SS1, BM1, BM2, PR1, and PR2. We include several of these sites around Liberty Island to compare a restoring wetland (BM1 and BM2) to adjacent waterways (SS1 and PR1). Site data are tabulated in Appendix I.

Water Quality

<u>Water Quality</u>

Water-quality data were collected monthly with handheld meters (concomitant with fish sampling) and whole water grab analysis. In 2016, 2018, and 2019, water-quality surveys were conducted more frequently to measure the immediate impact of flows from storm events on water quality. Various flow events were used as triggers for increased sampling frequency, including any storms that resulted in greater than 0.5 inches of local precipitation, flow releases on Putah Creek or Cache Creek, and increased flows down the Toe Drain or across Yolo Bypass.

For each fish-sampling event, temperature (degrees Celsius, °C), dissolved oxygen (DO, milligrams per liter (mg/L), and % saturation), and specific conductivity (microSiemens, µS) were recorded with a Yellow Springs Instruments (YSI) PRO2030 handheld device. Water clarity (Secchi depth, centimeters (cm)), tidal stage (ebb, flood, high, low), and water depths (m) were also recorded. Data from each site were graphed through time.

Water grabs were taken at eight sites within the CLC. Phytoplankton samples were also collected, preserved in Lugol's solution, and archived for later identification. Lab analyses of water grabs for water-quality constituents were performed by the at UC Davis biogeochemistry laboratory (using standard analysis techniques from Eaton et *al.* [1998]) and included the following:

- *pH*. Low pH can indicate increased heterotrophy, or respiration; high pH suggests increased autotrophy, or carbon fixation.
- *Indicators of suspended sediment or detritus*. These can be useful to determine what/how much organic or mineral material is suspended in the water column. Turbidity is an optical measurement of particle concentration; dissolved organic carbon (DOC) is a measurement of the total concentration of organic carbon dissolved in the water; total suspended solids (TSS) is a measurement of the mass of suspended particles in the water (including carbon); and volatile suspended solids (VSS) is a measurement of the mass of suspended carbon in the water.
- *Nutrients*. Phosphorus was measured as phosphate (PO_4), total dissolved phosphorus (TDP), and total phosphorus (TP). Nitrogen was measured as nitrate (NO_3), ammonium (NH_4), total dissolved nitrogen (TDN), dissolved inorganic nitrogen (DIN; $NO_3 + NH_4$), and total nitrogen (TN). The ratio of DIN to PO_4 is the moles of nitrogen from $NO_3 + NH_4$ to moles of phosphorus from PO_4 and is compared to the Redfield ratio, a standard ratio of 16:1 nitrogen to phosphorus in phytoplankton cells.
- *Chlorophyll.* Chlorophyll serves as a proxy for phytoplankton density. Chlorophyll *a* is a measurement of chlorophyll from living cells. Pheophytin *a* is a measurement of ambient chlorophyll from dead cells.

Fish and Aquatic Vegetation Sampling

Fish sampling was conducted in diverse near-shore and mid-channel habitats. To account for different habitat types, boat electrofishing and otter-trawling were used for sampling. All sampling was conducted from UC Davis boats, including a 21-foot-long Workskiff outfitted for trawling and water-quality sampling, and a custom 18-foot-long Smith-Root electrofishing vessel.

Trawling targeted mid-channel habitats and was conducted monthly using a four-seam otter trawl with a 1.5-m X 4.3-m opening, a length of 5.3 m, and mesh sizes of 35-millimeter (mm) stretch in the body and 6 mm stretch in the cod end. The otter trawl was towed at a speed of approximately 4 kilometers/hour (relative to the water) for 5 minutes at 14 or more sites. Contents of each trawl were placed into large containers of water. Fishes were identified to species using Wang (1986) and Moyle (2002), measured to the nearest mm standard length, and returned to the water. Siberian prawn (*Palaemon modestus*), red swamp crayfish (*Procambarus clarkii*), Asian clam (*Corbicula fluminea*), and Mississippi grass shrimp (*Palaemonetes kadiakensis*) were also identified and counted. Amphipods in the suborders Gammaroidea or Corophioidea were given an abundance ranking. Other invertebrates, including insects, isopods, mysids, and snails, were also given a ranked abundance. Volume of debris, including aquatic vegetation, was also estimated for each trawl. Aquatic vegetation was identified to genus or species and estimated volumetrically. Catch per unit effort (CPUE) of trawl catches was calculated by dividing catch by minutes trawled.

Electrofishing targeted near-shore habitats and was conducted biannually (spring and autumn) since 2013, with some sites sampled more frequently from 2013 to 2016. Electrofishing was conducted with a Smith-Root 7.5 GPP boat-mounted electrofisher at a constant pulse width of 60 pulses per second and variable power to maintain a constant electrical current of 8 ± 1 amperes. Approximately 300 m of shoreline at each site were sampled in the down-current direction, with effort being measured in time spent electrofishing. Stunned fish were collected using long-handled dipnets and placed in an aerated live-well; once recovered, they were identified, measured, and released. Sampling was conducted within restoration project areas where possible, as well as in close vicinity of the projects, to detect possible influences of restoration on fish assemblages. CPUE was calculated by dividing catches by minutes spent electrofishing.

To evaluate changes in fish assemblages, we chose the most-abundant species from trawls and electrofishing, grouped them by habitat association or origin (native or non-native), and then graphed them. The habitat associations indicate if a species spends most of its lifespan in benthic, pelagic, or littoral (*i.e.*, near-shore) habitat. Grouping fishes by habitat association offers a way to delineate patterns more easily without being overwhelmed by the complexity of viewing many species at once (See Appendix II).

Species associated with benthic habitat include bottom fishes that feed largely on invertebrates. Eleven species comprise the benthic group, including three natives — prickly sculpin (*Cottus asper*), Sacramento splittail (*Pogonichthys macrolepidotus*), and Sacramento sucker (*Catostomus occidentalis*) — and eight non-natives — bigscale logperch (*Percina macrolepida*), channel catfish (*Ictalurus punctatus*), brown bullhead (*Ameiurus nebulosus*), black bullhead (*Ameiurus melas*), white catfish

(*Ameiurus catus*), common carp (*Cyprinus carpio*), yellowfin goby (*Acanthogobius flavimanus*), and shimofuri goby (*Tridentiger bifasciatus*).

Fish associated with pelagic habitat are often planktivorous during at least one stage in their life history and occupy open-water habitat. We identified eight species as pelagic, including the pelagic organism decline (POD) species (Sommer *et al.* 2007)—striped bass (*Morone saxatilis*), Delta smelt, longfin smelt (*Spirinchus thaleichthys*), American shad (*Alosa sapidissima*), and threadfin shad (*Dorosoma petenense*)— and other species—wakasagi (*Hypomesus nipponensis*), Sacramento pikeminnow *(Ptychocheilus grandis*), hitch (*Lavinia exilicauda*), and Chinook salmon *(Oncorhynchus tshawytscha*).

We identified ten species that are associated with littoral habitat. Most of this group is comprised of non-native sunfishes (Centrarchidae) that were introduced for sport fisheries from the Mississippi River Watershed and southeastern United States, including bluegill (*Lepomis macrochirus*), redear sunfish (*Lepomis microlophus*), largemouth bass (*Micropterus salmoides*), white crappie (*Pomoxis annularis*), and black crappie (*Pomoxis nigromaculatus*). Sunfishes favor fresh water, warm temperatures, low flows, weedy habitats, and eat various invertebrates and fishes. The rest of the littoral group is made up of two native species – tule perch (*Hysterocarpus traski)* and threespine stickleback (*Gasterosteus aculeatus*) - and three non-native species – golden shiner (*Notemigonus crysoleucas*), Mississippi silverside (*Menidia audens*), and western mosquitofish (*Gambusia affinis*).

Results

Climatic Conditions: Mean Daily Outflow

The UC Davis North Delta Arc Study began in the winter of 2012, at the onset of a drought. Delta outflow was rather low in 2013 and very low in 2014 and 2015, which were the driest years of the drought. In 2016, Delta outflow increased as the drought began to lessen (Figure 3). The following year, 2017, was extremely wet and much of the Delta was flooded, causing an interruption to some sampling. 2018 was a drier year, followed by a wet year in 2019, but 2020 marked the onset of another severe California drought that continued through 2022.

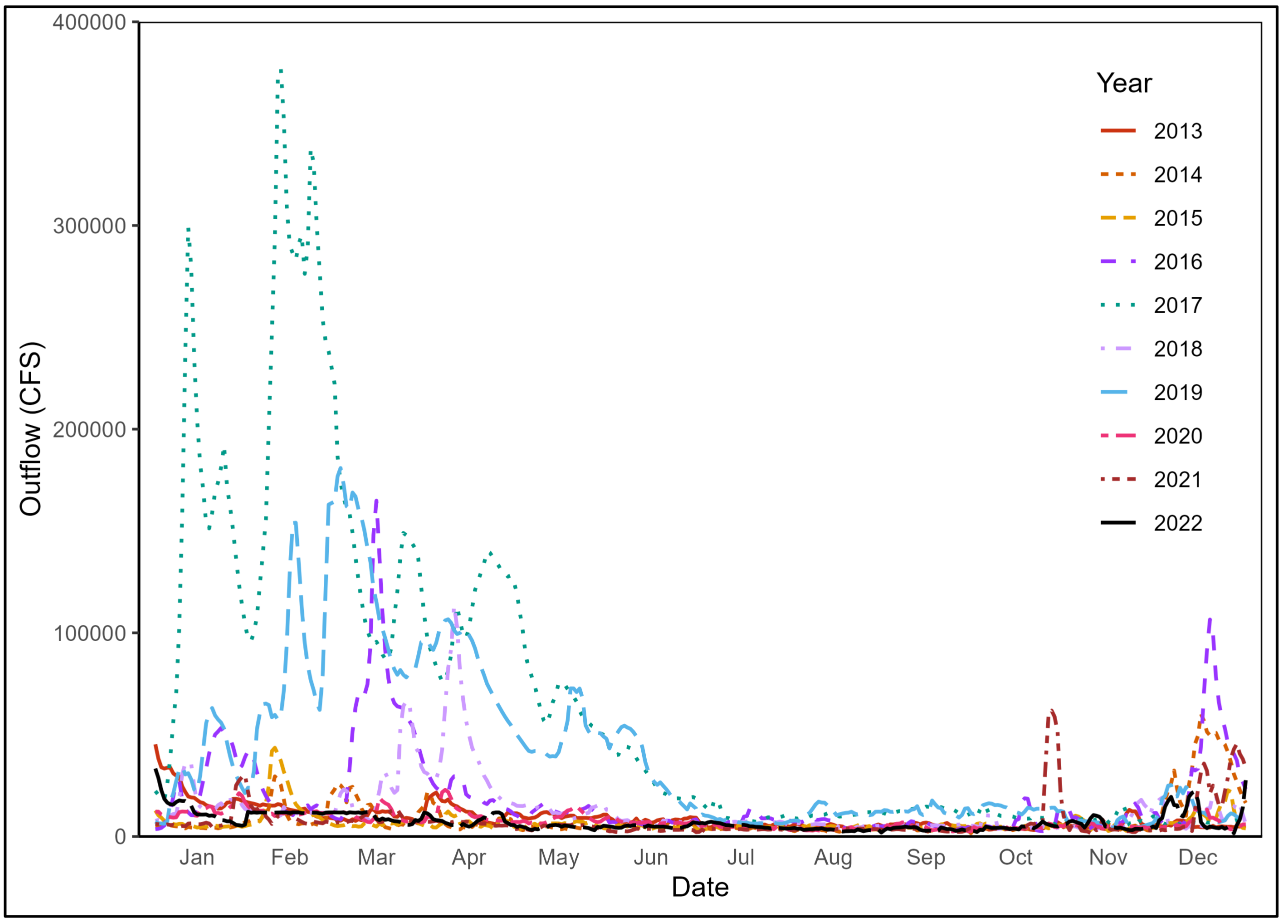

Figure 3. Mean daily Delta outflow (CFS) for 2013 to 2022 (DWR 2023).

Water Quality

<u>Water Quality at Otter Trawl Sites (Handheld Measurements)</u>

Temperature - Temperatures were typical of California's Mediterranean climate, with hot summers and cool winters (Figure 4). Due to its inland location, limited marine cooling influence in the CLC allowed summer temperatures to exceed 20°C for prolonged periods. Summers in 2014 and 2015 were among the hottest on record and had the highest number of months with mean water temperatures above 20°C. Differences in mean annual temperature among sample sites were minimal, although the terminal end of Cache Slough (CA1) and Ulatis Creek (UL1) had slightly higher maxima in most years. In 2022, maximum summertime water temperatures were higher than the preceding year but lower than 2013, 2017, and 2019, and minimum temperature never fell below 8°C.

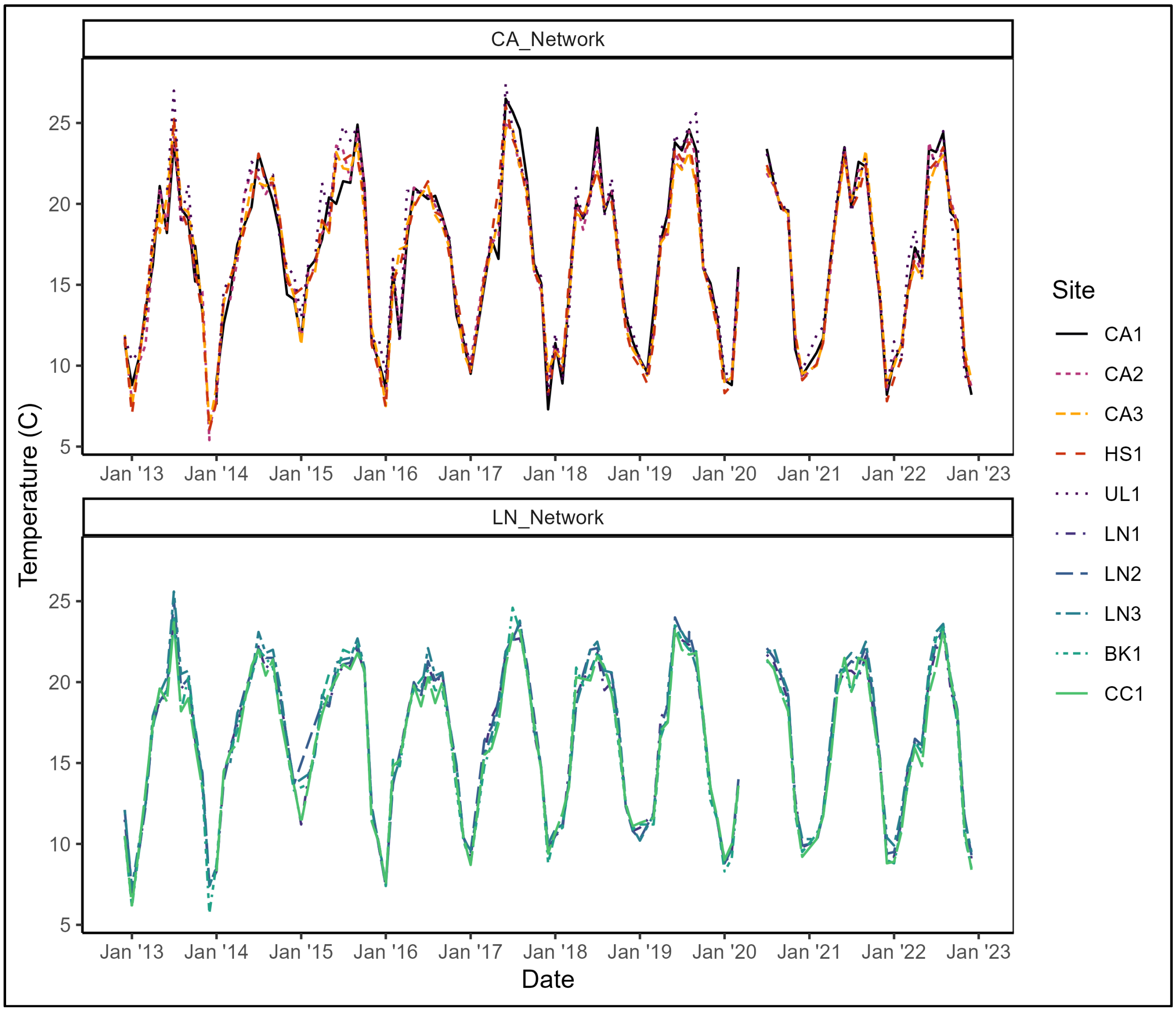

Figure 4. Monthly water temperature (°C) at otter-trawl sites.

Dissolved oxygen- Highest and lowest DO values occurred in upstream slough sites such as UL1, CA1, and CC1. Timing of minimum DO differed between the two slough complexes (Figure 5). In general, DO in the Cache Network was highest in winter and spring, and decreased throughout the summer and autumn. The Lindsey Network had highest values in autumn and winter, which then decreased and stabilized during spring and summer. Over the past three years the trends have been similar between networks. DO was at sufficient concentrations (>3 mg/L) for most fishes at all sites, except for several occasions until 2022. In 2022, low DO was driven by a hypoxia event in upper Cache (CA1) and Hass (HS1 and HS2) sloughs in September (0.7, 2.1, and 0.5 mg/L, respectively).

