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RESEARCH

# Regional Diversity Trends of Nearshore Fish Assemblages of the Upper San Francisco Estuary

Ryan McKenzie*[1], Christian Gredzens[1], Brian Mahardja[2]

## ABSTRACT

The loss of biodiversity and biotic homogenization are on the rise in ecosystems around the world as a result of species invasions, habitat degradation, and the effects of climate change. In the Sacramento–San Joaquin Delta, non-native species make up the majority of the fish community, and declines in native species have been well documented; however, little is known about whether these trends have resulted in biotic homogenization. In this study, we used data from a long-term beach seine survey to analyze regional beta diversity trends of nearshore fish assemblages in the Delta from 1995 to 2019. Overall, we found no evidence of regional biotic homogenization occurring over the study period. Regional beta diversity increased moderately over time and was significantly influenced by the high interannual variability of freshwater inflow. These beta diversity patterns were driven by the non-native Mississippi Silverside that has proliferated in the system in recent years, but also by a handful of native fish species such as the Sacramento Sucker, Tule Perch, and Splittail. Overall, our results offer a contrast to other highly invaded ecosystems around the world and suggest that despite the near extinction of some native fish species, there remain pockets of suitable habitat in the Delta that may play a key role in the conservation of remnant native fish diversity.

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## KEY WORDS

beta diversity, biotic homogenization, diversification, fish communities, long-term monitoring, California, Sacramento–San Joaquin Delta, Sacramento River, climate change

## INTRODUCTION

It is well recognized that worldwide biodiversity has declined because of both the extinction of endemic species and spread of cosmopolitan species. For many places, native species are being replaced by highly successful invaders that can better tolerate a broader range of environmental conditions and human activities (Olden and Poff 2003). Yet biodiversity patterns can be complex, and vary depending on the ecosystem or taxa, as well as the spatial and temporal scale examined (Levin 1992). Anthropogenic disturbances can result in a reduction of overall habitat complexity, which may lead to the homogenization of biota, a process by which species invasions and extirpations reduce the distinctiveness (i.e., increased similarity) of biological communities over time (Olden 2006). However, establishment of non-native species without concurrent extirpations can result in an increase for local biodiversity (Sax et al. 2002). Identifying patterns of species diversity at multiple spatial and temporal scales can help us understand which ecosystems are most resistant to non-native species, as well as the risk for of further shifts in biological communities.

Patterns of diversification or homogenization of biodiversity can be evaluated through measurements of species beta diversity, a measure of differences in species composition between two or more sites (Whittaker 1972). Loss of distinct communities—as indicated by temporal declines in beta diversity—can reduce the overall resiliency of an ecosystem to disturbances such as climate change, and there is also a growing recognition among managers and policy-makers that biodiversity is often linked with valuable ecosystem services (Weiskopf et al. 2020). To understand the ecological causes of biodiversity changes, it is important to decompose beta diversity into its two main components: nestedness and spatial turnover (Baselga 2010; Zbinden and Matthews 2017). Nestedness is a non-random process that occurs when species are lost from one site to the next, resulting in species-poor sites being subsets of species-rich sites, and is thought to be driven by spatial processes that promote the orderly disaggregation of assemblages. These processes include many environmental and biological factors that regulate species dispersal, immigration, and extinction rates (Taylor and Warren 2001; Bie et al. 2012; Peláez and Pavanelli 2019). Spatial turnover, on the other hand, occurs when species are replaced by others from one site to the next, and is thought to be driven mainly by environmental processes that filter out individuals (similar to niche partitioning), and include interspecific variation in habitat suitability, physiological tolerances, and biotic interactions (Nicolas et al. 2010; Henriques et al. 2017; Cunha et al. 2019; García–Girón et al. 2020). Nestedness and spatial turnover apply to incidence-based measures of beta diversity; however, the concept of beta diversity partitioning was extended to abundance-based measures by Baselga (2013a), who introduced the two analogous components of beta diversity used in our study: abundance gradients (nestedness) and balanced variation in species abundance (spatial turnover).

The highly invaded Sacramento–San Joaquin Delta (Delta) of California, USA, provides an excellent opportunity to study this topic. The Delta drains over half of the surface runoff that occurs in California, and it is at the heart of the Central Valley and State Water projects that provide drinking water to over 25 million people and support a multi-billion-dollar agricultural economy (Luoma et al. 2015). The potential effects from the impoundments and water diversions that result from these projects on the Delta's fish community led to the establishment of multiple long-term monitoring programs, some of which collected data at suitable spatial and temporal scales for assessment of beta diversity patterns. In addition, several native fish species have suffered population declines and have been subsequently listed under the US and California Endangered Species Acts (ESAs), and recovery of these species has become a management priority (Moyle et al. 2016; Johnson et al. 2017). Yet species do not live in isolation. Biological communities are a critical component of the ecosystems on which endangered and threatened species depend, and improving our understanding of community dynamics can provide better context for the expected population trajectory of these key species of interest.

The overall fish fauna of California has been homogenized at a broad scale (Marchetti et al. 2001) and non-native species have become the dominant component of the Delta fish assemblage (Feyrer and Healy 2003; Nobriga et al. 2005; Brown and Michniuk 2007; Mahardja et al. 2017); however, the extent of biotic homogenization that has occurred over time and space in the Delta is unknown. Because of the existence of floodplain, natural drainage patterns, and relatively high habitat connectivity, the northern and western regions of the Delta have been posited as a refuge for native species and targeted for restoration efforts (Quiñones and Moyle 2014). Yet it is unclear whether these regions have remained unique relative to other parts of the Delta in recent years, and if overall regional homogenization within the Delta or tributaries upstream has increased over time. Furthermore, climate-change models predict shifts in the magnitude and timing of freshwater input into the system, with increased periods of drought and more sporadic high-flow events in the future (Herbold et al. 2022). As observed in other ecosystems, shifts in water flow regimes can significantly affect the composition and biodiversity of ecological communities (Boulton et al. 1992; Bêche et al. 2006; Bogan et al. 2015). Therefore, understanding the dynamics between water inflow and beta diversity in the Delta is a critical component for forecasting the future effects of climate change on the system.

The objective of our study was to assess trends of fish beta diversity over time, and to test for relationships with freshwater inflow rates in the Delta. To assess these patterns, we used data from a multi-decade beach seine survey of nearshore fish assemblages. Higher fish diversity has been observed in the nearshore, littoral habitat of the Delta than in the open water (McKenzie and Mahardja 2021), and this habitat appears to have played a more dominant role in the food web over recent years (Conrad et al. 2016; Santos et al. 2016; Mahardja et al. 2017; Young et al. 2021). Results from our study can provide key insights into the biodiversity patterns and interspecific interactions among common fish taxa within the Delta that may be used as indicators of overall ecosystem function and provide important information for successful management of key species.

