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Effects of Working Landscapes and Tidal Restoration on Aquatic Ecosystems of the North Delta
Arc

By

BRIAN OLIVER WILLIAMSHEN
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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Abstract

The San Francisco Estuary (Estuary) is a novel ecosystem consisting of a unique community of native and nonnative organisms and a mosaic of human-constructed and naturalistic waterways, wetlands, and landscapes. The Estuary is highly altered and managed to support California's waterfowl hunting heritage and valuable agriculture industry and is considered one of the most invaded in the world, leading to declines of native and pelagic fishes. Most estuaries suffer from eutrophication and harmful algal blooms, but the modifications and introduced species of the estuary create a situation where phytoplankton is limited. Tidal restoration has become a primary tool to recover diminished ecosystem function and conserve native species. The North Delta Arc (Arc), an arc of habitat in the upper Estuary, contains more habitat heterogeneity, hosts a higher proportion of native species, and has a geomorphology that allows for adaptation to sea-level-rise. These attributes of the Arc make it a seemingly prime candidate for tidal restoration within the Estuary; however, outcomes of restoration are largely unknown and effects of human-managed wetlands and landscapes on aquatic ecosystems are poorly understood. To address these knowledge gaps, I studied different aspects of restoring wetlands, tidal sloughs that are influenced by human managed wetlands and landscapes, and the managed wetlands and landscapes themselves.

Suisun Marsh lies within the brackish water portion of the Arc and is primarily managed by private landowners and state agencies for waterfowl production and hunting. A common assumption has been that wetlands managed for waterfowl hunting created more harm than benefit for native fish species, which led to legislation requiring that much of the managed wetlands be restored to tidal wetlands. The first tidal restoration in Suisun Marsh was completed

in 2006 and fishes within the restoration went largely unmonitored. I designed a study to describe fish communities and metrics of primary and secondary production within the restoring wetland, adjacent tidal slough channels, and a wetland actively managed for waterfowl hunting. I found that the restoration supported mainly nonnative species and a lower fish diversity than surrounding tidal habitats and the managed wetland. I also found far higher concentrations of chlorophyll *a* and zooplankton in the managed than the restoring marsh.

The Cache Slough Complex makes up a majority of the freshwater portion of the Arc, is surrounded by agricultural land, and has more phytoplankton, zooplankton, and pelagic and native fishes than other freshwater regions of the Estuary. To understand the contribution of upstream agriculture in providing pelagic productivity and habitat for native fishes, I designed two research projects within the Cache Slough Complex and its watersheds. The first project measured nutrients, phytoplankton, and rates of pelagic primary production and respiration across sites with varying areas of upstream cropland. My study indicates that upstream cropland is important for phytoplankton production within the Cache Slough Complex. I also sampled fishes and invertebrates within the agricultural canals and ditches in watersheds that connect to the Cache Slough Complex. I found assemblages of native and nonnative fishes in the agricultural waterways and an abundance of invertebrates to feed them. Sites in watersheds with more irrigated cropland and no barrier to upstream migration supported the highest number of species.

Contrary to common belief, my studies indicate that there are beneficial aspects of the working lands to aquatic ecosystems in the Estuary. Instead of a pure focus on restoring estuarine habitats to some unattainable historic state, my research suggests that management of working lands should be harnessed to benefit aquatic communities. Working landscapes have

infrastructure to easily manipulate hydroperiods and water flows, so future research should be focused on how to best use these tools to attain specific ecosystem functions and conservation goals.

Chapter 1

Tidal restoration of a managed wetland in a California marsh favors non-native fishes

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Abstract

Tidal wetland restoration is commonly used to recover ecosystem functions and services that were lost when wetlands were diked for reclamation or management. Less research has been conducted on the response of invertebrate and fish assemblages to tidal restoration than on plants and physical attributes. Blacklock Marsh, a wetland in Suisun Marsh, USA, was once managed

for waterfowl hunting and cattle grazing until its dike was breached, restoring full tidal action. We sampled water quality, zooplankton, macroinvertebrates, and fishes in Blacklock Marsh, and compared these metrics to adjacent naturalistic waterways and to a managed wetland focused on waterfowl. Our goal was to compare food production and community assemblage on a restoring marsh to other types of nearby waterways. Blacklock Marsh had less chlorophyll-*a* and dissolved organic carbon than nearby dead-end sloughs and the managed wetland, less zooplankton biomass than the managed wetland, and lower fish diversity – with a fish assemblage dominated by non-native species – compared to all other waterways. The most abundant fish species in the restoring site, Mississippi silverside (*Menidia audens*), is a non-native fish and known predator of Delta smelt larvae (*Hypomesus transpacificus*), for which the restoration was targeted. Our research suggests that restoring tidal action to managed wetlands alone may worsen rather than improve conditions for at-risk and native fishes.

Introduction

Tidal wetland restoration is commonly used to revive hydrodynamic processes (Turner and Lewis 1996; MacBroom and Schiff 2012), to improve habitat connectivity (Weinstein and Kreeger 2000; Talley et al. 2006), and to re-establish emergent vegetation (Zhang et al. 1997; Smith and Warren 2012). Restoration can elevate diversity of native aquatic organisms by increasing both food production and foraging/refuge habitat (Boesch and Turner 1984; Kneib 1997; Simenstad et al. 2000). Nevertheless, effectiveness of tidal wetland restoration remains poorly understood because it is often unmonitored (Malakoff 1998; Zedler and Callaway 2001; Zedler 2007).

Although restorations are expected to return to a historic state favoring native species, managed wetlands, floodplains, reclaimed farmland, and other novel ecosystems may have

intractable conditions (Suding and Hobbs 2009) that render a return to a historically “natural” state unfeasible (Hilderbrand et al. 2005). When a wetland is diked and then intensively farmed, subsidence can occur, increasing the time needed for sediment accretion to form intertidal habitat (Callaway et al. 2011). Presence of invasive organisms further impedes creation of desirable habitat (Anisfeld 2012). Additional complications arise from climate-change-induced sea-level rise, which increases both inundation depth at restoration sites and salinity, potentially inhibiting the species restoration was meant to help (Callaway et al. 2007).

Many reclaimed tidal wetlands remain intermittently or permanently flooded (Roman et al. 1984; Zou et al. 2006; Warner et al. 2018). These managed wetlands differ from tidal wetlands because their water exchange with adjacent waterways is controlled by gates. Managed wetlands around the world (*e.g.*, South Asia, Europe, and North America) are used for controlling floods, limiting saltwater intrusion, abating coastal erosion, providing irrigation water, growing desirable vegetation and fishes, and enhancing waterfowl and wading-bird habitat (Kaminski and Prince 1981; Bamber et al. 1991; Rogers et al. 1994; de Graaf and Marttin 2003; Frisch et al. 2006). Many managed wetlands are novel environments that exhibit diverse geomorphic and water-quality conditions, which then support a distinctive suite of native and non-native species (Hobbs et al. 2006; Aguilar-Medrano et al. 2019). For example, managed wetlands can have lower densities of large migratory fish species, but higher densities of small resident fishes, than tidal wetlands (Rozas and Minello 1999). The control of hydroperiods with gates offers opportunities to improve conditions for at-risk native species, but this option has received scant scientific attention (Kloskowski and Nieoczym 2015).

One of the largest tidal marshes on North America's western coast is Suisun Marsh in the San Francisco Estuary, California – a highly invaded estuary (Cohen and Carlton 1998) – with an

area of about 47,000 ha (116,000 acres). Suisun Marsh is comprised of both managed and naturalistic landscapes. Nearly half of the area is diked and is managed by private landowners or state agencies, while the rest consists of tidal sloughs, bays, wetlands, and fringing grasslands. Tidal wetlands were altered as a consequence of myriad human activities, including farming, livestock production, mosquito abatement, and both accidental and intentional introduction of invasive species. Most managed landscapes are wetlands focused on waterfowl habitat that are seasonally flooded and exhibit muted tidal exchange. These managed wetlands are novel ecosystems supporting a mixture of native and non-native aquatic species (Moyle et al. 2014; Aguilar-Medrano et al. 2019).

Because Suisun Marsh is a nursery for key species (Moyle et al. 2014; Colombano et al. 2020), such as endangered Delta smelt (*Hypomesus transpacificus*), striped bass (*Morone saxatilis*), and endemic Sacramento splittail (*Pogonichthys macrolepidotus*), it has been the focus of large-scale ongoing tidal restoration (U.S. Department of the Interior [DOI] et al. 2013). With the pelagic ecosystem collapsing in the San Francisco Estuary (Sommer et al. 2007), planktonic food production has become a restoration goal. Other incentives for restoration are the threats of sea-level rise and seismic activity, which undermine dike integrity and could result in unplanned flooding and conversion of managed wetlands to open water (Knowles 2010; Moyle et al. 2014). The 2013 Suisun Marsh Habitat Management, Preservation and Restoration Plan mandates that over the next thirty years 2,000-3,000 ha (4,900 – 7,400 acres) of managed wetlands will be restored, and that 16,000-20,000 ha (40,000-50,000 acres) of managed wetlands will be enhanced to benefit important species (DOI et al. 2013).

We wanted to evaluate if restoration goals, such as endangered-species recovery, are being met in Suisun Marsh to inform future management throughout the San Francisco Estuary.

We compared water quality and invertebrate and fish assemblages in a restoring wetland, Blacklock Marsh, with nearby waterways, including a managed wetland. We expected the aquatic community and water quality in the restored wetland to be similar to adjacent naturalistic waterways, and to outperform the managed wetland in fish diversity and in primary and secondary production.

Methods

Waterways and Sampling Sites

Sampling sites were located in the Nurse-Denverton Slough complex, a distinct sub-region in Suisun Marsh (Moyle et al. 2014). Suisun Marsh is a large brackish tidal marsh located in the geographic center of the northern San Francisco Estuary (SFE), between the Sacramento-San Joaquin Delta to the east and San Pablo Bay to the west. The Nurse-Denverton complex includes a mosaic of wetland habitats, dominated by emergent vegetation (*Schoenoplectus* spp., *Typha* spp., and *Phragmites australis*), that supports many native and non-native fishes.

This study focused on Blacklock Marsh (hereafter “Blacklock” or “BL”), which was restored in 2006 (California Department of Water Resources [DWR] 2007). Blacklock was managed for waterfowl and cattle prior to purchase by DWR in 2003. Restoration was intended to increase both food production for Delta smelt and habitat for other endangered species, such as salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*) and Suisun Song Sparrow (*Melospiza melodia maxillaris*) (DWR 2007). The restoration plan included little earth-moving or vegetation management in the interior landscape, focusing instead on carefully engineered dike breaches designed to maximize sediment accretion (DWR 2007). When an unplanned

breach occurred in the perimeter dike in 2006 before the planned excavation, the property was left flooded. A second breach was subsequently excavated, with the intent of increasing tidal exchange. The wetland consists of shallow interior intertidal ponds (0.25 – 1.5 m deep at mean high water, 5 ha), a deep perimeter ditch (3 - 4 m deep, 3 ha, 2.2 km long), a network of intertidal channels (0.25 – 2 m deep, 5 ha), and patches of emergent aquatic vegetation (12 ha) (Fig. 1).

Blacklock was compared to five nearby tidal waterways from October 2013 to June 2015, where each had one to three fixed sites for water-quality and fish sampling (Table 1). Little Honker Bay (LH) is a shallow (1.25 m), open-water embayment that connects to Blacklock through two breaches on Blacklock's northwest dike (Fig.1). Arnold Slough (AS) is a sinuous dead-end channel of intermediate depth (2 m) connected to Blacklock by a culvert on its south dike. Luco (LS) and Denverton (DS) sloughs are both nearby dead-end slough systems of intermediate depth (1.5 m and 2.7 m, respectively). Both sloughs connect to adjacent managed wetlands by gates that can be used to either flood or drain. Linking all waterways in the complex is Nurse Slough (NS), a meandering, deep (6 m) channel.

Blacklock was also compared to a managed wetland, Luco Pond (LP), a shallow waterway at Luco Slough's upper end. The wetland connects to the slough via three gates that were open for muted tidal exchange from about October to May during the study. Fresh water may enter Luco Pond during rain events from northerly grazing lands. Water level within Luco Pond varies by season, to grow plants for waterfowl. If the wetland is drained in summer, it is sometimes graded and disked to maintain a mix of open shallow water, open deep water, and emergent vegetation.

Water Quality Sampling

Water quality was measured monthly at all fish-sampling sites from October 2013 through June 2015 (Table 1), using a Yellow Springs Instruments 85 meter to record temperature (°C), salinity (ppt), specific conductance (μS), and dissolved oxygen (mg/l and % saturation). Water transparency (Secchi depth, cm) and tidal stage (ebb, flood, high, low) were also recorded. Whole water grabs were collected monthly at one site in each waterway to determine chlorophyll-*a* ($\mu\text{g/l}$) and dissolved organic carbon (DOC, mg/l) concentrations. Lab analyses were performed by the Dahlgren geochemistry laboratory at University of California, Davis, using standard techniques (Eaton et al. 1998).

Zooplankton Sampling

Zooplankton were collected in Blacklock and Luco Pond during the same week on eight occasions (November 2013; February, March, and April 2014; February, April, May, and June 2015). We used a tapered, 2-m-long, 50- μm -mesh plankton net with a 0.5-m-diameter mouth and a 1-L closed cod end, hand-towed 0.25 m below the water surface for 20 m. A float attached to the mouth maintained constant depth. A flowmeter suspended in the mouth estimated sample volume. Contents were concentrated in the cod end, transferred to a container, preserved in 5% formaldehyde, and dyed with rose Bengal for identification. Zooplankton density was estimated in the lab by subsampling with a Stempel pipette until all species and life-history stages with more than 5 individuals in the first subsample (1/500) reached a count of 200 individuals.

Fish and Macroinvertebrate Sampling

Fishes and macroinvertebrates were sampled monthly using otter trawls and seines. Because of limited boat access, we could not trawl Luco Pond, so we compared Luco Pond to Blacklock with beach seines. Beach seines in both waterways were pulled in water less than 1.4 m deep.

Trawling was performed with a four-seam otter trawl with a 1.5 m X 4.3 m mouth, a length of 5.3 m, with mesh sizes of 35 mm stretch in the body and 6-mm stretch in the cod end (O'Rear and Moyle 2012). The trawl was towed at 4 km/hr for 5 minutes at two or three sites within each tidal waterway. Two to five seine hauls, with a 10-m beach seine featuring a stretched mesh size of 6 mm, were pulled in both the managed and restoring wetland. Catches were placed into large tubs filled with water. Fishes were identified, counted, measured to the nearest mm standard length (SL), and returned to the water. Macroinvertebrates that commonly measure >1 cm along their long axis (clams, shrimp, crayfish, and jellyfish) were identified, counted, and returned to the water. Sampling did not take place January 2015 for Blacklock, Little Honker Bay, Arnold Slough, and Luco Slough due to dangerous conditions.

Data Processing and Analysis

We graphed water-quality measurements for each waterway as Tukey boxplots, showing median (horizontal black line), first and third quartiles (upper and lower hinges of box), and largest and smallest values within $3/2$ the interquartile range of first and third quartiles (whiskers).

For zooplankton data, we calculated total density (individuals/m³) of each species per sample by calculating the total number of zooplankton per sample and dividing by the total

estimated volume of water sampled. We estimated biomass ($\mu\text{gC}/\text{m}^3$) for the most abundant taxa and life stages of copepods collected by multiplying the density of each species by dry weights from Dumont et al. (1975) and Kimmerer (unpublished data) . When dry-weight estimates were not available for a species' specific life stage, we applied estimates from similar taxa.

For macroinvertebrate and fish data, we calculated monthly trawl catch per unit effort (CPUE) by dividing total catch by species of all sites in a waterway by total number of minutes spent trawling in the same waterway. Similarly, monthly seine CPUE was calculated by dividing total catch by species per waterway by the number of seine hauls per waterway, resulting in catch per seine haul. Fish and macroinvertebrate CPUE values were graphed by waterway as box plots (see above).

To calculate fish species richness and evenness among waterways for both trawl and seine samples, we used the Shannon Diversity index, which was highly correlated with Simpson and Inverse Simpson indices (Table S2 and S3). All diversity indices were calculated in R with the diversity function in the vegan package (Oksanen et al. 2019; R Core Team 2020).

We employed two non-parametric tests, because data were not normally distributed, to determine differences in water quality, in zooplankton biomass, and in macroinvertebrate, and fish assemblages among waterways. First, we used the Kruskal-Wallis test (`kruskal.test` function) to ascertain differences between the waterways for a specific parameter or species (R Core Team 2020). If the test indicated differences ($p < 0.02$), then the Wilcoxon two-sample test (`pairwise.wilcox.test` function) was utilized to assess pairwise differences ($p \leq 0.045$) between Blacklock and each other waterway (R Core Team 2020). To evaluate fish-assemblage differences among waterways, we used non-metric multidimensional scaling (NMDS), invoking the `metaMDS` function in the vegan package (Oksanen et al. 2019) to create a dissimilarity

matrix of Bray-Curtis distances. CPUE variability among sampling events and sites were plotted. Ordination values were assigned a color by waterway, and ellipses were drawn using standard deviation of point scores by the geomorphic groups: managed wetland, embayment, tidal slough, and restoring wetland.

Results

Water Quality

Temperature and salinity differed little between Blacklock and other waterways (Fig. 2). The widest temperature range was observed in Blacklock: 6.5°C (December 2013) – 26.2°C (June 2014). Salinity was lowest across all sites in February and March and highest in August and September. Lowest salinity was measured in Denverton Slough in December 2014 (0.1 ppt), and highest in Luco Pond during September 2014 (50.1 ppt) when the wetland was mostly drained and remaining water evaporating.

In contrast, dissolved oxygen (DO) concentrations and water clarity differed among waterways. At all locations, DO generally remained between 5 and 10 mg/L, with occasional extreme values. The lowest DO concentration (2.6 mg/L) was observed in Luco Slough during June 2015 and the highest (12 mg/L) in Denverton Slough during February 2015. In general, the lowest values tended to occur in dead-end or pond waterways (Arnold, Luco, Denverton sloughs, and Luco Pond). DO was higher in Blacklock than in Arnold Slough, Luco Slough, and Luco Pond (p -values < 0.015), but lower than in adjacent Little Honker Bay ($p = 0.007$; Fig. 2). DO did not differ between Blacklock and Denverton/Nurse sloughs (Fig. 2). Secchi depth varied greatly across waterways (4 cm in Luco Pond to 75 cm in Little Honker Bay). Blacklock had

higher water clarity than Luco Slough, Denverton Slough, and Luco Pond (p-values < 0.0002) but did not differ from immediate waterways (Little Honker Bay, Arnold Slough, and Nurse Slough; Fig. 2). Secchi depths were, on average, favorable for species of concern, such as Sacramento splittail (Feyrer et al. 2015), threadfin shad, Delta smelt, and juvenile striped bass (Feyrer et al. 2007).

As with DO, dead-end and pond waterways tended to have higher levels of chlorophyll-*a* and DOC. Chlorophyll-*a* concentrations varied widely, with extreme low and high values occurring in Luco Pond (0.2 µg/L and 157.5 µg/L). Chlorophyll-*a* concentrations in Blacklock were higher than in Little Honker Bay and Nurse Slough (p-values < 0.009; Fig. 2); about the same as in Arnold Slough; and lower than in Luco Slough, Denverton Slough, and Luco Pond (p-values < 0.0001; Fig. 2). DOC varied greatly among waterways, from 0.6 mg/L in Little Honker Bay to 162 mg/L in Luco Pond. Blacklock had slightly higher levels of DOC than Little Honker Bay and Nurse Slough (p-values < 0.002), and lower values than Arnold Slough, Luco Slough, Denverton Slough, and especially Luco Pond (p-values < 0.00003; Fig. 2).

Invertebrates

We compared zooplankton for Blacklock and Luco Pond only. Copepod biomass was much higher in Luco Pond (mean biomass: 155 mg C m⁻³) than in Blacklock (mean biomass: 25.1 mg C m⁻³; Fig S1). Although the *p*-value from a Kruskal-Wallis test was somewhat high (*p* = 0.115), a difference was evident in the boxplot. The species accounting for the highest biomass in both locations were *Eurytemora affinis* and *Acanthocyclops vernalis*. Calanoid and cyclopoid nauplii comprised the highest numerical proportion of life stages in both Blacklock and Luco Pond.

Macroinvertebrates were captured in trawls (few were captured in seines) and compared among all waterways except Luco Pond. Four species, totaling 4,375 individuals, were caught in abundance: Harris mud crab (*Rhithropanopeus harrisii*; 3% of macroinvertebrate catch), Black Sea jellyfish medusae (*Maeotias marginata*; 26% of catch), Siberian prawn (*Palaemon modestus*; 47% of catch), and California bay shrimp (*Crangon franciscorum*; 24% of catch). All except bay shrimp are non-native. Blacklock, Arnold Slough, and Little Honker Bay generally had low macroinvertebrate CPUE, except for Harris mud crab, which were caught only in Blacklock. Jellyfish were abundant only in Nurse Slough. Siberian prawn were less abundant in Blacklock than in Nurse, Luco, and Denverton sloughs (p-values < 0.0004; Fig. S2). Bay shrimp were captured more frequently in those same sloughs, but not at numbers different than Blacklock.

Fish

We captured 30,755 individual fish from 25 species. The most abundant species were threespine stickleback (*Gasterosteus aculeatus*), Mississippi silverside (*Menidia audens*), black crappie (*Pomoxis nigromaculatus*), western mosquitofish (*Gambusia affinis*), and splittail (Table S1). Only stickleback and splittail are native.

Otter-trawling captured 8,916 fish representing 23 species. The dominant species in trawls were splittail (30% of total catch), Mississippi silverside (21% of total catch), striped bass (*Morone saxatilis*, 10%), tule perch (*Hysterocarpus traski*, 9%), and shimofuri goby (*Tridentiger bifasciatus*, 5%) (Table S1).

Most fish species generally had lower CPUE in Blacklock than in other waterways except for two non-native species: Mississippi silverside and shimofuri goby CPUE was higher in

Blacklock than any other location (p-values < 0.046; Fig. 3). Native splittail and tule perch had lower CPUE in Blacklock than most other sloughs (lower for splittail compared to Luco, Denverton, and Nurse sloughs; lower for tule perch compared to all waterways except Luco Slough) (Fig. 3). Striped bass, a valuable non-native sport fish, had lower CPUE in Blacklock than all other locations (p-values < 0.045).

Fish diversity calculated from trawl data was lowest in Blacklock (Shannon Diversity Index [SDI] = 0.95), driven by the dominance of Mississippi silverside (73% of catch). Fish diversity in tidal sloughs Denverton (SDI = 1.87), Nurse (SDI = 1.6), and Luco (SDI = 1.72) was moderately higher, and adjacent sites Little Honker Bay (SDI = 2.03) and Arnold Slough (SDI = 2) had the highest diversity indices (Table S2). Fewer fish species were captured by trawl in Blacklock (17) than Denverton (21) and Arnold sloughs (18), but more than Little Honker Bay (14), Nurse Slough (16), and Luco Slough (16).

The NMDS ordinations showed differences in fish assemblages among waterways. Trawl data separated Blacklock from other waterways (Fig. 4). Fishes most associated with the Blacklock points (BL) were Mississippi silverside and shimofuri goby. In the other direction and closer to the centroid, the sloughs (AR, DV, LC, NS) clustered together and overlapped with the shallow embayment (LH). These sites were somewhat associated with the native splittail and tule perch, as well as non-native striped bass and black crappie.

Beach-seining was only conducted in Blacklock and Luco Pond and captured 21,839 fish representing 14 species. The dominant species in beach seines were threespine stickleback (51% of total catch), Mississippi silverside (25% of total catch), black crappie (7% of total catch), western mosquitofish (7% of total catch), and common carp (*Cyprinus carpio*; 3% of total catch) (Table S1). Threespine stickleback, black crappie, and western mosquitofish were seined nearly

exclusively in Luco Pond (Fig. 4). Splittail were found in both Blacklock (total CPUE = 4.25 fish/seine) and Luco Pond (total CPUE = 2.19 fish/seine).

Both fish CPUE and diversity were lower in beach seine captures in Blacklock (SDI = 1.15) than in Luco Pond (SDI = 1.88; Table S3), mostly due to dominance of Mississippi silverside in Blacklock (Fig. 5). Species richness was lower in Blacklock (9) than Luco Pond (12) for beach seine catch.

Based on the beach seine data, Blacklock (circle) and Luco Pond (triangle) were clearly segregated in ordination space. Blacklock samples were strongly associated with Mississippi silverside (Fig. S3), while the defining fishes of the Luco Pond assemblage were threespine stickleback and black crappie. (Fewer points were displayed for Blacklock because samples with zero catch for all five target species were omitted from the analysis, which was a common occurrence in Blacklock.)