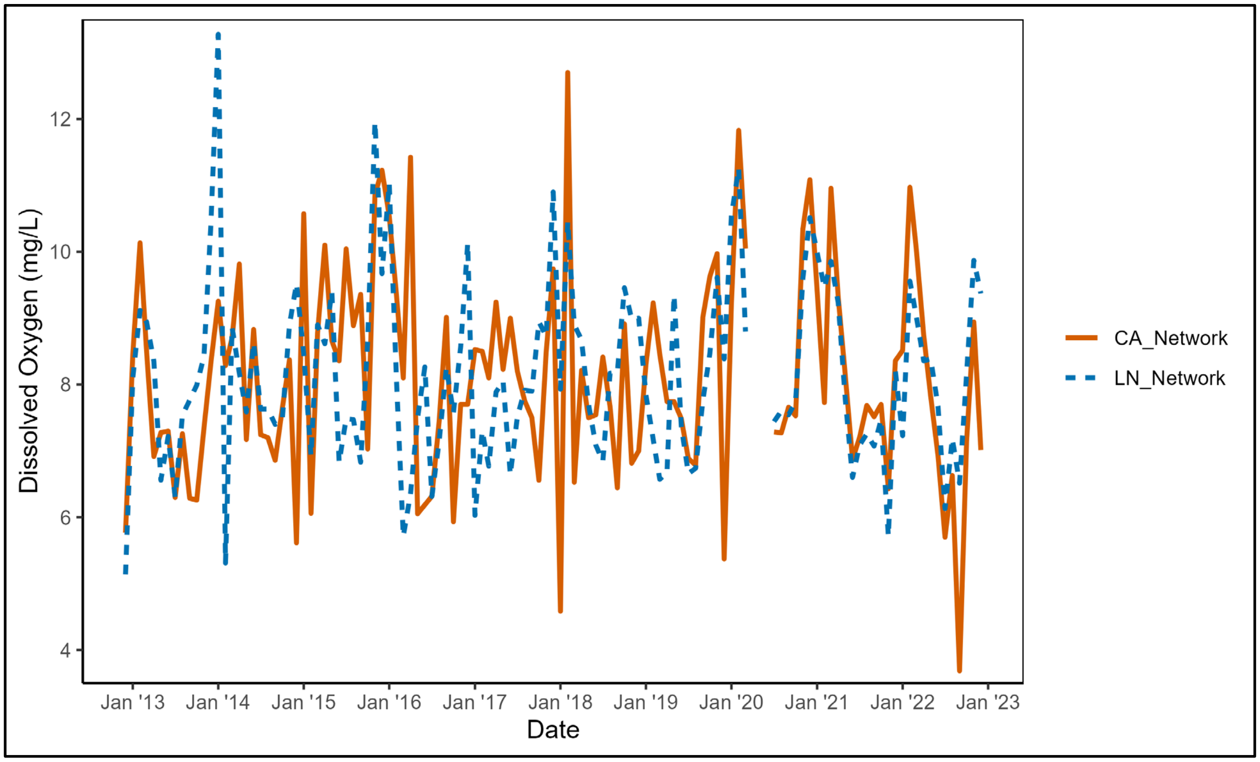

Figure 5. Monthly average DO (mg/L) for each network (CA_Network = Cache Network; LN_Network = Lindsey Network).

Specific conductivity- Specific conductivity was generally much higher in the Cache Network than in the Lindsey Network. Specific conductivity was highest at UL1 and decreased downstream toward CA3. Lindsey Slough was less variable from end to mouth, especially in summer. In spring, specific conductivity became elevated, increasing variation along slough length, with highest values in Barker Slough and lowest values at LN3 near the mouth (Figure 6). Seasonal variation occurred in both sloughs, with specific conductivity decreasing during summer when runoff was low. In 2022, upper slough sites in UL1 remained much higher than the other Cache Network sites, while the Lindsey Network remained lower than pre-2020 levels the entire year.

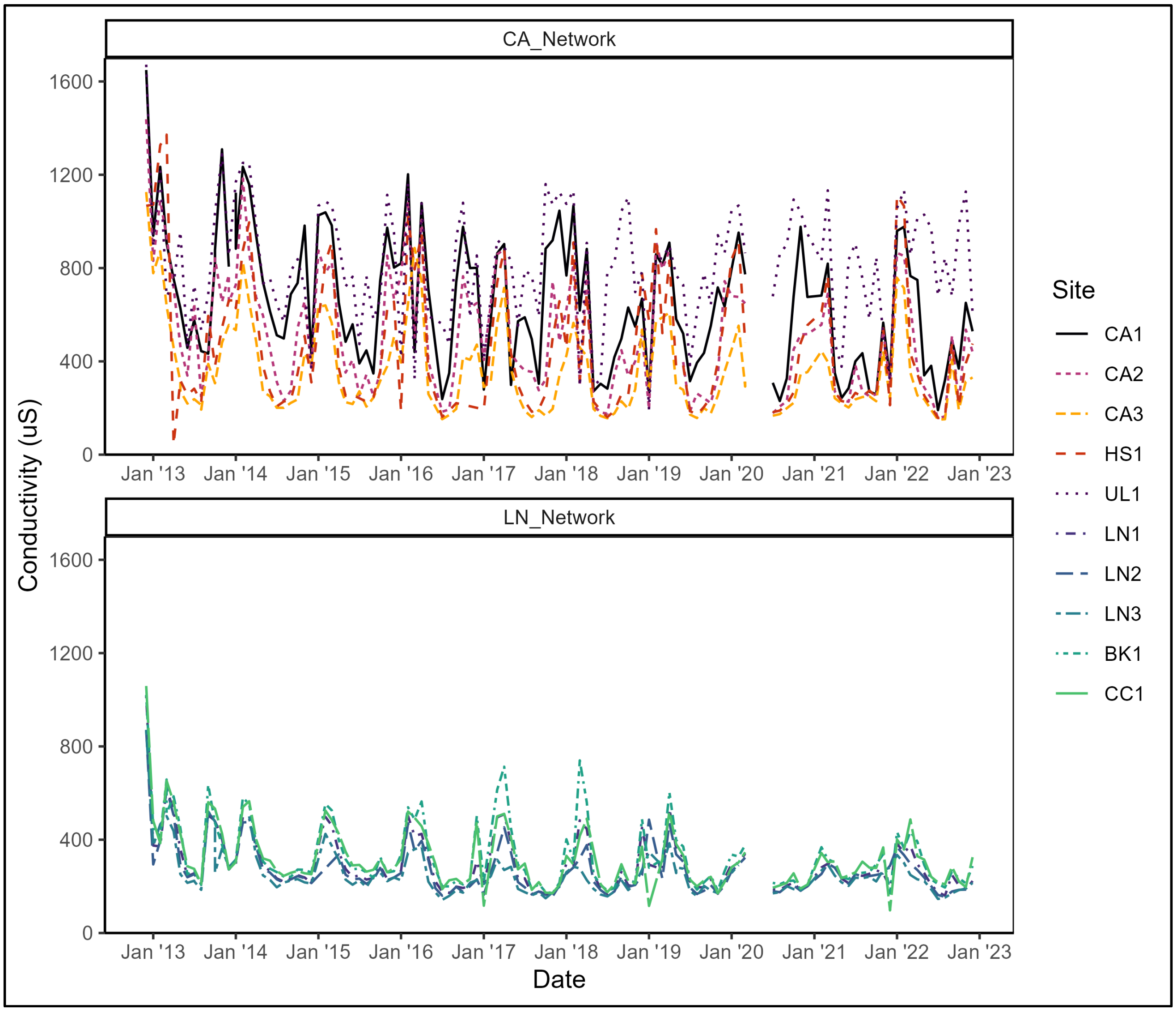

Figure 6. Monthly specific conductivity (µS) at otter-trawl sites. Top panel (CA_Network) includes Cache Network sites and bottom panel (LN_Network) includes Lindsey Network sites.

Secchi depth- Secchi depth increased throughout most of the study, especially in Lindsey Slough, Barker Slough, and lower Cache Slough (Figure 7). Sites with the slowest rate of increase in water clarity (i.e., Secchi depth) were UL1 and CA1. Each year saw a pattern of increasing clarity in late summer and autumn, followed by a decrease in the winter. Wet years, such as 2017 and 2019, decreased the water clarity. In 2022, Secchi depth rebounded from the depressed levels observed in 2021 and reached the highest recoded depth of the study in 2022 (473 cm at LN3) with elevated levels at downstream sites of both networks (LN3 and CA3).

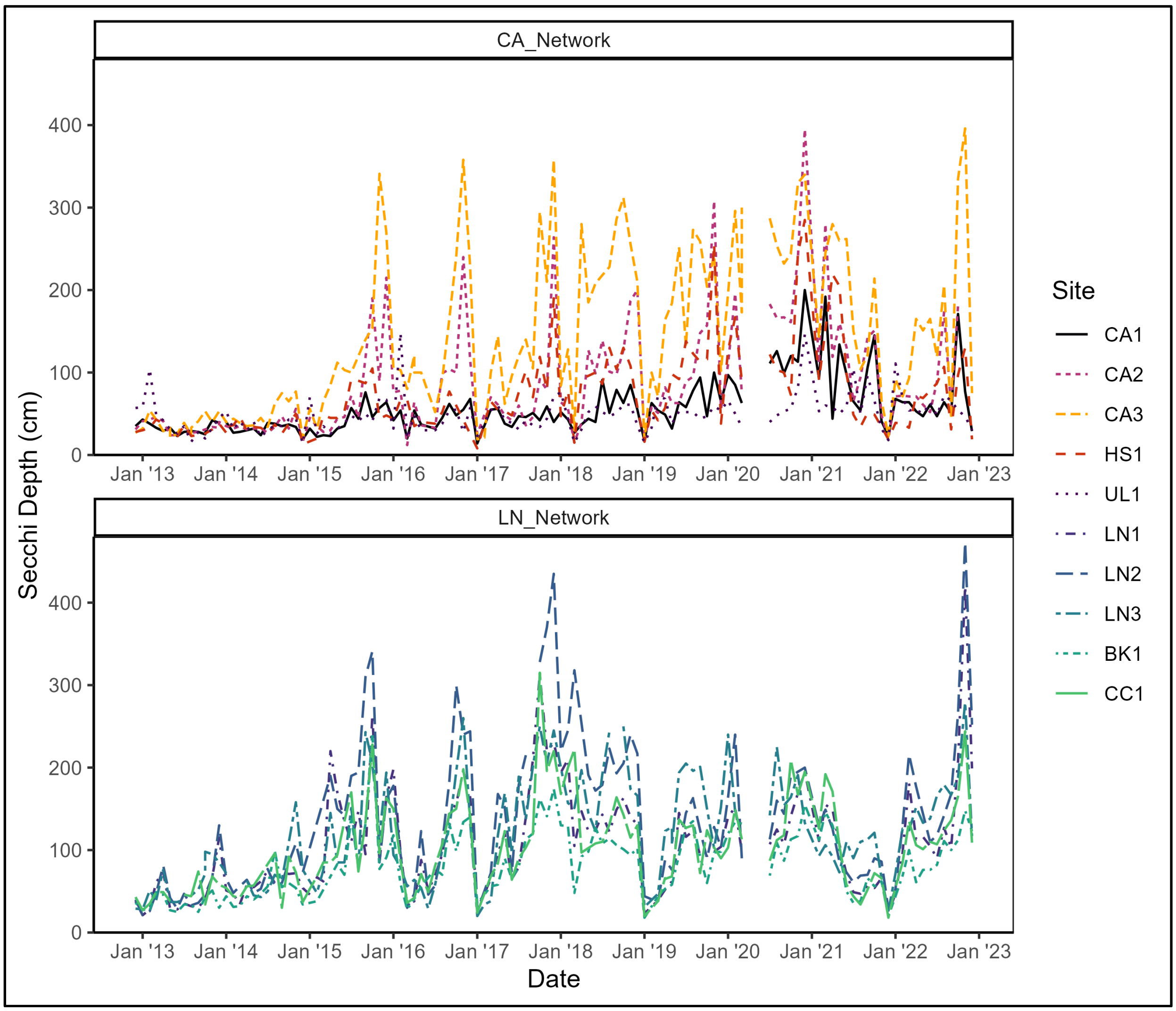

Figure 7. Monthly Secchi depth (cm) at otter-trawl sites. Top panel (CA_Network) includes Cache Network sites and bottom panel (LN_Network) includes Lindsey Network sites.

Water Quality Constituents (Water Grabs)

pH- pH has generally increased throughout the study, with peaks in spring of most years (Figure 8). UL1 consistently had the highest pH of all sites. The entire region has become more alkaline over time, possibly a result from increased primary production. In 2022, pH was at its highest levels in February in the Lindsey Network and March in the Cache Network, staying above pH 7 for the entire year across all sites.

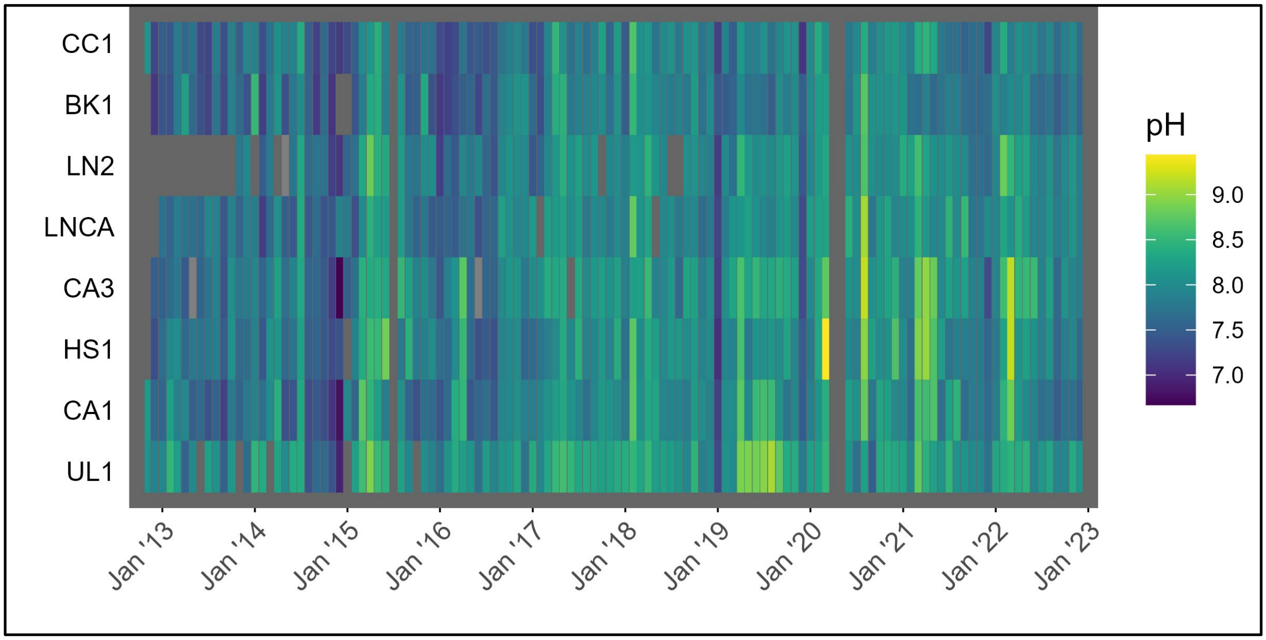

Figure 8. Monthly pH at water-quality sites.

Indicators of suspended detritus or sediment- Spatial patterns were observed for all four indicators, with highest values at UL1, CA1, and HS1. Samples from lower Cache Slough and from Lindsey Slough had lower values (Figure 9), including Calhoun Cut near the Lindsey Slough Restoration Project, but upper Lindsey Network sites (Bk1 and CC1) had seasonally high DOC. All sites showed seasonal changes, with increasing values early in the year – especially during the very wet winters of 2017 and 2019.

Turbidity, VSS, and TSS decreased after 2014 in samples from Lindsey and lower Cache sloughs and generally remained low, even through wetter years following the drought. In 2022, turbidity and DOC, and to a lesser extend TSS and VSS, spiked in the Cache Network in September and December, both months when precipitation occurred.

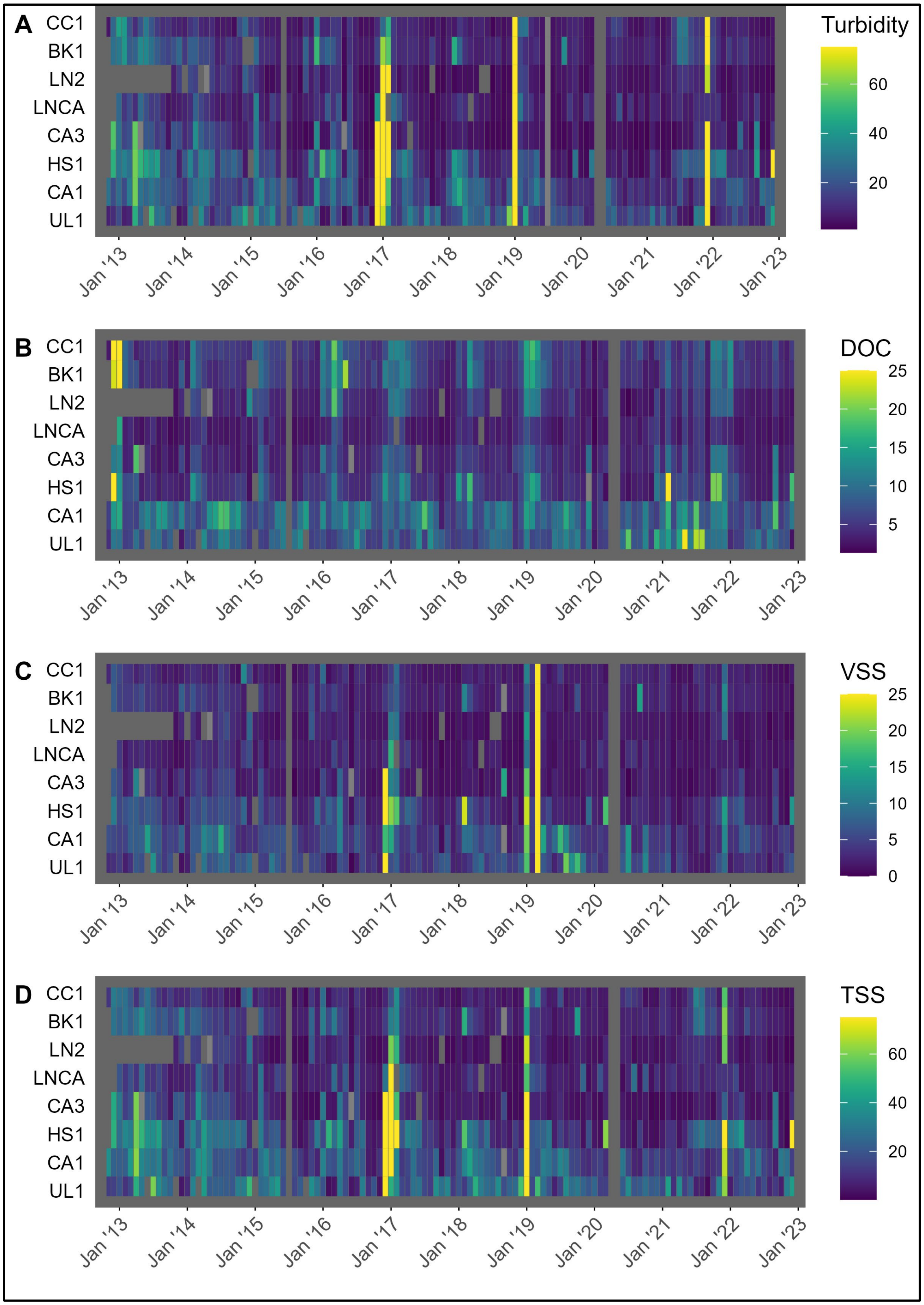

Figure 9. Indicators of suspended detritus or sediments. Monthly turbidity (NTU), dissolved organic carbon (DOC; mg/L), volatile suspended solids (VSS; mg/L), and total suspended solids (TSS; mg/L) at water-quality sites.