## METHODS

### Study Area

The Delta is an inverted river delta located in the Central Valley of California that is formed by the confluence of the Sacramento and San Joaquin rivers. The Delta experiences a Mediterranean climate characterized by cool, wet winters and hot, dry summers. The once-tidal marsh system has been heavily modified since the mid-19th century and is now composed of a patchwork of levee-lined agricultural islands interlaced with a network of canals, sloughs, and flooded islands (Whipple et al. 2012). For our analysis, we examined beta diversity trends across regions that were delineated using professional judgement and were loosely based on the US Geological Survey (USGS) hydrologic unit code (HUC 8) hydrological units and water-conductivity levels (*https://water.usgs.gov/GIS/huc.html*, Figure 1). The lower Sacramento River region included sites along the American and Sacramento rivers north of Sacramento, California. The North Delta included sites along the Sacramento River and Steamboat Slough from Sacramento to Rio Vista, California. The South Delta included sites along the Mokelumne, Middle, and San Joaquin rivers. The West Delta included sites along the Sacramento and San Joaquin rivers west of Rio Vista, California, that experienced higher levels of saltwater intrusion in some years indicated by specific water conductivities that exceeded 2,000 µS $cm^{-1}$ in the dataset (IEP et al. 2020). For the temporal grain in our analyses, we used the California water year (WY), which begins on October 1 of each calendar year and ends on September 30 of the following calendar year (e.g., WY 2019 begins on October 1, 2018, and ends on September 30, 2019).

### Data Sources

The US Fish and Wildlife Service (USFW) Delta Juvenile Fish Monitoring Program (DJFMP) has conducted beach seine surveys since 1976 to evaluate the abundance and distribution of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) and various resident fish species within the Delta (IEP et al. 2020). The DJFMP beach seine survey has been the primary monitoring program in the Delta that evaluates fish community changes in the nearshore, littoral habitat (Brown and May 2006; Mahardja et al. 2017). Although the DJFMP began in 1976, sampling in the summer months (when non-salmonid juvenile fishes typically recruit into the gear) did not become part of standard protocol until 1995. Since 1995, the DJFMP has conducted year-round sampling at 44 fixed sites within the Delta and the lower Central Valley. Before data analysis, we removed samples collected under poor sampling conditions, and filtered the catch to include only fish species with more than 100 total individuals captured over the study period (Table 1). The genus *Micropterus* was not resolved to species level because of moderate misidentification rates (Kirsch et al. 2018), and the genus *Lampetra* was not resolved to species level because early life stages (ammocoetes) were not identified to species level. Species counts for each seine haul were converted to catch-per-unit effort (CPUE) by dividing the counts of each species captured by sampling volume ($m^3$).

For comparisons between average flow rates, we used data from the California Department of Water Resources's Dayflow dataset (CDWR 2023) for annual freshwater inflow into the Delta. Specifically, the Effective Western/Central Delta Inflow (QEFFECT) parameter was used in analysis, which is the daily estimated inflow that reaches the western and central Delta after accounting for water use and diversions in the southern Delta. We chose the QEFFECT because it was originally developed for Striped Bass (*Morone saxatilis*) studies within the Delta and accounts for water use and diversions that can affect water-quality parameters important to fish (e.g., salinity). For our analysis, the daily QEFFECT cubic feet per second (cfs) was converted to million acre-feet (maf) per water year by converting the mean cfs per day to daily million-acre feet, and then summing those values across each day of the water year:

$$maf_{Year} = \sum_{i=1}^{365} QEFFECT_i \times \frac{1.98347_{acre-feet\ per\ day}}{1 ft^3 s{-1}} \times \frac{1\ maf}{10^6 acre-feet} \qquad \textbf{Eq 1}$$

maf = million-acre-feet
QEFFECT = daily mean $ft^3\ s^{-1}$

## Sample-Based Rarefaction

The number of species detected within surveys is positively correlated with sampling effort, because rare species are more likely to be encountered as sampling effort increases, which can influence diversity measures (Gotelli and Colwell 2001). On inspection of the DJFMP seine dataset we found that sampling effort at seine sites was somewhat inconsistent over time. This resulted from a higher frequency of sampling during winter months to track the out-migration of juvenile salmonids as well as from changes in site accessibility from year to year (e.g., high tides, encroachment of aquatic vegetation, site construction). Therefore, we took a series of steps to ensure balanced sample size over time. First, we limited our analysis to seine sites that were successfully sampled a minimum of three times in the "wet" (October to April) and three times in the "dry" (May to September) seasons of each year between 1995 and 2019. Subsequently, 23 DJFMP fixed beach seine sites met this criterion and were used in the analysis (Figure 1). Second, we performed sample-based rarefaction within each seine site. Specifically, the "wet" and "dry" seasons were used as the temporal grain to find the minimum number of samples taken within each season across all years of sampling for each site. Data were then re-sampled (without replacement) within each year using these minimum sample sizes to obtain a constant number of samples from each site for each season across all years of the dataset (see Appendix A). Species CPUE within each site were then averaged across these rarefied samples by season, water year, and region to create the mean annual species assemblages for each region. To account for the variation associated with sub-sampling the dataset during the rarefaction process, 1,000 permutations were run to calculate CPUE estimates and for subsequent beta diversity calculations.

## Beta Diversity Trends

Many indices are available to calculate beta diversity, and each can offer a different perspective, depending on their unit of measure (i.e., occurrence vs. abundance) and how they weight dominant and rare species (Anderson et

**Table 1** Catch summary from the US Fish and Wildlife Service Delta Juvenile Fish Monitoring Program beach seine survey from 1995 to 2019. Species with less than 100 individuals captured were removed from the dataset before analysis.