Discussion

Much post-restoration monitoring has focused on plants and sediment, with fewer studies examining aquatic invertebrates and fishes (Atkinson et al. 2001; Konisky et al. 2006; Weinstein et al. 2019). Studies on fishes in tidally restored wetlands have found mixed results, with some finding fish and invertebrate assemblages similar to reference sites (Burdick et al. 1996; Lechêne et al. 2018), and others finding increased fish density but with different assemblages than reference sites (Simenstad and Thom 1996; Roman et al. 2002; Prahalad et al. 2019) or dominance of invasive species (Grimaldo et al. 2012). Results of our study corresponded most with Grimaldo *et al.* (2012): the restored wetland was dominated by invasive species, and, further, it did not grow much phytoplankton or zooplankton.

The aquatic habitat and fauna of Blacklock Marsh differed from that of nearby tidal waterways and the managed wetland in many ways. Chlorophyll-*a* concentrations in Blacklock were lower than those found in the dead-end sloughs and the managed wetland. Zooplankton biomass in Blacklock was much less than in the managed wetland. Vulnerable fish species, such as striped bass and splittail, were less abundant; fish species diversity was less; and fish assemblage was most distinct in Blacklock than other tidal habitats. Further, the most abundant fish species in Blacklock - Mississippi silverside – has been shown to feed on Delta smelt larvae (Baerwald et al. 2012), the most endangered species in the SFE, and one of the main targets of tidal wetland restoration in Suisun Marsh (DOI et al. 2013). Below we discuss the likely mechanisms leading to the deficiencies of Blacklock – physical environment and invasive species – as well as lessons for future management.

Physical Environment

Differences in water quality, invertebrates, and fishes were attributable to differences in geomorphology, hydrodynamics, and connectivity among the restoring Blacklock, adjacent waterways, and the managed wetland. The geomorphology of Blacklock likely results in residence time lower than dead-end sloughs and the managed wetland, which may support fewer native and at-risk fishes with less accumulation of organic material and production of phytoplankton and zooplankton.

Un-diked naturalistic tidal marshes typically have a sinuous main slough connected to dendritic tributaries that exchange water with marsh plains during very high tides (Moyle et al. 2014). Such complex morphology creates hydrodynamic patterns that feature regions of mixed residence time, with water exchanging more frequently at mouths of sloughs than in dead-end,

upstream reaches (Downing et al. 2016). Bi-directional flows, extended residence times (Jassby and Cloern 2000; Stumpner et al. 2020), and increased nutrient retention (Nixon et al. 1996) can induce phytoplankton blooms and support the accumulation of DOC and plankton that supplement wetland food webs. Dead-end Denverton and Luco sloughs most resembled historic tidal marshes, although the sloughs are largely separated from marsh plains. Instead, they exchange seasonally with managed wetlands that, depending on the management strategy, function similarly to marsh plains through exchange and accumulation of nutrients and DOC. High concentrations of chlorophyll-*a* and DOC in Denverton and Luco sloughs correspond with higher residence times.

In contrast, Blacklock only faintly resembles a historic tidal marsh. The site was breached without construction of sinuous starter channels, resulting in tidal flows mainly moving through a perimeter borrow ditch with rapid, multidirectional exchange with central ponded areas. This flow pattern probably decreases residence time while increasing dispersion, which would limit nutrient retention and explain why chlorophyll-*a* and DOC concentrations were generally lower throughout Blacklock than in dead-end sloughs in this and another study (Strong 2015). Dike failures at other managed wetlands may create similar habitat with low residence time and little phytoplankton production.

Managed wetlands in Suisun Marsh have a relatively controlled hydrology compared to tidal wetlands, with gates moderating water exchange with sloughs. In Suisun Marsh, they are generally drained during summer to grow terrestrial plants for waterfowl (Rollins 1981). When flooded, water on managed wetlands is spread over a large, shallow area – increasing residence time and area exposed to sunlight – allowing for phytoplankton blooms similar to seasonal floodplains and rice ponds in the Sacramento Valley (Corline et al. 2017). Luco Pond possessed

all these features during our study, and thus not only had the highest chlorophyll-*a* concentrations compared to all other waterways during our study, but also had higher concentrations than Blacklock, large sloughs, and a historic wetland in a concurrent study (Strong 2015).

The degree of hydrodynamic connectivity can determine both the assemblage and abundance of organisms in wetlands (Meynecke et al. 2008; Fernandes et al. 2015). The breaches at Blacklock provide considerable exchange with the adjacent embayment through which aquatic organisms can enter and leave the restoring marsh. Despite the high degree of connectivity, the restoring marsh had lower fish diversity than the embayment, with both invertebrate and fish catches dominated by just one or two species. In contrast, dead-end sloughs had only one point of connectivity and exhibited high diversity and distinctive assemblages dominated by native species. The managed wetland was even more constrained, with muted exchange and seasonal disconnection with tidal sloughs. Gates may discourage larger organisms, such as adult splittail and striped bass, from entering managed wetlands (Kimball et al. 2012) while allowing small fishes, such as the native threespine stickleback, to flourish.

The high productivity of managed wetlands can transfer to sloughs when they are connected. For example, copepods were abundant during flushing/draining cycles of Luco Pond, a time of punctuated exchange of pond and slough water. Zooplankton became highly concentrated in the pond and were transported to Luco Slough, where they could have fed planktivorous fish. Such a scenario has been corroborated by juvenile salmon growing faster in managed-wetland outlets in Suisun Marsh, where zooplankton biomass was greatest, than in tidal sloughs adjacent to historic marsh plains (Aha et al. 2021). Macroinvertebrates and small fish produced on managed wetlands can also be transported to tidal sloughs and consumed by larger

fish. Diets of white catfish (*Ameiurus catus*) in tidal sloughs were seasonally dominated by managed-wetland-associated species such as threespine stickleback and the amphipod *Eogammarus confervicolus* (O'Rear 2012). In addition, striped bass, an economically important sport fish, are known to eat exported species at wetland discharge points (Moyle 2002; O'Rear & Moyle 2014; O'Rear unpublished data). Because timing/magnitude of flooding/draining managed wetlands is controlled, the wetlands can be leveraged to boost plankton and small-fish numbers in adjacent waterways at key periods, such as the summer rearing period for many pelagic fishes when zooplankton is scarce (Kimmerer 2004).

Invasive Organisms

Invasive organisms present one of the biggest challenges to restoration within the San Francisco Estuary (Lopez et al. 2006; Callaway et al. 2011), as it is one of the world's most invaded estuaries (Cohen and Carlton 1998). Additionally, the invaders come from myriad environments (e.g., the Mississippi River Watershed, watersheds that drain to the Atlantic Ocean, the Black Sea region, and Japanese estuaries), so potential always exists for some non-native species to dominate a restoration site. The most prevalent invader in the study was the Mississippi silverside, a species that eats pelagic larval fish and may compete for food with pelagic species (Moyle and Bennett 2008). Among the waterways, Blacklock hosted the highest numbers of Mississippi silverside.

The tidal sloughs and embayment generally had low numbers of Mississippi silverside. Luco Slough was the only dead-end slough with significant numbers of Mississippi silverside, likely because of the many shallow mud flats in the slough where the species tends to shoal (Moyle 2002). Blacklock's shallow, warm water provided attractive habitat for Mississippi

silverside. The dominance of Mississippi silverside in Blacklock was consistent with an experiment in a different SFE restoring wetland, where Mississippi silverside were used because native fishes were too rare for adequate sample sizes (Cohen and Bollens 2008). In contrast, hardly any Mississippi silverside were captured in Luco Pond while threespine stickleback were very abundant, a difference best explained by hydroperiod. While Luco Pond is flooded during the peak spawning period of threespine stickleback (winter/spring), it is often dry during the spawning window for Mississippi silverside (summer). Our findings in Luco Pond are consistent with other studies of managed wetlands. A managed wetland in southwestern Suisun Marsh was dominated by threespine stickleback and western mosquitofish, as well as some species not found in Luco Pond (O'Rear and Moyle 2012), and small resident fishes tended to dominate managed wetlands in Louisiana (Rozas and Minello 1999). The difference in abundance between Mississippi silverside and threespine stickleback in the managed wetlands highlights their ability to favor one or the other based on the hydroperiod - which is controlled - overlapping the fishes' reproductive periods, an option not available in tidal restorations.

Management Recommendations

Restoration of brackish tidal wetlands has potential for improving habitat for endangered and valued invertebrates and fishes, but our research shows that restoration actions can harm the organisms they intend to benefit. Future restorations can be compromised if they do not comprehensively consider (1) the risk posed by invasive non-native species, (2) the effect of geomorphology, or (3) the potential value of the existing environments they are to supersede. Therefore, we recommend that (1) restoration designs include dendritic channels longer than the tidal exchange, coupled with partially isolated ponds to increase water residence time; (2)

contingencies such as structures with ability to dewater restorations be included in designs to allow for adaptive management and invasive-species control; and (3) research be conducted on diked wetlands management strategies and alternative gate designs that maximize benefits to desirable aquatic organisms. Further, we recommend that coordination occurs between large-scale excavation of restoration sites and enhancement of managed wetlands (*e.g.*, using fill from excavations for bolstering dikes of key managed wetlands) to meet the challenge of sea-level rise. Otherwise, unplanned breaches in existing managed wetlands can increase the incidence of open water habitats that work against desirable restoration outcomes.

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Tables and Figures

Table 1 Waterway description, control structures, and sample site number for Study. WCG = water control gate used to drain or flood water from managed wetland. Distance from BL= distance of nearest point of a waterway from a hydrologic connection to Blacklock Marsh by way of Nurse Slough. EAV = Emergent Aquatic Vegetation.

	Blacklock Marsh	Little Honker Bay	Arnold Slough	Nurse Slough	Luco Slough	Denverton Slough	Luco Pond
Code	BL	LH	AS	NS	LS	DS	LP
Waterway Type	Restoring Wetland	Adjacent Embayment	Adjacent Tidal Slough	Large Tidal Slough	Tidal Slough	Tidal Slough	Managed Wetland
Depth (m)	0.5-4	1-2.5	1-3	2-10	1-3	1-4	0.5-2
# WCG	1	1	3	3	12	7	3
Distance from BL (km)	0	0	0	0.6	3.75	3.75	5.3
EAV Area (km²)	0.12	0.13	0.43	0.85	0.40	0.59	0.78
Open Water (km²)	0.14	0.34	0.10	0.73	0.14	0.33	0.95
# Trawl Sites	3	2	3	3	3	3	-
# Seine Sites	3	-	-	-	-	-	2
# Zooplankton tows	1	-	-	-	-	-	1

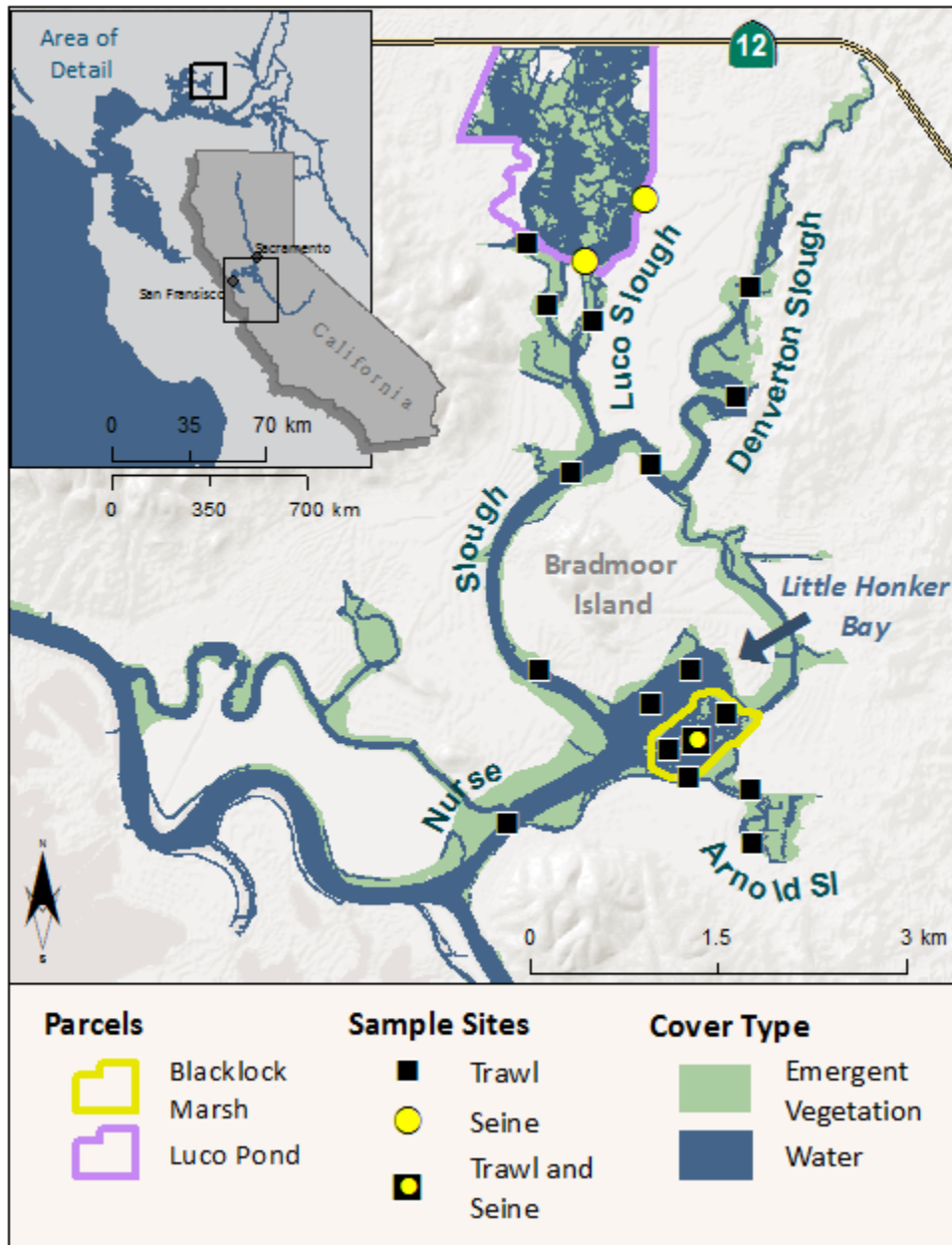


Figure 1 Study region. Suisun Marsh is in the northern San Francisco Estuary. The study was conducted in the Nurse-Denverton complex in northwest corner of the marsh.

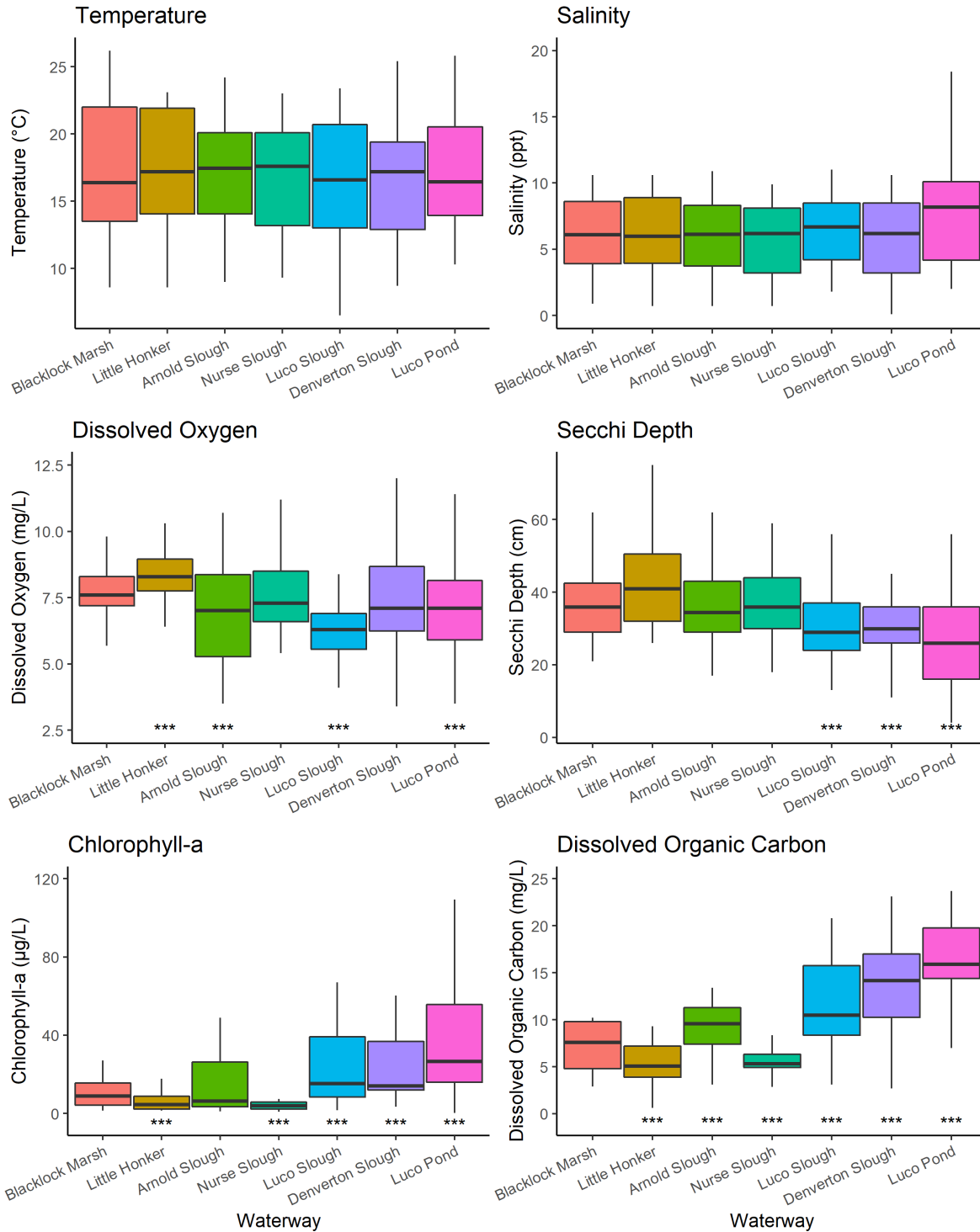


Figure 2 Water quality by waterway. Range of water-quality values observed in each waterway during trawl and seine surveys – outliers omitted. Stars indicate sites with measurements different than Blacklock (p -value ≤ 0.045) according to Wilcoxon two-way test.

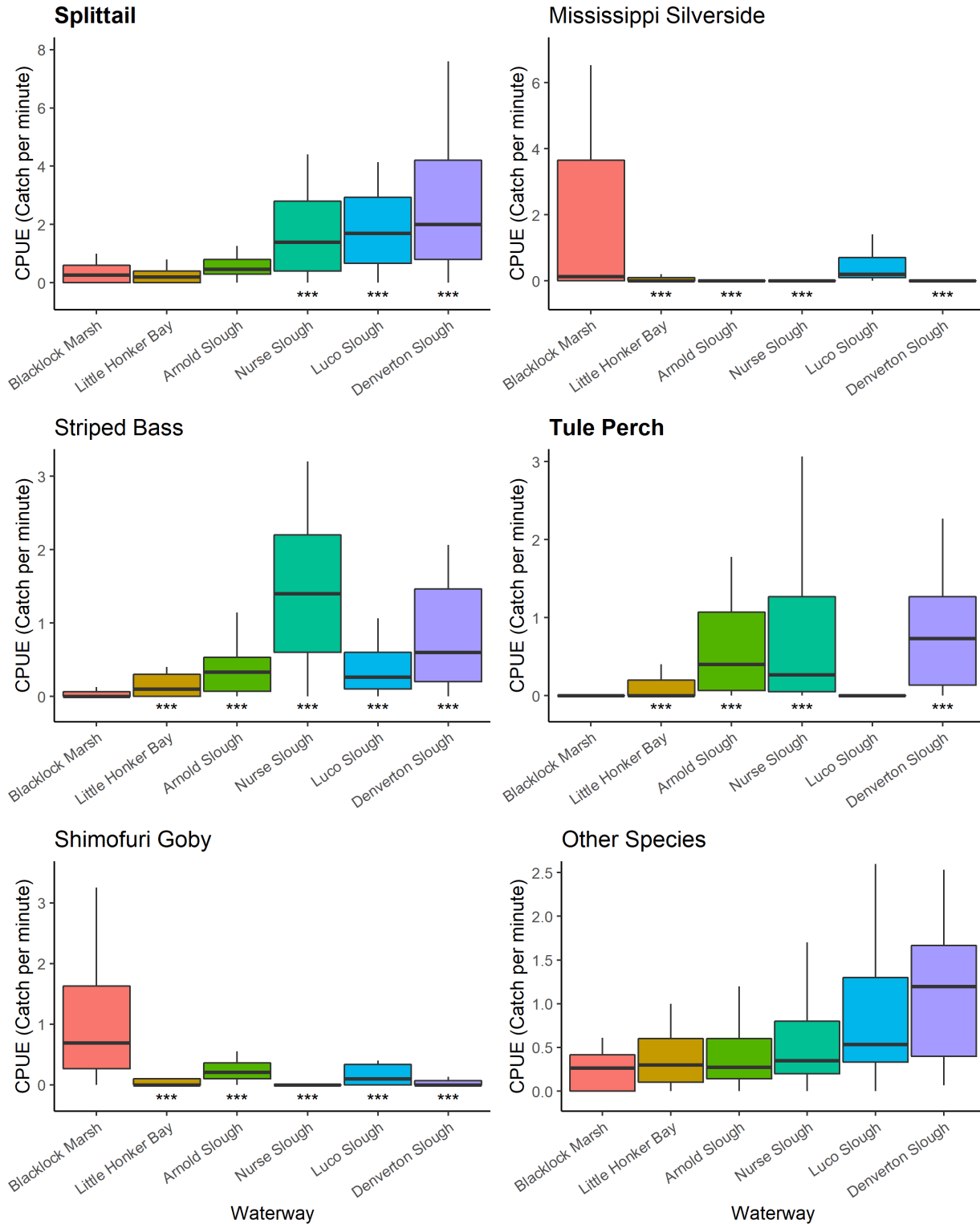


Figure 3 Monthly trawl CPUE by fish species and waterway – outliers omitted. Any species with a total catch of less than 400 individuals is classified as other. Stars indicate sites with measurements different than Blacklock (p -value ≤ 0.045) according to Wilcoxon two-way test. Y-axis varies by plot. **Bold** indicates native species.

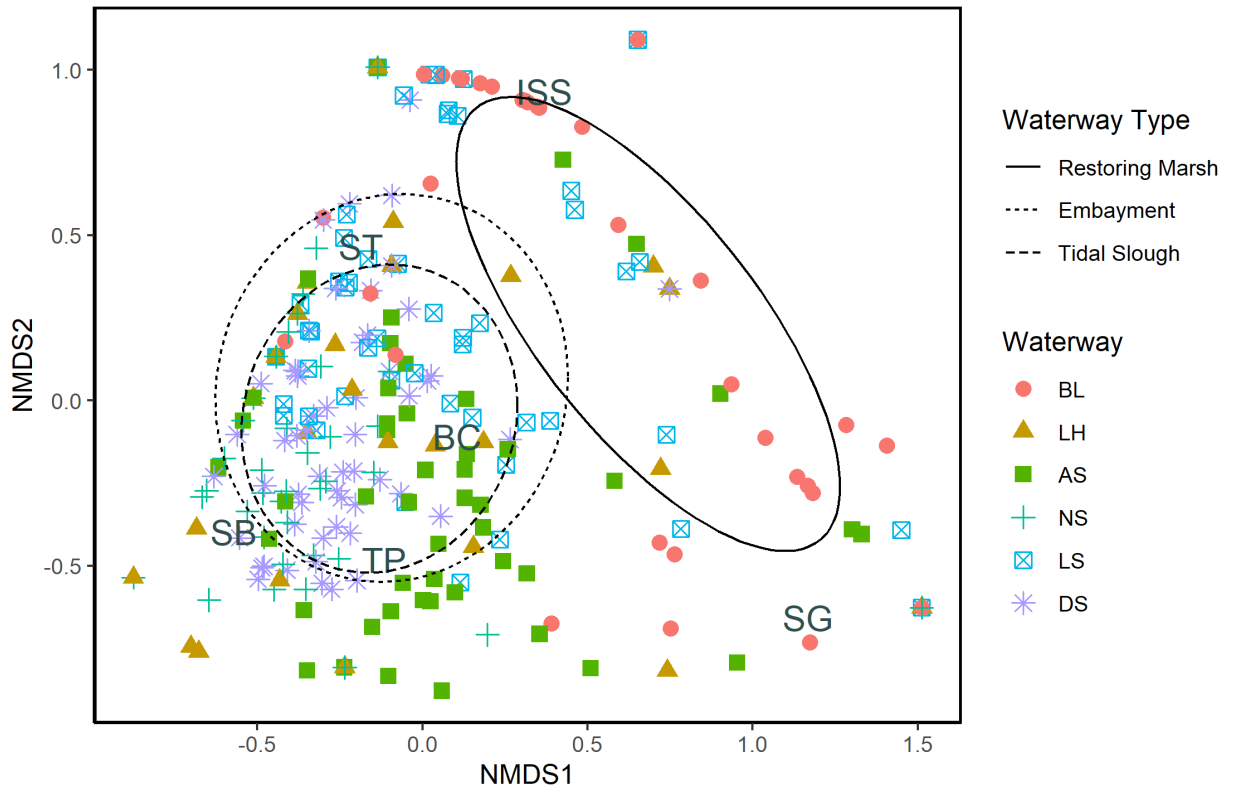


Figure 4 NMDS plot of fish captured in trawls (Stress = 0.083. See Table 1 for waterway codes. BC = black crappie, ISS = Mississippi silverside, SB = striped bass, SG = shimofuri goby, **ST = splittail**, and **TP = tule perch**). Bold indicates native species.