Phosphorus- All measurements showed similar seasonal and spatial patterns (Figure 10). Upstream Cache Network sites (UL1, CA1, and, to a lesser degree, HS1) had the highest phosphorus concentrations. Phosphorus was higher at Cache Network sites than Lindsey Network sites. Concentrations were highest during winter, following similar temporal patterns of suspended and dissolved materials. In 2022, phosphorous concentrations remained high CA1 and UL1 and spiked at HS1 in September and December.

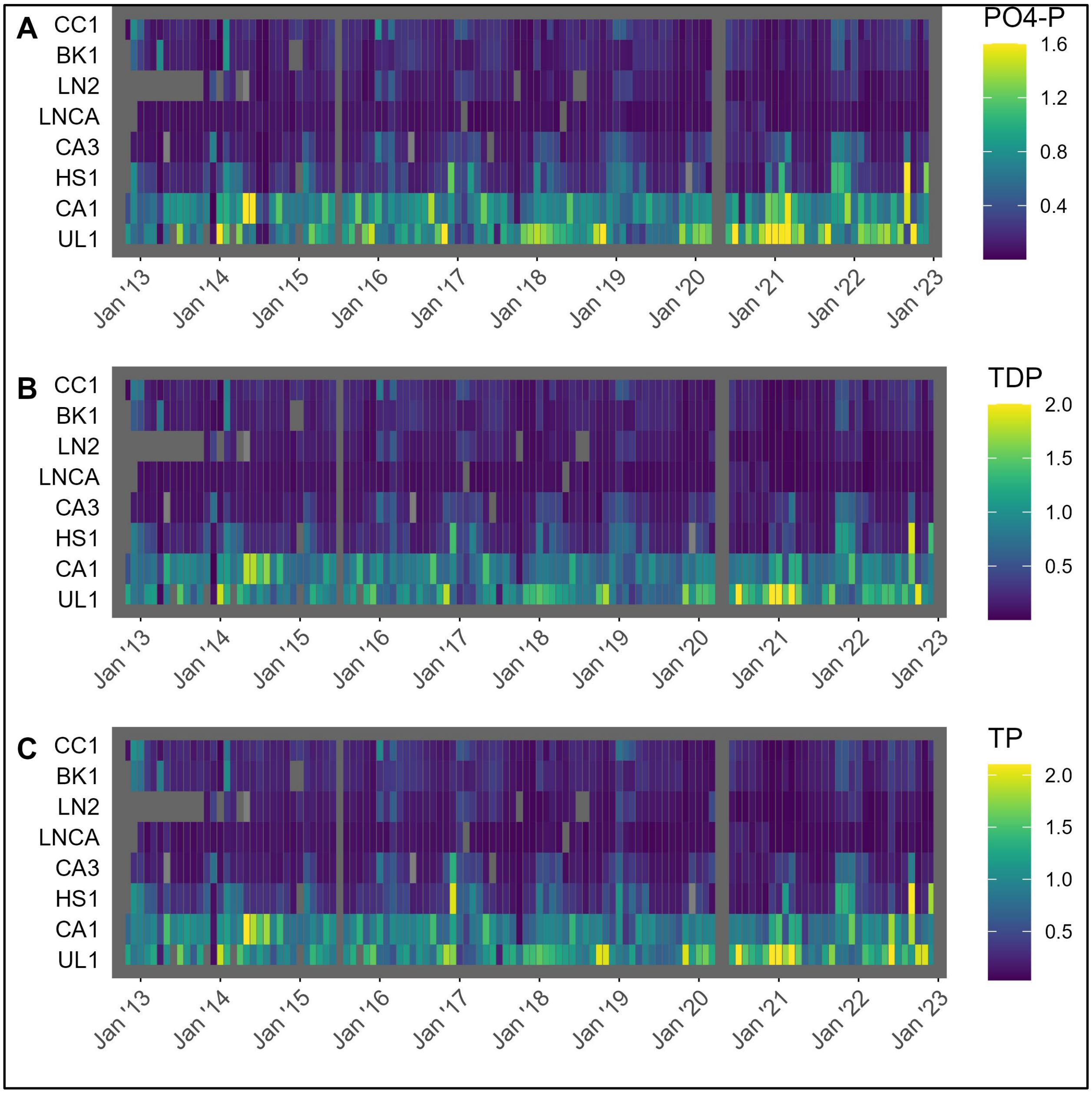

Figure 10. Monthly phosphorus as phosphate (PO_4), total dissolved phosphorous (TDP), and total phosphorous (TP), in mg/L, at water-quality sites.

Nitrogen- Relative patterns of nitrogen concentrations were similar for NO_3, TDN, and TN (Figure 11). Upstream sites in the Cache Network had the highest concentrations (UL1, CA1, and HS1, in descending order). Seasonal increases occurred from late autumn to early spring across all sites. NH_4 did not follow strong seasonal patterns, and highest concentrations were found at the upstream CA1 site and the most downstream site, LNCA. Since January 2021, NH_4 concentrations have remained low at LNCA and have been elevated at HS1. The general trends were maintained in 2022, except for spikes in TDN at CC1 and LN2, and in NH_4 at HS1 and CA3 in September.

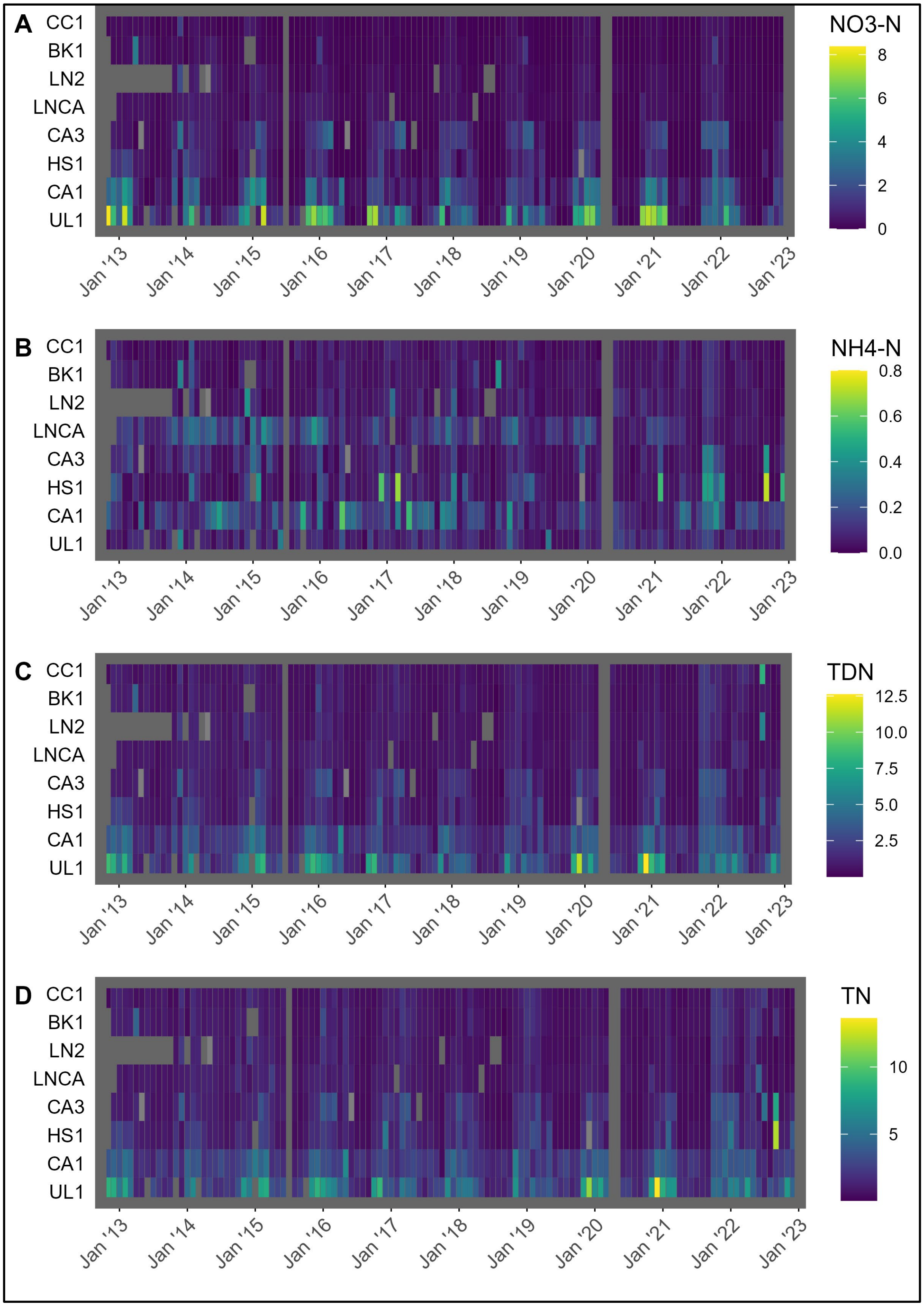

Figure 11. Monthly nitrogen as nitrate (NO_3), ammonium (NH_4), total dissolved nitrogen (TDN), and total nitrogen (TN), in mg/L, at water-quality sites.

Dissolved Inorganic Nitrogen to Phosphate Ratio (DIN:PO4)- All sites followed seasonal trends in the molar DIN to PO_4 ratio. In winter, primary producers at sites were generally phosphate-limited, as indicated by ratios above the Redfield ratio line. In summer, primary producers at sites were generally nitrogen-limited, as indicated by ratios below the Redfield ratio line (Figure 12). Locations of winter excess nitrogen levels varied among years. In 2022, all sites appeared nitrogen limited year-round with a DIN-to-PO_4 ratio below the Redfield ratio line, except for LNCA which had a ratio above the line in January, February, March, and December.

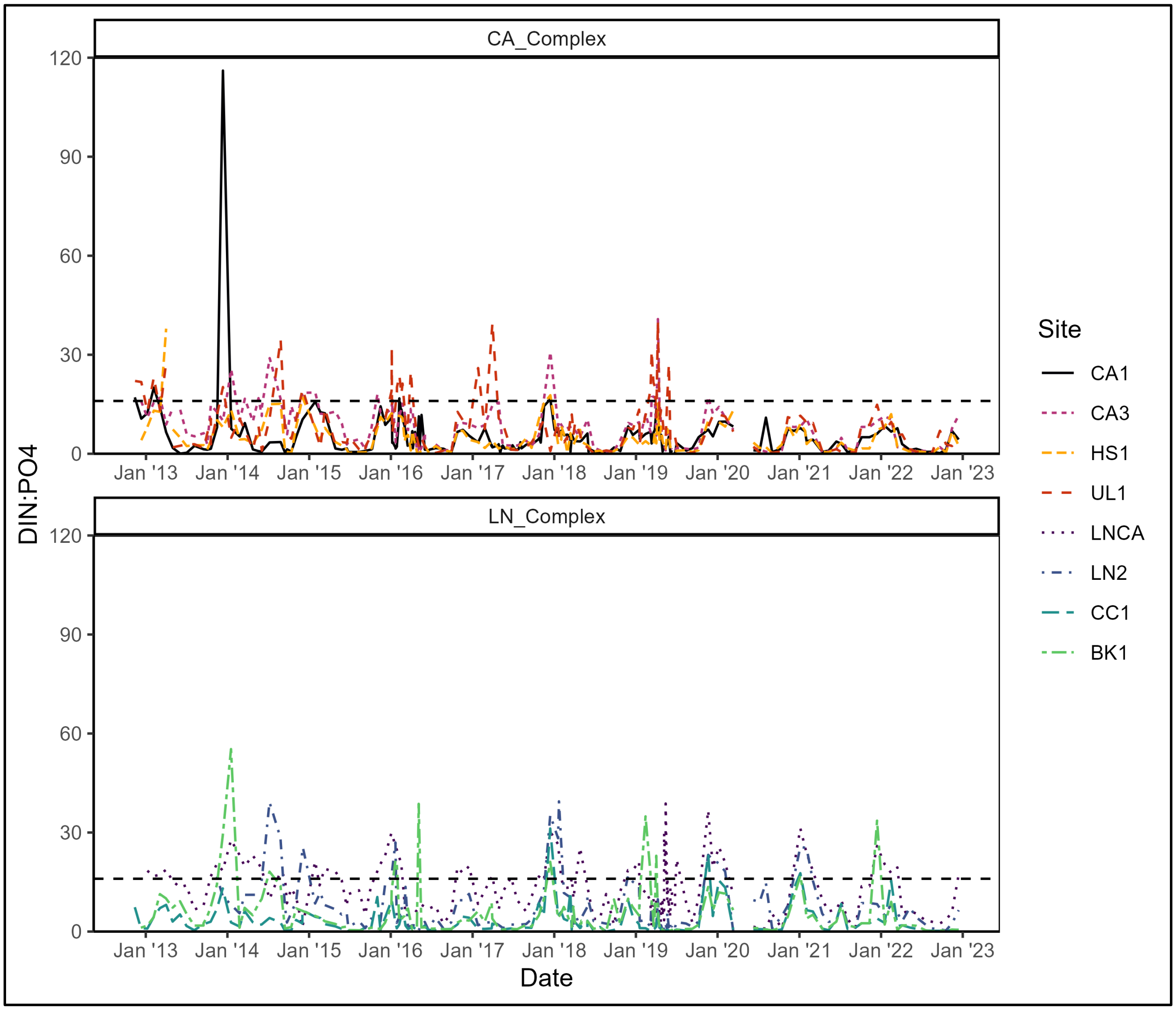

Figure 12. Molar ratio of dissolved inorganic nitrogen to phosphate (DIN:PO4) based upon monthly values at water-quality sites. The horizontal dashed line is the Redfield ratio (16:1), which is the ratio of nitrogen to phosphorus in phytoplankton – values above this line indicate phosphorus limitation and those below the line indicate nitrogen limitation for phytoplankton growth. Top panel (CA_Network) includes Cache Network sites and bottom panel (LN_Network) includes Lindsey Network sites.

Chlorophyll- Generally paralleling suspended-sediment and nutrient concentrations, both chlorophyll *a* and pheophytin *a* were highest in upstream sites of the Cache Network (CA1 and UL1, followed by HS1; Figure 13). Concentrations at the Cache-Lindsey confluence and in the Lindsey Network were consistently low, except for the occasional high value at BK1 and LN2. In 2022, there were very high chlorophyll-*a* and somewhat high pheophytin-*a* concentrations at HS1, CA3, and CA1 in spring.

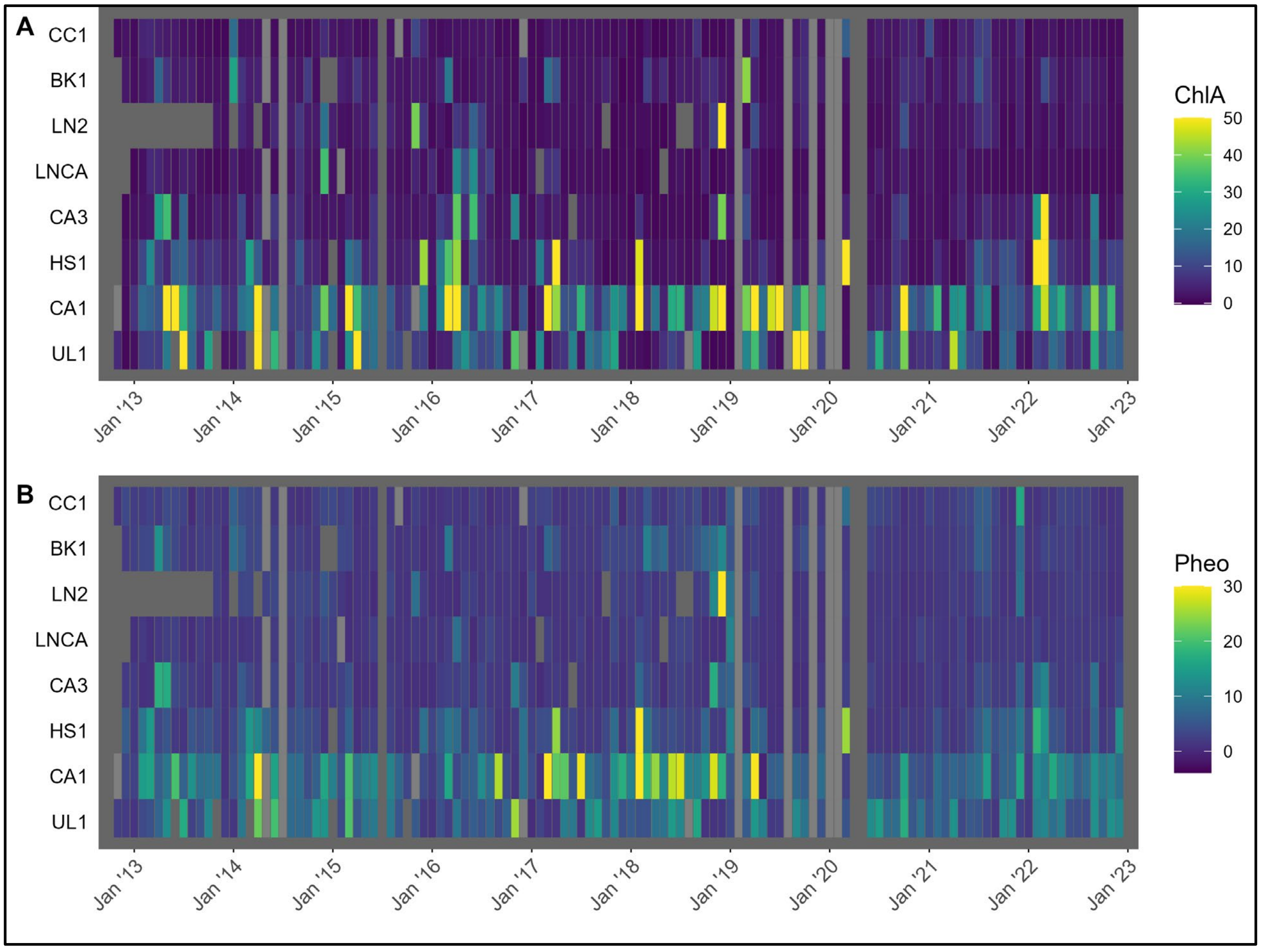

Figure 13. Monthly chlorophyll *a* (ChlA) and pheophytin *a* (Pheo), in micrograms per liter (µg/L), at water-quality sites.