| Species Code | Name | Native | Total Count |
|---|---|---|---|
| AMS | American Shad (*Alosa sapidissima*) | No | 2964 |
| ARG | Arrow Goby (*Clevelandia ios*) | Yes | 1 |
| BAS | Black Bass (*Micropterus* spp.) | No | 12642 |
| BFK | Bluefin Killifish (*Lucania goodei*) | No | 2 |
| BGS | Bluegill Sunfish (*Lepomis macrochirus*) | No | 5898 |
| BKB | Black Bullhead (*Ameiurus melas*) | No | 48 |
| BKS | Black Crappie (Pomoxis nigromaculatus) | No | 1614 |
| BRB | Brown Bullhead (*Ameiurus nebulosus*) | No | 21 |
| C | Common Carp (*Cyprinus carpio*) | No | 3358 |
| CAR | California Roach (*Hesperoleucus symmetricus*) | Yes | 184 |
| CHC | Channel Catfish (*Ictalurus punctatus*) | No | 96 |
| CHG | Chameleon Goby (*Tridentiger trigonocephalus*) | No | 31 |
| CHN | Chinook Salmon (*Oncorhynchus tshawytscha*) | Yes | 220846 |
| DSM | Delta Smelt (*Hypomesus transpacificus*) | Yes | 958 |
| FHM | Fathead Minnow (*Pimephales promelas*) | No | 27208 |
| GF | Goldfish (*Carassius auratus*) | No | 1247 |
| GSF | Green Sunfish (*Lepomis cyanellus*) | No | 90 |
| GSN | Golden Shiner (*Notemigonus crysoleucas*) | No | 13781 |
| HCH | Hitch (*Lavinia exilicauda*) | Yes | 2594 |
| HH | Hardhead (*Mylopharodon conocephalus*) | Yes | 604 |
| LAM | Lamprey (*Lampetra* sp.) | Yes | 176 |
| LFS | Longfin Smelt (*Spirinchus thaleichthys*) | Yes | 26 |
| LP | Bigscale Logperch (*Percina macrolepida*) | No | 8752 |
| MQF | Western Mosquitofish (*Gambusia affinis*) | No | 29438 |
| MSS | Mississippi Silverside (*Menidia audens*) | No | 1107198 |
| NAN | Northern Anchovy (*Engraulis mordax*) | Yes | 1 |
| PAH | Pacific Herring (*Clupea pallasii*) | Yes | 18 |
| PRS | Prickly Sculpin (*Cottus asper*) | Yes | 915 |
| PSF | Pumpkinseed Sunfish (*Lepomis gibbosus*) | No | 2 |
| PSS | Pacific Staghorn Sculpin (*Leptocottus armatus*) | Yes | 778 |
| RBT | Rainbow Trout/Steelhead (*Oncorhynchus mykiss*) | Yes | 1050 |
| RES | Redear Sunfish (*Lepomis microlophus*) | No | 6978 |
| RFK | Rainwater Killifish (*Lucania parva*) | No | 2767 |
| RSN | Red Shiner (*Cyprinella lutrensis*) | No | 88738 |
| SAPM | Sacramento Pikeminnow (*Ptychocheilus grandis*) | Yes | 34863 |
| SASU | Sacramento Sucker (*Catostomus occidentalis*) | Yes | 119289 |
| SCB | Sacramento Blackfish (*Orthodon microlepidotus*) | Yes | 232 |
| SHG | Shokihaze Goby (*Tridentiger barbatus*) | No | 2 |
| SHM | Shimofuri Goby (*Tridentiger bifasciatus*) | No | 3309 |
| SMU | Striped Mullet (*Mugil cephalus*) | No | 3 |
| SPLT | Sacramento Splittail (*Pogonichthys macrolepidotus*) | Yes | 122754 |
| STB | Striped Bass (*Morone saxatilis*) | No | 2619 |
| STF | Starry Flounder (*Platichthys stellatus*) | Yes | 35 |
| TFS | Threadfin Shad (*Dorosoma petenense*) | No | 155369 |
| TP | Tule Perch (*Hysterocarpus traskii*) | Yes | 6993 |
| TSS | Three-spined Stickleback (*Gasterosteus aculeatus*) | Yes | 1145 |
| W | Warmouth (*Lepomis gulosus*) | No | 26 |
| WAG | Wakasagi (*Hypomesus nipponensis*) | No | 1971 |
| WHC | White Catfish (*Ameiurus catus*) | No | 235 |
| WHS | White Crappie (*Pomoxis annularis*) | No | 1870 |
| YEB | Yellow Bullhead (*Ameiurus natalis*) | No | 1 |
| YFG | Yellowfin Goby (*Acanthogobius flavimanus*) | No | 10632 |

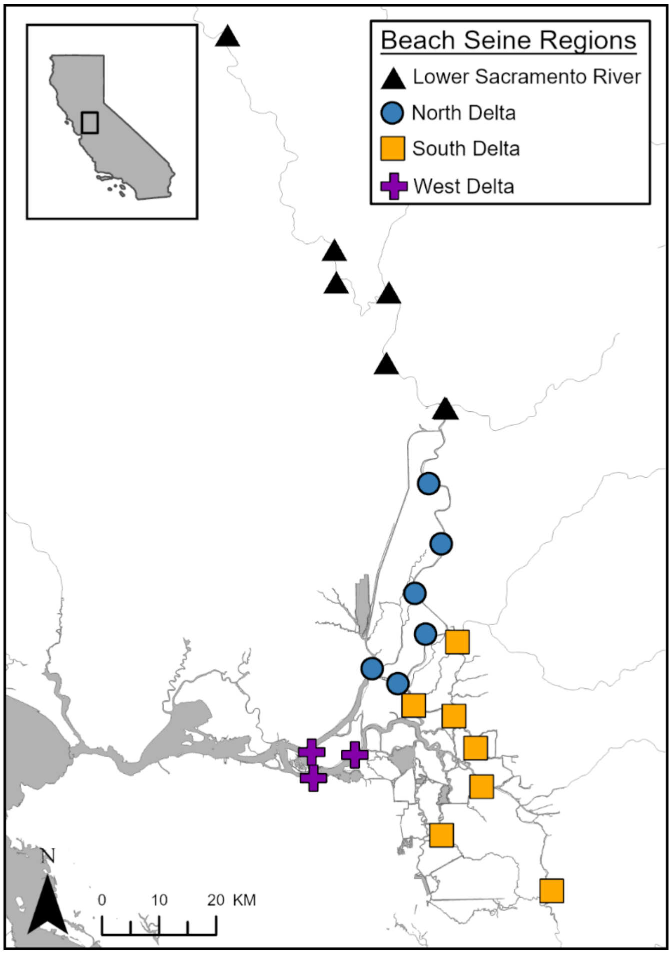

**Figure 1** Map of the US Fish and Wildlife Service Delta Juvenile Fish Monitoring Program beach seine sites and study regions

al. 2011; Tuomisto 2010a, 2010b). For our primary analysis, we calculated beta diversity using the Bray–Curtis dissimilarity index, which is an abundance-based measure that provides more weight to dominant species (Schroeder and Jenkins 2018). The Bray–Curtis dissimilarity index is a proportion bound between 0 and 1, where a value of 0 indicates that sites have the same species composition, and a value of 1 indicates that sites are completely different in species composition. Before running our analysis, we inspected species CPUE plots, and applied a fourth-root transformation to normalize CPUE across species and mitigate the influence of the highly abundant species on our beta diversity estimates (Appendix A). The Bray–Curtis dissimilarity index on fourth-root-transformed data was chosen as our primary analysis because it provided a more balanced view of the community in terms of the weight given to rare vs. dominant species; however, we repeated our analysis with the Jaccard dissimilarity index using presence–absence data and the Bray–Curtis dissimilarity index using untransformed CPUE data for comparison purpose and include them in Appendix B.