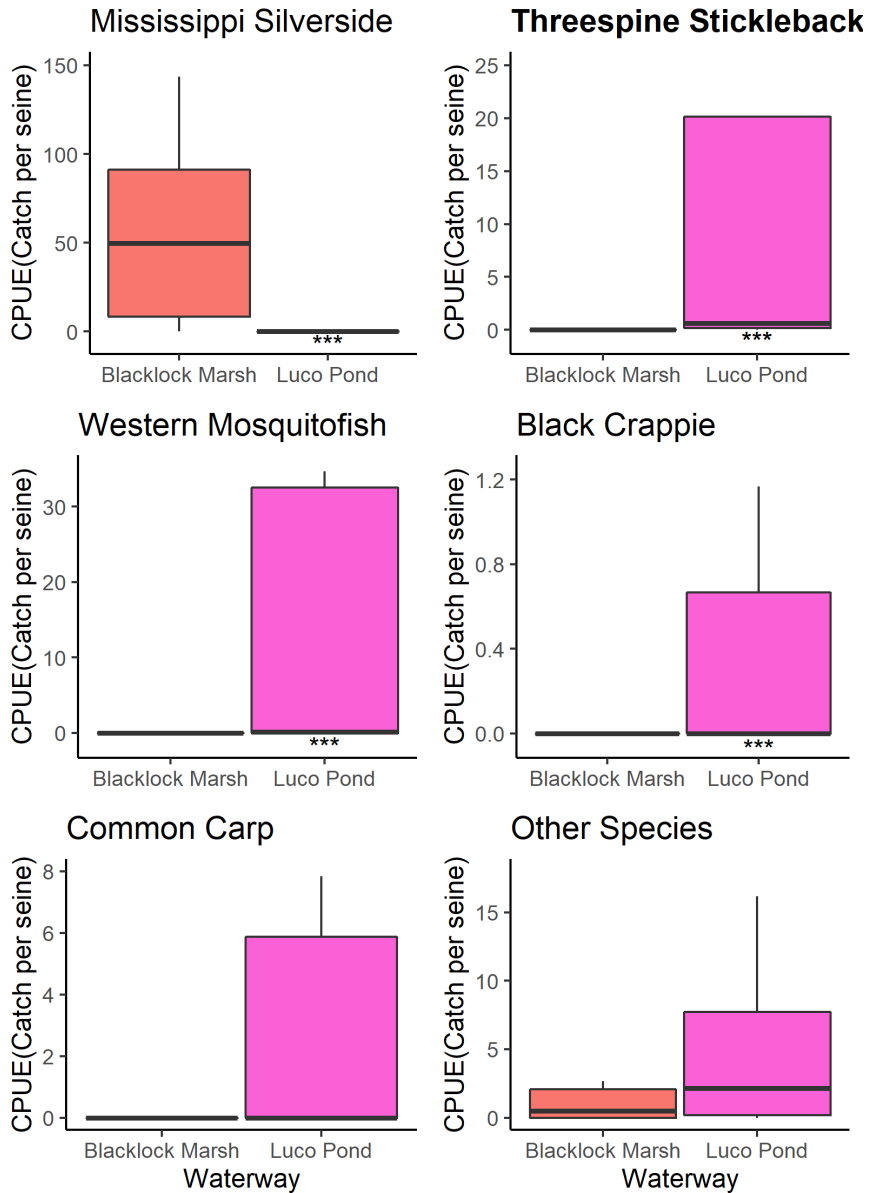


Figure 5 Monthly seine CPUE by fish species and waterway – outliers omitted. All species where fewer than 600 individuals were captured are classified as other. Stars indicate sites with measurements different than Blacklock according to Wilcoxon two-way test ($p\text{-value} \leq 0.045$). Y-axis varies by plot. **Bold** indicates native species.

Appendix

Table A1 Fish species by trawl and seine of all fishes sampled. **Bold*** indicates native species.

Common Name	Scientific Name	Species Code	Total	Otter Trawl	Beach Seine
threespine stickleback*	<i>Gasterosteus aculeatus</i>	STBK	13087	115	12972
Mississippi silverside	<i>Menidia audens</i>	ISS	5512	1866	3646
Splittail*	<i>Pogonichthys macrolepidotus</i>	ST	3061	2646	415
black crappie	<i>Pomoxis nigromaculatus</i>	BC	3026	1122	1904
western mosquitofish	<i>Gambusia affinis</i>	MQF	1760	0	1760
striped bass	<i>Morone saxatilis</i>	SB	916	914	2
common carp	<i>Cyprinus carpio</i>	CP	911	201	710
tule perch*	<i>Hysterocarpus traski</i>	TP	776	775	1
shimofuri goby	<i>Tridentiger bifasciatus</i>	SG	643	465	178
prickly sculpin*	<i>Cottus asper</i>	SCP	311	119	192
threadfin shad	<i>Dorosoma petenense</i>	TFS	202	201	1
white catfish	<i>Ameiurus catus</i>	WCF	249	249	0
yellowfin goby	<i>Acanthogobius flavimanus</i>	YFG	95	40	55
American shad	<i>Alosa sapidissima</i>	ASH	123	123	0
longfin smelt*	<i>Spirinchus thaleichthys</i>	LFS	23	23	0
shokihaze goby	<i>Tridentiger barbatus</i>	SKG	19	19	0
Sacramento sucker*	<i>Catostomus occidentalis</i>	SKR	12	12	0
rainwater killifish	<i>Lucania parva</i>	RWK	2	0	2
staghorn sculpin*	<i>Leptocottus armatus</i>	STAG	4	4	0
northern anchovy*	<i>Engraulis mordax</i>	NAC	8	8	0
Pacific herring*	<i>Clupea pallasii</i>	PH	5	5	0
Delta smelt*	<i>Hypomesus transpacificus</i>	DS	3	2	1
goldfish	<i>Carassius auratus</i>	GF	2	2	0
black bullhead	<i>Ameiurus melas</i>	BLB	3	3	0
bay pipefish*	<i>Syngnathus leptorhynchus</i>	BYP	1	1	0
golden shiner	<i>Notemigonus crysoleucas</i>	GSH	1	1	0
Total		25	30755	8916	21839

Table A2 Diversity indices for fishes captured with otter trawl.

Waterway	Shannon Diversity Index	Simpson Diversity Index	Inverse Simpson Diversity Index
Blacklock	0.95	0.44	1.78
Little Honker Bay	2.03	0.83	5.98
Arnold Slough	2.00	0.81	5.40
Nurse Slough	1.60	0.72	3.57
Luco Slough	1.72	0.75	3.97
Denverton Slough	1.87	0.77	4.42

Table A3 Diversity indices for fishes captured with beach seine.

Waterway	Shannon Diversity Index	Simpson Diversity Index	Inverse Simpson Diversity Index
Blacklock	1.15	0.13	0.28
Luco Pond	1.88	0.47	1.04

Table A4 Wilcoxon two-sided test results between Blacklock Marsh and other waterways for water quality. **Bold** p-values indicate a difference in parameter values.

Parameter	Waterway	Estimate	Statistic	p-value	Conf low	Conf high
Dissolved Oxygen	DV	0.449963	6907.5	0.061264	-0.01993	0.879942
	LC	1.330047	3927.5	5.89E-07	0.909964	1.699964
	AR	0.600028	3228.5	0.037041	0.02999	1.149985
	LH	-0.59993	1251.5	0.007023	-0.90001	-0.16002
	NS	0.270029	3077.5	0.193258	-0.16995	0.600047
	LP	0.540022	5038	0.015703	0.099958	1.080043
Secchi Depth	DV	6.000042	8159.5	5.83E-06	3.999963	8.999907
	LC	6.000038	3607	0.000166	2.999973	9.999951
	AR	0.999998	2764.5	0.744282	-3.00005	4.000011
	LH	-3.99998	1423.5	0.063741	-8.99995	6.27E-05
	NS	0.99996	2840.5	0.679016	-3.00006	4.000083
	LP	11.99994	5949.5	3.05E-08	7.999953	15.99996
Chlorophyll- <i>a</i>	DV	-8.4461	2974	8.65E-10	-10.3601	-5.87408
	LC	-6.7	1579.5	5.82E-05	-11.7	-3.39997
	AR	-0.59999	2523.5	0.559151	-3.10005	1.799972
	LH	2.500046	2342.5	0.008231	0.599984	5.29998
	NS	3.49892	3733	2.15E-05	1.791366	6.245102
	LP	-21.5	1524	4.26E-10	-27	-15
Dissolved Organic Carbon	DV	-6.81009	1756	1.23E-19	-7.67181	-5.72531
	LC	-4.29995	1191	3.48E-08	-5.79995	-2.90003
	AR	-2.30001	1556.5	2.09E-05	-3.40005	-1.10004
	LH	1.599975	2459	0.001305	0.699966	2.699936
	NS	1.857852	3803	5.84E-05	0.980524	2.667484
	LP	-9.60009	468	9.47E-22	-11	-8.40003

Table A5 Wilcoxon two-sided test results between Blacklock Marsh and other waterways for trawl CPUE of macroinvertebrates. **Bold** p-values indicate a difference in macroinvertebrate CPUE.

Species	Waterway	Estimate	Statistic	p-value	Conf low	Conf high
Siberian Prawn	DV	-2.53325	63	3.46E-05	-4.06674	-0.59994
	LC	-3.68E-05	118.5	0.003951	-0.20004	-2.50E-05
	AR	-2.10E-05	178.5	0.275281	-5.83E-06	4.95E-05
	LH	-2.39E-05	178.5	0.275281	-4.39E-05	2.61E-05
	NS	-3.03964	73.5	0.000171	-3.99997	-2.06E-05
Black Sea Jellyfish	DV	-2.17E-05	190	1	-4.33E-05	6.91E-06
	LC	-8.50E-05	191	0.614695	-3.99E-05	6.38E-05
	AR	0	210	0.342112	0	0
	LH	-3.43E-05	190	0.573704	-4.42E-05	1.89E-05
	NS	-2.97E-05	132	0.040015	-5.28E-06	5.02E-05

Table A6 Wilcoxon two-sided test results between Blacklock Marsh and other waterways for trawl CPUE of fishes. **Bold** p-values indicate a difference in fish CPUE. **Bold** species names indicate native species.

Species	Waterway	Estimate	Statistic	p-value	Conf low	Conf high
Mississippi Silverside	DV	0.133329	337.5	0.000966	7.26E-05	1.846329
	LC	1.62E-05	223	0.959499	-0.13334	1.433956
	AR	-0.13332	110	0.001842	-1.64633	-2.61E-05
	LH	0.074576	295.5	0.04509	-9.48E-06	1.634007
	NS	0.133345	357	2.96E-05	8.14E-05	1.634016
Shimofuri Goby	DV	0.689607	407.5	1.33E-06	0.266742	1.399975
	LL	0.466658	328.5	0.006558	0.069993	1.066684
	AR	-0.45912	117	0.009394	-1.12903	-0.06673
	LH	0.666712	392	8.46E-06	0.26151	1.343325
	NS	0.689643	404.5	1.26E-06	0.266672	1.343302
Tule Perch	DV	-0.7333	29	2.79E-07	-0.8667	-0.20002
	LC	-2.16E-05	189	0.229613	-2.60E-05	3.28E-05
	AR	0.399984	375.5	1.64E-05	0.067873	0.66673
	LH	-7.64E-06	155.5	0.029762	-0.09996	6.55E-06
	NS	-0.26668	66.5	1.86E-05	-0.59998	-0.09996
Sacramento Splittail	DV	-1.2667	82.5	0.000506	-2.00004	-0.60508
	LC	-1.19991	103	0.003044	-2.06669	-0.36664
	AR	0.204699	284.5	0.108389	-0.06663	0.428616
	LH	6.33E-05	225	0.918287	-0.13335	0.266729
	NS	-0.90003	122.5	0.013524	-1.53336	-0.06668
Striped Bass	DV	-0.56922	37.5	2.30E-06	-1.11589	-0.20001
	LC	-0.24924	71	9.38E-05	-0.40005	-0.10002
	AR	0.208119	358.5	0.000282	0.071457	0.40906
	LH	-0.03341	147.5	0.04304	-0.19997	8.75E-06
	NS	-1.39994	18.5	1.83E-07	-1.73338	-1.06664

Table A7 Wilcoxon two-sided test results between Blacklock Marsh and other Luco Pond for seine CPUE of fishes. **Bold** p-values indicate a difference in fish CPUE. **Bold** species names indicate native species.

Species	Estimate	Statistic	p-value	Conf low	Conf high
Threespine Stickleback	-0.50002	61	3.12E-05	3.12E-05	-0.3333
Mississippi Silverside	48.99996	370	2.47E-06	2.47E-06	77.13329
Black Crappie	-7.77E-05	120	0.002085	0.002085	0
Western Mosquitofish	-0.20052	100	0.0004	0.0004	0
Common Carp	-4.61E-05	156	0.134508	0.134508	1.30E-05

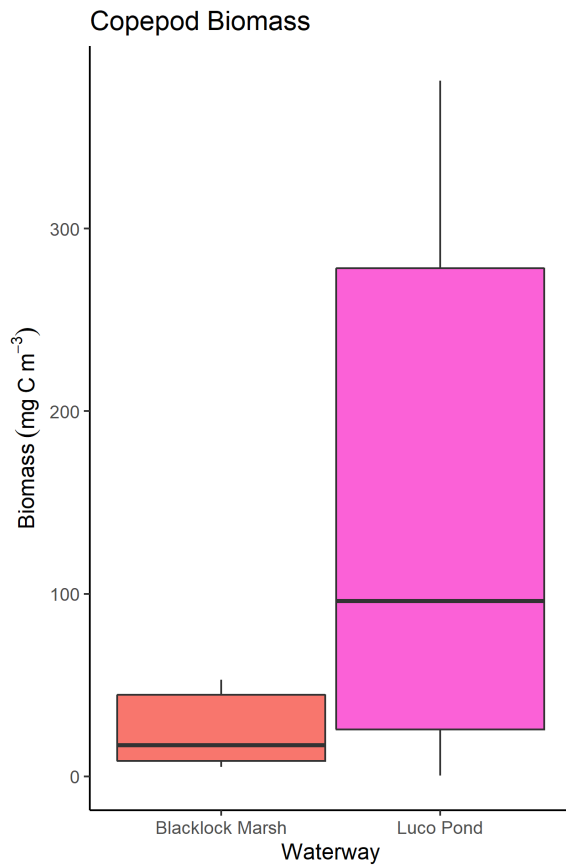


Figure A1 Copepod biomass (mg C m⁻³) for months where samples were collected both in Blacklock Marsh (BL) and Luco Pond (LP).

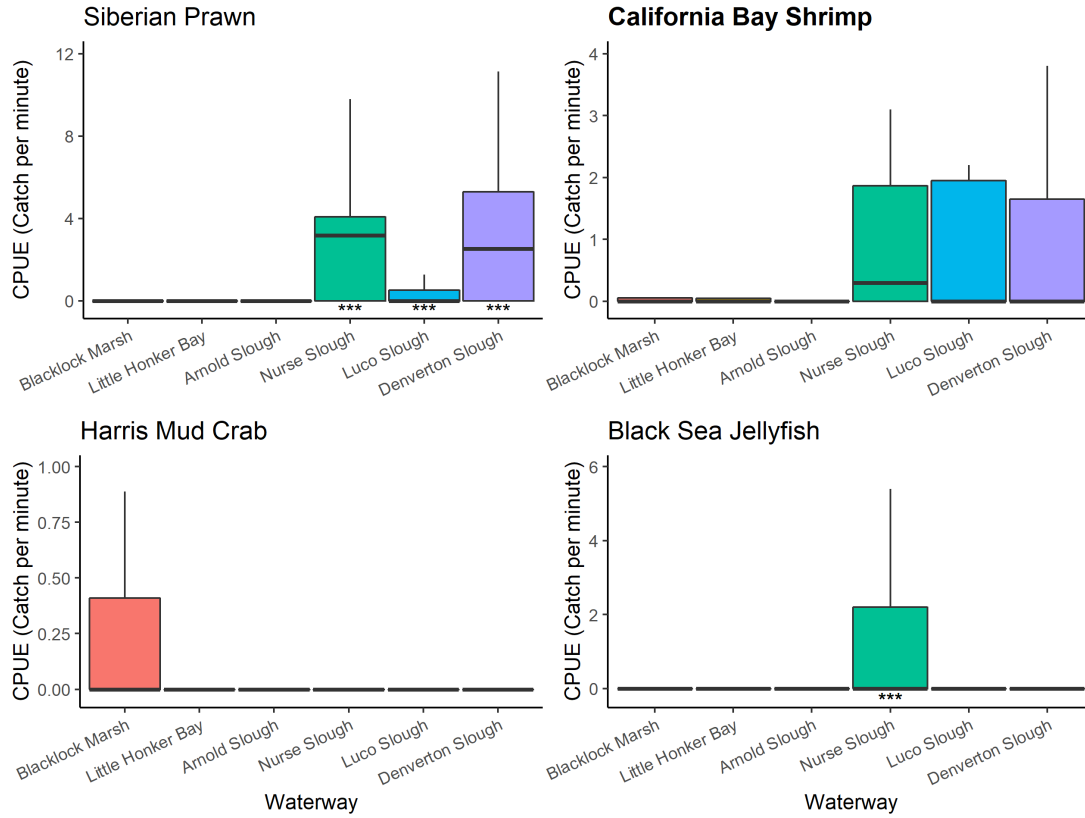


Figure A2 Trawl CPUE by macroinvertebrate species and waterway. Stars indicate sites with measurements different than Blacklock ($p\text{-value} \leq 0.045$) according to Wilcoxon two-way test. Y-axis varies by plot. **Bold** indicates native species.

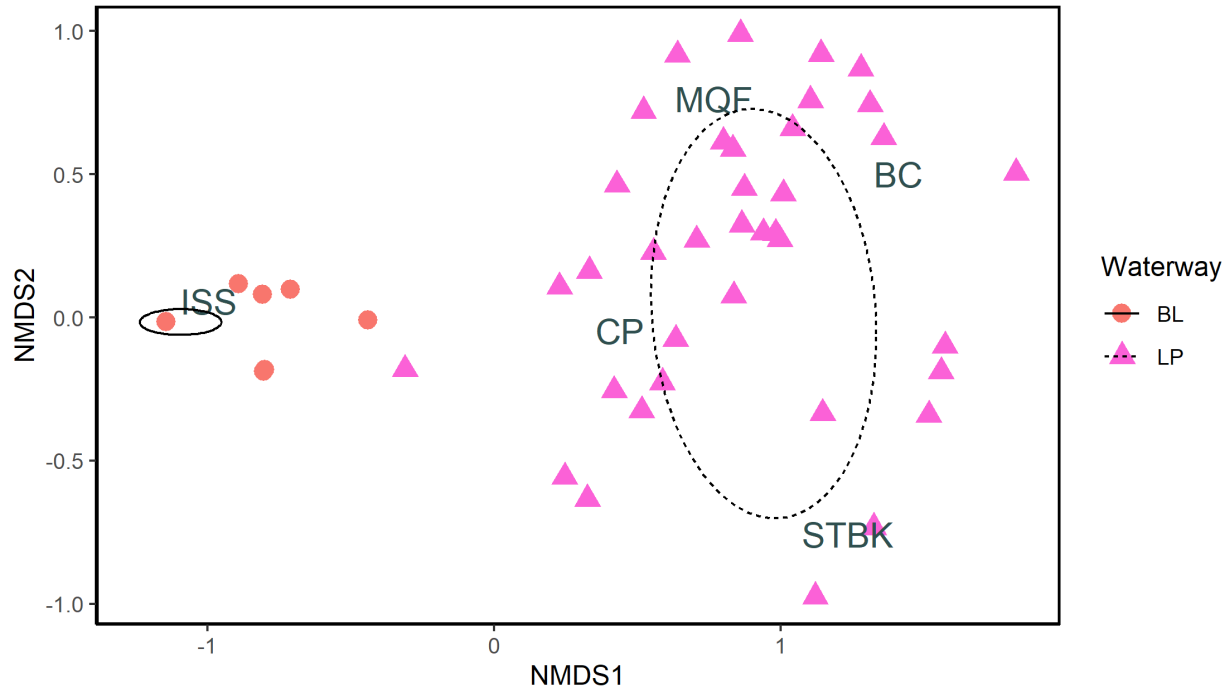


Figure A3 NMDS plot of fish captured in seines (Stress = 0.029. See Table 1 for waterway codes. BC = black crappie, CP = common carp, ISS = Mississippi silverside, MQF = western mosquitofish, and STBK = threespine stickleback).

Chapter 2

Agricultural affects water chemistry and primary production in the San Francisco Estuary

Brian Oliver Williamshen

Abstract

Phytoplankton are the base of estuarine pelagic food-webs, and a reduction of phytoplankton in the San Francisco Estuary (SFE) has contributed to a decline of zooplankton and pelagic fishes. The Cache Slough Complex within the SFE still supports higher densities of phytoplankton, zooplankton, and pelagic fishes than other freshwater regions. A unique feature of the Cache Slough Complex is the connection of small upland agricultural watersheds directly to dead-end tidal sloughs. To determine if the agricultural landscapes are important to phytoplankton production in the Cache Slough Complex, I measured rates of pelagic metabolism using bottle incubations, nutrient concentration, and organic carbon across tidal sloughs with varying areas of upstream irrigated cropland during a wet and a dry year. Sites with more upstream cropland had higher nutrient (ammonium, nitrate, and phosphorus) concentrations, greater chlorophyll-*a* concentrations and higher rates of pelagic primary production. However, there was little difference in dissolved organic carbon and rates of pelagic respiration among sites. Years with largely different precipitation amount also had different chlorophyll *a*, pelagic metabolism rates, and nutrients which seems to be tied to upstream land use and watershed size. Results from my study suggests that upstream irrigated agriculture is an important determinant of phytoplankton biomass in tidal sloughs of the Cache Slough Complex.

Introduction

Phytoplankton are the base of pelagic estuarine food-webs that support commercially and recreationally important fish species, but some estuaries have limitations to phytoplankton production that can adversely affect fisheries (Cloern 2001; Domingues et al. 2011; Saulnier et al. 2020). Phytoplankton produced within the estuary and bacterioplankton sustained by organic carbon support zooplankton that are prey for juvenile and pelagic fishes (Day et al. 2012; Andersson et al. 2018). Growth of phytoplankton is controlled by nutrient concentration, light availability, and temperature – which in addition to hydrodynamics and loss (*e.g.*, grazing), determines phytoplankton biomass (Ketchum 1954; Boynton et al. 1982; Cloern et al. 2014).

Most study and management of estuarine ecosystems have focused on the detrimental effects of agriculture, but nutrient-rich agricultural runoff can also increase fish production in certain cases (Watzin and Gosselink 1992; Patrick 1994; Matson et al. 1997; Nixon and Buckley 2002). Agricultural and other terrestrial inputs can increase phytoplankton in nutrient limited estuaries (Domingues et al. 2011; Paczkowska et al. 2019). Agricultural runoff is a major contributing factor to eutrophication and harmful algal blooms in many estuaries, but despite nutrient loading, California's largest estuary is phytoplankton limited (Nixon 1995; Cloern 2001; Rabalais 2002).

Over the past half century, pelagic productivity has declined across trophic levels in the Sacramento-San Joaquin River Delta (Delta) and aquatic communities have changed drastically (Bennett and Moyle 1996; Jassby et al. 2002; Nobriga et al. 2005). The Delta comprises the freshwater portion of the tidally influenced San Francisco Estuary (SFE) and has been highly modified by conversion of wetlands and diversion of water for agriculture. Populations of pelagic fishes in the SFE have been declining over the past several decades, with a sharp drop in

the year 2000 (Feyrer et al. 2007; Sommer et al. 2007; Stompe et al. 2020), likely due, in part, to a decline in plankton production caused by water diversions and species introductions (Cloern and Jassby 2012). The reduction in pelagic productivity in the SFE affects the zooplankton food supply needed by pelagic and juvenile fishes (Moyle 2002; Winder and Jassby 2011).