Fish and Aquatic Vegetation

Aquatic Vegetation

Aquatic vegetation captured in otter trawls increased through 2020 before declining in 2021 and 2022 (Figure 14). Most samples were dominated by the invasive Brazilian waterweed (*Egeria densa*). The largest volumes previously occurred at CC1 until 2018 when BK1 and CA3 were heavily colonized, then another shift occurred in 2020 when dense beds of Brazilian waterweed formed at HS1. Substantial increases occurred at BK1, CA1, CA2, CA3, and HS1 over the study period. Several sites had little to no aquatic vegetation at the onset of the study, including all the Cache Network, but all contained some by 2018. In 2022, vegetation dropped to its lowest annual average since 2015. Vegetation drastically decreased after July 2021 and remained low to July 2022, hit a peak in August (with Lindsey Network somewhat denser than Cache) and then slowly declined in catch throughout the year (Figure 15).

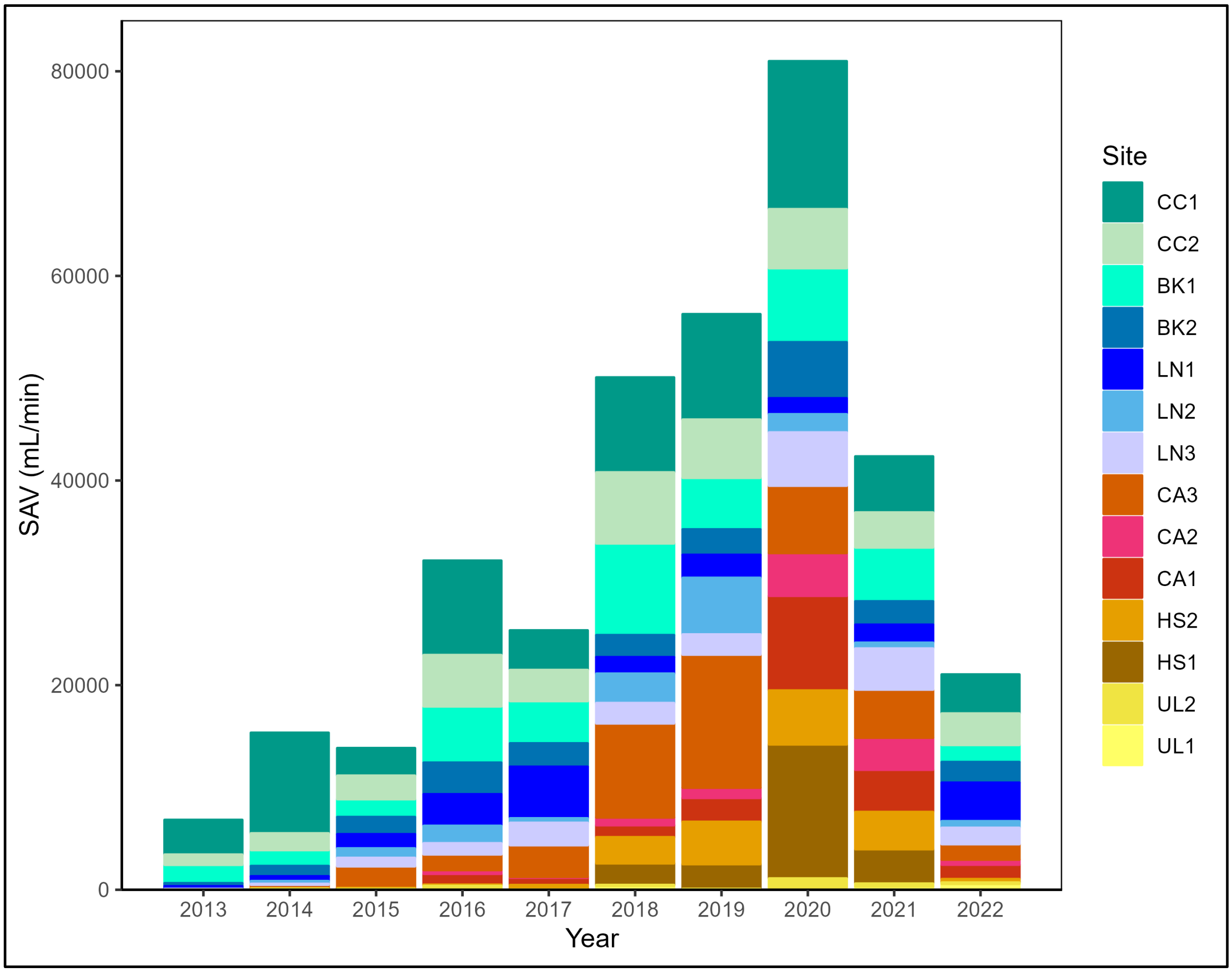

Figure 14. Annual CPUE of submersed aquatic vegetation (SAV) (mL/minute) retrieved in otter trawls at different sites from 2013-2021.

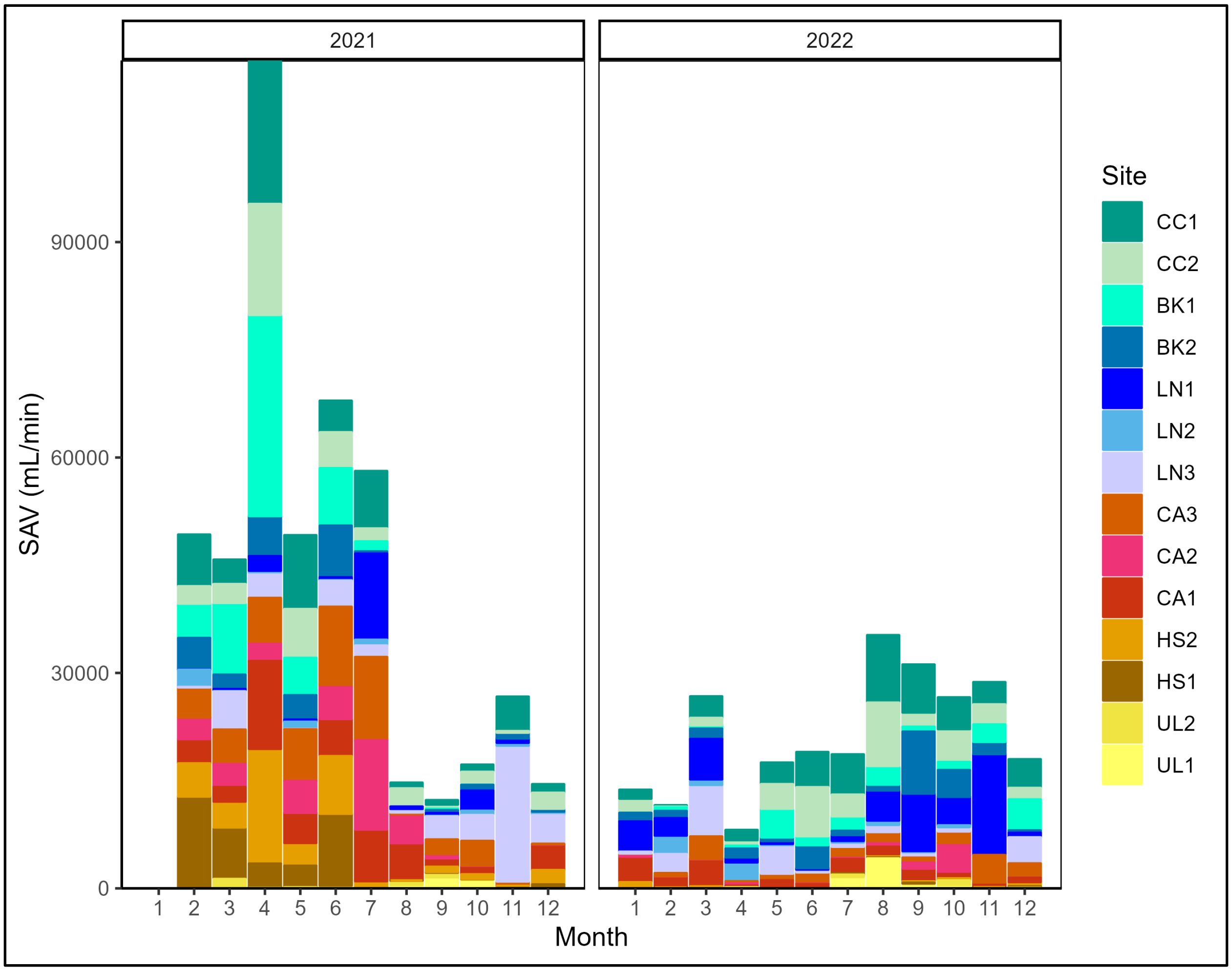

Figure 15. Monthly CPUE of SAV (mL/minute) retrieved in otter trawls at different sites from 2021 - 2022.

Fish Assemblage

Temporal patterns

Non-native fishes made up a greater proportion of catch than natives throughout the study period. Non-native fish proportion increased in otter trawls from 2013 to 2015, remained high until 2020, and then became more variable and lower overall through 2022 (Figure 16). Non-native fish proportion was variable in electrofishing catch, with a peak in 2016 and 2017 (Figure 17). Native fishes were typically at higher abundance during spring in both otter-trawl and electrofishing catches. In 2022, a relatively high proportion of native fishes persisted through most the year, with the highest proportion for otter trawl since 2014 and the highest-ever proportion for electrofishing captured in spring (Figure 16 and 17). Three native species – hitch, prickly sculpin, and tule perch – made a resurgence in 2021 and continued to be high in 2022, with the highest-ever otter-trawl CPUE for a given month for hitch and prickly sculpin (Figure 18), and highest catch of prickly sculpin in spring electrofishing (Figure 19).

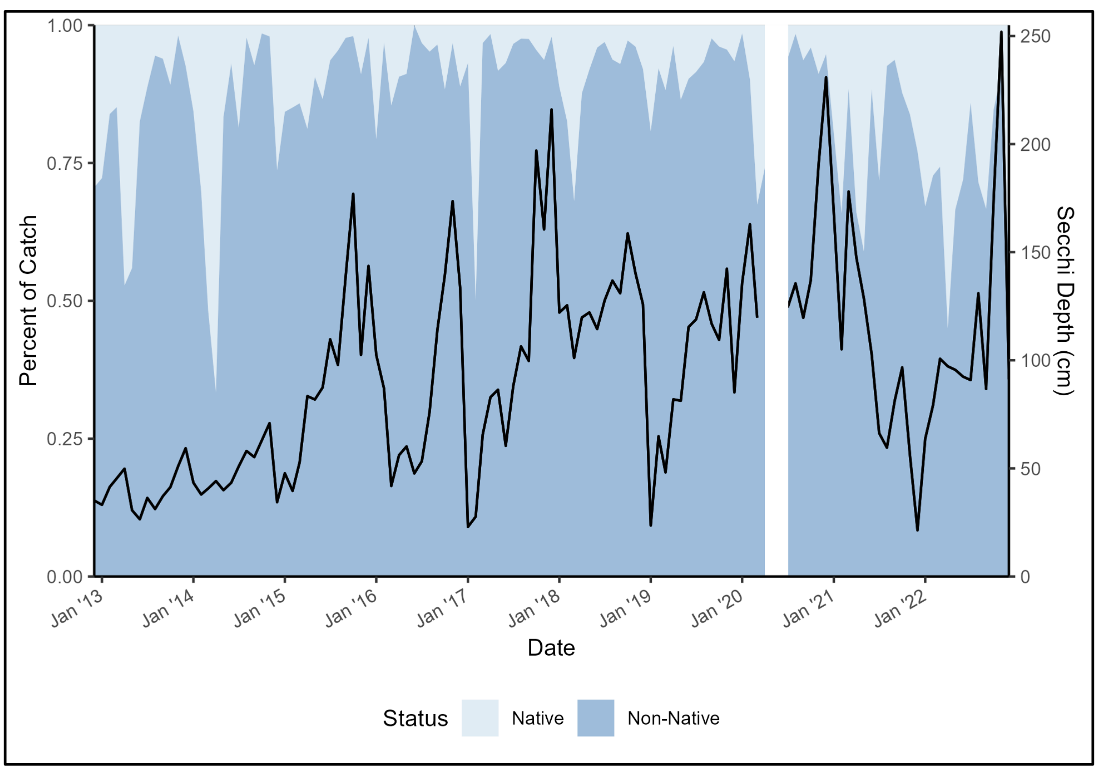

Figure 16. Percent of CPUE of fishes by native or non-native status from otter trawls. Secchi depth, a measure of water clarity, is represented by the black line. White space = no sample.

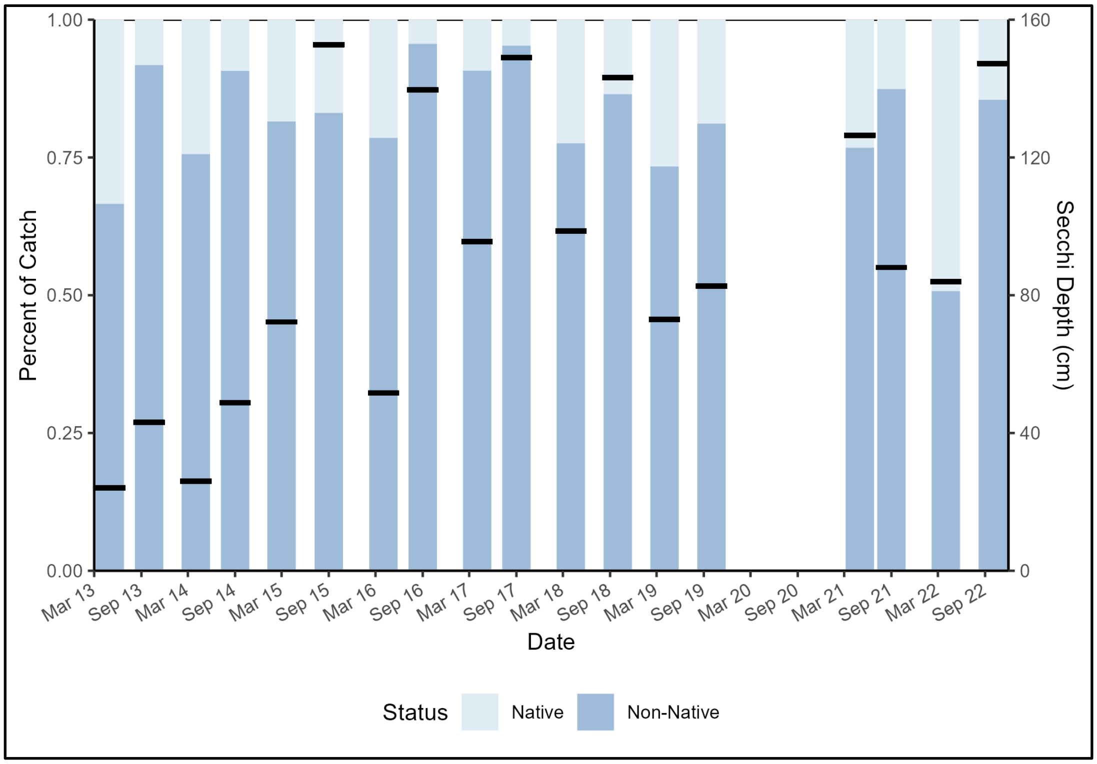

Figure 17. Percent of CPUE of fishes by native or non-native status from electrofishing. Mean Secchi depth, a measure of water clarity, is represented by the horizontal black lines. White space = no sample.

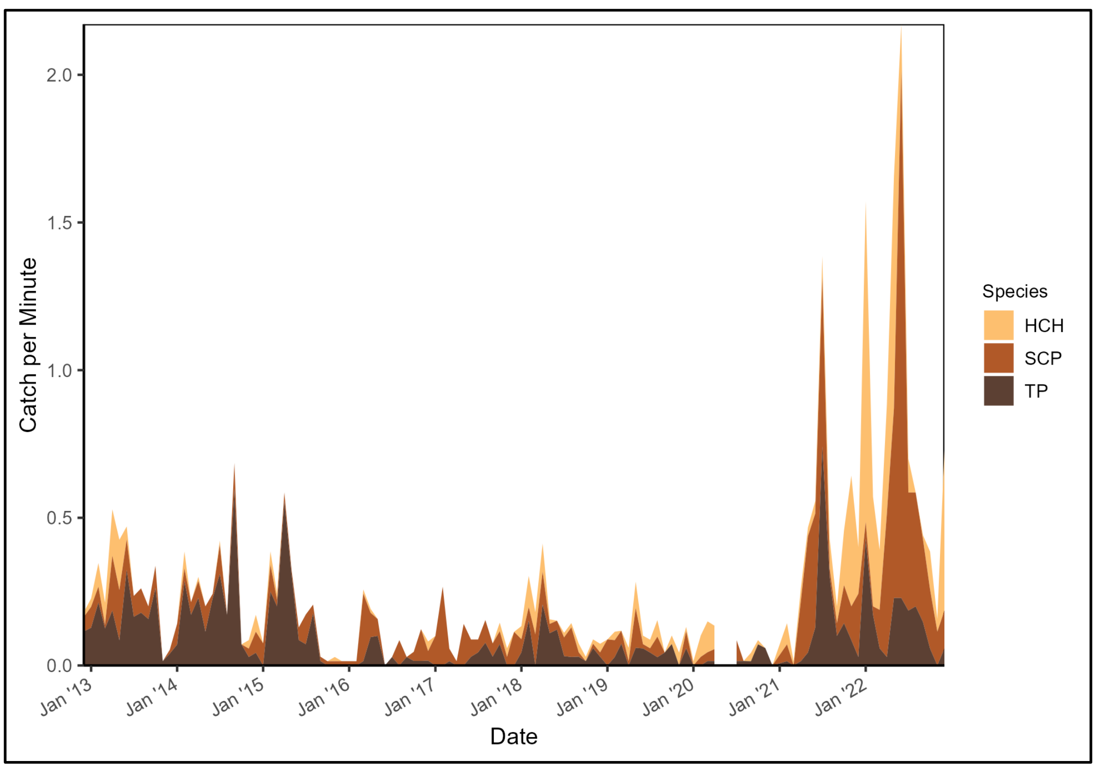

Figure 18. Monthly catch per minute of hitch (HCH), prickly sculpin (SCP), and tule perch (TP) from otter-trawling. White space = no sample.