For each permutation of the dataset, we computed the Bray–Curtis multi-site dissimilarity index and the two components of the index: (1) balanced variation in species abundance, whereby the individuals of some species in one region are substituted by the same number of individuals of different species in another region; and (2) abundance gradients, whereby some individuals of the same species are lost from one region to the other (Baselga 2013a, 2013b). We also conducted separate pairwise analyses between regions to identify which specific regions were driving the overall beta diversity trends within the Delta. All indices were calculated using the betapart package in R (Baselga et al. 2023; R Development Team 2022). For each water year, the mean dissimilarity index was obtained by calculating dissimilarity indices for permutations of the region × species matrix and averaging across permutations.

We fit a series of linear models using ordinary least squares (OLS) regression to test two null hypotheses: (1) that there was no significant change in the mean annual dissimilarity indices over water years (time), and (2) that there was no effect of annual water inflow on mean annual dissimilarity indices. A significant positive slope indicates increasing divergence in species composition between regions (i.e., diversification) and a significant negative slope indicates increasing similarity between regions (i.e., homogenization). We also assessed heterogeneity and normality for each model using standardized residual and quantile–quantile plots, and collinearity between water years and annual inflow had an acceptable Pearson correlation coefficient of -0.3 and variance inflation factor of 1.10 (Dormann et al. 2013).

### Species Trends

To assess regional species associations, we constructed non-metric multi-dimensional scaling (NMDS) ordinations to visualize species assemblage differences between regions across time and annual water inflow. For our temporal exploration, we split the dataset in half between early (1995 to 2007) and late (2008 to 2019) time-periods. For our inflow exploration, we split the data into high (>21,000 maf) and low (<21,000 maf) inflow years, with the delineation set at the minimum inflow level that consistently resulted in high-inflow years corresponding to the "Above Normal" and "Wet" water-year types used by the CDWR for the Sacramento River basin (SWRCB Decision 1641) to align both metrics. Given that NMDS ordination analysis is an exploratory tool, our primary goal was to identify general patterns of regional species associations over time and inflow levels, and seed future hypothesis testing studies. For NMDS ordinations, we consolidated the species assemblage dataset by averaging the CPUE of each species across the 1,000 permuted species assemblages for each region and year combination. Ordinations based on pairwise Bray–Curtis dissimilarity indices were then constructed using the vegan package in R with 100 random starts (Oksanen et al. 2022). To reduce clutter and help visualize differences in species composition among regions, the top 25 species—based on ordination correlation coefficients—were displayed as vectors of increasing CPUE on ordinations. In addition, we performed a similarity percentage (SIMPER) analysis using the vegan package in R with 999 permutations (Oksanen et al. 2022) to determine which species were primarily responsible for the observed changes in regional beta diversity across time and annual water inflow. Similarity percentage analysis performs pairwise comparisons of groups of sampling units and finds the contribution of each species to the mean between-group Bray–Curtis dissimilarity. Separate SIMPER analyses were run—using regions as the grouping factor and annual species assemblages as sampling units—to compute the mean between-region Bray–Curtis dissimilarity for the early and late time-periods, and high- and low-annual-inflow years. To determine their contribution to change in the dissimilarity index, the contributions of each species were averaged across pairwise comparisons, and the difference in the mean contribution between the early and late and periods and between high-flow and low-flow years were calculated. Using this method, positive values indicated that species contributed to increased regional dissimilarity (i.e., differentiation), and negative contributions indicated that species contributed to decreased dissimilarity (i.e., regional homogenization).

In addition to our main analyses, we have included a supplemental analysis using only data collected after WY 2000 (Appendix C). We chose this alternative period for a comparison to our main analysis to ensure that our main results were robust and not overly influenced by the consecutive "wet" years that occurred from water years 1995 to 1999, and because the 2000 to 2019 period was characterized by prolonged periods of intense drought punctuated by extended high inflows only in 2006, 2011, 2017, and 2019. Therefore, the hydrological regime of this period may better represent future conditions within the Delta that result from climate change (Dettinger et al. 2016; Swain et al. 2018).

## RESULTS

In the DFJMP beach seine dataset, we observed 52 fish species among the 23 seine sites between 1995 and 2019. Out of these species, 36 (15 native and 21 non-native species) had more than 100 individuals captured over the study period and were used in analysis (Table 1). Results from our primary analysis using the Bray–Curtis dissimilarity index on fourth-root-transformed CPUE data are reported in the subsequent sections. However, we observed variation in the beta diversity trends over time, depending on the dissimilarity index and data transformation used for analysis (Figure 2). Trends of beta diversity based on water inflow rates were consistent across all analyses. In addition, the results of our supplemental analysis using data collected only after WY 2000 were consistent with our main analysis reported here (see Appendix C).