There are important connections between aquatic and terrestrial ecosystems, with energy and nutrients moving between them, and terrestrial subsidies are particularly important to estuarine production (Polis et al. 1997; Nakano et al. 1999; Nixon and Buckley 2002; Hoffman et al. 2008). Flow pulses can enhance the connection between landscapes in estuaries and lead to increased nutrient concentration and phytoplankton production (Eyre and Twigg 1997; Pinckney et al. 1998; Saeck et al. 2013). Estuarine-terrestrial linkages have been recognized elsewhere in the SFE, such as marsh derived carbon playing an important role in estuarine food webs (Sobczak et al. 2002; Colombano et al. 2020), but little research has explored how landscape processes in agriculture-dominated watersheds upstream of the Delta may drive pelagic food webs within tidal sloughs.

The Cache Slough Complex (CSC) is a unique slough complex within the freshwater North Delta, near the Sacramento River, that receives inflow from a managed floodplain and several watersheds of varying size, geomorphology, and land use, and has been identified to have high potential for successful restoration (Durand et al. 2016; Moyle et al. 2018). The two main sloughs of the CSC, Cache Slough and Lindsey Slough, are geographically close but have varying food-web structure, phytoplankton, zooplankton. A majority of carbon contribution to fishes comes from phytoplankton in upper Cache Slough and from submerged macrophytes in upper Lindsey Slough (Young et al. 2021). The upper reaches of the Cache Slough Network typically have higher chlorophyll-*a* (Chl *a*; a proxy for phytoplankton biomass) concentration

and zooplankton density than the upper Lindsey Slough Network (Montgomery 2017; Jasper 2020; Luke 2023). High residence time and connectivity to upslope landscapes likely play a significant role in the disparity of phytoplankton and zooplankton observed between two adjacent channels within the complex (Jasper 2020). However, the mechanisms driving production at the tidal slough-landscape interface is largely unknown.

To better understand components of the base of the pelagic food web and its connection with human-dominated landscapes I evaluated nutrient concentrations, Chl *a*, and rates of pelagic primary production and respiration between a wet and a dry year across sites with varying upstream land use.

I tested three hypotheses: (H1) tidal sloughs with greater areas of upstream irrigated cropland would have higher concentrations of nutrients, rates of pelagic autotrophic production, and Chl *a* concentrations. In addition, (H2) tidal sloughs with more upstream cropland would have higher dissolved organic carbon concentrations that would contribute to higher pelagic respiration. Finally, (H3) in a wet year, tidal sloughs would have higher nutrient concentrations, dissolved organic carbon (DOC), pelagic productivity and respiration, and phytoplankton abundance than in a dry year.

Methods

Study Site

All sampling sites were located within the Cache Slough Complex (CSC), a wetland complex located in the North Delta that is comprised of tidal sloughs, fringing emergent marsh, and flooded agricultural tracts. I chose sites in five CSC sloughs that had varying areas of upstream landcover (Fig 1; Table 1). All sites fall within a low water exchange zone of the CSC

(Stumpner et al. 2020b), so they have high residence time and varying proportions of Sacramento River water (Fig 2; Durand et al. 2019).

The two distinct slough networks within the CSC are the Cache Network and Lindsey Network, with each network comprised of three smaller sloughs. The Cache Network includes Cache (and site CA), Hass (HS), and Ulatis (UL) sloughs and the Lindsey Network includes Lindsey Slough, Barker Slough (BK), and Calhoun Cut (CC; Table 1; Fig 1). The study took place from January through June in 2019 and 2021; 2019 is classified as a wet year (687 mm precipitation from November 2018 through June 2019) and 2021 as a critically dry year (166 mm precipitation from November 2020 through June 2021; California Department of Water Resources 2023; National Oceanic and Atmospheric Administration 2024). Sites were sampled one to three times each month in 2019 and once each month in 2021. HS, UL, BK, and CC were sampled in both 2019 (nine total samples at each site) and 2021 (six total samples at each site), and CA was only sampled in 2021 (six samples; Table 1).

The Cache Network receives water from the 375 km² Ulatis Creek Watershed, which encompasses the southeastern Coast Range and city of Vacaville, and from the 154 km² Hass Slough Watershed (Table 1; Fig 1). Ulatis Creek receives water from urban runoff, Vacaville's Easterly Wastewater Treatment Plant, and cropland irrigation – the watershed is the major source of sediment and nitrogen for the CSC (Morgan-King and Schoellhamer 2013; Fackrell et al. 2022). During all years, there is some discharge of water into Ulatis Creek, which keeps a constant supply of water flowing to UL. An additional source of agricultural water constituents is the Hass Slough Watershed, a laser-graded network of cropland and irrigation canals which both draws water from and drains into Hass Slough.

Lindsey Slough receives water from the 94 km² Calhoun-Big Ditch drainage, and the 45 km² Barker Creek Watershed (Table 1; Fig 1). Inflows from both drainages are ephemeral through rangeland (grassland sometimes used for grazing), with Barker Slough also receiving some urban and cropland runoff. The terminus of Barker Slough is the Barker Slough Pumping Plant which supplies water to the Solano and Napa counties via the North Bay Aqueduct – BK is located within 50 meters of the pumps. The portion of Barker Slough above the tidal excursion is dammed and a large pond, Campbell Lake, halts flow of water until enough precipitation has fallen to raise the stage and crest the dam. Calhoun Cut is a straight channel that was excavated through the middle of the historic upper Lindsey Slough channel. A recent restoration project reconnected Calhoun Cut with the historic slough channel, increasing the area of tidal marsh in the region. CC is located at the mouth of the restoration site.

Water Quality

I collected surface water in a thoroughly rinsed 20-liter bucket from which water quality, phytoplankton, and incubation samples were drawn. I filled 1-liter high density polyethylene (HDPE) bottles from the thoroughly mixed bucket to measure turbidity, soluble reactive phosphorus (SRP), nitrogen from nitrate and nitrite (NO₃), and nitrogen from ammonium (NH₄), DOC, and Chl *a*. Samples were stored on ice and were filtered and analyzed within five days of collection. Subsamples of approximately 100 mL were filtered through a 0.2 μm pore size polycarbonate membrane for quantification of SRP, NO₃, NH₄, and DOC. SRP was measured using ammonium molybdate spectrophotometric method. The two forms of dissolved inorganic nitrogen (DIN) were measured as follows: NO₃ using vanadium chloride spectrophotometric method (Doane and Horwath 2003) and NH₄ using spectroscopy with the Berthelot reaction

using a salicylate analog of indophenol blue (Forster 1995). DOC was measured with a UV enhanced-persulfate TOC analyzer (Phoenix 8000) in accordance with EPA Standard Method 5310C (Clesceri et al. 1998).

Chl *a* concentration was determined using fluorescence. A subsample was filtered through a Whatman porous GF/F filter, placed into vials, freeze-dried, suspended in 90% ethanol warmed to 78°C for ten minutes for extraction, and analyzed using a Turner Trilogy Laboratory Fluorometer (Sartory and Grobbelaar 1984; Clesceri et al. 1998). Turbidity was measured by placing a subsample of each water grab into a turbidity meter (Oakton T-100).

Phytoplankton

Phytoplankton were collected in 250 mL opaque bottles from the thoroughly mixed buckets of whole surface water and preserved in 5% Lugol's solution by volume. Phytoplankton identification and enumeration were performed by BSA Environmental Services, Inc. using the Utermöhl method (Utermöhl 1931, 1958) in accordance with Standard Methods 10200 (Clesceri et al. 1998). A Leica DMLB compound microscope was used for random field counts of at least 400 natural units and taxa were identified to the lowest possible taxonomic level. Cell biovolumes were quantified on a per milliliter basis (Hillebrand et al. 1999).

Pelagic Community Metabolism Rates

We measured changes in dissolved oxygen in bottle incubations to model pelagic ecosystem metabolic rates. To collect water for the bottle incubations, I poured surface water from the mixed 20-liter bucket through a 150-micrometer (μm) filter to exclude zooplankton,

placed in thoroughly rinsed opaque HDPE bottles, sealed, and stored on ice. Water samples were transported to the laboratory and placed in a temperature-controlled grow chamber set to ambient temperatures where they were allowed to equilibrate in the dark for approximately 8 hours. Chamber temperature was held constant throughout each incubation and ranged from 11.5 to 21°C.

Water from each site was poured into four replicate 1-pint (0.59 L) mason jars and dissolved oxygen (DO) concentration was measured using a Presens Fibox 4 fiberoptic oxygen sensor (detection from 1-15 mg/L and $\pm 0.05\%$ accuracy). Four replicate jars for each of the five sites were randomly placed under fluorescent grow lights and exposed to 10-14 hours of light (25 hours on 1/15/2019) with photosynthetic active radiation ranging from 83.3 to 126.7 $\mu\text{mol/s}$. Light and dark bottles were incubated concurrently in 2019; four jars were exposed to light from each site while four were enclosed in dark chambers. In 2021, light and dark jars were incubated sequentially; jars from each site were exposed to a period of light followed by a period of dark. DO was recorded for each jar immediately before light exposure at the end of the light period and at the end of the dark period. Two glass marbles were placed in each jar and jars were agitated at the beginning of incubation and prior to each measurement. I attributed declines in DO within dark jars to respiration alone, and assumed respiration within the dark jars was representative of respiration in the light jars and calculated the metabolism rates as follows:

$$\text{Net Community Production (NCP)} = \frac{\Delta DO_{\text{light}}}{\Delta t}$$

$$\text{Community Respiration (CR)} = \frac{\Delta DO_{\text{dark}}}{\Delta t}$$

$$\text{Gross Primary Production (GPP)} = \text{NCP} - \text{CR}$$

Where NCP, CR, and GPP are standardized to a volume of 1 Liter (L) and a time of one day (d) giving units of $\text{mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$.

To standardize rates from incubations carried out at different temperatures for a comparison between sites and years, a Q10 of 2.5 and 1.8 were used for CR and GPP, respectively (Lomas et al. 2002; Apple et al. 2006; Wielgat-Rychert et al. 2010). To examine primary productivity per unit of Chl *a*, I calculated Chl *a* normalized GPP (NGPP) by dividing GPP by Chl *a* concentration.

Analysis

All analyses and data visualization were performed in R (R Core Team 2022). Site differences for water constituents (NH_4 , NO_3 , SRP, DOC, turbidity, EC, and Chl *a*), phytoplankton (density and biovolume), and metabolism rates (GPP, CR, and NCP) were analyzed using a Wilcoxon signed-rank test. The Wilcoxon test is a nonparametric test that is ideal for pairwise testing data that are not normally distributed. A Benjamini-Hochberg p-adjustment was calculated for all site comparisons using the package GGPUBR (Kassambara 2023). To compare differences between years within each site for all variables, GGPUBR was used to perform the test and display p-values on figures (Kassambara 2023).

To model drivers of the metabolism rates and Chl *a* concentration, generalized linear mixed models were used. Models were created with all combinations of the biologically relevant predictor variables (NH_4 , NO_3 , SRP, DOC, and Chl *a*) for each response variable (Q10 corrected GPP, CR, NCP, and NGPP) using the lmer function in the lme4 package (Bates et al. 2015). Only EC was used as a predictor variable for Chl *a* because phytoplankton uptake

nutrients and can draw down concentration when abundant. Site and month were assigned as random effects in the models to account for unmeasured spatial and temporal differences. I checked that model residuals met assumptions of normality and homoscedasticity. All models were compared against each other using both AICc (AIC corrected for small sample size bias) and BIC, both are information criterion that penalize model complexity in different ways (Aho et al. 2014). The models within 4 points of the top-ranked model for both AICc and BIC were considered (Burnham and Anderson 2001) and the the highest R^2 that fit this criterion were chosen. Maximum likelihood was used when performing model selection and restricted maximum likelihood was used for final model output.

Results

Metabolism Rates

Overall, Cache Network sites with greater area of cropland had higher rates of GPP than Lindsey sites (Fig 3A; Fig 8A), CR rates were similar between networks and cropland area (Fig 3B; Fig 8B), and NCP was somewhat higher at Cache Network sites (Fig 3C; Table 2), and there were differences between years at each site (Fig 3). Mean GPP varied from 1.3 to 13 $\text{mg O}_2 \text{L}^{-1} \text{d}^{-1}$ at CC and CA, respectively (Fig 3A). Mean GPP was higher in 2019 at HS and higher in 2021 at BK and CC (Fig 3A). Mean CR ranged from 3.5 $-\text{mg O}_2 \text{L}^{-1} \text{d}^{-1}$ at BK and CC to 6.3 $-\text{mg O}_2 \text{L}^{-1} \text{d}^{-1}$ at CA (Fig 3B). There were stark differences in CR between years at each site – rates were higher in 2019 at all sites but UL, which was higher in 2021 (Fig 3B). Mean overall NCP varied from -2.2 $\text{mg O}_2 \text{L}^{-1} \text{d}^{-1}$ at CC to 7 $\text{mg O}_2 \text{L}^{-1} \text{d}^{-1}$ at CA (Fig 3C). NCP was higher in 2021 at UL, BK, and CC and was autotrophic ($\text{NCP} > 0$) for most incubations in 2021 at CA and UL (Fig

3C). There was little difference in NGPP between networks, but there were differences between years with NGPP higher in 2021 at UL and BK (Fig 3D; Table 4). Mean NGPP was between 0.56 and 0.92 mgO₂ ugChl⁻¹ d⁻¹ among sites.

Drivers of Metabolism

To determine drivers associated with H1, I fit models for GPP, NCP, NGPP, and Chl *a*. Best fit models for GPP included Chl *a* and NH₄ as fixed effects (Fig 4A), Chl *a* and DOC as fixed effects for NCP (Fig 4C), and NH₄ and turbidity for NGPP (Fig 4D). Chl *a* concentration had a positive ($p < 0.001$) effect on GPP (Fig 4A). Chl *a* concentration had a positive effect ($p < 0.001$), and DOC had a negative effect ($p = 0.001$) on NCP (Fig 7C). NH₄ had a positive effect ($p = 0.011$) and turbidity had a negative effect ($p = 0.002$) on NGPP (Fig 4D).

To determine drivers associated with H2, I fit a model for CR. The best fit model for CR included Chl *a* and DOC as fixed effects, (Fig 4B). Chl *a* concentration and DOC both had a positive effect ($p < 0.001$) on CR (Fig 7B)

Phytoplankton

To determine the quantity and quality of phytoplankton present at sites I measured Chl *a* and phytoplankton biovolume. Overall, Chl *a* concentration and total phytoplankton biovolume were higher in Cache than Lindsey Network sites (Fig 5; Table 3) and higher in 2021 than 2019 (Fig 5). Mean Chl *a* concentration varied from 2.7 ug/L at CC to 18 ug/L at CA and was higher in 2019 at HS and higher in 2021 at UL and CC (Fig 5A).

Diatoms made up the greatest biovolume of phytoplankton across sites for both years, and diatoms, chlorophytes, and cryptophytes had higher biovolume in 2021 than 2019 across sites (Fig 5B). Mean total phytoplankton biomass was lowest at HS ($2.2 \times 10^9 \text{ um}^3/\text{L}$) and highest at CA ($5.7 \times 10^9 \text{ um}^3/\text{L}$) and UL ($4.1 \times 10^9 \text{ um}^3/\text{L}$; Fig 5B). Microcystis was only found at three sites (CC, BK, and HS) on a single sampling day in April 2021.

Water Chemistry

To answer parts of H1, H2, and H3 nutrients and other water constituents were compared across sites and years. Ammonium, nitrate, and soluble reactive phosphorus all followed similar site and year differences – overall, Cache Network sites that had more upstream cropland had much higher NH_4 , NO_3 , and SRP concentrations than Lindsey Network sites (Fig 6; Fig 8; Table 4). Mean NH_4 concentrations varied from 0.49 mg/L at CC to 0.15 mg/L at HS and concentrations were higher in 2019 than 2021 at HS, while higher in 2021 at BK and UL (Fig 6A). Mean NO_3 concentration ranged from 0.09 mg/L at CC to 2.6 mg/L at UL (Fig 6B) and were higher in 2019 than 2021 at HS and higher in 2021 at CC (Fig 6B). Mean SRP concentration varied from 0.13 mg/L at BK to 1.1 mg/L at CA (2021 only; Fig 6C) and were higher in 2019 at HS and CC and higher in 2021 at UL (Fig 6C). Ratio of moles of nitrogen from dissolved inorganic nitrogen (DIN; $\text{NH}_4 + \text{NO}_3$) to moles of SRP was nearly always below 10, except for several occasions at UL in 2019 when SRP was exceptionally high.

Compared to the inorganic nutrients, DOC did not differ greatly across sites (Fig 7A; Table 2), but turbidity and EC were overall higher in Cache Network Sloughs with greater upstream cropland area (Fig 7; Fig 8; Table 4). DOC, Turbidity, and EC showed similar patterns

between years at each site, with HS, BK, and CC being elevated in 2019 and UL being elevated in 2021 (Fig 7). Mean DOC varied from 9.6 mg/L at BK to 11 mg/L at CA (Fig 7A). Mean turbidity was lowest at BK (12 NTU) and highest at HS (37 NTU; Fig 7B). Mean EC varied from 337 uS/cm at CC to 799 uS/cm at UL and was the only variable that diverged from the spatial pattern stated above: no difference at HS between 2019 and 2021 (Fig 7C).

Discussion

In contrast with other large estuaries in the United States, such as the Chesapeake Bay Estuary, eutrophication is not an issue in the SFE and phytoplankton abundance has been in decline (Cloern 2001; Cloern and Jassby 2012). Phytoplankton depletion within the Delta region of the SFE is thought to have created a pelagic organism decline of zooplankton and fishes (Feyrer et al. 2007; Sommer et al. 2007; Winder and Jassby 2011). Because agricultural runoff contributes to excess phytoplankton in other estuaries, I attempted to relate agriculture to phytoplankton production within the CSC through comparison of sites with a range of agricultural influence. My results suggest that factors in connected to agricultural landscapes are influencing phytoplankton production within the CSC, though not through my hypothesized mechanisms.

There are well-documented differences Chl *a* concentrations within the CSC, with upper Cache Network Slough sites (HS and UL) having much higher concentrations than upper Lindsey Network Sloughs sites (BK and CC; Jasper 2020; Luke 2023). Because there are more nutrient sources to HS and UL from agricultural runoff and wastewater effluent, I expected that these sites would have higher nutrients, that nutrient concentrations would be a driver of higher

NGPP, and that higher NGPP would lead to the higher Chl *a* concentration at those sites (H1). I refuted this hypothesis by showing that although nutrients were higher at HS and UL, NGPP rates did not differ among sites and nutrients were at concentrations unlikely to limit production at most sampling events across sites. An alternate explanation was that higher residence time would lead to more accumulation of Chl *a* at HS and UL than BK and CC; however, it has been shown that residence time is similar across sites (Durand et al. 2019), making that explanation unlikely. This led me to believe that phytoplankton is being produced and concentrated in upstream agricultural waterways and subsequently transported to high-residence-time tidal slough sites where it accumulates. Although nutrient concentration is not driving phytoplankton production in tidal slough sites, where nutrients are abundant from upstream sources and the Sacramento River (Durand et al. 2019; Fackrell et al. 2022), it likely is important for upstream phytoplankton production since there are no nitrogen sources upstream of BK and CC to fuel production. These findings suggest that management of water for irrigation is important for the high phytoplankton concentration in Cache Network Sites.

Croplands can be sources of DOC to adjacent waterways (Eckard et al. 2017), which led me to hypothesize that DOC would be higher at sites with greater upstream cropland area and would drive higher rates of respiration there (H2). I refuted this hypothesis by finding similar DOC concentration and respiration rates across sites. My finding suggesting that wetlands, rangeland, and estuary produced DOC are all likely contributing to heterotrophic respiration.

Finally, precipitation increases connectivity between the landscape and tidal sloughs, which led me to hypothesize that in a wet year there would be an increase in all nutrients and measured water quality constituents (H3), which according to my first two hypotheses, would lead to higher GPP, CR, and NGPP, thus higher Chl *a* concentration. I refuted this hypothesis by

finding differing water constituents and metabolism rates between the wet and dry year at different sites. My results suggest that there are geomorphologic and landscape-level differences that respond differently to precipitation. First, it appears that watershed area may be important, since the largest catchment (UL) seemed to have a dilution of water constituents, depression in all measured metabolism rates, and lower Chl *a* concentration during the wet year. Second, upstream land use seems to be important, as sites with no upstream nitrogen sources (BK and CC) will have no nitrogen to deliver with increased landscape connectivity and can lead to dilution of nitrogen coming from Sacramento River water. In a small cropland-dominated watershed (HS) there was higher nutrient concentrations, DOC, GPP, CR, and Chl *a*, suggesting that increased connectivity to cropland with precipitation, when the watershed is appropriately sized, creates ideal conditions for upstream phytoplankton production and delivery to tidal sloughs.

Phytoplankton Production

The interaction of water originating from wastewater and cropland runoff, combined with high residence time at Cache Network sites, fuels pelagic primary productivity that is much higher in Cache Network than at Lindsey Network and sites along the main axis of the estuary from the Sacramento River to San Pablo Bay (Parker et al. 2012). Spatial differences in nutrient concentration and phytoplankton between slough networks are likely tied to upstream land use and water source. Sloughs with more upstream cropland have higher nutrient loads and pelagic primary productivity, while sloughs with little upstream cropland have the potential for occasional nutrient limitation.

Residence time is the biggest determinant of Chl *a* concentration in the CSC (Stumpner et al. 2020a). The combination of residence time and connectivity to croplands is likely a key driver of Chl *a* in my study, which in turn is driving pelagic GPP. Samples from sites within the upstream watersheds had much higher Chl *a* concentrations than within the tidal sloughs in 2019 (Jasper 2020), suggesting that there is a phytoplankton pool to be transported to the tidal sloughs. Water spread across irrigation ditches or cropland has access to abundant sunlight, somewhat resembling historic floodplains, fueling phytoplankton production that is then transported down to the high residence time area of the tidal slough where it can accumulate (Fig 9). Normalized GPP rates did not vary greatly among sites, indicating that accumulation, not differences in NGPP, is driving the differences in phytoplankton abundance.

I hypothesized that nutrients would be the greatest driver of phytoplankton production and lead to the site differences observed in phytoplankton production (H1), but my results suggest an interaction of nutrients, upstream production, and accumulation drives phytoplankton abundance (Fig 10). NH₄, the energetically favorable form of nitrogen for phytoplankton to uptake, did have a small positive effect of NGPP, suggesting it can contribute to increased phytoplankton abundance (Cresswell and Syrett 1979).

Cropland and urban landscapes export high concentrations of DIN and phosphorus (Omernik and Development 1976), and the differences I observed in nutrients are likely due to water that enters the networks from the surrounding landscapes. Consistent with hypothesis 1, the Cache Network sites had much higher NH₄, NO₃, and SRP, which appear to be tied to inputs from upstream land use (Fig 10). Ratio of DIN to SRP was nearly always below 10, suggesting that nitrogen is in higher demand than phosphorus, as is common in estuaries (Redfield 1934; Nixon et al. 1986; Nixon 1995).

Phytoplankton production in the Lindsey Network may sometimes be inhibited by low nitrogen concentrations from the Sacramento River, an occurrence that may become more common in the future with a change to the nitrogen supply. At both BK and CC in 2019, DIN was measured at concentrations that were found to limit primary production in a nearby CSC channel (Loken et al. 2022). An operational change to a wastewater treatment plant on the Sacramento River, implemented July 2021, virtually eliminated NH₄ from the plant's effluent and reduced the amount of NO₃. This decrease to the amount of available DIN in sites which receive nutrients primarily from the Sacramento River is likely to slow rates of pelagic primary production the Lindsey Network.

Phytoplankton quality is a concern within the CSC (Stumpner et al. 2020a), but phytoplankton biovolume in my study was comprised mostly of large diatoms and cryptophytes, which are nutritionally important for zooplankton (Hansen et al. 1994; Müller-Navarra et al. 2000; Lehman et al. 2008). The three dominant phytoplankton clades for biovolume were the same as sampled in a nearby tidal channel, but my study found diatoms and cryptophytes at higher biovolume (Smits et al. 2023). Cryptophytes made up a much higher proportion of phytoplankton biovolume in 2019, indicating that conditions of a wet year are more conducive to their production. Additionally, *Microcystis spp.*, a toxic cyanobacteria known to create water quality problems in the SFE (Lehman et al. 2005, 2020), was only observed at three sites in April 2021.

Other Pelagic Carbon Sources

Rates of respiration correspond to both the biomass of phytoplankton respiring and the amount of organic carbon in the system being respired by bacteria and fungi. Mean DOC was similar across sites, but the sources are likely different. The primary sources of DOC are likely the wastewater, agricultural runoff, and carbon of planktonic origin. The Lindsey Network sites have more surrounding emergent marsh and submerged macrophytes than the Cache Network sites, with CC located adjacent to a tidal marsh restoration project. These tidal marshes and submerged macrophytes likely contribute DOC to the two sites, while rangeland is another DOC source when there is connection to the landscape.