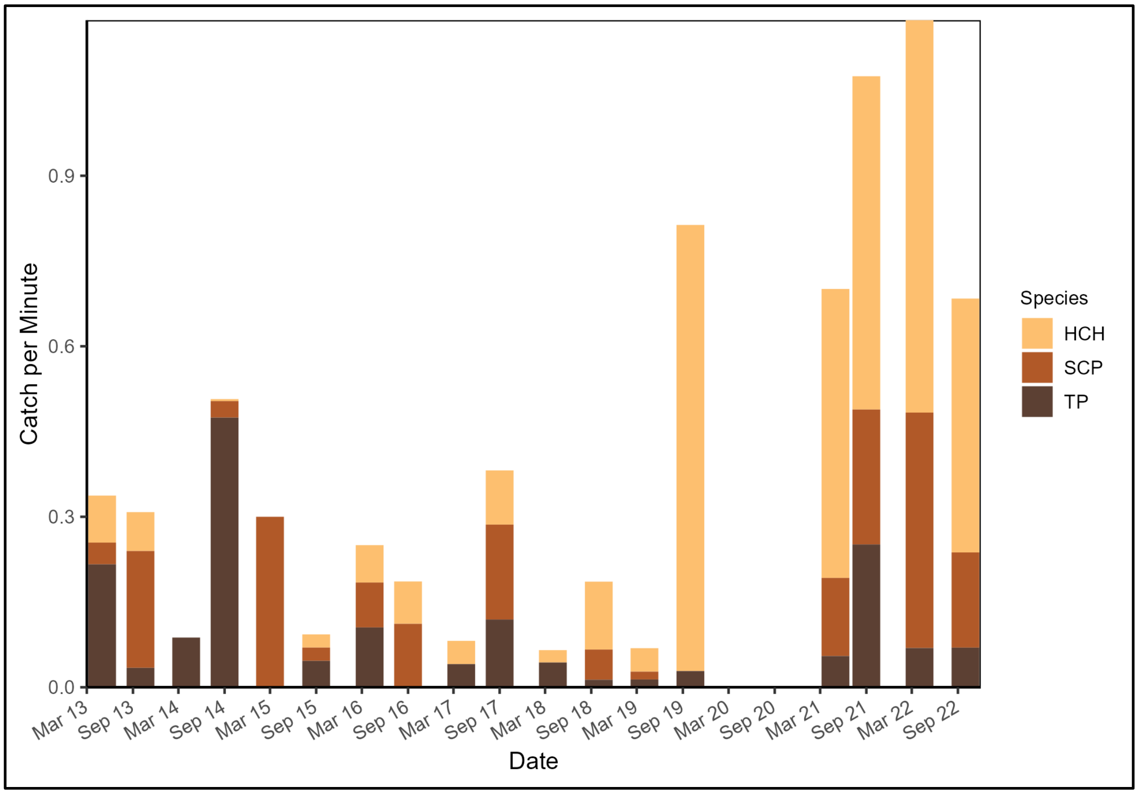

Figure 19. Monthly catch per minute of hitch (HCH), prickly sculpin (SCP), and tule perch (TP) from electrofishing. White space = no sample.

Both otter-trawl and electrofishing CPUE in the CLC was dominated by pelagic and littoral fishes (Figure 20 and 21), with the littoral group generally having increased over the study period. Otter-trawl CPUE underwent seasonal shifts, with fish generally being least abundant during winter. Abundances of the habitat-associated groups were somewhat seasonal, with littoral fishes typically dominating otter-trawl catches in spring and pelagic fishes dominating otherwise (Figure 22). All habitat-associated groups were typically more abundant in autumn than spring for electrofishing (Figure 23). Littoral-associated species seasonally dominated otter-trawl CPUE for the duration of the study, with year-round elevated CPUE in 2018 and 2019, and dominated all electrofishing samples (Figure 22 and 23). There have been shifts in habitat associated groups, with pelagic fishes being dominant at the beginning of the study, then 2016 to 2021 generally having relatively low pelagic catch and higher littoral and benthic catch, and since 2021, an increase in both pelagic and benthic species.

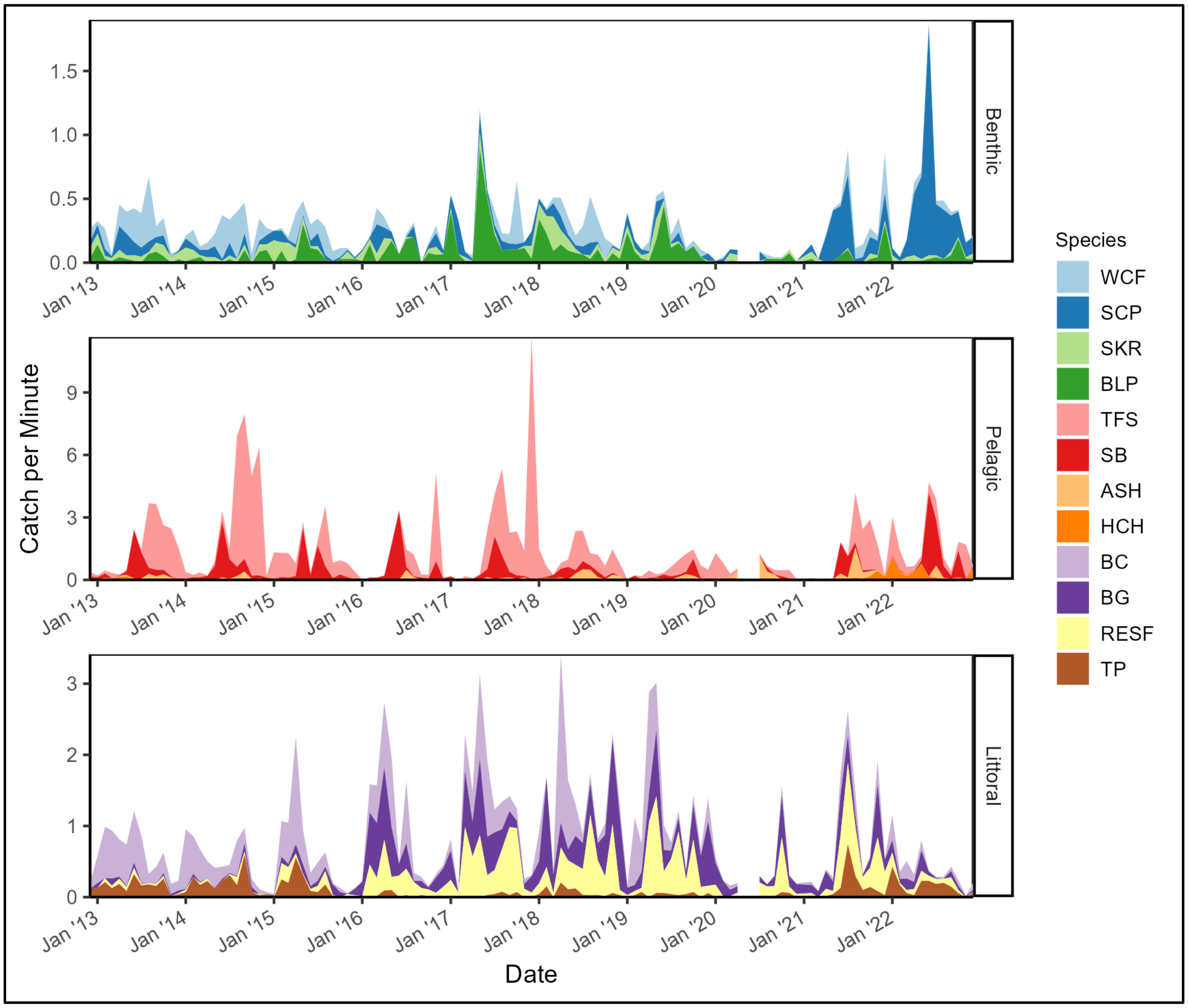

Figure 20. Monthly catch per minute of fishes from otter trawls separated by habitat association (benthic, pelagic, and littoral species). Included are the four most abundant species in otter trawl catch for each habitat-association grouping over the survey period (2013-2022). Note differences in scale along the Y-axes. White space = no sample. WCF = white catfish, SCP = prickly sculpin, SKR = Sacramento sucker, BLP = bigscale logperch, TFS = threadfin shad, SB = striped bass, ASH = American shad, HCH = hitch, BC = black crappie, BG = bluegill, RESF = redear sunfish, TP = tule perch.

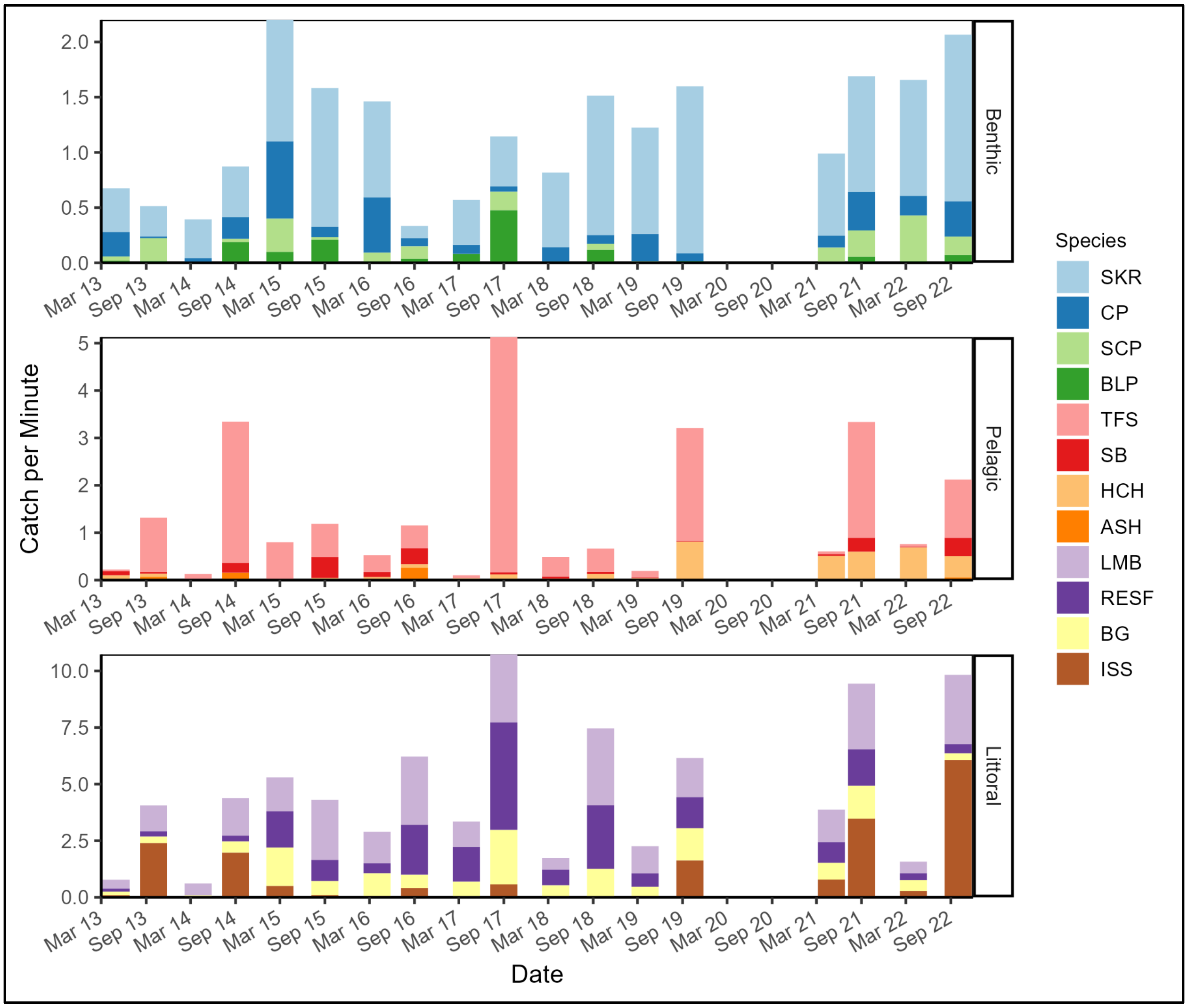

Figure 21. Monthly catch per minute of fishes from spring and autumn electrofishing separated by habitat association (benthic, pelagic, and littoral species). Included are the four most abundant species in electrofishing catch for each habitat association grouping over the survey period (2013-2022). Note differences in scale along the y-axes. White space = no sample. CP = common carp, LMB = largemouth bass, ISS = Mississippi silverside.

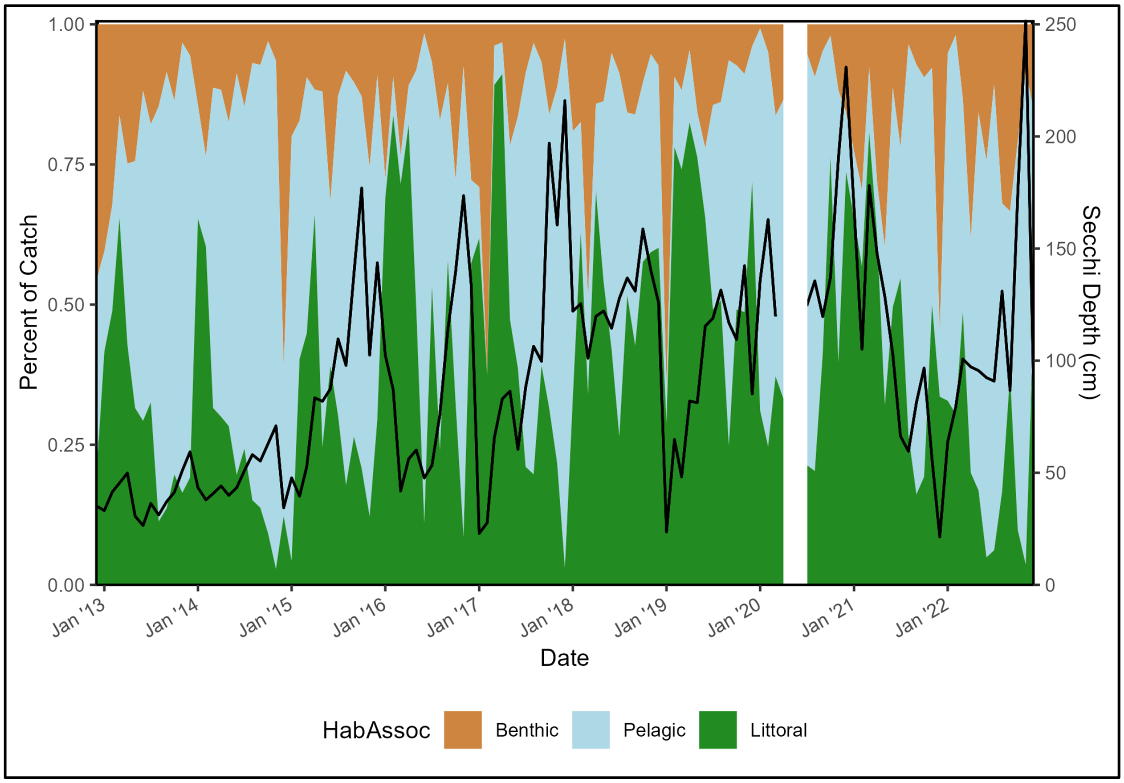

Figure 22. Percent of CPUE of fishes by habitat association from otter trawls. Secchi depth, a measure of water clarity, is represented by the black line. White space = no sample.

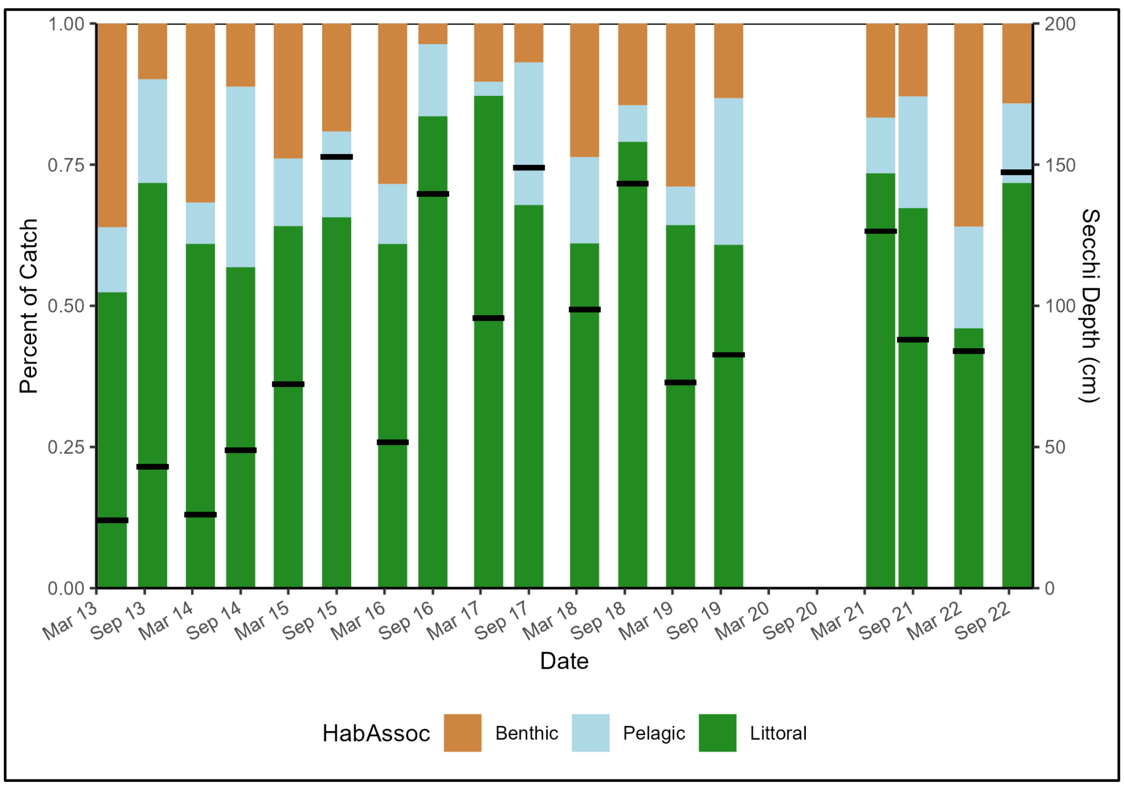

Figure 23. Percent of CPUE of fishes by habitat association from spring and autumn electrofishing. Secchi depth, a measure of water clarity, is represented by the horizontal black lines. White space = no sample.