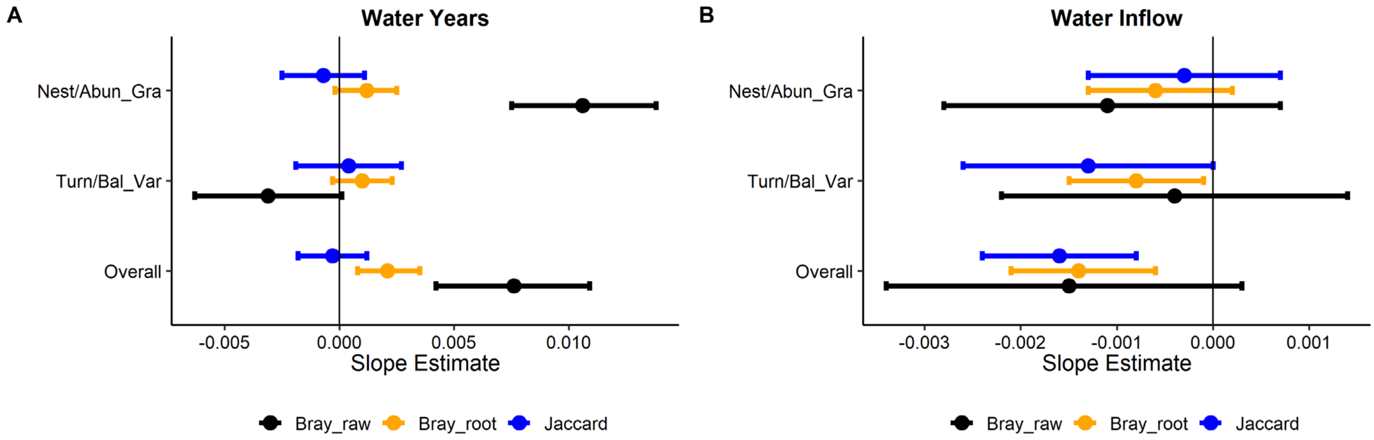

**Figure 2** Slope estimates from multi-variate linear regressions of different beta diversity indices (Bray_raw: Bray–Curtis multi-site dissimilarity index using raw CPUE data; Bray_root: Bray–Curtis multi-site dissimilarity index using fourth-root-transformed CPUE data; Jaccard: Jaccard multi-site dissimilarity index) and their components (Nest/Abun_Gra: species nestedness or species abundance gradient component; Turn/Bal_var: species turnover or balanced variation in species abundance component; Overall: overall dissimilarity index) over: (**A**) water years (1995 to 2019) and (**B**) water inflow (million acre-feet). *Vertical line* marks a slope estimate of 0.

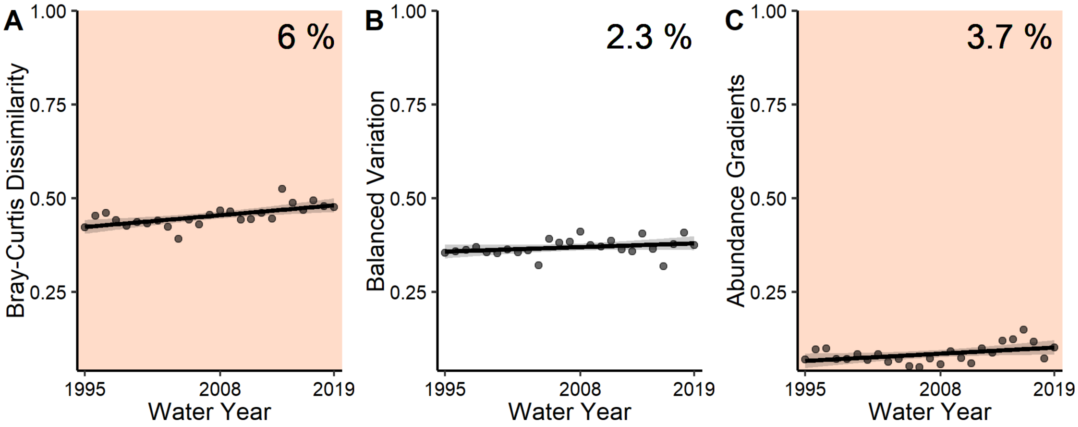

**Figure 3** Effect plots of the (**A**) Bray–Curtis dissimilarity index and its components, (**B**) balanced variation in species abundance and (**C**) abundance gradients, over water years 1995 to 2019. *Points* represent partial residuals of the data after accounting for the effect of annual water inflow. *Shading around the line* re,presents a 95% confidence interval around the mean (*solid line*). Significant ($\rho < 0.05$) trends indicated by our multi-variate linear regression model are highlighted by *red*. Overall percent change of the mean is indicated for each plot in the *top right*.

### Beta Diversity and Species Temporal Trends

Beta diversity across regions increased significantly over time (Slope = 0.0024, $\rho = 0.001$), resulting in an overall increase of 6% in the mean Bray–Curtis dissimilarity index over the 25-year study period (Figure 3A). Balanced variation in species abundance was the dominant component of regional diversity (0.37 ± 0.005 standard error [SE]) compared to species abundance gradients (0.08 ± 0.005 SE); however, changes in regional diversity over time were significantly higher for species abundance gradients (Figures 3B and 3C). The differentiation of the West Delta was the largest contributor to the change over time, as we observed significant ($\rho < 0.05$) divergence of this region from the lower Sacramento River region (7.5%), and the North Delta (9.5%) and South Delta (9.5%) (Figure A4; Table 2).

Non-metric multi-dimensional scaling ordinations showed consistently clear separations between

**Table 2** SIMPER analysis results showing changes in species distribution and dissimilarity contributions during late time period (2008 to 2019) relative to early time period (1995 to 2007). Changes in the mean fourth-root-transformed (CPUE) values are provided for the lower Sacramento River (LSAC), North Delta (North), South Delta (South), and West Delta (West) regions. Δ DI: change in mean species contribution to dissimilarity index during late time period; Trend: Hom–homogenization or decrease n regional dissimilarity; Dif–differentiation or increase in regional dissimilarity. *Green* indicates positive values, *orange* represents negative values, and the *degree of shading* indicates the degree of change.