Although phytoplankton are important for the pelagic food web, it has been shown that zooplankton will also feed on allochthonous carbon sources (Harfmann et al. 2019), representing an alternative trophic pathway for the pelagic food web. However, phytoplankton is far more important for zooplankton growth than allochthonous organic carbon in the Delta (Jassby and Cloern 2000; Müller-Solger et al. 2002; Sobczak et al. 2002), so it is beneficial to have sloughs that have an NCP that is more positive (more autotrophic).

Wet and Dry year differences

Flow pulses can increase nutrient concentration, respiration, and primary productivity, but responses can be inconsistent (Eyre and Twigg 1997; Pinckney et al. 1998; Shen et al. 2016). Natural and managed flow pulses through restored floodplain and agriculturally managed floodplains upstream of the Delta produce high concentrations of both phytoplankton and zooplankton which are transported downstream (Ahearn et al. 2006; Corline 2014; Frantzych et

al. 2021). In my CSC sites, increased runoff during a wet year affected sites differently; most sites had an increase in DOC, resulting in increased pelagic respiration during a wet year, but the largest watershed had lower concentrations of all water constituents and primary productivity. The year with higher precipitation only stimulated greater primary productivity at HS, the site that is used almost entirely for irrigated crop production (Table 1).

During wet years, runoff from cropland can transport nutrients and materials to estuaries (Baker et al. 2018). My two sites with the most upstream cropland, HS and UL, had different responses to the wet year. Agricultural runoff may explain the elevated nutrients, DOC, and turbidity in the cropland-dominated Hass Slough Watershed, but watershed size and the corresponding large volume of water with high precipitation seems to be diluting water constituents at UL (Fig 10A).

During dry years, the Lindsey Network sites have higher water residence time, with water and nitrogen originating almost entirely from the Sacramento River and during wet years water discharges into the network from rangeland runoff (Durand et al. 2019; Fackrell et al. 2022; Huntsman et al. 2023). Water flowing through rangeland is not likely to be rich in nitrogen but could carry phosphorus and organic carbon from sediment and vegetation. During 2019, NH₄ and NO₃ originating from the Sacramento River seemed to be somewhat diluted by runoff from the surrounding landscape (Fig 10A).

Turbidity is expected to be higher in wet years, as runoff carries organic material and sediment from the landscape into waterways (Coulliette and Noble 2008). This increase was observed at every site except UL, which was surprising because of the comparatively large size of the Ulatis Creek Watershed and the high-gradient streams of its headwaters. As with nutrients, it seems the volume of water that flows through the watershed dilutes the generally turbid waters

of Ulatis Creek. Also, a fair portion of the watershed is within the city of Vacaville and the cement surfaces have little sediment. Furthermore, phytoplankton can contribute to higher turbidity, so the higher Chl *a* in 2021 may be a reason that the turbidity pattern was reversed in Ulatis Slough.

It seems that salt was tied to landscape inputs in the Lindsey Network, leading to elevated EC at BK and CC during the wet year when residence time would be expected to be lower. EC increases in the CSC can be tied to either landscape inputs or high residence time (Downing et al. 2016; Gross et al. 2019). At UL, returns of irrigation water that are not diluted by precipitation combined with evaporation explain high EC during the dry year of 2021.

Unmeasured Potential Controls on Phytoplankton Abundance

Invasive bivalves and submerged macrophytes may be exerting some control on phytoplankton abundance in the CSC that were not measured (Fig 9). The introduction of two clam species have caused a shift in species assemblage and a decline in abundance of both phytoplankton and zooplankton (Alpine and Cloern 1992; Kimmerer and Orsi 1996; Kimmerer 2006; Winder and Jassby 2011). Clams were not found in abundance in most upstream regions of the CSC, so although they have a great effect on plankton elsewhere in the SF Estuary, they are unlikely playing a role at my sites (Brown et al. 2024). There was, however, a high density of clams found near CC, which could potentially be depressing phytoplankton (Williamshen et al. 2023).

Subtidal habitat in the Delta has been colonized by submerged aquatic macrophytes that produce allelopathic (*i.e.*, phytoplankton controlling) compounds and compete with

phytoplankton for light and nutrients (Søndergaard and Moss 1998; Mulderij et al. 2007; Vanderstukken et al. 2011). Submerged macrophytes reached very high abundance during the study period at CC, BK, and HS during 2021, which may have contributed to depressed Chl *a* concentrations at BK and HS (Williamshen et al. 2023; Smits et al. 2024).

Withdrawals from the Barker Slough Pumping Plant could be affecting Chl *a* at BK, with the pump located immediately upstream of the site (Fig 9). During wet years pumping is slowed because of diminished water quality, so 2019 that had lower export rates than 2021. There is some evidence that decreased pumping increases Chl *a* in this slough (Jasper 2020). In 2019 Chl *a* concentration was slightly higher, but there was no difference in GPP between years. There was a large pump situated near the HS site as well, but this pumping system functions differently; some of the pumped water is returned to the slough, whereas the Barker Slough Pumping Plant exports water out of the system.

Contaminants are a potential factor that could be affecting metabolism rates in the CSC. High contaminant concentrations can potentially inhibit phytoplankton production, such as the herbicide, Durion, found in the CSC; however, it was found that the herbicide seems to have no effect on production in the region (Stumpner et al. 2020a). Since areas with the highest pelagic primary production and phytoplankton density were those with irrigation return, which carries the highest contaminant loads, it is unlikely they are affecting phytoplankton at my sites.

Caveats

A caveat to my study is that it was carried out during the first six months of only two years and did not capture the large volumes of irrigation return water that are returned to the

system in Autumn at the end of the irrigation season. Also, differences in methods between years could affect the between-year metabolism comparisons in the study. There could also be differences between the two years besides precipitation that could be driving observed temporal differences. Finally, I was unable to directly determine sources of nutrients and DOC, so there may be sources that I did not account for.

CA was added as a site in 2021, so a temporal comparison is lacking for this site. However, the site is of interest because it had the highest Chl *a* concentration, GPP, CR, and NCP of all sites sampled in 2021. The site is a small, dead-end offshoot of Ulatis Slough with high water residence time, little direct upstream inputs, and water supply originating nearly entirely from Ulatis Creek.

EC cannot be reliably used as a proxy for residence time in the system because both residence time and landscape inputs affect it. Because of this, the relationship of Chl *a* to EC in the linear model signifies a relationship to both residence time and inputs from upstream landscapes.

Management Implications

Tidal marsh restoration has become a prominent conservation measure within the CSC, with several restorations completed, a major one under construction, and several more planned. A primary goal of tidal marsh restoration in the area is to increase pelagic primary production to support pelagic fishes that have been in decline (California Department of Water Resources and California Department of Fish and Game 2010). CC is located at the mouth of a tidal restoration and has a large area of tidal marsh surrounding it; however, this site had the lowest Chl *a*

concentration and rates of GPP. My results corroborate others from the SFE, that restoration is not contributing to a notable increase and export of pelagic primary production (Lehman et al. 2010; Williamshen et al. 2021; Yelton et al. 2022).

Irrigation provides a connection between the landscape and tidal waterways during all years and that connection is amplified during a wet year, while only wet years connect non-irrigated rangeland to waterways. Increased concentrations in Chl *a* were not always observed during the wet year, so the increase in phytoplankton with increased flows seen elsewhere in the Delta is not consistent with my sites. Flow pulses have the potential to deliver phytoplankton downstream if there are suitable conditions for producing phytoplankton on the landscape. It seems scenarios in which water is spread across the landscape, as it would be on the cropland and ditches of the Hass Slough watershed, is when increased water moving through the landscape can boost production.

Site and connection to upland watersheds should be considered when planning and implementing restorations in the Delta, so conditions are conducive to phytoplankton production. Restoring sloughs that are connected to areas that are hydrologically isolated from Sacramento River water with their own water supply could generate more plankton than those located close to the main axis of the estuary. The extremely high Chl *a* concentrations and metabolism rates observed at CA demonstrate how high-residence-time offshoots of nutrient and phytoplankton rich watersheds can function to produce a pelagic food source.

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Figures and Tables

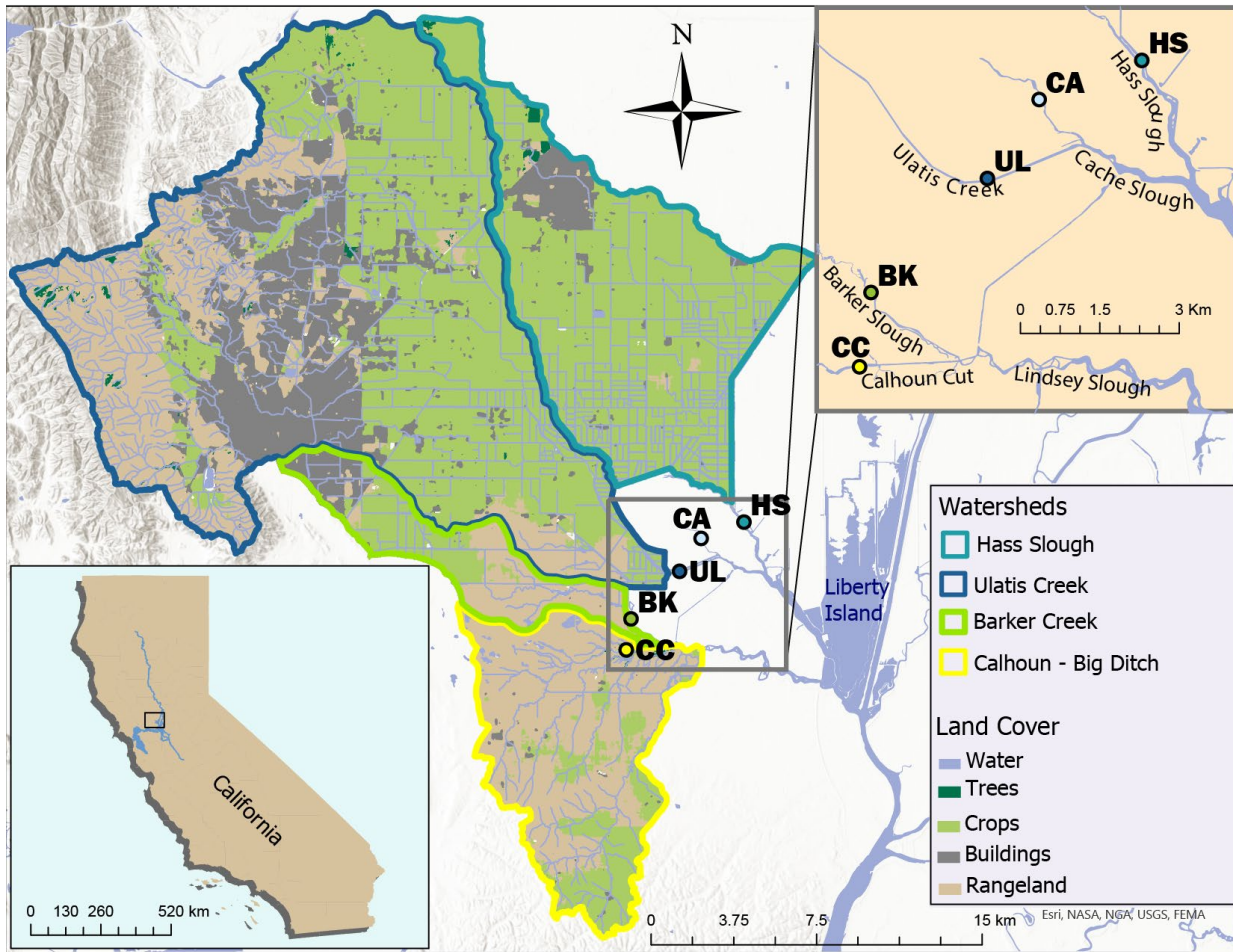


Figure 1 Map of study sites and connecting watersheds. Land use within watersheds indicated by color: light green = crops, tan = rangeland, and grey = buildings.

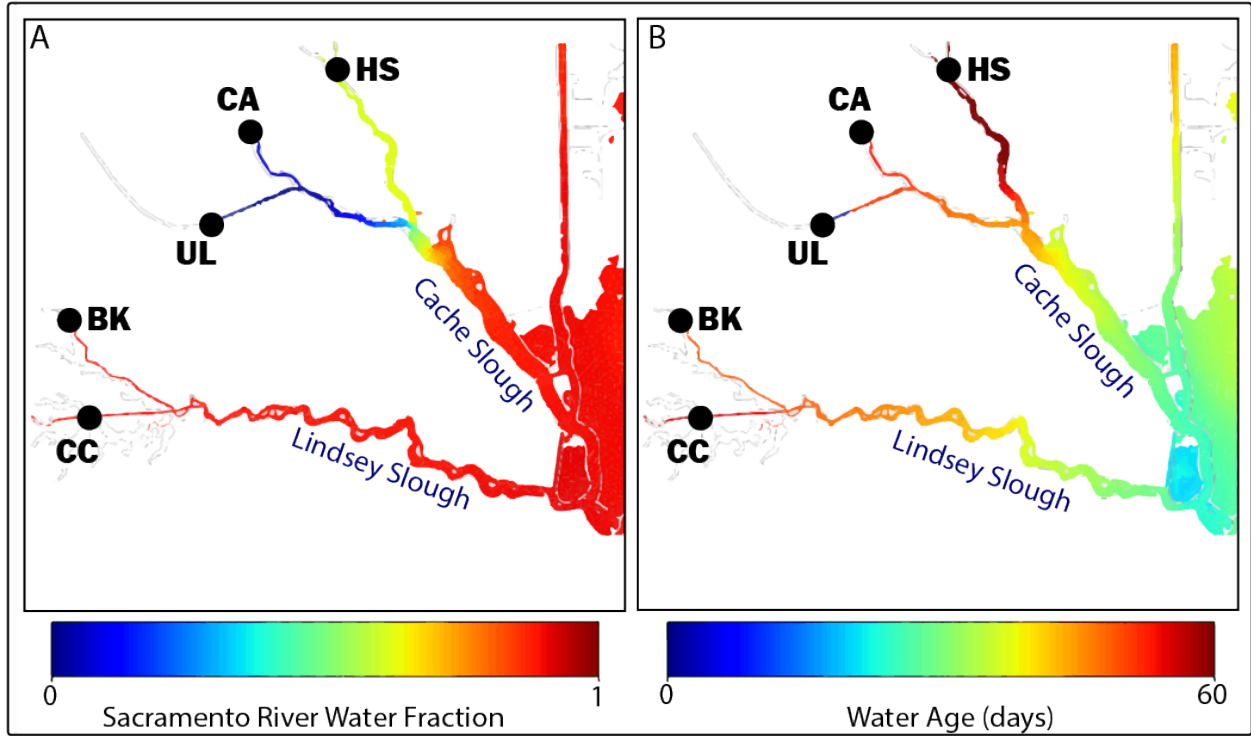


Figure 2 Map of study area with (A) Sacramento River water fraction and (B) water age in days at low tide adapted from Durand et al. (2019).

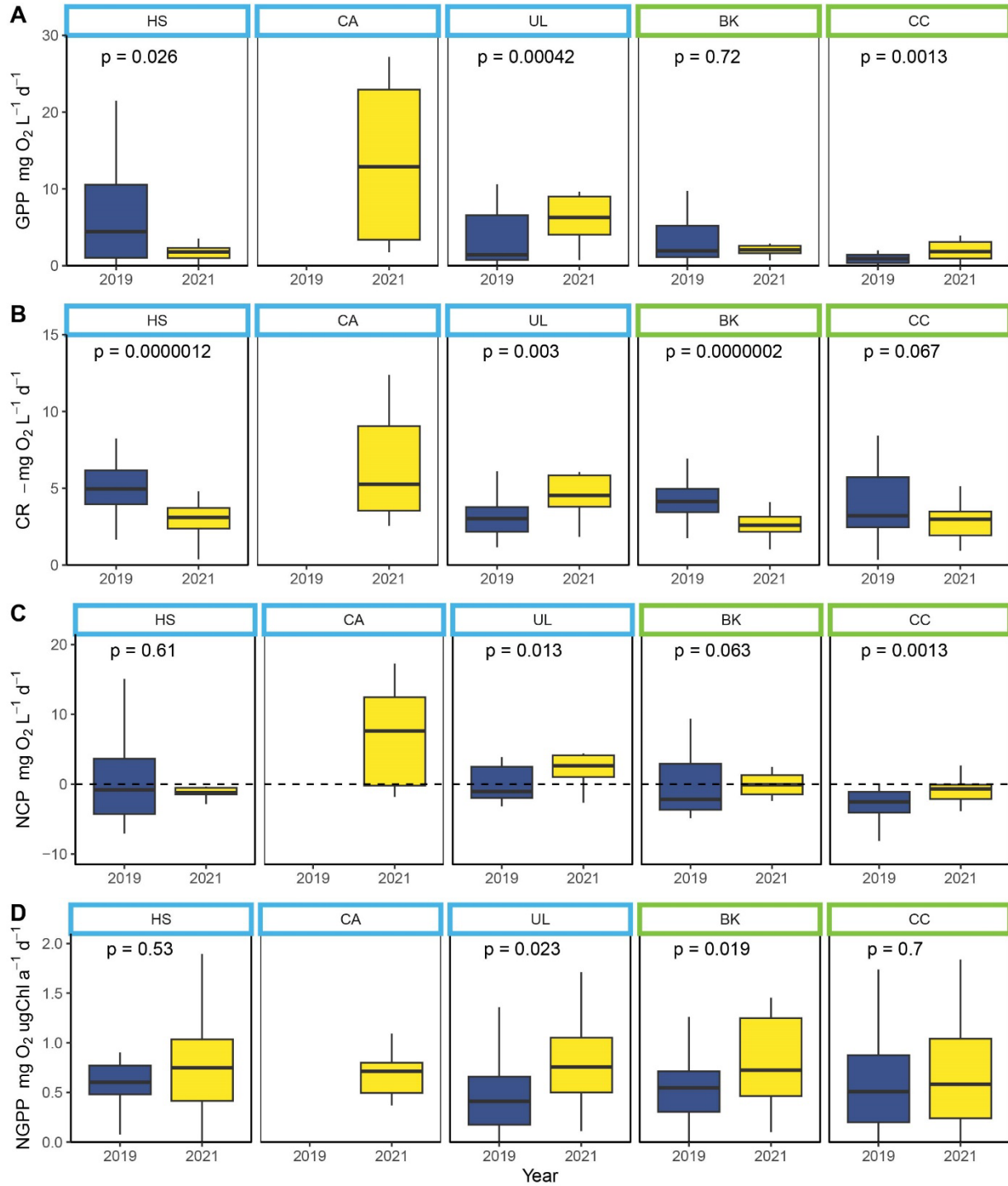


Figure 3 Comparison of pelagic metabolism rates: (A) gross primary production, (B) community respiration, (C) net community production, and (D) Chl *a* normalized gross primary production among sites and years. P-values for Wilcoxon sign-ranked test between years for each site. Outliers removed from plots. Cache Slough Network sites bordered in blue and Lindsey Slough Network sites bordered in green.

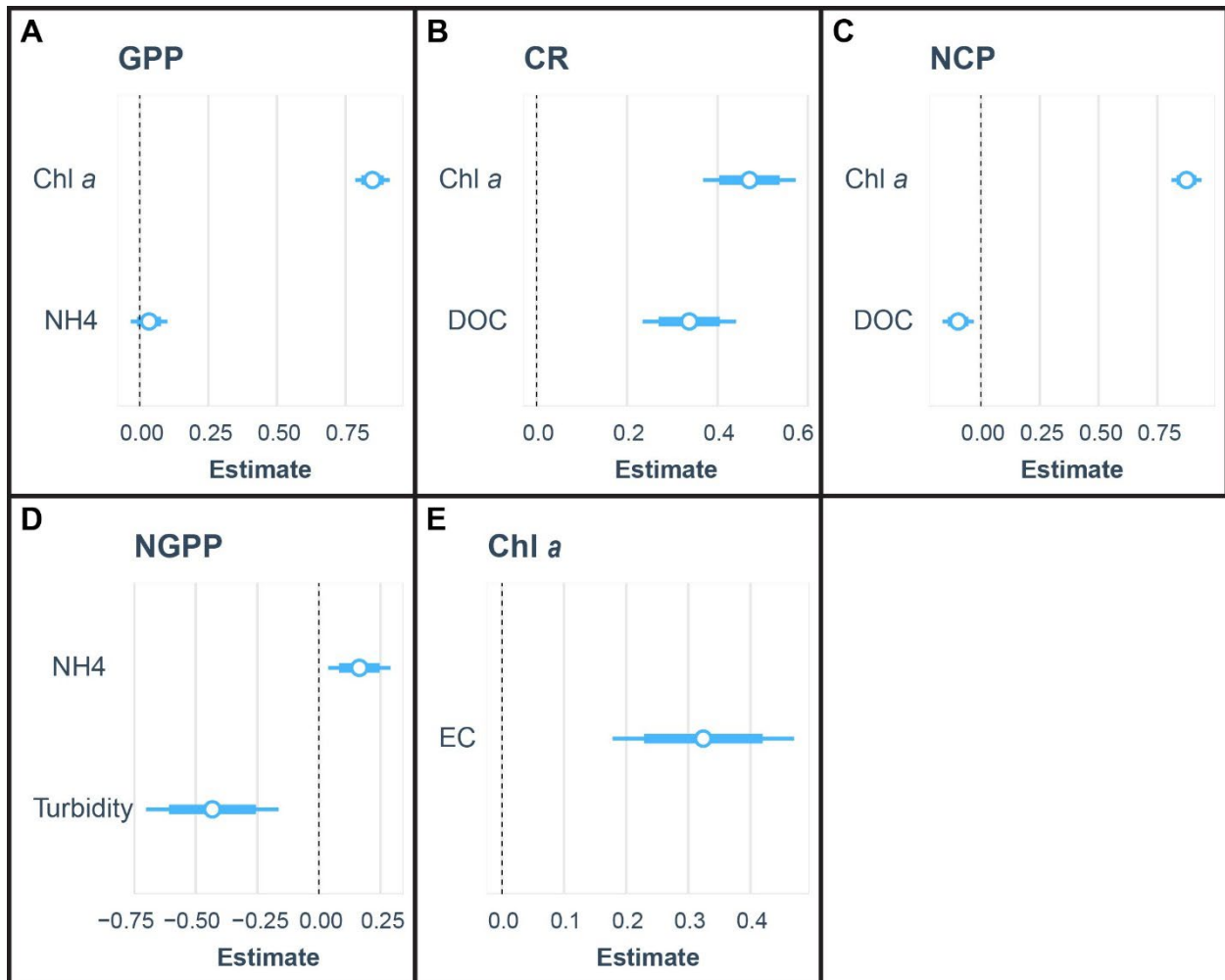


Figure 4 Coefficients for each predictor variable in the best fit model for each response variable (A) gross primary production, (B) community respiration, (C) net community production, (D) chlorophyll-normalized gross primary production, and (E) chlorophyll *a*. Thin whiskers = 0.95 and thick whiskers = 0.8 confidence intervals.