The benthic-associated group was comprised mostly of Sacramento sucker (SKR) in electrofishing catch and shifted from white catfish (WCF; 2013-2015) to bigscale logperch (BLP; 2015-2020) to prickly sculpin (SCP; 2020-2022) in otter-trawl catch (Figures 20 and 21). Benthic species often accounted for the highest proportion of total catch in winter and their relative proportion remained fairly stable throughout the study period (Figures 22 and 23).

The pelagic-associated group was dominated by threadfin shad (TFS; Figures 20 and 21), with peak numbers occurring in late summer and early autumn. Also seasonally abundant were striped bass (SB), which appeared mostly in early summer as juveniles. Both striped bass and threadfin shad remained seasonally abundant throughout the study but declined in catch from 2017 to 2021 and subsequently became the most abundant pelagic species in 2022 in otter-trawl catch. Listed Delta smelt and longfin smelt numbers, while never high, were negligible after 2014. Delta smelt were never abundant during the study, and the last capture occurred in May 2015. Longfin smelt were captured at a slightly higher rate, but only rarely after spring 2014 and none after April 2018.

Non-native sunfishes dominated across most of the study period (Figures 20 and 21). Representing a relatively small fraction of the CPUE in 2012-13, they came to dominate catches by 2015 and continued increasing in abundance until 2022. In 2022, sunfish abundance decreased in both otter-trawl and electrofishing catches. Comparing the otter-trawl CPUE of the most abundant sunfishes, bluegill (BG) and redear sunfish (RESF), with the ecologically similar native tule perch (TP; Figures 20 and 21), tule perch became rare in catches from 2015 to 2021, while redear sunfish and bluegill increased dramatically. A big change occurred in 2022, when redear and bluegill were replaced by tule perch, with tule perch making up the highest proportion of littoral fish catch in otter trawls. A shift from sunfish to Mississippi silverside (ISS) also occurred, with Mississippi silverside making up the highest proportion of electrofishing catch in 2021 and 2022 (Figure 21). Electrofishing showed similar trends but captured many more largemouth bass (LMB) as a proportion of the overall CPUE.

Spatial Differences

Non-native fishes dominated at all sites, although some sites appeared more favorable to natives than others. Natives comprised a higher proportion of the otter-trawl CPUE at CA3, CC1, and CC2 (Figure 24). The proportion of natives in otter-trawl catch was greatest at the most downstream site (CA3) for the Cache Network but increased from downstream to upstream sloughs (LN to BK and CC) in the Lindsey Network. In contrast to otter trawl, natives comprised a higher proportion of the electrofishing CPUE in all Cache Network sites than in the Lindsey Network sites (Figure 25). Proportion of natives in electrofishing catch increased from downstream to upstream for both slough networks.

Prickly sculpin and tule perch were the two most abundant native species in otter trawls, and Sacramento sucker and tule perch in electrofishing samples (Figures 26 and 27). Sacramento sucker were more commonly caught in Cache Network sites, while tule perch tended to be well-distributed across all sites. Hitch were most abundant in Cache Network sites in otter-trawl sampling but most abundant in Lindsey Network sites in electrofishing samples. Threadfin shad were the most abundant non-native species in both slough networks in otter-trawl catch. Threadfin shad and largemouth bass dominated electrofishing catch in the Cache Network, and redear sunfish and largemouth bass were most abundant in the Lindsey Network.

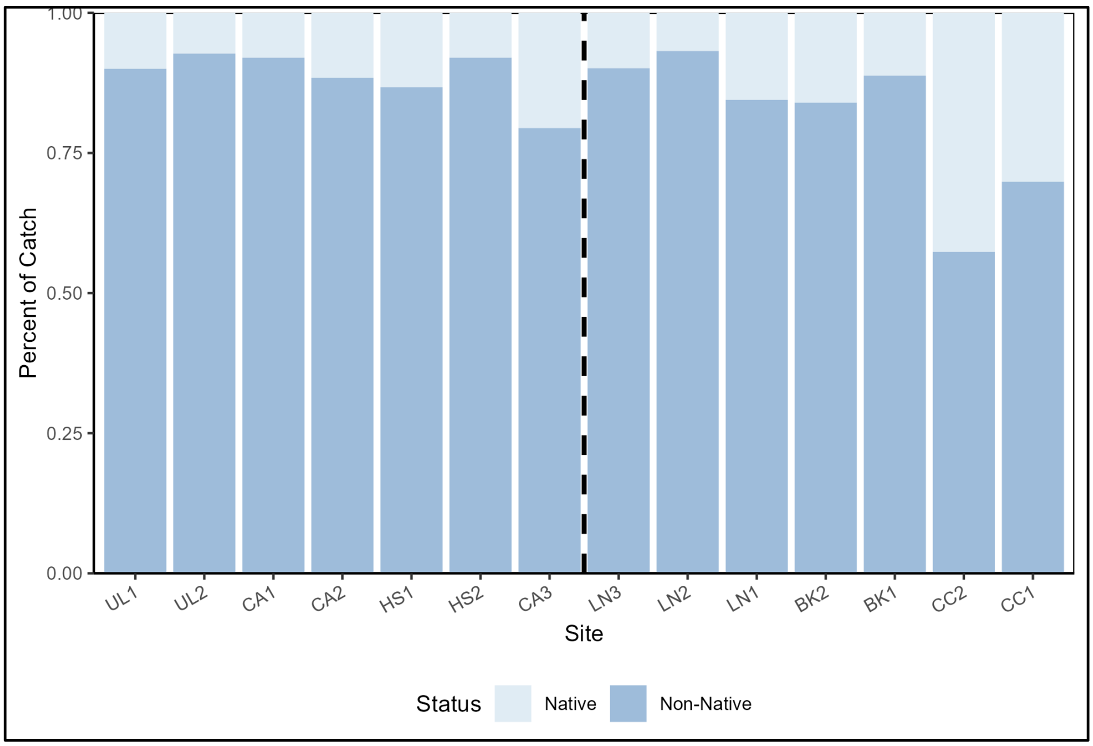

Figure 24. Percent of CPUE of fish species by native/non-native status across otter-trawl sites from January 2013 to December 2022.

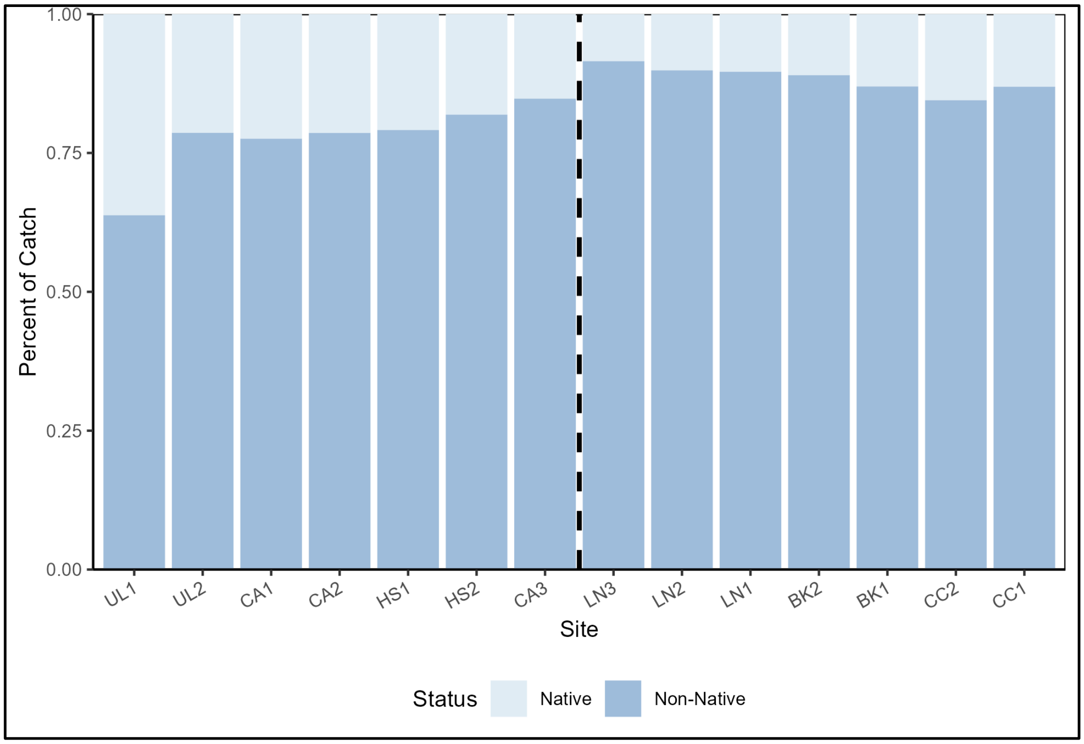

Figure 25. Percent of CPUE of fish species by native/non-native status across electrofishing sites from January 2013 to December 2022.

CPUE was overall greater in the Cache Network than the Lindsey Network for otter-trawl catch (Figure 26). Abundance increased from downstream to upstream in the Cache Network, with lowest CPUE at CA3 and highest at CA1 and UL1 (Figure 26). In the Lindsey Network, total CPUE increased from downstream to upstream through Barker Slough, but Calhoun Cut, although further upstream, had the lowest otter-trawl CPUE of any slough (Figure 26). CPUE was somewhat uniform between Cache and Lindsey networks for electrofishing (Figure 27). No strong longitudinal patterns existed, but Lindsey Slough tended to have a higher CPUE than the smaller upstream sloughs in the Lindsey Network, and Ulatis Slough had the highest abundance in the Cache Network (Figure 27).

Otter-trawl CPUE of pelagic and benthic fishes increased from downstream to upstream in the Cache Network, driving the overall abundance pattern (Figure 26). Otter-trawl CPUE of littoral and benthic fishes increased from downstream to upstream in the Lindsey Network, except that littoral CPUE was lowest in Calhoun Cut (Figure 26). Electrofishing CPUE of benthic fishes increased and littoral fishes decreased from downstream to upstream in the Cache Network (Figure 27). No strong patterns existed longitudinally for electrofishing CPUE for any of the habitat-associated fishes in the Lindsey Network (Figure 27).

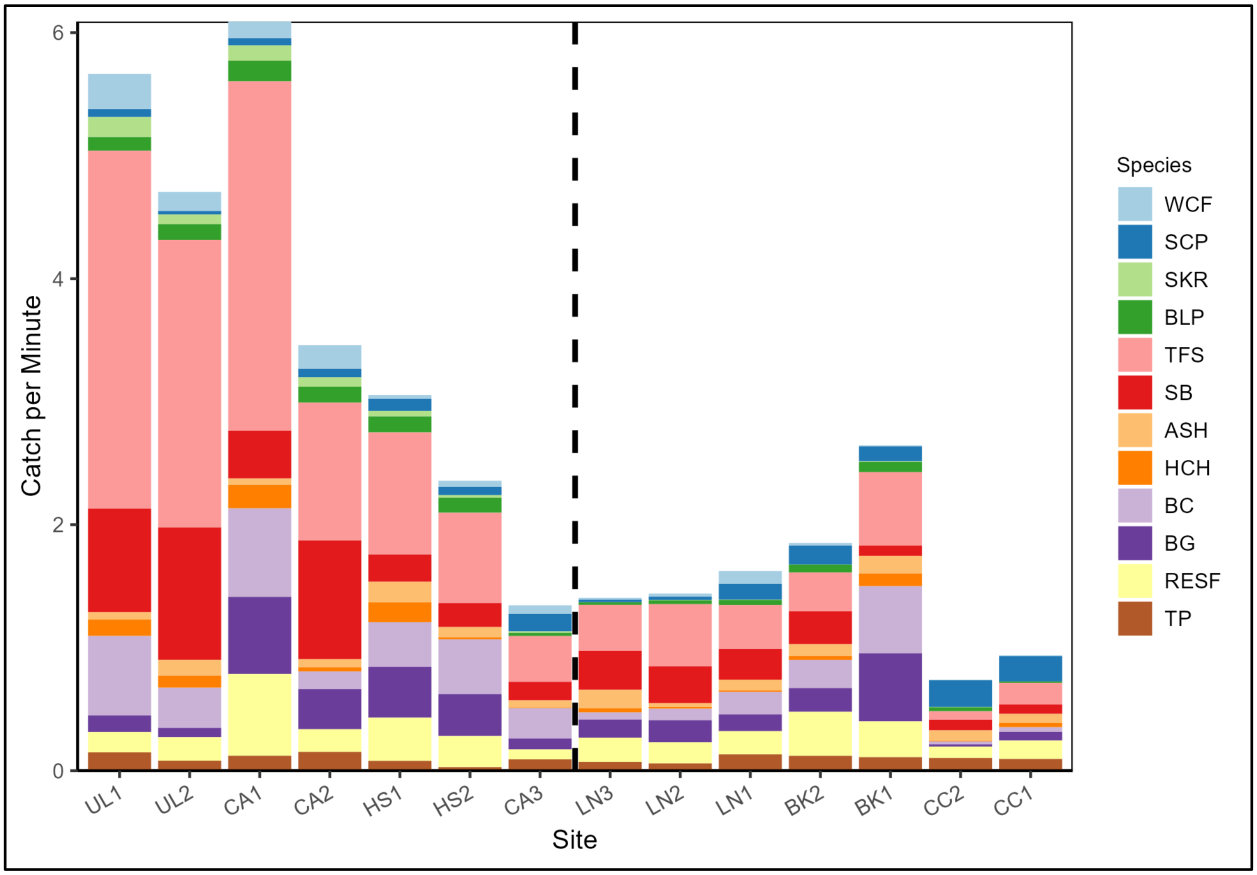

Figure 26. Catch per minute of fish species across otter-trawl sites from January 2013 to December 2022. Included are the four most abundant species in otter trawl catch for each habitat association grouping (benthic, pelagic, littoral) over the survey period (2013-2022). Dashed vertical line separates Cache and Lindsey networks.

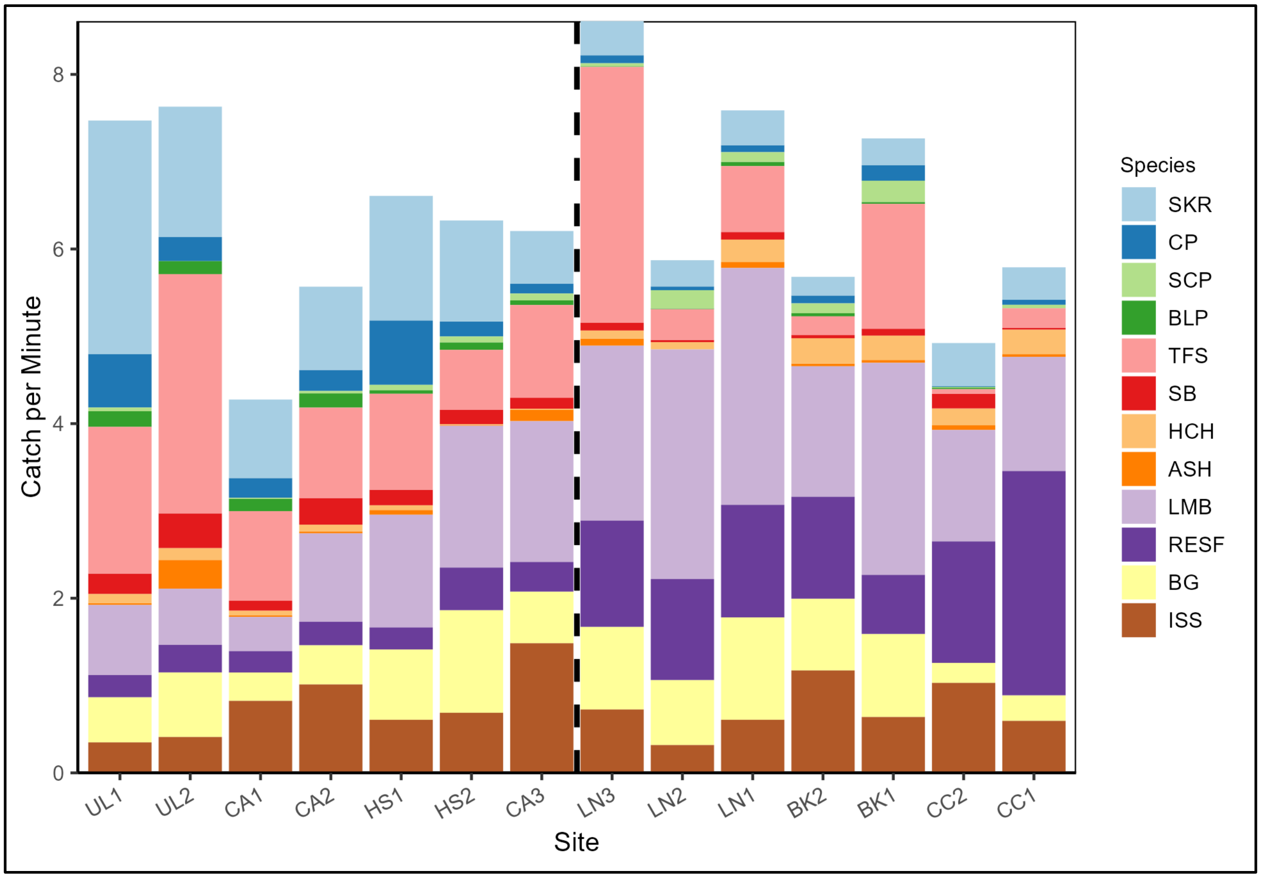

Figure 27. Catch per minute of fish species across electrofishing sites from January 2013 to December 2022. Included are the four most abundant species in electrofishing catch for each habitat association grouping (benthic, pelagic, littoral) over the survey period (2013-2022). Dashed vertical line separates Cache and Lindsey networks.