| Species code | Δ DI | Trend | LSAC | North | South | West |
|---|---|---|---|---|---|---|
| MSS | 0.87 | Dif | 0.13 | 0.21 | 0.07 | 0.49 |
| RFK | 0.73 | Dif | 0.04 | 0.07 | 0.15 | 0.28 |
| SASU[a] | 0.64 | Dif | 0.19 | 0.20 | – 0.05 | 0.00 |
| TP[a] | 0.61 | Dif | 0.01 | 0.00 | – 0.02 | 0.21 |
| SHM | 0.54 | Dif | 0.01 | 0.18 | 0.09 | 0.17 |
| TSS[a] | 0.51 | Dif | 0.02 | 0.05 | 0.00 | 0.19 |
| SPLT[a] | 0.48 | Dif | 0.13 | 0.15 | – 0.01 | – 0.01 |
| TFS | 0.37 | Dif | – 0.13 | – 0.21 | – 0.06 | – 0.01 |
| HH[a] | 0.31 | Dif | 0.13 | 0.00 | – 0.02 | 0.05 |
| CHN[a] | 0.26 | Dif | – 0.12 | – 0.09 | – 0.18 | – 0.16 |
| SAPM[a] | 0.26 | Dif | 0.01 | – 0.01 | – 0.07 | – 0.02 |
| PSS[a] | 0.23 | Dif | 0.00 | – 0.01 | 0.02 | 0.10 |
| BKS | 0.20 | Dif | 0.09 | 0.02 | 0.00 | – 0.02 |
| STB | 0.18 | Dif | – 0.03 | – 0.09 | 0.06 | – 0.02 |
| LP | 0.18 | Dif | 0.08 | 0.04 | 0.01 | 0.08 |
| GSN | 0.17 | Dif | 0.04 | – 0.07 | 0.01 | 0.06 |
| GF | 0.14 | Dif | 0.00 | 0.01 | 0.06 | 0.00 |
| MQF | 0.13 | Dif | – 0.03 | 0.03 | 0.03 | 0.13 |
| RES | 0.10 | Dif | 0.07 | 0.13 | 0.20 | 0.09 |
| BAS | 0.09 | Dif | 0.10 | 0.10 | 0.12 | 0.11 |
| HCH[a] | 0.06 | Dif | – 0.03 | – 0.07 | – 0.07 | – 0.01 |
| AMS | 0.01 | Dif | – 0.04 | – 0.07 | – 0.10 | – 0.03 |
| BGS | – 0.01 | Hom | 0.00 | 0.05 | 0.17 | 0.05 |
| WHC | – 0.02 | Hom | – 0.05 | 0.06 | – 0.02 | 0.02 |
| WAG | – 0.02 | Hom | – 0.04 | 0.00 | – 0.01 | 0.01 |
| FHM | – 0.05 | Hom | – 0.08 | – 0.07 | – 0.14 | – 0.07 |
| LAM[a] | – 0.05 | Hom | – 0.03 | 0.01 | – 0.01 | 0.00 |
| PRS[a] | – 0.08 | Hom | 0.04 | 0.06 | 0.10 | 0.15 |
| C | – 0.14 | Hom | – 0.01 | 0.00 | – 0.05 | 0.01 |
| SCB[a] | – 0.16 | Hom | 0.00 | – 0.03 | – 0.05 | – 0.01 |
| RBT[a] | – 0.18 | Hom | – 0.01 | – 0.11 | – 0.05 | – 0.01 |
| YFG | – 0.20 | Hom | – 0.02 | – 0.11 | – 0.10 | – 0.04 |
| CAR[a] | – 0.20 | Hom | – 0.03 | – 0.02 | – 0.01 | – 0.01 |
| DSM[a] | – 0.33 | Hom | – 0.02 | – 0.13 | – 0.09 | – 0.09 |
| WHS | – 0.36 | Hom | – 0.10 | – 0.03 | – 0.02 | – 0.02 |
| RSN | – 0.69 | Hom | 0.14 | 0.06 | – 0.22 | 0.06 |

a. Native species. See species codes and names in Table 1.

**Table 3** SIMPER analysis results showing changes in species catch- per- unit effort (CPUE) and dissimilarity contributions during high- fnflow conditions (> 21 maf) relative to low- inflow conditions (<21 maf). Mean fourth- root-transformed CPUE values are provided for the lower Sacramento River (LSAC), North Delta (North), South Delta (South), and West Delta (West) regions. Δ DI: change in mean species contribution to dissimilarity index during High Flow conditions; Trend: Hom – homogenization or decrease in regional dissimilarity; Dif – differentiation or increase in regional dissimilarity. Green indicates positive values, orange represents negative values, and the degree of shading indicates the degree of change from 0.

| Species code | Δ DI | Trend | LSAC | North | South | West |
|---|---|---|---|---|---|---|
| SASU[a] | – 0.74 | Hom | – 0.14 | – 0.03 | 0.03 | 0.10 |
| MSS | – 0.56 | Hom | – 0.11 | – 0.15 | – 0.04 | – 0.34 |
| CHN[a] | – 0.45 | Hom | 0.05 | 0.07 | 0.14 | 0.19 |
| TFS | – 0.41 | Hom | 0.04 | 0.10 | – 0.06 | – 0.16 |
| SHM | – 0.37 | Hom | 0.01 | – 0.07 | – 0.05 | – 0.11 |
| RFK | – 0.36 | Hom | 0.00 | 0.01 | – 0.06 | – 0.14 |
| TSS[a] | – 0.32 | Hom | – 0.01 | – 0.05 | – 0.02 | – 0.10 |
| PSS[a] | – 0.26 | Hom | 0.00 | 0.01 | 0.01 | – 0.11 |
| MQF | – 0.21 | Hom | 0.04 | – 0.01 | – 0.05 | – 0.15 |
| FHM | – 0.18 | Hom | – 0.01 | 0.03 | 0.04 | 0.02 |
| TP[a] | – 0.15 | Hom | – 0.05 | – 0.04 | 0.00 | – 0.06 |
| HCH[a] | – 0.15 | Hom | 0.05 | 0.11 | 0.10 | – 0.05 |
| RSN | – 0.13 | Hom | – 0.20 | – 0.08 | 0.02 | 0.01 |
| YFG | – 0.12 | Hom | – 0.03 | – 0.05 | 0.02 | – 0.05 |
| WAG | – 0.09 | Hom | – 0.01 | 0.00 | 0.00 | – 0.02 |
| RES | – 0.08 | Hom | – 0.01 | 0.00 | – 0.08 | 0.02 |
| STB | – 0.04 | Hom | 0.00 | – 0.02 | – 0.07 | – 0.02 |
| SAPM[a] | – 0.02 | Hom | 0.05 | 0.03 | 0.07 | 0.10 |
| BKS | – 0.01 | Hom | 0.01 | 0.08 | 0.04 | 0.03 |
| GSN | 0.02 | Dif | 0.03 | 0.10 | 0.07 | – 0.06 |
| WHC | 0.03 | Dif | 0.05 | – 0.04 | 0.01 | – 0.01 |
| HH[a] | 0.04 | Dif | – 0.01 | 0.07 | 0.06 | 0.00 |
| PRS[a] | 0.04 | Dif | 0.04 | 0.02 | 0.00 | 0.02 |
| BAS | 0.08 | Dif | – 0.03 | – 0.06 | – 0.02 | 0.00 |
| BGS | 0.08 | Dif | 0.04 | – 0.04 | – 0.05 | 0.10 |
| LAM[a] | 0.13 | Dif | 0.05 | 0.02 | 0.01 | 0.00 |
| RBT[a] | 0.13 | Dif | 0.00 | 0.06 | 0.04 | 0.02 |
| AMS | 0.14 | Dif | 0.08 | 0.03 | 0.04 | – 0.04 |
| DSM[a] | 0.15 | Dif | 0.00 | 0.05 | 0.08 | 0.02 |
| SCB[a] | 0.15 | Dif | 0.02 | 0.02 | 0.06 | – 0.01 |
| LP | 0.17 | Dif | 0.04 | – 0.03 | – 0.02 | – 0.07 |
| C | 0.22 | Dif | 0.02 | 0.04 | 0.11 | 0.02 |
| CAR[a] | 0.24 | Dif | 0.03 | 0.03 | 0.01 | 0.02 |
| GF | 0.27 | Dif | 0.02 | – 0.01 | 0.12 | 0.00 |
| WHS | 0.32 | Dif | 0.11 | 0.03 | 0.01 | 0.00 |
| SPLT[a] | 0.52 | Dif | 0.10 | 0.07 | 0.23 | 0.39 |

a. Native species. See species codes and names in Table 1.