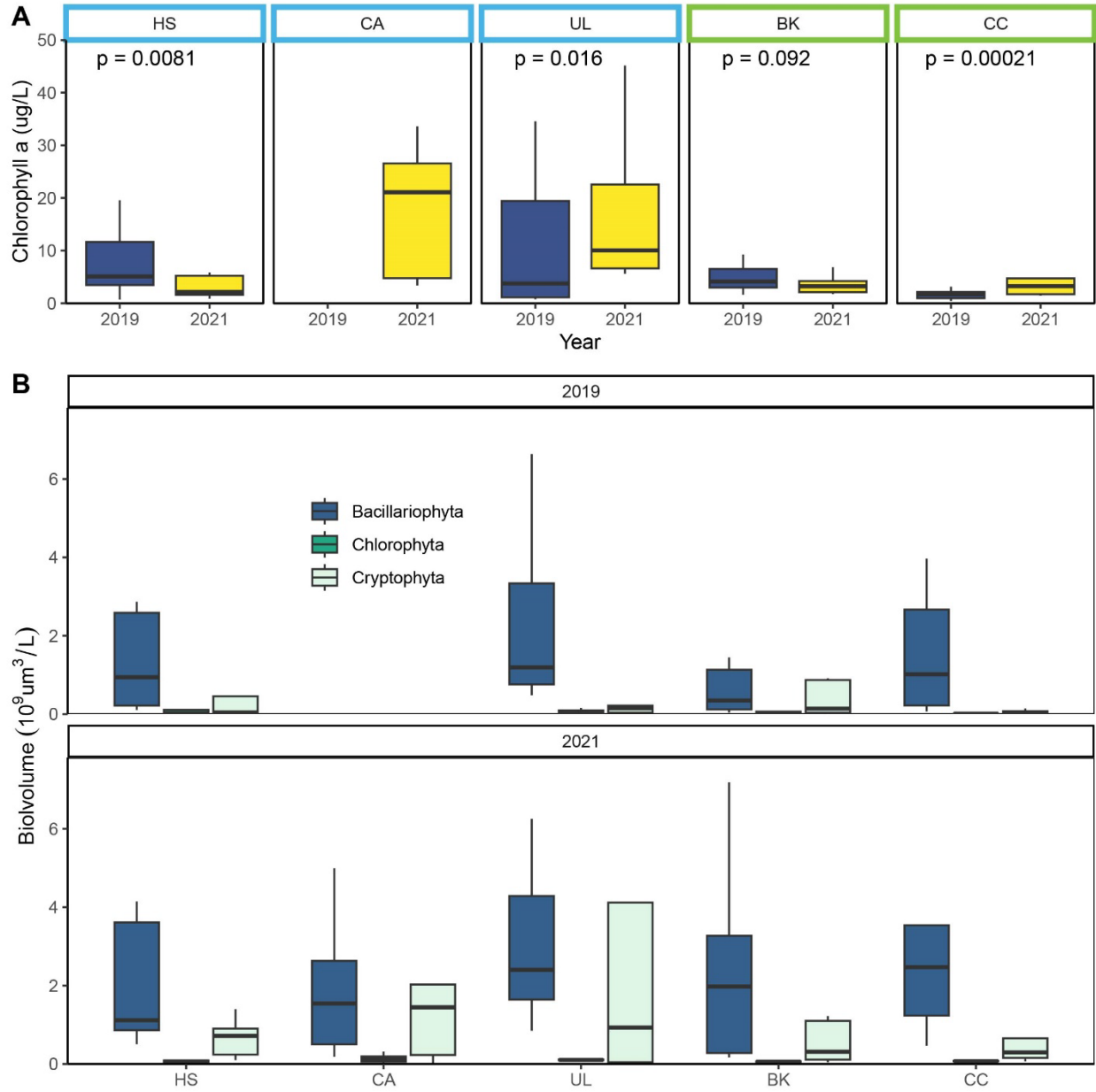


Figure 5 Comparison of (A) Chl *a* concentration, and (B) phytoplankton biovolume for the three dominant taxonomic clades among sites and years. Outliers removed from plots and CA1 only sampled in 2021. Cache Slough Network sites bordered in blue and Lindsey Slough Network sites bordered in green.

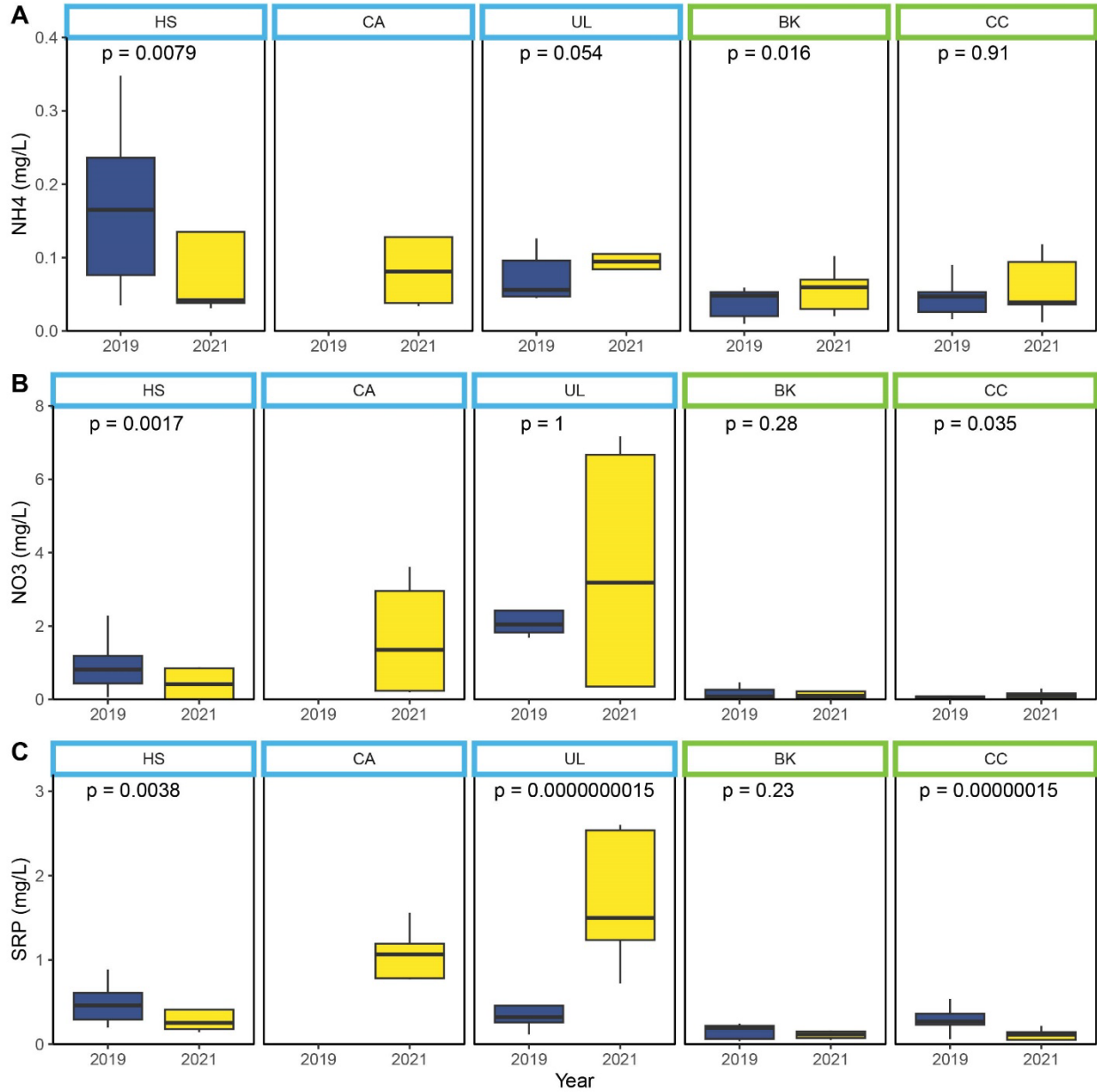


Figure 6 Comparing nutrients (A) NH₄, (B) NO₃, and (C) SRP among sites and years. P-values for Wilcoxon sign-ranked test between years for each site. Outliers removed from plots and CA1 only sampled in 2021. Cache Slough Network sites bordered in blue and Lindsey Slough Network sites bordered in green.

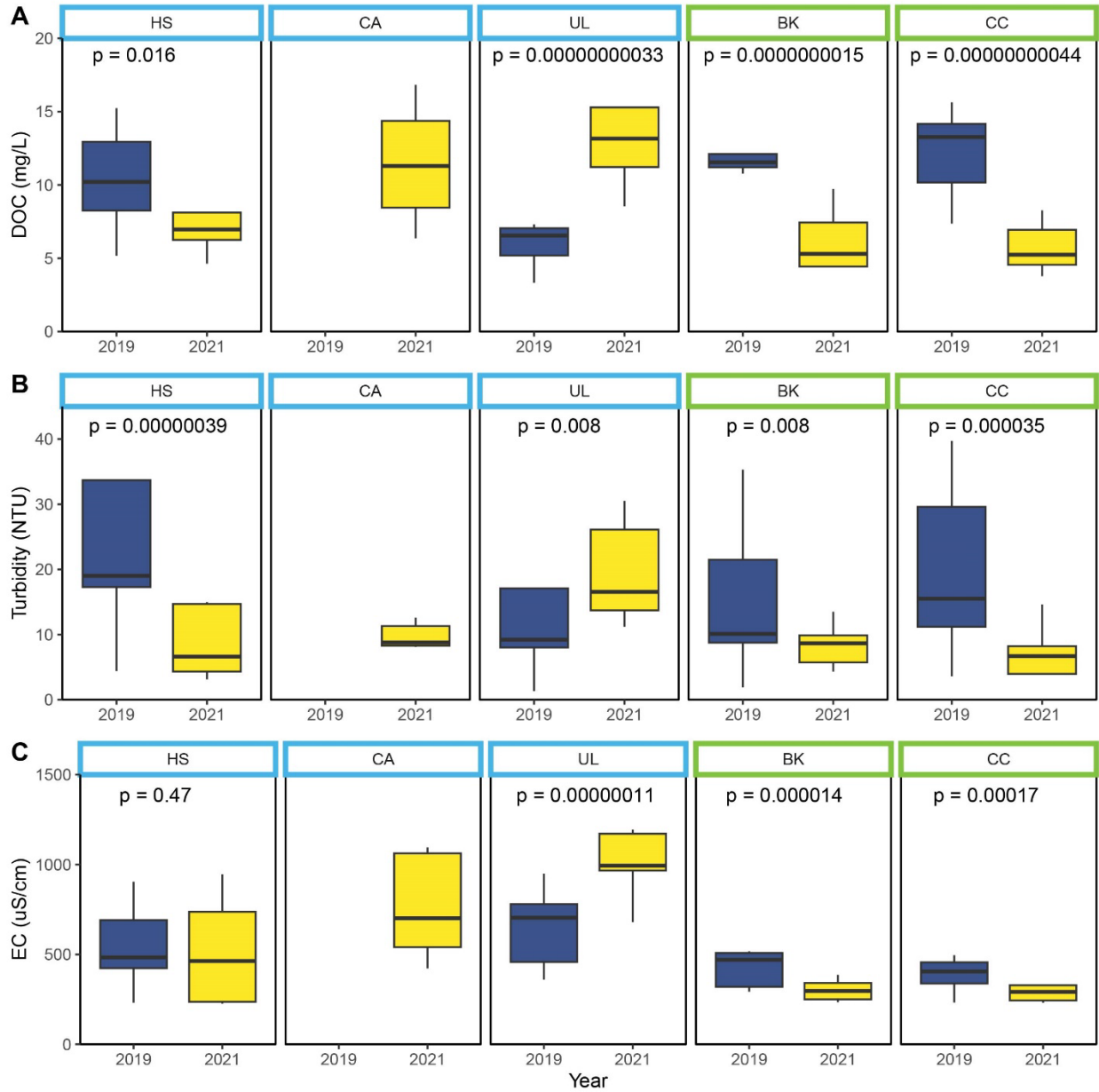


Figure 7 Comparison of water quality (A) DOC, (B) turbidity, and (C) electrical conductivity among sites and years. P-values for Wilcoxon sign-ranked test between years for each site. Outliers removed from plots and CA1 only sampled in 2021. Cache Slough Network sites bordered in blue and Lindsey Slough Network sites bordered in green.

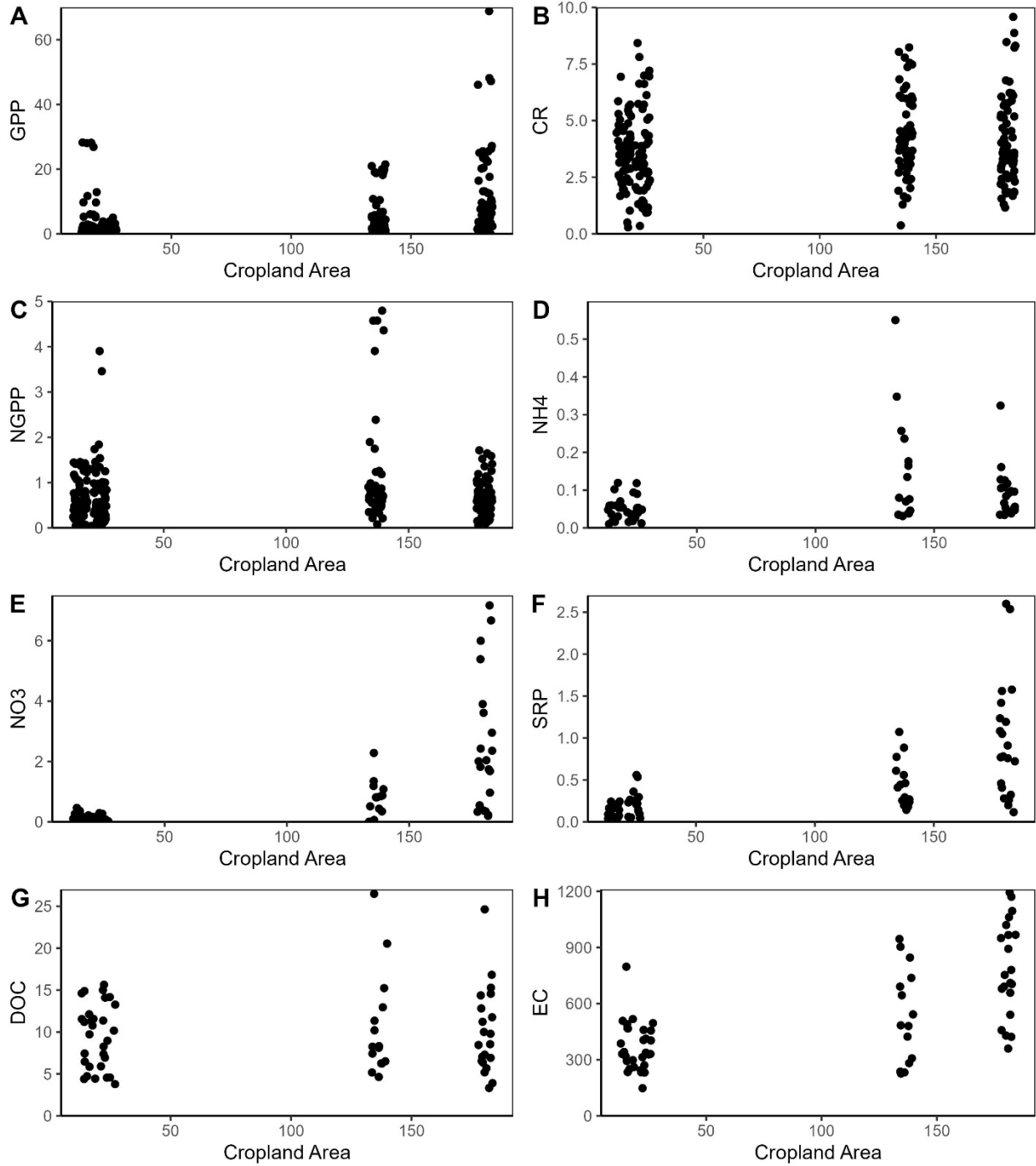


Figure 8 Plots comparing (A) gross primary productivity, (B) community respiration, (C) *Chl a* normalized gross primary productivity, (D) NH_4 , (E) NO_3 , (F) SRP , (G) DOC and (H) electrical conductivity with jittered points along the gradient of cropland area upstream of the different sites.

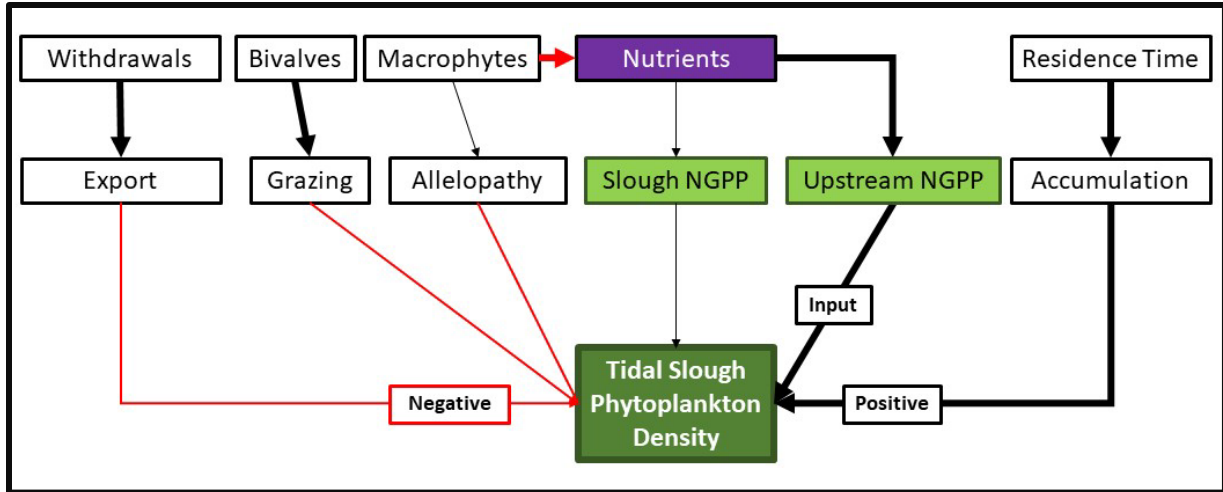


Figure 9 Conceptual model diagram for tidal slough phytoplankton biomass. Black lines indicate a positive effect and red lines a negative. Arrow thickness corresponds to magnitude of effect.

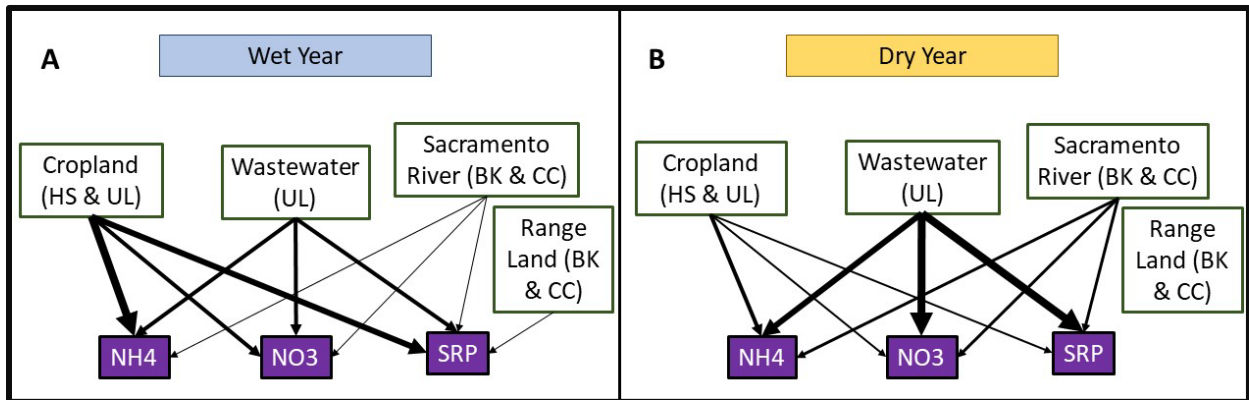


Figure 10 Conceptual model diagram for nutrient sources for (A) a wet year and (B) a dry year. Arrow thickness corresponds to magnitude of effect.

Table 1 Site attributes. Network is the slough network each site is in; CA = Cache Slough Network and LN = Lindsey Slough Network. WS Area = watershed area, Crop% = percentage of watershed area that is cropland, Urb% = percentage of watershed area that is buildings, and Range% = percentage of watershed area that is rangeland.

SITE	WATERSHED	NETWO RK	WS AREA (KM²)	CROP %	URB%	RANGE %	2019 Sampl es	2021 Sampl es
HS	Hass Slough	CA	154	88.8%	9.0%	1.3%	9	6
UL	Ulatis Creek	CA	375	48.2%	23.4%	27.4%	9	6
CA	Ulatis Creek	CA	375	48.2%	23.4%	27.4%	-	6
BK	Barker Creek	LN	45	34.9%	16.7%	47.0%	9	6
BD	Calhoun-Big Ditch	LN	94	25.3%	1.0%	72.4%	9	6

Table 2 Wilcoxon sign-ranked test p-value results for metabolism rates.

SITE	GPP	CR	NCP	NGPP
CC1-BK1	<0.001	0.470	0.024	0.650
CC1-UL1	<0.001	0.290	<0.001	0.850
CC1-HS1	<0.001	0.024	0.005	0.640
CC1-CA1	<0.001	0.001	<0.001	0.640
BK1-UL1	0.160	0.580	0.034	0.650
BK1-HS1	0.580	0.040	0.800	0.650
BK1-CA1	<0.001	0.002	<0.001	0.640
UL1-HS1	0.230	0.270	0.150	0.640
UL1-CA1	0.002	0.015	0.004	0.640
HS1-CA1	<0.001	0.040	<0.001	0.650

Table 3 Wilcoxon sign-ranked test adjusted p-value results for Chl *a* and phytoplankton.

SITES	Chl <i>a</i>	Biovolume
CC1-BK1	<0.001	0.500
CC1-UL1	<0.001	0.019
CC1-HS1	0.002	0.930
CC1-CA1	<0.001	0.019
BK1-UL1	0.017	0.001
BK1-HS1	0.480	0.430
BK1-CA1	<0.001	0.019
UL1-HS1	0.011	0.019
UL1-CA1	0.044	0.430
HS1-CA1	<0.001	0.019

Table 4 Wilcoxon sign-ranked test adjusted p-value results for nutrients.

SITES	NH4	NO3	PO4	DOC	EC	Turbidity
CC1-BK1	0.380	0.150	<0.001	0.810	0.020	0.780
CC1-UL1	<0.001	<0.001	<0.001	0.610	<0.001	0.130
CC1-HS1	<0.001	<0.001	<0.001	0.810	<0.001	0.130
CC1-CA1	0.002	<0.001	<0.001	0.150	<0.001	0.780
BK1-UL1	<0.001	<0.001	<0.001	0.610	<0.001	0.019
BK1-HS1	<0.001	<0.001	<0.001	0.810	0.020	0.042
BK1-CA1	0.004	<0.001	<0.001	0.130	<0.001	0.380
UL1-HS1	0.220	<0.001	0.002	0.610	<0.001	0.780
UL1-CA1	0.750	0.013	0.018	0.130	0.530	0.009
HS1-CA1	0.340	0.006	<0.001	0.130	0.004	0.019

Chapter 3

Fishes in Ditches: Fish habitat in agricultural waterways of the North Sacramento-San Joaquin River Delta

Brian Oliver Williamshen

Abstract

Irrigated agriculture is important for the world's food supply, and the ditches and canals used for irrigation create novel habitats for fishes. Agriculture surrounds the Sacramento-San Joaquin River Delta, but little is known about fishes inhabiting the waterways in upland agricultural watersheds that connect directly to the Delta's tidal sloughs. I found eighteen fish species across four small watersheds that connect to the northern Delta. Fish assemblages included both native and nonnative species and were distinct across watersheds and sites with varying degrees of connectivity to tidal Delta sloughs. Waterways cut through irrigated cropland were perennial and supported more fish species, while those with less cropland supported a high abundance of few species. I found water quality was suitable to warm-water fishes across watersheds and average turbidity was higher than tidal Delta sloughs. I documented an abundance and diversity of zooplankton and benthic invertebrates across watersheds that are available as prey for fishes. This study establishes fish assemblages in agricultural waterways upstream of the Delta, which include native fish species, and indicates the importance of managing these waterways as fish habitat.

Introduction

Seventy percent of the world's surface water withdrawals are used for agriculture, with corresponding impacts on the ecology of nearby waterbodies (United Nations Educational, Scientific and Cultural Organization 2012; Raven and Wagner 2021). Irrigated agriculture creates the need for water storage and delivery, and often uses chemical fertilizers, pesticides,

and herbicides. Water management for irrigation and agricultural practices leads to diversion of fish to unsuitable habitats, reduced stream flows, water storage impoundments, and introduction of contaminants into waterways (Minckley et al. 1991; Marchetti and Moyle 2001).

There is much focus on the harm of agricultural irrigation to fish, but evidence exists that it can provide fish habitat. Agricultural waterways (canals, ditches, and reservoirs) across the Northern Hemisphere support a diversity of native and nonnative fish species, including threatened species like the Rio Grande silvery minnow (*Hybognathus amarus*) that live in irrigation canals connected to the Rio Grande River (Katano et al. 2003; Williams et al. 2004; Cowley et al. 2007). Agricultural waterways can also be used as tools for fish conservation in highly altered ecosystems, such as irrigation ditches that create a source for fish diversity to the Darance River in France (Aspe et al. 2016).

California's agricultural production was worth more than \$50 billion in 2022 and uses an estimated 7.19 million m³ of water per day for agricultural irrigation (Dieter et al. 2018; California Department of Food & Agriculture 2023). A complex network of waterways was constructed throughout the state to enable this valuable agricultural industry. Much of California's richest agricultural land lies adjacent to the floodplains of the Sacramento and San Joaquin rivers and their confluence at the Sacramento-San Joaquin River Delta (Delta). The Delta is the hub of the state's complex water conveyance system, which includes reservoirs, two massive export pumping facilities, and thousands of smaller pumps and siphons that divert approximately 8 km³ of water per year to thousands of kilometers of agricultural waterways (Herren and Kawasaki 2001; Kimmerer 2002; Kimmerer and Nobriga 2008).

Native fish populations have been in decline in the Delta due to habitat alteration and management to support agricultural production, including diking and draining of wetlands, upstream dam construction, water diversions, and use of harmful chemicals. Waterways have been disconnected from historic floodplains and tidal marsh by the construction of levees to drain land for crops and grazing (Nichols et al. 1986; Whipple et al. 2012). Continued dam operation has reduced Delta turbidity, which creates habitats favored by submerged plants and nonnative fishes (Moyle 2002). Water diversions reduce inflows and export plankton and fishes from the Delta, which likely plays a substantial role in a reduction of some native fishes

(Sommer et al. 2007; Kimmerer 2008). Finally, ongoing use of pesticides harms fishes and aquatic invertebrates through chemical laden runoff (Weston and Lydy 2010).