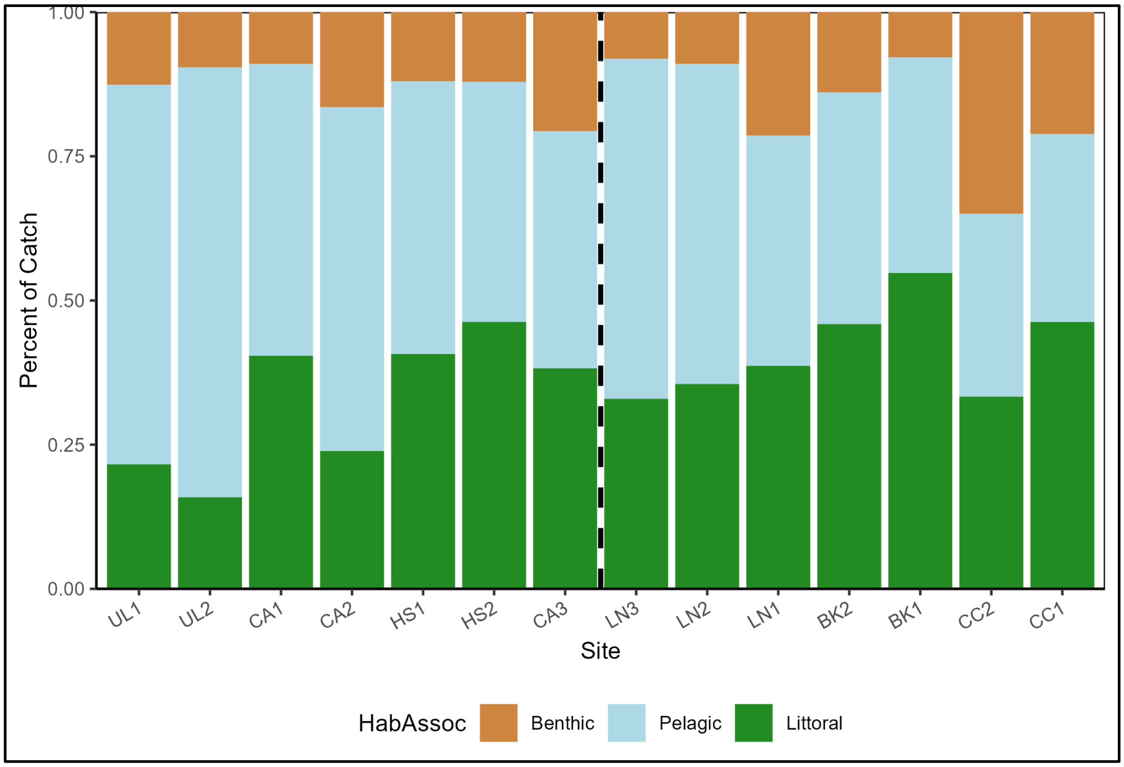

Figure 28. Percent of CPUE of fish species by habitat association (benthic, pelagic, littoral) across otter-trawl sites from January 2013 to December 2022.

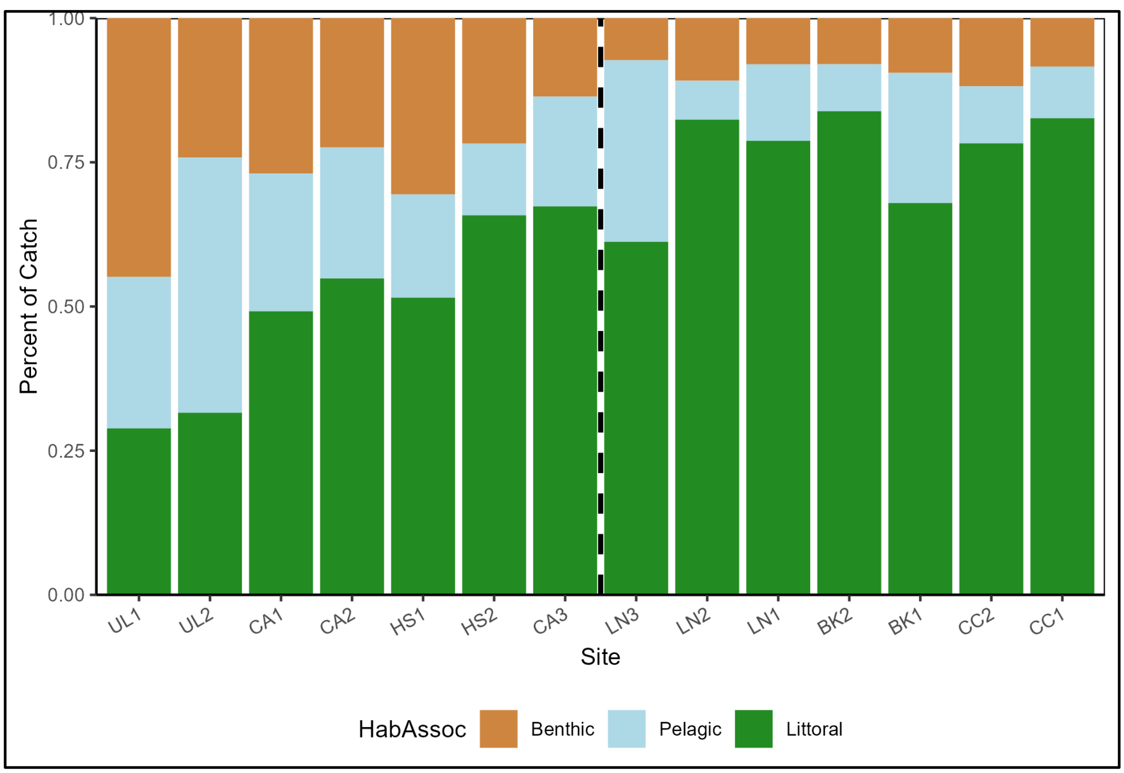

Figure 29. Percent of CPUE of fish species by habitat association (benthic, pelagic, littoral) across electrofishing sites from January 2013 to December 2022.

Benthic species did not vary much between the networks in otter trawls but were much more abundant in the Cache Network in electrofishing catch (Figures 26 and 27). Benthic species made up the highest proportion of the otter-trawl catch at two Lindsey Network sites, CC2 and LN1, and a higher proportion of electrofishing catch in all the Cache Network sites (Figures 28 and 29). Sacramento sucker, white catfish, common carp, and bigscale logperch were more abundant in the Cache Network, while prickly sculpin and Sacramento sucker were the dominant benthic fish in the Lindsey Network (Figures 26 and 27).

Pelagic species were more abundant in the Cache Network but made up a fairly even proportion of catch between networks for otter-trawl catch (Figures 26 and 28). Pelagic species were overall more abundant and made up a higher proportion of electrofishing catch in the Cache Network, but they were also quite abundant and made up a high proportion of the catch at two Lindsey Network sites, LN3 and BK1 (Figures 27 and 29). For both networks, threadfin shad were the most abundant pelagic species in otter-trawl and electrofishing catches; striped bass and hitch tended to be the second most-abundant pelagic fishes in the Cache Network and the Lindsey Network, respectively.

Sunfishes made up a majority of the littoral CPUE in otter-trawl and electrofishing samples (Figures 26 and 27). Black crappie were the most abundant littoral fish caught with otter trawls in the Cache Network and Barker Slough, with redear sunfish or bluegill being the dominant littoral species in other Lindsey Network sites. Largemouth bass were the dominant littoral species in electrofishing catch, and largemouth bass and redear sunfish were more abundant in Lindsey Slough sites. Bluegill appeared to be somewhat evenly distributed across all sites and both gear types. Mississippi silversides were common in electrofishing catch across both complexes.

Restoration Comparison

The Lindsey restoration generally had lower catches than surrounding waterways, but a similar proportion of native fishes (Figure 30). Both the Lindsey restoration and surrounding waterways hit peak abundance in autumn 2017, declined until 2021, and exhibited increasing abundance since. In 2022, the Lindsey restoration had a similar abundance of fish to surrounding sites in spring and lower abundance in autumn, but virtually no natives were caught within the restoration during the year.

The North Liberty Island Mitigation Bank restoration generally had a lower abundance and proportion of natives compared to surrounding sites (Figure 30). NLIMB autumn electrofishing CPUE steadily increased until 2019 and plateaued, while spring CPUE peaked in 2018 then remained low – this pattern was similar to surrounding sites, except adjacent sites had more pronounced peaks in autumn in wet years (2017 and 2019; Figure 30). In 2022, abundance of fishes was much higher in NLIMB surrounding sites than in the restoration itself, and proportion of natives was similar. March had the highest proportion of native fishes in NLIMB for our study period in the region, which was driven by hitch abundance.

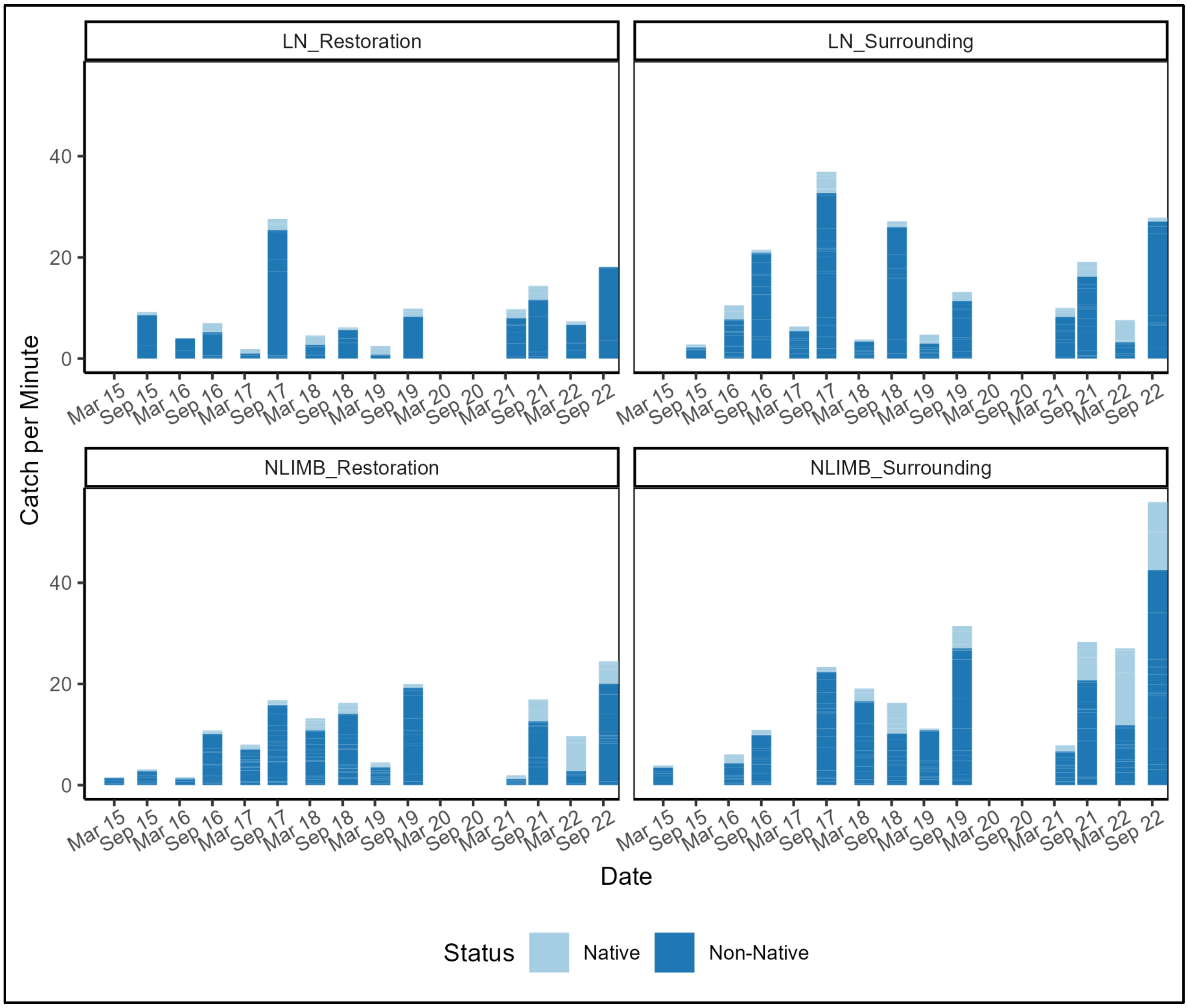

Figure 30. Percent of CPUE of fish species by native/non-native status across sites from electrofishing in restoration and restoration-adjacent sites (CC1 and CC2 for Lindsey Restoration; SS1 and PR1 for NLIMB). White space = no sample.

Discussion

From 2012 - 2022, the CLC was subject to drought, record floods, experimental water releases from the Yolo Bypass, changes to upstream wastewater treatment discharge, and tidal restoration. Our study captured a suite of responses to these dynamic conditions, with the most profound being the proliferation and subsequent die back of aquatic weeds. During the 2012-16 drought, aquatic weeds expanded concurrently with much clearer water, decreased zooplankton abundance, and increased abundance of non-native sunfishes. Persistence and expansion of weeds and sunfishes during the wet years of 2017 and 2019 seemed to indicate a shift to a stable, littoral-dominated ecosystem. Upstream ends of small sloughs with freshwater inflows appeared resilient to the ecosystem shift, remaining turbid and supporting relatively high numbers of plankton and native fishes, but by 2020 even upstream reaches were weed-choked and dominated by non-native species. However, in 2021, aquatic weeds declined substantially, accompanied by an increase in several native species and a decrease in nonnative sunfishes that persisted through 2022. Determining the trigger of weed decline and ongoing suppression is important for managing the ecosystem to support native fishes and maintain pelagic habitat.

Temporal Changes

Over the study period, water quality changed substantially in the Lindsey Network and near the confluence, with decreasing measures of suspended material in the water column (i.e., turbidity, VSS, and TSS). These water-quality changes were likely driven by the expansion of aquatic weeds in the area. Submersed vegetation, such as Brazilian waterweed, has been shown to slow water and capture sediment in the southern Delta (Santos et *al.* 2011; Hestir et *al.* 2016) . While proximity of the CLC to Yolo Bypass and Ulatis Creek (both of which provide detritus, sediment, and scouring flows) may have delayed the spread of aquatic weeds, the duration and intensity of the 2012-16 drought, which limited flooding on the bypass and reduced flows, appeared to offer an opportunity for invasion. The pattern of invasion changed in July 2021, when we observed rooted aquatic weeds coated in filamentous algae; by the following month, the weeds had died back and remained low through 2022. We hypothesize that the algae blocked sunlight from reaching the rooted weeds and caused them to senesce. The die-back coincided with the upgrade of the Sacramento Regional Wastewater Treatment Plant to tertiary treatment, which virtually eliminates ammonium from the water and reduces the total amount of nitrogen released. However, nitrogen in the CSC comes mostly from local upstream sources and not the Sacramento River (Fackrell et *al.* 2022), and no changes to nitrogen concentrations were noted after the upgrade, except for a reduction in ammonium at the most downstream site, LNCA. Water quality did not vary notably before the die back, so the mechanism that caused the flourishing of the filamentous algae remains unknown.

Delta outflow seems to have an impact on fish abundance and species presence in the North Delta, but the magnitude of that impact has changed. Prolonged low flow with drought drove a shift in the assemblage, but subsequent wet years did not shift it back. Wet years and decreased water clarity often correspond to increased fish numbers in the estuary, particularly for natives (O'Rear *et al.* 2021). Although high flows and slightly decreased water clarity both occurred in 2019, fish abundance in the CLC did not increase notably. Also, the proportion of native to non-native species remained low in otter-trawl catch through the wet year of 2019, with an increase in the dry year of 2021. Changes in habitat association in the CLC did not change as expected with water-year type. These trends indicate that some of the changes associated with aquatic weeds may dampen the effects of delta outflow.

The rapid expansion of aquatic weeds during the drought co-occurred with changes in the fish assemblage. Historically the Delta was much more turbid, and native fishes are adapted to these conditions. Increasing water clarity tends to decrease habitat for native species while improving conditions for many nonnative fishes, especially sunfishes – such as bluegill, redear sunfish, and largemouth bass. Consistent with shifting conditions, native smelt species nearly disappeared while abundance of sunfishes dramatically increased. Tule perch, a normally ubiquitous species endemic to lowland rivers and estuaries in California, declined dramatically during the study until 2021, when it increased with decreasing volume of aquatic weeds and remained common through 2022. Catch of other species – notably native prickly sculpin and hitch, and non-native threadfin shad, American shad, striped bass, and Mississippi silverside – increased during 2021 and 2022 to abundances not observed since 2017. We did not see a resurgence of any smelt species, likely indicating a temperature threshold has been passed that inhibits these cool-water fishes. Mississippi silverside, although a littoral species, appeared to be negatively associated with aquatic weeds, corroborating a study that found the species more associated with marsh habitat and shallow water than with aquatic weeds (Young et *al.* 2018).

Spatial Differences

Spatial differences between the two slough networks were exacerbated by the drought. Early in the study, the upper Cache Network remained more resilient to changes than the Lindsey Network and the confluence: turbidity, VSS, TSS, phosphorus, nitrogen, and chlorophyll *a* all remained considerably high. However, 2018-2020 saw major shifts in all but Ulatis Creek and the uppermost Cache Slough site. Concomitantly, zooplankton densities were often higher in the Cache Network, in particular CA1 and UL1 (Williamshen et *al.* 2022). The resiliency of the Cache Network was surprising because it lacks the complex physical structure and habitat (emergent wetlands and a restoration site) of the Lindsey Network. But Ulatis Creek and agricultural runoff provided Cache Slough with fresh water, detritus, and nutrients, and may have slowed the encroachment of aquatic weeds into the network's upper reaches.