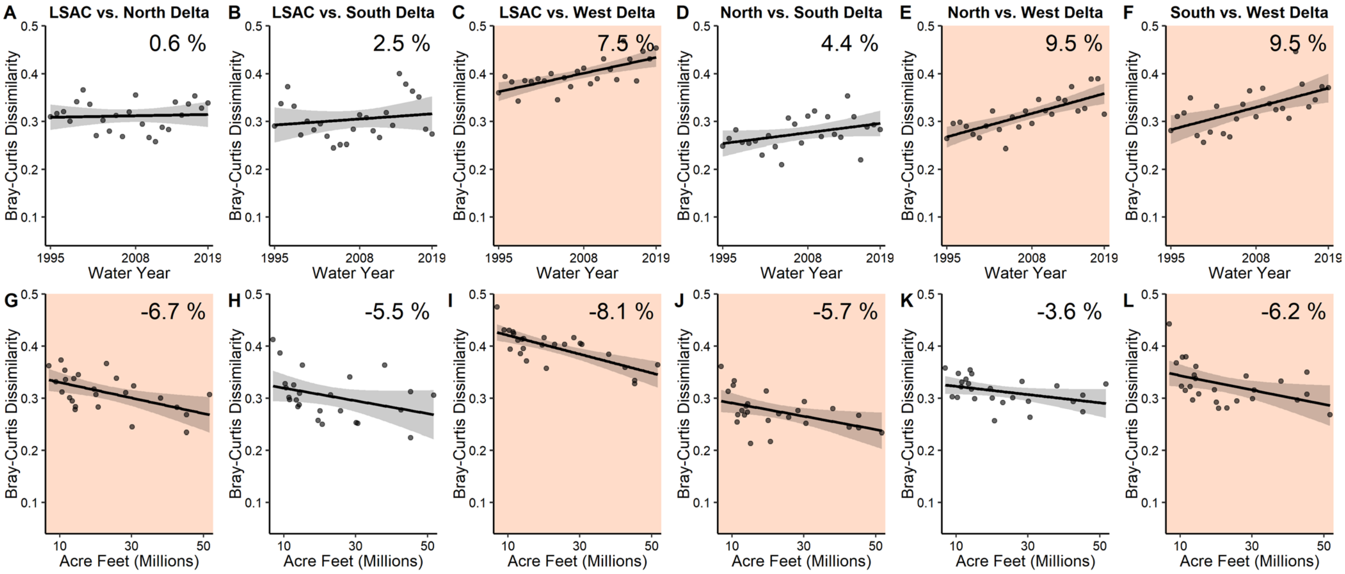

**Figure 4** Effect plots of regional pairwise comparisons of Bray–Curtis dissimilarity index over water years (**A–F**) and water inflow (**G–L**). Significant ($\rho < 0.05$) trends indicated by our multivariate linear regression model are highlighted by red. Overall percent change of the mean is indicated for each plot in the *top right*.

regions for both early and late periods, with the lower Sacramento River region associated with a mixture of native and non-native species; the North Delta associated with native species (Delta Smelt [*Hypomesus transpacificus*], *Lampetra* spp.); the South Delta associated with warm-water non-native species (*Micropterus* spp., Bluegill [*Lepomis macrochirus*], Redear Sunfish [*Lepomis microlophus*], Red Shiner [*Cyprinella lutrensis*]); and the West Delta associated with a number of salt-tolerant species (Mississippi Silverside [*Menidia audens*], Pacific Staghorn Sculpin [*Leptocottus armatus*], Rainwater Killifish [*Lucania parva*], Shimofuri Goby [*Tridentiger bifasciatus*], Striped Bass, Three-spined Stickleback [*Gasterosteus aculeatus*], Yellowfin Goby [*Acanthogobius flavimanus*]; Figure 5). We observed many species that contributed to the overall increase in regional dissimilarity through time as a result of changes in their regional CPUE. Some of the top contributors included several native and non-native salt-tolerant species (Mississippi Silverside, Pacific Staghorn Sculpin, Rainwater Killifish, Tule Perch [*Hysterocarpus traskii*], Three-spined Stickleback, Shimofuri Goby) that had relatively large increases in CPUE during the late period in the West Delta (Table 2). We also observed relatively large decreases in CPUE for several native species (Chinook Salmon, Hardhead [*Mylopharodon conocephalus*], Sacramento Pikeminnow [*Ptychocheilus grandis*], Sacramento Sucker [*Catostomus occidentalis*], Sacramento Splittail [*Pogonichthys macrolepidotus*]) in the South Delta along with increases—or smaller decreases—in other regions, which contributed to regional differentiation over time. In contrast, we also observed several species that promoted regional homogenization and counteracted the overall differentiation trend. These species included the Delta Smelt and the White Crappie (*Pomoxis annularis*), which decreased in CPUE across all regions, and the Red Shiner, which had decreased CPUE in the South Delta and increased CPUE in all other regions.