Agricultural waterways can provide warm, turbid habitat and reconnect the landscape to tidal Delta waterways, ameliorating some of the harm to aquatic ecosystems. The Yolo Bypass, a floodplain largely managed for rice production and flood protection, connects to the Delta and supports native fishes, including endangered species (Sommer et al. 2001). Experimental water management in rice farms and canals within the floodplain has demonstrated how water management can increase invertebrate production and lead to rapid growth of Chinook salmon (Sommer et al. 2004; Corline 2014; Katz et al. 2017).

Faunal filters from landscape level features to biotic interactions shape the assemblage of organisms that occur in a given waterway (Tonn et al. 1990; Poff 1997; Quist et al. 2005). In agricultural waterways, water quality, connectivity to other aquatic habitat, and invertebrate abundance are likely filters to which fish can inhabit these waterways. Water quality can reach warm temperatures in shallow waterways in the Delta and excess organic material and algae blooms can lead to low dissolved oxygen, which structure fish assemblage in the Delta and surrounding waterways (May and Brown 2002; Feyrer and Healey 2003; Morgan et al. 2006). Connectivity between wetlands and agricultural waterways can lead to higher fish species richness (Katano et al. 2003; Ishiyama et al. 2014). Additionally, perennial waterways can support a higher richness of species (Pusey et al. 2020). Prey availability in the forms of zooplankton and larger invertebrates can be a filter on which species and life stages of species will occur in an agricultural waterway (Bottom and Jones 1990).

Despite the prevalence of irrigated agriculture surrounding the Delta, and the known value of upstream habitats to fishes and aquatic invertebrates, irrigation canals and ditches in small watersheds connecting to the Delta have gone unstudied. I characterized the fish assemblages, sampled water quality, and measured invertebrate abundance of agricultural waterways connected to the Delta to answer the following research questions: (1) what fish assemblages are present in agricultural waterways that connect to the Delta? (2) Is water quality suitable for fish survival? and (3) are invertebrate food sources present to support native fish in the waterways?

Methods

Sampling Sites

The Cache Slough Complex (CSC) is a freshwater tidal slough complex in the North Delta that receives water from the Sacramento River, Cache and Putah creeks, and several smaller watersheds. The CSC has less land subsidence than elsewhere in the Delta, has elevation that can accommodate sea level rise, and supports a relatively high abundance of native and nonnative fishes, making it an important region for native fish conservation (Brown and Michniuk 2007; Moyle et al. 2018). The tidal sloughs of the CSC connect to hundreds of kilometers of creeks, canals, and ditches that are used to irrigate or drain land that mainly produces tomatoes, cattle, alfalfa, and nut trees (Solano County 2023).

I chose sampling sites across four small watersheds that connect to different tidal sloughs in the CSC. I assigned each site within the waterways a connectivity ranking of high (HI), medium (MD), or low (LO). A site was assigned high rank if there were no barriers, medium if there were seasonal barriers, and low if there were permanent barriers to upstream migration from the tidal slough.

The Hass Canal (HSLO) and Hass Drain (HSHI) are in the 154 km² irrigated cropland-dominated Hass Slough Watershed (HS; Fig 1; Table 1). Much of the water used for irrigation during the growing season (March to October) is pumped from Hass Slough, an offshoot of Cache Slough. HSLO is in the main irrigation canal distributing water pumped from Hass Slough, fish must pass through the pump to get to the site. HSHI is in the main drain that returns water back, unimpeded, to Hass Slough.

The Alamo Creek Wastewater Drain (ULLO), Alamo Creek Reservoir (ULMD1), Ulatis Reservoir (ULMD2), and Ulatis Creek Tidal Channel (ULHI) are in Alamo and Ulatis creeks within the 375 km² Ulatis Creek Watershed (UL; Fig 1; Table 1). The watershed originates in the Coast Range and its waterways flow through rangeland, cropland, urban land, and receive wastewater effluent before entering the Delta via Cache Slough (Fig 1). ULLO was located 4.1 km downstream of the wastewater treatment plant and has a permanent barrier to upstream migration from the lower creek. From mid-March through October irrigators construct small barriers (check dams) to create impoundments within canals in the Ulatis Creek and Alamo

Creek canal channels to facilitate irrigation of adjacent farmland; I sampled two such reservoirs, ULMD1 and ULMD2. Tide affects water stage at ULHI, but there is little to no tidal exchange with the slough (Durand et al. 2019). More sites were chosen within the Ulatis Creek Watershed because of its large size, year-round flows, and variety of habitat types.

The 45 km² Barker Creek Watershed (BK) and 94 km² Big Ditch Watershed (BD) consist of mostly ephemeral channels that receive seasonal flow through rangeland, non-irrigated grassland that is sometimes used for livestock grazing (Fig 1; Table 1). A permanent dam forms a barrier above the Barker Creek Channel (BKHI), but upstream migration from the tidal slough to the site is unimpeded. Water flows from the small reservoir to the site when water stage surpasses dam height, usually during winter and spring. The Big Ditch (BDLO) is an ephemeral waterway that I could not sample after May because the waterway dried. There is a permanent barrier of thick emergent vegetation that the ditch flows through to the tidal slough, blocking upstream migration to fish except during years when the area floods.

Fish Sampling

In shallow waterways (<1.5 m), I used beach seines to sample fishes. I pulled seines once monthly from February to September 2022 at BKHI, HSHI, and ULHI – sampling at BDLO occurred from February through May because of drying and at ULLO from February through June because of increased depth. I sampled a similar volume of water with the net at all sites. I placed catch into a bucket of water, identified fishes to species, counted, measured to the nearest millimeter (mm) standard length, and returned to the water. I only measured thirty individuals for each species and counted the remainder.

At sites too deep to seine, I deployed gillnets from canoes. I used gillnets once monthly from April through September 2022 at HSLO, ULMD1, ULMD2, and ULHI. I fished gillnets from the bottom, extending 2.44 m up, with six 4.57-m long panels of varying mesh size stretch (2.5 cm, 5.1 cm, 7.6 cm, 10.2cm, 12.7 cm, and 15.2 cm). I deployed nets for 60 minutes and checked at least every 30 minutes to minimize harm to captured fishes. I removed fishes from the net quickly and placed into an aerated tub of water. I identified, counted, and returned fishes as with seine net sampling.

I collected water quality at every fish sampling site using a Yellow Springs Instruments Professional 2030 to record monthly temperature (°C), specific conductivity ($\mu\text{S}/\text{cm}$), and dissolved oxygen (DO; mg/L). I also collected water in pre-rinsed 1-liter high density polyethylene (HDPE) bottles to measure turbidity (NTU) in an Oakton T-100 turbidity meter at the laboratory.

Invertebrate Sampling

To capture invertebrates in shallow waterways, I use a beach seine and a d-frame sweep net. Large invertebrates (crayfish, clams, and shrimp) captured in beach-seine hauls were identified to species and counted along with fish (see fish sampling).

I used a 25 cm x 30 cm d-frame net with 500 μm mesh for all sweep-net samples. At each site the net was swept across and 3 cm above the same 1 m length of benthos three times in alternating directions at three fixed points across a stream channel. I preserved samples in 70% ethanol and transported them to the laboratory for processing. I identified invertebrates by life stage and to family for insects and Cladocera, order for copepods, and coarser taxonomic levels for other invertebrates. For samples that were exceptionally dense with vegetation, detritus, or organisms I subsampled by weight until at least 200 total individual invertebrates were counted, counts from subsamples were multiplied by the inverse of the fraction of the subsample weight (Sebastien et al. 1988; Williamshen et al. 2023b). I divided sample counts by the area swept to get a density of individuals per m^2 of benthos.

To sample zooplankton in deep waterways ($>2\text{m}$), I used a conical net with a 30 cm diameter mouth, 90 cm length, and 150 μm mesh. I threw the net 10 m and retrieved perpendicular to the current, if any, three times for a total sample volume of 2.12 m^3 . Samples were preserved in 5% Formaldehyde, stained with rose Bengal, and transported to the laboratory for processing. I diluted samples to a volume of 500 mL and subsampled using a stemple pipette. Subsamples were taken until at least 140 total individuals were counted for the sample (Wu and Culver 1992; Roseman 1997). Copepods and Cladocera were identified to the lowest possible taxonomic group, usually genus, while other invertebrates were identified to a coarser taxonomic

level. I calculated density (zooplankton per m³) by multiplying the number of individuals by the inverse fraction of each subsample and dividing by the total volume sampled.

Analysis

To visually compare fish and invertebrate assemblages from seine and gillnet catch I used non-metric multidimensional scaling (NMDS) to ordinate Bray-Curtis dissimilarity distances. NMDS was chosen as the ordination method because data do not need to be normally distributed (Zuur et al. 2007). Each point in the plots corresponds to a sampling event and points were assigned a color by watershed and shape by connectivity and plotted in an ordination biplot. Ellipses were plotted using standard deviation around the centroid of points from each watershed and connectivity ranking.

To statistically test differences in fish and invertebrate species assemblages from gillnets and seines I performed permutational analysis of variance (PERMANOVA; Anderson 2001) using watershed and connectivity as factors. PERMANOVA is a non-parametric test and does not require data to be normally distributed. HSLO was excluded from NMDS and PERMANOVA because only a single fish on a single sampling event was captured. All NMDS and PERMANOVA analyses were performed using the vegan package (Oksanen et al. 2019) in program R (R Core Team 2022). To compare differences in species richness for seine and gillnet samples I used a Wilcoxon signed-rank test. The Wilcoxon test is a nonparametric test that is ideal for pairwise comparisons of data that are not normally distributed. GGPUBR was used to perform the test and display p-values on a figure (Kassambara 2023).

Results

Fish Catch

I captured a total of 2,845 fishes belonging to 18 species: 6 native and 12 nonnative. In seines I captured 2,811 fishes belonging to 16 species and in gillnets 34 individuals belonging to 5 species (Table 2). Fish catch was less abundant, but more species rich in watersheds with more cropland than rangeland (Fig 1).

Seines selected for smaller fishes (mean standard length 43mm; std dev 24) and 93% of individuals caught were nonnative (Table 2). Seine catch was dominated by three nonnative species: western mosquitofish (*Gambusia affinis*; 58% of total catch), black bullhead (*Ameiurus melas*; 13%), and fathead minnow (*Pimephales promelas*; 11%; Table 2). The most abundant native fish was prickly sculpin (*Cottus asper*; 5%; Table 2). Barker Creek and Big Ditch watersheds had more fish per seine (139 and 98.3, respectively) than Ulatis Creek and Hass Slough watersheds (29.4 and 28.5, respectively).

Gillnets selected for larger fishes (330 mm; 138) and 71% of individuals caught were native (Table 2). Gillnets captured two additional species and catch was comprised mostly of Sacramento sucker (*Catostomus occidentalis*; 59% of catch) and largemouth bass (*Micropterus salmoides*; 21%; Table 2). I only caught a single fish in the Hass Slough Watershed in gillnets, a Sacramento hitch (*Lavinia exilicauda*).

I captured postlarval and small juvenile (< 25 mm SL) fishes in seines, sweep-nets, and zooplankton-nets. I captured small juvenile western mosquitofish, Mississippi silverside (*Menidia audens*), Sacramento sucker, prickly sculpin, threespine stickleback (*Gasterosteus aculeatus*), fathead minnow, largemouth bass, and black bullhead across watersheds in seines. I sampled post-larval prickly sculpin, western mosquitofish, Sacramento sucker, Mississippi silverside, and fathead minnows with zooplankton and sweep nets. Additionally, I saw and captured postlarval Sacramento sucker with aquarium net at ULMD1 (personal observation).

Assemblages

I found distinct assemblages of fishes and invertebrates across watersheds and habitat types in seine and gillnet samples (PERMANOVA p-values = 0.001; Appendix 1). Hass Slough and Ulatis Slough watersheds had the highest species richness (13 and 12, respectively) followed by Barker Creek and the Big Ditch watershed (8 and 4, respectively; Fig 2). Highly connected habitat had the highest total species richness (17), while medium and low had 4 and 5, respectively. When comparing the species richness of all samples taken at each habitat connectivity ranking, high connectivity sites had greater richness than low and medium

connectivity sites ($p \leq 0.0016$), while there was no difference between low and medium connected sites ($p = 1$; Fig 4).

The NMDS plot that included fish and invertebrates from seines and gillnets showed groupings by watershed and connectivity ranking. There was minimal overlap in assemblages among watersheds (Fig 3). The Hass Slough Watershed was associated with golden shiner (*Notemigonus crysoleucas*) and fathead minnow. The Ulati Creek Watershed had a wide distribution associated with largemouth bass and Sacramento sucker. The Barker Creek Watershed was associated with Mississippi silverside and black bullhead (Fig 3A), and the Big Ditch watershed was most associated with western mosquitofish. There was no overlap in ellipses by connectivity ranking (Fig 3B). Low connectivity habitat was most associated with red swamp crayfish and western mosquitofish, medium connectivity associated with Sacramento sucker, and high connectivity had the widest distribution in ordination space that was associated with many species, particularly Mississippi silverside and prickly sculpin (Fig 3B).

Water Quality

There was minor variation in DO and temperature and greater variation between specific conductivity and turbidity among watersheds (Table 3). Mean DO was 6.8 or greater across watersheds (Table 3) but reached hypoxic levels (<3 mg/L) on four occasions at ULHI. I recorded a minimum temperature of 7.2°C and a maximum of 23°C , with mean watershed temperature between 15 and 19°C (Table 3). Mean SC was lowest in the Hass Slough Watershed (539 uS/cm) and highest in the Barker Creek Watershed (1124; Table 3). Mean turbidity was above 15 NTU across watersheds with occasional extreme values from 4.75 to 200.3 NTU during the study (Table 3).

Invertebrates

In seine hauls I captured 1,247 individual invertebrates belonging to four species. The two dominant invertebrate species captured were red swamp crayfish and Asian clam (19%; Fig

5A). There were more invertebrates per seine in Hass Slough and Ulatis Creek watersheds (56 and 41.1, respectively) than at Barker Creek and Big Ditch watersheds (30 and 3.5, respectively)

The most numerous invertebrates in sweep-net samples were cladocerans (63% of the total catch) and insects (10%) which were found across all watersheds (Fig 5B). The highest total sweep-net invertebrate catch was in Ulatis Creek Watershed (54%). Copepods and cladocerans were the two dominant clades found across watersheds with reservoir habitat in zooplankton nets (Fig 5C). Copepods made up a majority the total zooplankton abundance (55%) and were dominated by the genera *Eurytemora* (52% of copepod catch) and *Pseudodiaptomus* (27%). Cladocerans made up 39% of the total zooplankton catch. I found copepods in the highest density in the Hass Slough watershed and cladocerans in highest density at the Ulatis Creek Watershed (Fig 5C).

Discussion

This study shows the potential of California's vast network of agricultural waterways to support distinctive assemblages of native and nonnative fishes. Watersheds with mostly cropland have a diversity of perennial habitats, so I expected that watersheds with more irrigated cropland would have more fish species. I confirmed this expectation as the two cropland dominated watersheds (HS and UL) had the highest species richness. Because there is potential for upstream fish migration, I expected fish species richness to be highest in sites with a high degree of connectivity. I confirmed this hypothesis, catching far more species in sites with high connectivity than medium and low connectivity. I thought fish abundance would be greater in watersheds with more cropland, because they have perennial waters and a diversity of habitat types. However, great abundance of few species occurred in watersheds with more rangeland than cropland. Water quality was suitable for persistence of tolerant fish species and there was an abundance of zooplankton and macroinvertebrates to support fishes inhabiting the waterways. Cropland dominated watersheds were perennial and offered year-round, diverse habitats, while ephemeral waterways that drain mostly non-irrigated rangeland provide limited, seasonal fish habitat.

The mixed assemblage of natives and nonnatives I observed in upstream irrigation-waterways resembled that of the Delta. Small-bodied fishes were mostly nonnative, large-bodied fishes were mostly native, and native fishes were found in every watershed. The dominance of nonnative fishes and presence of tolerant native species like prickly sculpin, Sacramento sucker, and Sacramento pikeminnow corroborates a study in the late 1990s that found mostly nonnatives and the same native species associated with agricultural drains (May and Brown 2002). I caught fewer than half as many species as found on a nearby agricultural floodplain, the Yolo Bypass (Sommer et al. 2001). However, the Yolo Bypass connects to both to riverine and tidal habitat, has a larger perennial canal, mimics the natural floodplain-spawning habitat of fishes, and was sampled for many years, so it is expected that more species occur there.

These waterways are currently not good habitat for the more sensitive, threatened species that use the Delta. The species I captured are generally tolerant of warm temperatures and low dissolved oxygen and were mostly invertivores, with several species that switch to piscivory as adults (Moyle 2002). Although these agricultural waterways are not likely able to support sensitive species, they have the potential to export phytoplankton and invertebrates to the tidal sloughs where those species can access them (Ch. 2 this dissertation).

Native Fishes in Agricultural Waterways

The common small natives that I captured in seines were prickly sculpin and threespine stickleback. These two species were also found to be the most common native fishes occupying managed waterfowl hunting ponds lower in the San Francisco Estuary and threespine stickleback were abundant in agricultural ditches in Oregon (Colvin et al. 2009; Williamshen et al. 2021). These species seem the best adapted natives to take advantage of human managed landscapes/waterways within the Delta. They are both fairly tolerant of extreme water quality, can pass through barriers (*e.g.*, pumps and thick emergent vegetation), and can quickly colonize ephemeral waterways when flooded (Moyle 2002).

Sacramento sucker and Sacramento pikeminnow were common in the seasonal reservoirs in the Ulati Creek Watershed. Sacramento suckers are one of the few natives that have actually increased in abundance in the Delta since the 1990s and their ability to use agricultural

waterways may give them resilience in a changing ecosystem (Mahardja et al. 2017). Sacramento pikeminnow have been in decline in the Delta, and agricultural waterways may give them refuge when there are unfavorable conditions within the Delta (Mahardja et al. 2017). Both species can migrate long distances, so could be using both the Delta and Ulatris Creek Watershed during different seasons or life stages. The Sacramento pikeminnow I captured were at a size that mainly preys on smaller fish and crayfish, which were found in abundance within the Ulatris Creek watershed (Moyle 2002).

Nonnative Fishes in Agricultural Waterways

All watersheds were dominated by small-bodied fishes that are tolerant and can rapidly reproduce with favorable conditions, like Western mosquitofish and fathead minnows. Western mosquitofish have been widely introduced in California since 1922 for mosquito control and fathead minnow as a bait and forage fish (Dill and Cordone 1997; Moyle 2002). Western mosquitofish were common in sites with varying connectivity across watersheds, demonstrating their ability to rapidly colonize agricultural waterways. Fathead minnows were most common in habitat that drains wastewater effluent and irrigation return, suggesting they may be more reliant on perennial water and upstream population sources.

Largemouth bass, an important species for recreational angling, thrive in warm still-water habitats, but were curiously absent in my gillnet samples in reservoirs of the Ulatris Creek Watershed (Moyle 2002). Habitat within the small Ulatris Creek Watershed reservoirs seem suitable for largemouth bass, but the seasonal fluctuations in water may be excluding them from these sites. Largemouth bass were found at all sites with a high degree of connectivity to tidal sloughs, indicating they will utilize agricultural waterways they can easily move to from the Delta.

Temporary dams and pumps likely exclude some species from migrating upstream into agricultural waterways. Mississippi silversides have rapidly expanded their range throughout the Delta after introduction to an upstream lake, and there are concerns they harm native fishes through predation and competition (Baerwald et al. 2012; Mahardja et al. 2016). These fish were

most abundant in habitat highly connected to tidal sloughs, indicating that they may be blocked from upstream reaches of waterways and that there are few upstream source populations.

Fish Reproduction in Agricultural Waterways

Agricultural waterways have the potential to provide spawning habitat to native and nonnative species. Migratory species may migrate from the tidal waterways of the Delta to spawn in flowing waters found in agricultural waterways. The presence of post-larval and small juvenile fish across all waterways indicates that reproduction is occurring at, or upstream of my sites. Native fish tend to spawn earlier in the year than nonnatives, giving them the chance to utilize the ephemeral waterways when they are inundated from winter storms (Moyle 2002). In watersheds that maintain summer flows from irrigation water (*e.g.*, UL and HS), there is the potential for native species to utilize both spawning and rearing habitat.

Sacramento suckers can migrate long distances and typically spawn in riffles over gravel, which are present in the upper Ulatris Creek Watershed (Villa 1985; Moyle 2002). Spawning within the Ulatris Creek Watershed may contribute to the high abundance of Sacramento Suckers in tidal Ulatris Slough (Williamshen et al. 2023a).

Because Sacramento hitch became abundant in the CSC in 2019, have similar spawning requirements to Sacramento sucker, and were previously observed in Ulatris creeks (K. Martin Perales, personal communication), I hypothesized that Ulatris Creek may be good spawning habitat for the species (Williamshen et al. 2023a). Hitch have the highest temperature tolerance of any native California minnow and are commonly found in urbanized waterways in association with natives I sampled in Ulatris Creek (Leidy 1984; Moyle 2002). Hitch absence in my samples is likely because I sampled during a dry year and deployed gillnets after their spawning migration in early spring and could not sample with seines where juveniles were likely to be present.

Contrary to Mississippi silverside and largemouth bass, agricultural waterways may provide source populations of fish species that move downstream to the Delta. I found black bullhead in high abundance in the Barker Creek Watershed, with young of year fish appearing in July and remaining abundant through the study period. Black bullhead are often associated with

agricultural ponds and slow flowing creek/slough channels and are uncommon in the CSC (Moyle 2002; Huntsman et al. 2023), so the reservoir in Barker Creek likely contains a source population.

Water Quality

Temperature, DO, and specific conductivity during the study were within the physiological tolerance of most species found in the Delta (Moyle 2002). However, my sampling occurred in the morning or early afternoon, well before the hottest part of the day, so my data are biased towards cooler than the maximum water temperature that these waterways experience. Water temperature during the summer often exceeds 25°C in tidal sloughs in which these waterways connect (Williamshen et al. 2023a), which is stressful to cool-water associated fish like striped bass (Moyle 2002). It is likely that these waterways reach temperatures that are stressful to cool-water fishes during summer, thus the dominance of warm-water tolerant fish I captured. Dissolved oxygen was adequate for fishes across waterways, only reaching hypoxic levels (< 3 mg/L) ULHI, but nearly every species I caught can tolerate DO as low as 1 mg/L (Moyle 2002). The Big Ditch did dry completely during the study, making it unavailable to fish. Although I did not measure any extreme water quality, the dominance of highly tolerant fish suggests that water quality is a filter for the species that can occur in agricultural waterways.

Native Delta fishes tend to be associated with turbid water, while many nonnatives are associated with clear water and the submerged plants that inhabit clear water (Young et al. 2018). I found high mean turbidity (>15 NTU) in all watersheds, which is higher than mean turbidity in CSC slough during dry years, like 2022, and in other regions of the Delta that are generally below 10 NTU (Hestir et al. 2016; Williamshen et al. 2023a). This indicates that agricultural waterways provide a turbid-water area where submerged plants cannot grow and is unlikely to be colonized by many of the nonnative fishes that favor clear water. In addition to turbid water availability at my sites, agricultural watersheds are known to be sources of turbidity in the tidal sloughs of the Delta (Morgan-King and Schoellhamer 2013).

Invertebrates in agricultural waterways

Zooplankton are important food to early life stages of many fish species and are important for any native fishes spawning in agricultural waterways (Moyle 2002). Observed density of zooplankton was lower than in tidal sloughs in which these waterways connect (Luke 2023), but was similar to or much higher than nearby agricultural waterways adjacent to the Lower Sacramento River (de Vlaming et al. 2006). I found zooplankton belonging to a variety of taxonomic clades in the agricultural waterways (Fig 5). They were dominated by large-bodied cladocerans, and the copepods *Eurytemora spp* and *Pseudodiaptomus spp*, which may be of extra value to young fishes.

Amphipods and insects are also important prey for many Delta fishes (Moyle 2002). Although not as numerous as zooplankton, their presence indicates that there is food available for the fishes inhabiting agricultural waterways. Amphipod and insect abundance at some sites may be suppressed through predation by incredibly high density of small fishes.

Crayfish can be an important prey item for larger fishes, such as Sacramento pikeminnow and largemouth bass (Moyle 2002; Weinersmith et al. 2019). They were abundant in seine samples at several shallow water sites and were seen in the riprap at all reservoir sites (personal observation). Their presence indicates that there are prey available for large-bodied fishes in agricultural waterways.