In the Cache Network we observed a hypoxic event in Cache and Hass sloughs in September 2022. At HS2 we trawled up five dead fish – including a bigscale logperch, Mississippi silverside, Sacramento Sucker, tule perch, and yellowfin goby – and measured dissolved oxygen at 0.5 mg/L. This low DO event and fish-kill occurred following a short, intense storm that may have mobilized large quantities of organic material from recently harvested fields. Timing and duration of autumn storms may have the potential to cause events like this again at sights that have upstream connection to agricultural land.

Differences in water quality and plankton production between the Cache and Lindsey networks were paralleled by fish catch and assemblage. POD species, which need zooplankton for at least part of their life cycle, were most abundant in the upper Cache Network while being rarer in most of the Lindsey Network. The most abundant POD species in the region was threadfin shad, which moved seasonally into the upper reaches of the Cache Network where zooplankton concentrations were higher (Montgomery et *al.* 2016, Montgomery 2017). The second most-abundant POD species was juvenile striped bass, which was also seasonally more abundant in the Cache Network. Catch of sunfishes by electrofishing tended to be highest in the Lindsey Network, especially for redear sunfish and largemouth bass, likely because it was weedier, although bluegill were also common in the Cache Network. Black crappie tended to be more prevalent in Cache Slough and Ulatis Creek, probably because they are more well-suited for open-water, turbid conditions and are well-adapted for eating zooplankton. The somewhat higher otter-trawl catch of sunfishes in the Cache Network was likely due to higher turbidities coupled with less submersed vegetation, resulting in movement of sunfishes away from edges and into the channel thalweg where the trawl sampled (Todd and Rabeni 1989, Abrahams and Kattenfeld 1997, Ahrenstorff *et al.* 2009).

Conclusions

The CLC ecosystem has rapidly changed, a change facilitated by the drought. Whereas the region was once a stronghold for native species, that resiliency showed signs of weakening. In particular, the spread and persistence of non-native organisms indicate an ecological shift that may be difficult to reverse. However, a decrease in aquatic weeds in 2021 was coupled with an increase of several native fish species, indicating the ecosystem can recover given the right conditions. Tidal restorations, while providing habitat for some native species, may also support invaders, especially aquatic weeds, depending on where the restorations are in the landscape. Likewise, if conditions are unfavorable in channels adjacent to restorations, then connectivity to other parts of the Delta will be limited, inhibiting the movement of desirable fishes in and out of restoration sites.

Our study highlights some useful lessons and future directions:

1. Differences in physical structure between the two networks, as well as effects of tidal restoration, are superseded by the effects of hydrodynamic differences. In particular, the Cache Network benefits from periodic freshwater flows entering from Ulatis Creek and, to a lesser extent, from Hass Slough. Lindsey Slough has a small freshwater source entering from Campbell Lake into Barker Slough, but the effect of the lake's outflows and occasional high rates of primary production are muted by water withdrawals. Relocating the North Bay Aqueduct and increasing connectivity with upslope flows from Jepson and Maine Prairie may improve plankton productivity in the Lindsey Network while limiting distribution of aquatic weeds.

2. Flow pulses from upstream sources appear to support high local productivity in upper slough networks. Pulses may deliver important subsidies of nutrients to upstream reaches where phytoplankton-production potential is high, creating important regional blooms which may become rarer in the Delta with the elimination of ammonium coming from the Sacramento Wastewater Treatment Plant. Many fishes are able utilize local sources of primary and secondary production, as seen by relatively high catches of native and POD fishes in upper Cache Slough, upper Hass Slough, and Ulatis Creek. But care must be taken for timing of pulses to prevent harmful low DO events.

3. Any changes to flows or landscapes must account for aquatic weeds. Herbicides are currently used but are probably insufficiently effective over the long term and may harm the ecosystem in unknown ways. Directional flow pulses increase turbidity and help control weeds locally, presenting a management opportunity to maintain small areas of weed-free habitat. Also, promotion of filamentous algae growth to smother weed beds must be explored. The use of temporary or intermittently used

gates at restoration sites would provide a tool to drain sites and remove invasive organisms, allowing an ecosystem a fresh start. Creation of channels in restoration sites that are deep enough to inhibit colonization by aquatic weeds will favor pelagic and benthic habitat that is increasingly rare in the CLC.

4. Restorations that are designed to look like historic natural landscapes may fail to meet goals of aquatic restoration. Pervasive and permanent changes in the landscape favor the persistence of non-native species. Directing flows across tidal landscapes from upstream sources may be the most effective way of supporting restoration goals. Such directional flows increase local nutrient availability, mobilize sediment, and limit colonization by non-native weeds. New restoration projects should incorporate inflows from upland drainages that can direct sediment and nutrients into the area. An optimal hydrograph would include flow pulses in early spring to benefit food-web production for recruiting native fishes, followed by a late spring/early summer flow pulse to move them out and to help them avoid high summer temperatures. In winter, allowing increased flow could help reduce aquatic vegetation.

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Appendix I: Site data

Table A1. Site names and locations.

Site Code	Site Description	Subregion	Waterway	Latitide & Longitide	Channel Width (m)	Avg. Depth (m)
BK1	Barker Slough upstream	Upper Lindsey	Barker Slough	38°16'20.0"N 121°47'40.3"W	29.5	3
BK2	Barker Slough downstream	Upper Lindsey	Barker Slough	38°15'47.1"N 121°46'48.5"W	25.5	3.5
BM1	Liberty Isl Mitigation Bank upstream	Liberty Island	Stairsteps	38°19'44.0"N 121°40'23.8"W	10.6	2.4
BM2	Liberty Isl Mitigation Bank downstream	Liberty Island	Stairsteps	38°20'02.0"N 121°40'15.8"W	16.4	2.7
BP1	Beaver Pond 1	Liberty Island	Beaver Pond	38°19'29.5"N 121°40'60.0"W	32.9	NA
BP2	Beaver Pond 2	Liberty Island	Barker Slough	38°19'29.5"N 121°40'60.0"W	32.9	NA
CA1	Cache Slough upstream of conf with Ulatis	Upper Cache	Cache Slough	38°18'05.3"N 121°45'20.9"W	33.7	1.9
CA2	Cache Slough upstream of conf with Haas	Upper Cache	Cache Slough	38°17'45.1"N 121°44'41.4"W	55.1	2.8
CA3	Cache Slough downstream of conf with Haas	Lower Cache	Cache Slough	38°17'05.3"N 121°43'04.6"W	298.3	3.7
CC1	Calhoun Cut upstream	Upper Lindsey	Calhoun Cut	38°15'34.9"N 121°47'49.8"W	50.8	2.1
CC2	Calhoun Cut downstream	Upper Lindsey	Calhoun Cut	38°15'36.6"N 121°47'09.1"W	29.3	2.4
HS1	Haas Slough upstream	Upper Cache	Haas Slough	38°18'37.7"N 121°44'08.7"W	40.2*	2.3
HS2	Haas Slough downstream	Upper Cache	Haas Slough	38°18'06.2"N 121°43'47.0"W	159.3*	4
LN1	Lindsey Slough upstream	Upper Lindsey	Lindsey Slough	38°15'31.4"N 121°45'57.4"W	73.7	4.9
LN2	Lindsey Slough upstream of telephone line	Upper Lindsey	Lindsey Slough	38°15'31.4"N 121°44'41.5"W	90.9	5.7
LN3	Lindsey Slough upstream of bridge	Lower Lindsey	Lindsey Slough	38°15'00.8"N 121°42'50.1"W	140.1	5.2
LNCA	Conf of Cache/Lindsey	Lower Cache	Cache/Lindsey Confluence	38°14'39.9"N 121°41'19.6"W	229.2	NA
PR1	Downstream of USGS sonde	Liberty Island	Prospect Slough	38°19'44.2"N 121°40'02.2"W	62.5	5.6
PR2	Prospect Slough downstream trawl and lower prospect seining beach	Liberty Island	Prospect Slough	38°17'52.5"N 121°40'02.2"W	50.9	6.4
SG1	Upstream from side channel to Cache	Liberty Island	Shag Slough	38°18'10.7"N 121°41'34.3"W	88.9	7.7
SG2	Downstream from side channel to Cache	Liberty Island	Shag Slough	38°16'58.8"N 121°41'34.3"W	95.1	7.8
UL1	Ulatis Slough upstream	Upper Cache	Ulatis Slough	38°17'33.2"N 121°45'51.4"W	38.4	2.4
UL2	Ulatis Slough downstream	Upper Cache	Ulatis Slough	38°17'46.1"N 121°45'11.1"W	49.6	2.4

Appendix II: Fish data and catch totals

Table A2. Total fish catch from 2012-2022.

Species Code	*Common Name*	*Scientific Name*	*Habitat Association*	*Status*	*Otter Trawl*	*Electro-fishing*	*Total*
ASH	American Shad	*Alosa sapidissima*	Pelagic	Non-Native	133	727	860
BB	Brown Bullhead	*Ameiurus nebulosus*	Benthic	Non-Native	24	67	91
BC	Black Crappie	*Pomoxis nigromaculatus*	Littoral	Non-Native	419	2301	2720
BF	Sacramento Blackfish	*Orthodon microlepidotus*	Benthic	Native	21	4	25
BFG	American Bullfrog	*Lithobates catesbeianus*	Littoral	Non-Native	2	46	48
BG	Bluegill	*Lepomis macrochirus*	Littoral	Non-Native	1627	1857	3484
BGRE	Bluegill/Redear Hybrid	*Lepomis spp.*	Littoral	Non-Native	6	20	26
BLB	Black Bullhead	*Ameiurus melas*	Benthic	Non-Native	18	101	119
BLP	Bigscale Logperch	*Percina macrolepida*	Littoral	Non-Native	169	627	796
CCF	Channel Catfish	*Ictalurus punctatus*	Benthic	Non-Native	11	30	41
CENTRARCH	Unknown Centrarchid	*Centrarchid spp.*	Littoral	Non-Native	0	7	7
CLUPEIDAE	Unknown Clupeid	*NA*	Pelagic	Non-Native	2	72	74
CP	Common Carp	*Cyprinus carpio*	Benthic	Non-Native	469	130	599
CS	Chinook Salmon	*Oncorhynchus tshawytscha*	Pelagic	Native	43	2	45
DS	Delta Smelt	*Hypomesus transpacificus*	Pelagic	Native	1	16	17
FHM	Fathead Minnow	*Pimephales promelas*	Littoral	Non-Native	6	12	18
GF	Goldfish	*Carassius auratus*	Benthic	Non-Native	67	11	78
GSF	Green Sunfish	*Lepomis cyanellus*	Littoral	Non-Native	3	2	5
GSH	Golden Shiner	*Notemigonus crysoleucas*	Littoral	Non-Native	1232	216	1448
HCH	Sacramento Hitch	*Lavinia exilicauda exilicauda*	Pelagic	Native	301	487	788
ISS	Mississippi Silverside	*Menidia audens*	Littoral	Non-Native	1974	370	2344
LFS	Longfin Smelt	*Spirinchus thaleichthys*	Pelagic	Native	2	221	223

LMB	Largemouth Bass	*Micropterus salmoides*	Littoral	Non-Native	3559	185	3744
MQF	Western Mosquitofish	*Gambusia affinis*	Littoral	Non-Native	31	5	36
MSF	Unknown Sunfish	*Lepomis spp.*	Littoral	Non-Native	345	292	637
RESF	Redear Sunfish	*Lepomis microlophus*	Littoral	Non-Native	1790	1873	3663
RSNR	Red Shiner	*Cyprinella lutrensis*	Littoral	Non-Native	0	1	1
RT	Rainbow/Steelhead Trout	*Oncorhynchus mykiss*	Pelagic	Native	6	3	9
RWK	Rainwater Killifish	*Lucania parva*	Littoral	Non-Native	10	18	28
SB	Striped Bass	*Morone saxatilis*	Pelagic	Non-Native	318	2958	3276
SCP	Prickly Sculpin	*Cottus asper*	Benthic	Native	174	785	959
SF	Starry Flounder	*Platichthys stellatus*	Benthic	Native	0	2	2
SG	Shimofuri Goby	*Tridentiger bifasciatus*	Benthic	Non-Native	100	168	268
SKR	Sacramento Sucker	*Catostomus occidentalis*	Benthic	Native	1790	302	2092
SPM	Sacramento Pikeminnow	*Ptychocheilus grandis*	Pelagic	Native	114	39	153
ST	Sacramento Splittail	*Pogonichthys macrolepidotus*	Benthic	Native	9	158	167
STBK	Threespine Stickleback	*Gasterosteus aculeatus*	Littoral	Native	2	2	4
TFS	Threadfin Shad	*Dorosoma petenense*	Pelagic	Non-Native	2760	7768	10528
TP	Tule Perch	*Hysterocarpus traski*	Littoral	Native	423	790	1213
WAKASAGI	Wakasagi	*Hypomesus nipponensis*	Pelagic	Non-Native	0	477	477
WC	White Crappie	*Pomoxis annularis*	Littoral	Non-Native	38	272	310
WCF	White Catfish	*Ameiurus catus*	Benthic	Non-Native	51	625	676
WM	Warmouth	*Lepomis gulosus*	Littoral	Non-Native	72	23	95
YFG	Yellowfin Goby	*Acanthogobius flavimanus*	Benthic	Non-Native	51	41	92

Table A3. Fish catch in 2021.

Species Code	Common Name	Scientific Name	Habitat Association	Status	Otter Trawl	Electro-fishing	Total
ASH	American Shad	*Alosa sapidissima*	Pelagic	Non-Native	57	4	61
BB	Brown Bullhead	*Ameiurus nebulosus*	Benthic	Non-Native	6	0	6
BC	Black Crappie	*Pomoxis nigromaculatus*	Littoral	Non-Native	87	14	101
BF	Sacramento Blackfish	*Orthodon microlepidotus*	Benthic	Native	0	0	0
BFG	American Bullfrog	*Lithobates catesbeianus*	Littoral	Non-Native	6	0	6
BG	Bluegill	*Lepomis macrochirus*	Littoral	Non-Native	72	57	129
BGRE	Bluegill/Redear Hybrid	*Lepomis spp.*	Littoral	Non-Native	0	0	0
BLB	Black Bullhead	*Ameiurus melas*	Benthic	Non-Native	1	0	1
BLP	Bigscale Logperch	*Percina macrolepida*	Littoral	Non-Native	33	6	39
CCF	Channel Catfish	*Ictalurus punctatus*	Benthic	Non-Native	0	0	0
CENTRARCH	Unknown Centrarchid	*Centrarchid spp.*	Littoral	Non-Native	0	0	0
CFU	Unknown Catfish	*NA*	Benthic	Non-Native	0	0	0
CLUPEIDAE	Unknown Clupeid	*NA*	NA	NA	17	0	17
CP	Common Carp	*Cyprinus carpio*	Benthic	Non-Native	11	36	47
CS	Chinook Salmon	*Oncorhynchus tshawytscha*	Pelagic	Native	0	3	3
DS	Delta Smelt	*Hypomesus transpacificus*	Pelagic	Native	0	0	0
FHM	Fathead Minnow	*Pimephales promelas*	Littoral	Non-Native	1	0	1
GF	Goldfish	*Carassius auratus*	Benthic	Non-Native	0	1	1
GSF	Green Sunfish	*Lepomis cyanellus*	Littoral	Non-Native	0	0	0
GSH	Golden Shiner	*Notemigonus crysoleucas*	Littoral	Non-Native	27	92	119
HCH	Sacramento Hitch	*Lavinia exilicauda exilicauda*	Littoral	Native	267	82	349
ISS	Mississippi Silverside	*Menidia audens*	Littoral	Non-Native	95	454	549
LFS	Longfin Smelt	*Spirinchus thaleichthys*	Pelagic	Native	0	0	0
LMB	Largemouth Bass	*Micropterus salmoides*	Littoral	Non-Native	13	256	269

MQF	Western Mosquitofish	*Gambusia affinis*	Littoral	Non-Native	0	2	2
MSF	Unknown Sunfish	*Lepomis spp.*	Littoral	Non-Native	4	3	7
RESF	Redear Sunfish	*Lepomis microlophus*	Littoral	Non-Native	62	51	113
RSNR	Red Shiner	*Cyprinella lutrensis*	Littoral	Non-Native	0	0	0
RT	Rainbow/Steelhead Trout	*Oncorhynchus mykiss*	Pelagic	Native	3	3	6
RWK	Rainwater Killifish	*Lucania parva*	Littoral	Non-Native	7	3	10
SB	Striped Bass	*Morone saxatilis*	Pelagic	Non-Native	602	29	631
SCP	Prickly Sculpin	*Cottus asper*	Benthic	Native	324	42	366
SG	Shimofuri Goby	*Tridentiger bifasciatus*	Benthic	Non-Native	23	6	29
SKR	Sacramento Sucker	*Catostomus occidentalis*	Benthic	Native	19	184	203
SPM	Sacramento Pikeminnow	*Ptychocheilus grandis*	Pelagic	Native	0	2	2
ST	Sacramento Splittail	*Pogonichthys macrolepidotus*	Benthic	Native	2	0	2
STBK	Threespine Stickleback	*Gasterosteus aculeatus*	Littoral	Native	0	0	0
TFS	Threadfin Shad	*Dorosoma petenense*	Pelagic	Non-Native	550	92	642
TP	Tule Perch	*Hysterocarpus traski*	Littoral	Native	125	10	135
WAKASAGI	Wakasagi	*Hypomesus nipponensis*	Pelagic	Non-Native	251	0	251
WC	White Crappie	*Pomoxis annularis*	Littoral	Non-Native	0	0	0
WCF	White Catfish	*Ameiurus catus*	Benthic	Non-Native	24	0	24
WM	Warmouth	*Lepomis gulosus*	Littoral	Non-Native	2	2	4
YFG	Yellowfin Goby	*Acanthogobius flavimanus*	Benthic	Non-Native	12	2	2