Concerns of Agricultural Waterways

Although agricultural waterways support invertebrates and fishes, contaminant loads in these habitats are of concern. Pesticides washing from farmland to the waterways could be controlling the zooplankton population – pyrethroids are known to be toxic to, and can cause population declines in zooplankton (Day 1989; Hua and Relyea 2019). High concentrations of insecticides, especially pyrethroids, have been measured in Ulatis Creek during storm events (Weston et al. 2019). The presence of these pyrethroids have caused some invertebrates to become resistant to them which allows bioaccumulation that could have detrimental effects of fish that eat them (DeCourten et al. 2020; Huff Hartz et al. 2021).

There are also concerns with the effects of irrigation infrastructure that moves water onto cropland. Pumps can entrain fish and export them to unsuitable habitat while draining ditches can strand fish in drying pools (Minckley et al. 1991). All fish found in the Big Ditch were presumably stranded and killed as it dried. Further, irrigation return water can cause hypoxia through high dissolved organic carbon loads and eutrophication from nutrient loading, which is of most concern when a great volume of irrigation tailwater is released into the tidal sloughs at the end of the growing season. Hypoxia-related fish kills have been observed in Hass Slough and lower Putah Creek after early Autumn rain events, which likely occurred from an influx of organic material from the agricultural landscape (Rabidoux et al. 2022; Williamshen et al. 2023a).

Implications

This study demonstrates that a diversity of fishes and aquatic invertebrates are present in agricultural waterways connecting to the Delta and these waterways give the CSC heterogeneous habitat not found in other regions of the Delta. Irrigation infrastructure (pumps and check dams) give the ability to control water movement through waterways and can be operated to provide water during spawning and rearing time periods of native fishes, and exclude potentially harmful nonnatives, like Mississippi silverside. The waterways show potential as a tool for conservation of native minnows and suckers. Augmentation of ditch channels and promotion of emergent and riparian vegetation growth can improve fish habitat quality (DeZiel et al. 2019). Riparian vegetation may be particularly important to provide shade and cool summer water temperatures.

More research is needed on how to best manage these waterways to maximize benefit to native and important fish species. Additional sampling is needed, as I only sampled these waterways during spring and summer of a dry year, and additional species are likely found during other seasons and wetter years. Study is needed on the impacts of export and stranding of fish through water pumps. It is also important to understand the effects of agriculture-associated chemicals on fishes and potential impacts to human health of recreational anglers. Last, experimentation on creating spawning habitat, manipulating flow, and improving habitat within agricultural waterways is desirable to provide optimal conditions for spawning and rearing of native fishes.

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Figures and Tables

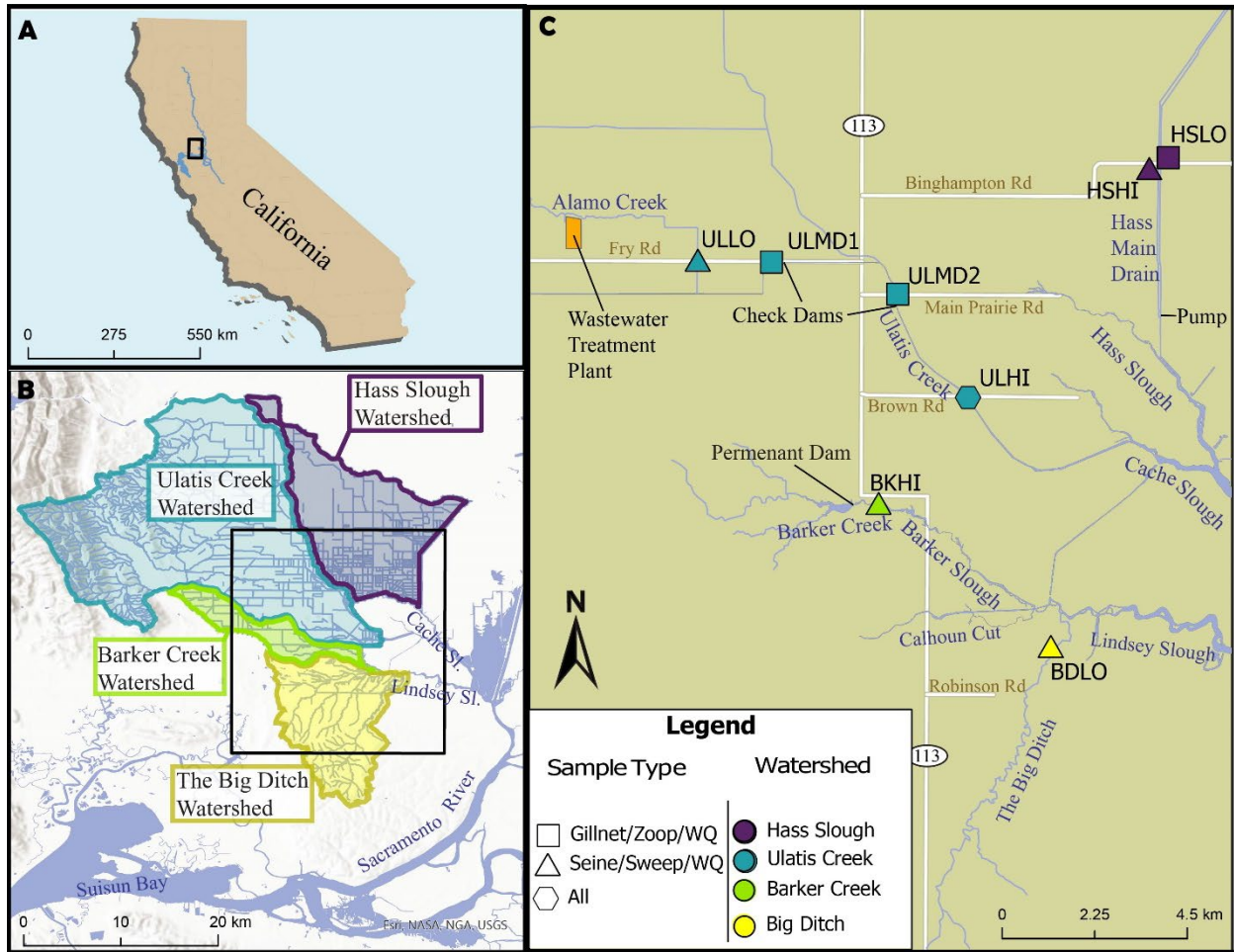


Figure 1 Map of study sites. Panel A shows the location of the study watersheds within California, Panel B shows the watersheds in which the study sites are in, and panel C shows the study sites with point color corresponding to watershed and point shape corresponding to what sample methods were used at the site.

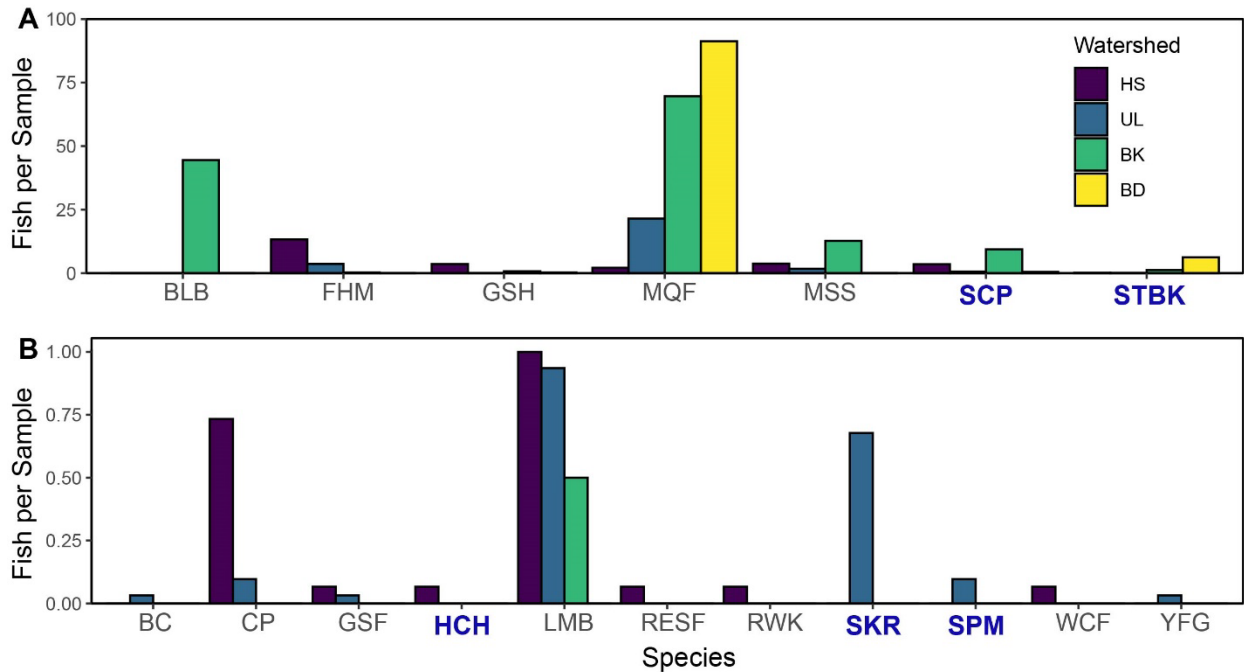
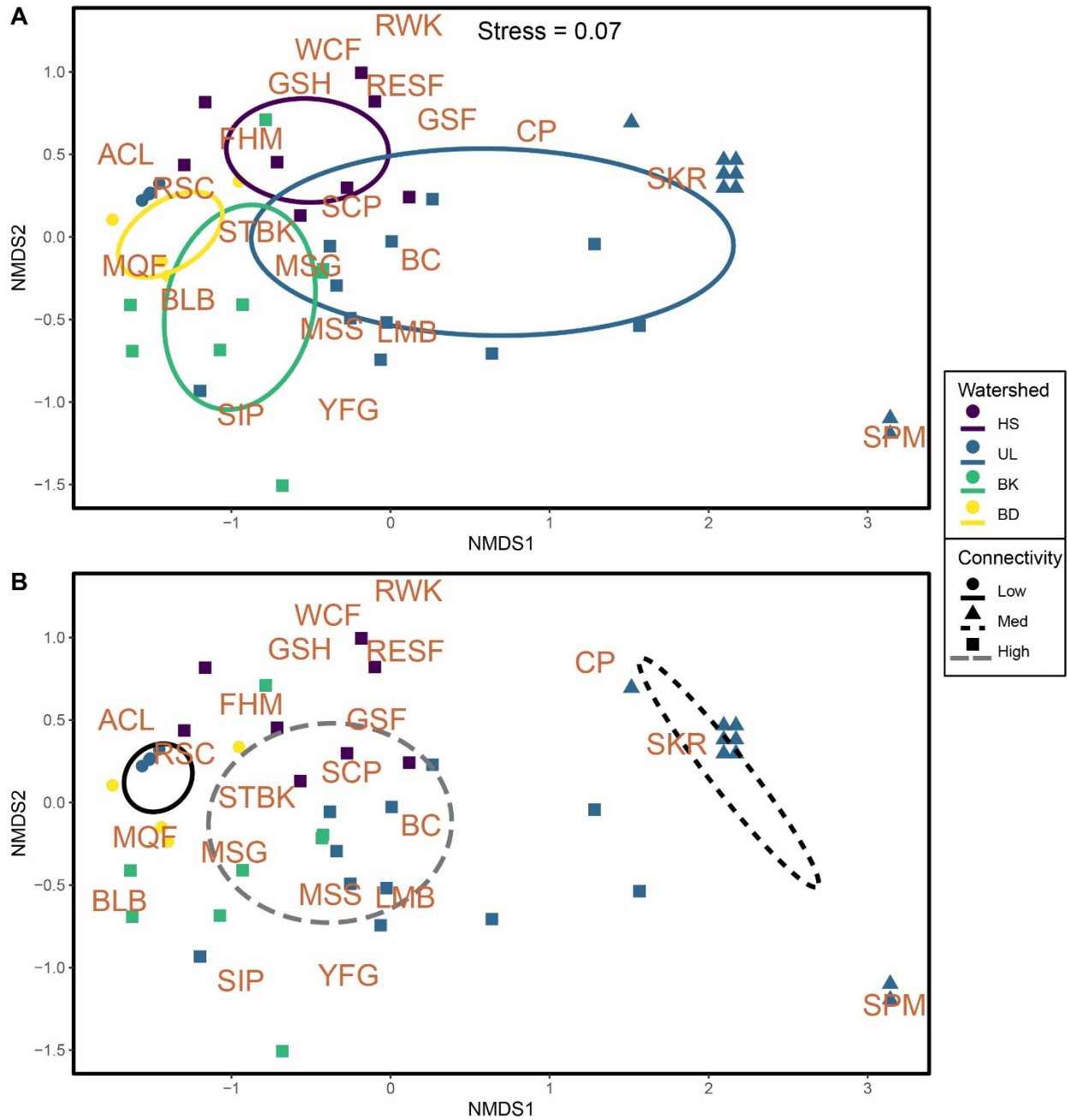


Figure 2 Plots of fish catch in seine and gillnet: (A) barplot showing common species (> 50 individuals) among watersheds in catch per sample and (B) showing uncommon species (<50 individuals) among watersheds in catch per sample. Native species codes are **bold and blue**. BC = black crappie, BLB = black bullhead, CP = common carp, FHM = fathead minnow, GSH = golden shiner, GSF = green sunfish, **HCH = Sacramento hitch**, LMB = largemouth bass, MQF = western mosquitofish, MSS = Mississippi silverside, RESF = redear sunfish, RWK = rainwater killifish, **SCP = prickly sculpin**, **SKR = Sacramento sucker**, **SPM = Sacramento pikeminnow**, **STBK = threespine stickleback**, WCF = white catfish, and YFG = yellowfin goby.



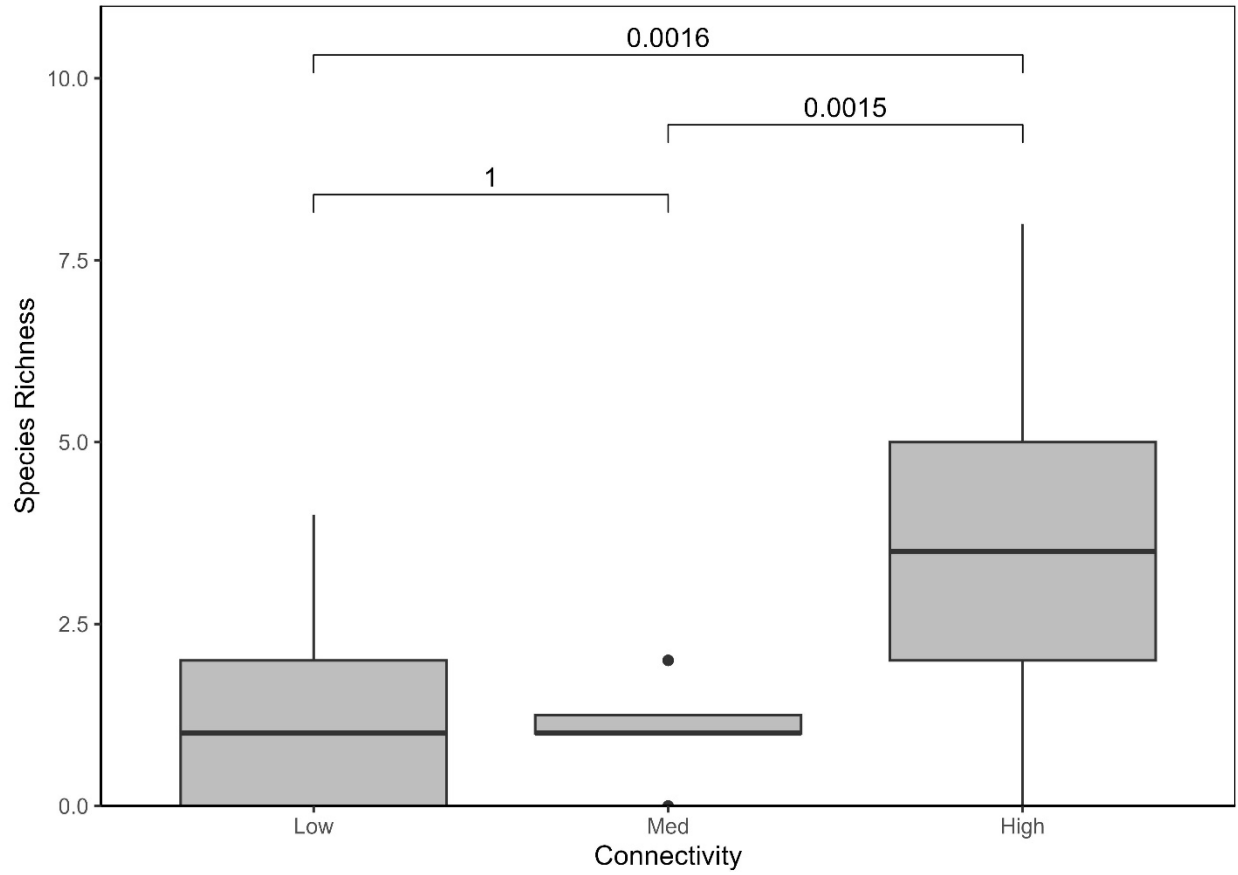


Figure 4 Boxplot of fish species caught in seines for by connectivity ranking. P-values for Wilcoxon tests between richness in each connectivity ranking.

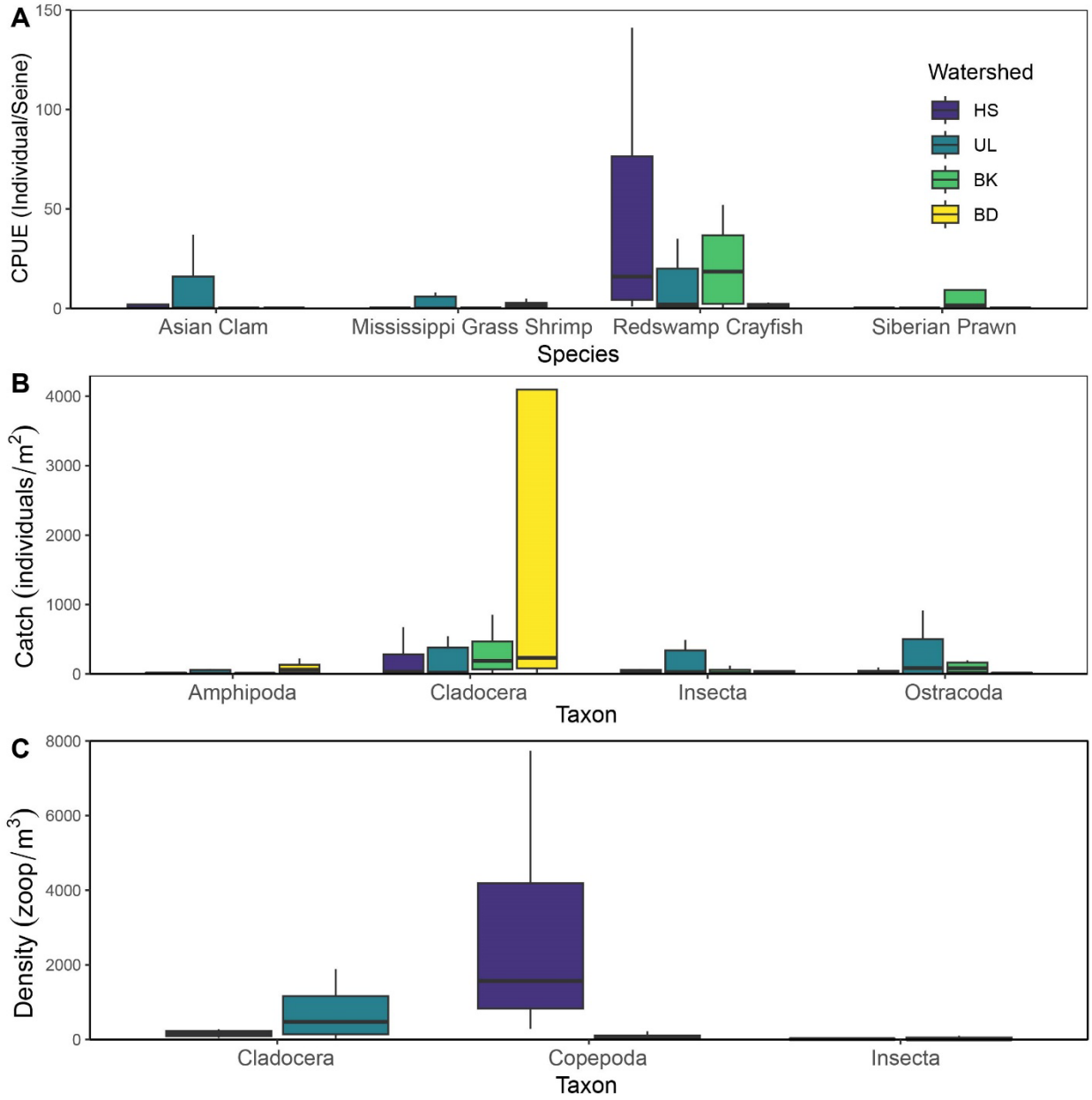


Figure 5 Boxplots of invertebrates captured using three different methods: (A) seine net, (B) sweep net, and (C) zooplankton net. Outliers removed.

Table 1 Site attributes: WS Area = watershed area in km², Distance = distance to tidal slough in km, Peren = whether the site is perennial, Cropland = % of watershed land area used for irrigated crop production, Rangeland = % of watershed land area that is non-irrigated rangeland. Conn = degree of connectivity to tidal slough; low = permanent barrier, med = seasonal barrier, and high = no barrier to upstream migration.

Site	Watershed	WS Area	Distance	Peren	Cropland	Rangeland	Conn
HSLO	Hass Slough	154	4.7	Yes	89%	1%	Low
HSHI	Hass Slough	154	4.7	Yes	89%	1%	High
ULLO	Ulatis Creek	375	12.6	Yes	48%	27%	Low
ULMD1	Ulatis Creek	375	9.2	Yes	48%	27%	Med
ULMD2	Ulatis Creek	375	5.6	Yes	48%	27%	Med
ULHI	Ulatis Creek	375	2.5	Yes	48%	27%	High
BKHI	Barker Creek	45	2.6	Some Years	35%	47%	High
BDLO	Big Ditch	95	1.2	No	25%	72%	Low

Table 2 Fish and invertebrate species captured in seine and gillnet sampling. Native species in bold font.

Common Name	Scientific Name	Code	Seine	Gillnet	Total
Western Mosquitofish	<i>Gambusia affinis</i>	MQF	1621	0	1621
Red Swamp Crayfish	<i>Procambarus clarkii</i>	RSC	418	0	418
Black Bullhead	<i>Ameiurus melas</i>	BLB	356	0	356
Fathead Minnow	<i>Pimephales promelas</i>	FHM	314	0	314
Asian Clam	<i>Corbicula fluminea</i>	ACL	241	0	241
Mississippi Silverside	<i>Menidia audens</i>	MSS	212	0	212
Prickly Sculpin	<i>Cottus asper</i>	SCP	148	0	148
Siberian Prawn	<i>Palaemon modestus</i>	SIP	67	0	67
Mississippi Grass Shrimp	<i>Palaemon kadiakensis</i>	MSG	67	0	67
Golden Shiner	<i>Notemigonus crysoleucas</i>	GSH	61	0	61
Largemouth Bass	<i>Micropterus salmoides</i>	LMB	41	7	48
Threespine Stickleback	<i>Gasterosteus aculeatus</i>	STBK	39	0	39
Sacramento Sucker	<i>Catostomus occidentalis</i>	SKR	1	20	21
Common Carp	<i>Cyprinus carpio</i>	CP	11	3	14
Sacramento Pikeminnow	<i>Ptychocheilus grandis</i>	SPM	0	3	3
Green Sunfish	<i>Lepomis cyanellus</i>	GSF	2	0	2
Black Crappie	<i>Pomoxis nigromaculatus</i>	BC	1	0	1
Sacramento Hitch	<i>Lavinia exilicauda</i>	HCH	0	1	1
Rainwater Killifish	<i>Lucania parva</i>	RWK	1	0	1
Redear Sunfish	<i>Lepomis microlophus</i>	RESF	1	0	1
White Catfish	<i>Ameiurus catus</i>	WCF	1	0	1
Yellowfin Goby	<i>Acanthogobius flavimanus</i>	YFG	1	0	1

Table 3 Mean (SD) of water quality taken during each seine and gillnet sample.

Water-shed	DO (mg/L)	SC (uS/CM)	TEMP (°C)	Turbidity (NTU)
HS	7 (1.4)	539 (383)	17 (4.6)	34 (20)
UL	6.8 (2.7)	836 (131)	19 (2.5)	26 (21)
BK	7.5 (4.2)	1124 (293)	18 (4.4)	65 (73)
BD	7.6 (3.1)	746 (221)	15 (4.2)	16 (9.9)

Table 4 Results of PERMANOVA with watershed and habitat type as factors.

	DF	SUM OF SQUARES	R²	F- Statistic	p- value
Watershed	3	3.10	0.17	3.74	0.001
Connectivity	2	4.17	0.22	7.54	0.001
Residual	41	11.33	0.61		
Total	46	18.60	1.00		