### Beta Diversity and Species Inflow Trends

Annual water inflow to the Delta ranged from 6.97 maf (WY 2014) to 51.72 maf (WY 2017) with a mean of 22.63 maf (± 2.62 SE) over the 25-year dataset. We found a significant inverse relationship between beta diversity and annual water inflow (Slope = -0.0013, $\rho = 0.001$), resulting in an overall decrease of 6.0% over the range of inflow rates (Figure A5; Table 2). Balanced variation of species

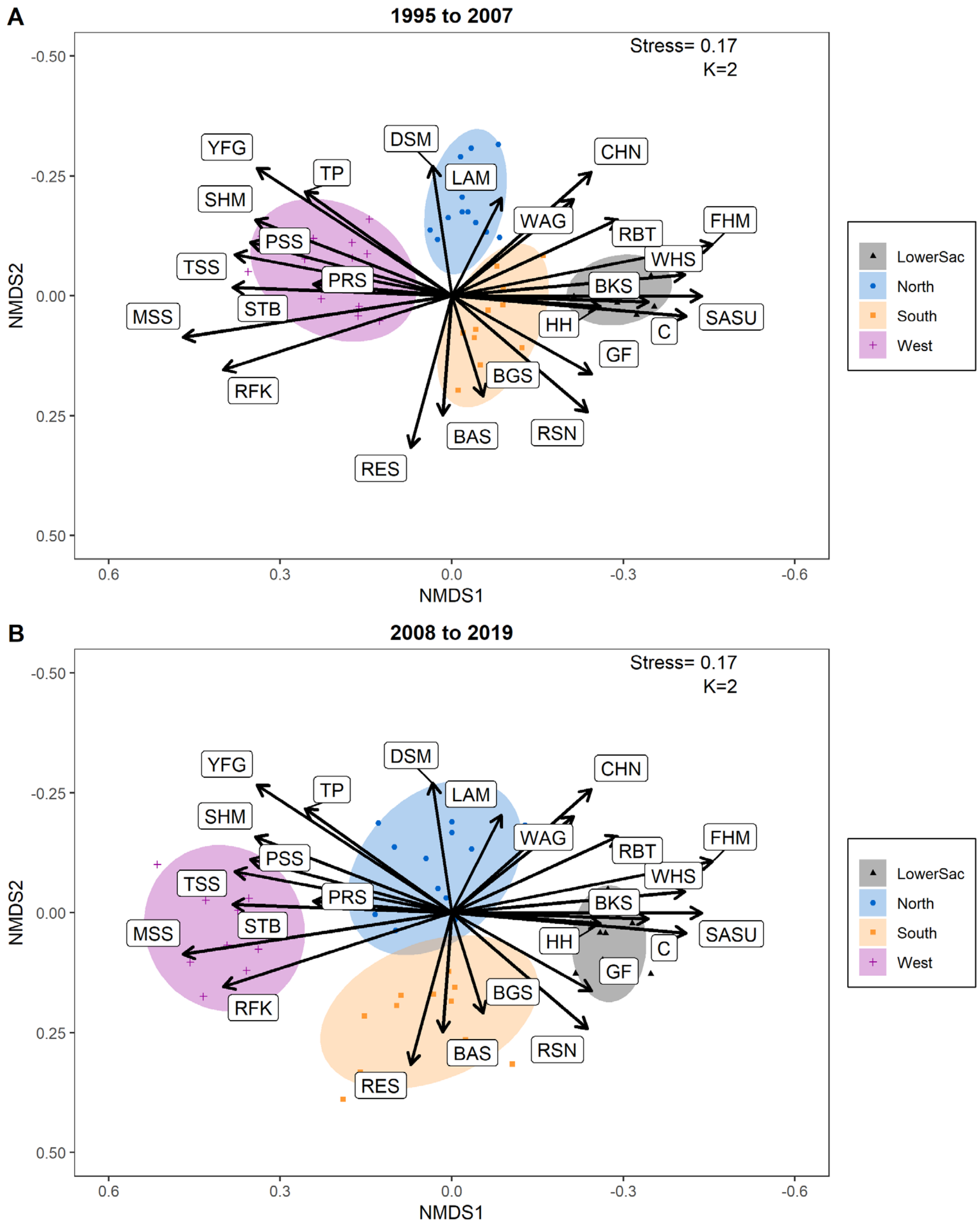

**Figure 5** Non-metric dimensional scaling ordinations based on Bray–Curtis dissimilarity index of beach seine regions' species compositions in the Sacramento–San Joaquin River Delta during (**A**) early (1995 to 2007) and (**B**) late (2008 to 2019) time-periods. Labeled vectors represent increasing catch-per-unit effort of species. Species code definitions can be found in Table 1. *Dots* represent annual species assemblages, and *colored polygons* represent a 95% confidence ellipses.

abundance and abundance gradients contributed to the overall change in the index over annual inflow rates, with a decrease of 3.0% for both components (Figures 6B and 6C). All region-by-region pairwise models indicated a negative relationship between annual water inflow and beta diversity, with four out of the six models having a significant ($\rho < 0.05$) decrease in beta diversity with increased water inflow, indicating that this trend was generally consistent across the study area (Figure 4).

Ordinations showed clear regional separations and species associations during low-inflow years and a higher degree of overlap in regional compositions during high-inflow years (Figure 7). Changes in species distributions that contributed to the regional homogenization during high-inflow years included the native Sacramento Sucker and Chinook Salmon, which had relatively large CPUE increases in the South and West Delta regions, and several salt-tolerant species (Mississippi Silverside, Threadfin Shad [*Dorosoma petenense*], Shimofuri Goby, Rainwater Killifish,

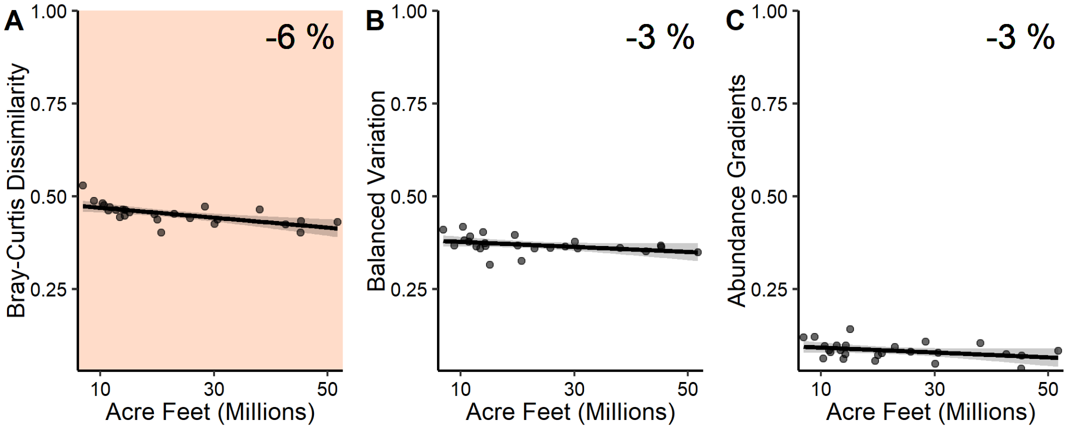

**Figure 6** Effect plots of the Bray–Curtis dissimilarity (**A**) balanced variation in species abundance, (**B**) abundance gradients, (**C**) over annual water inflow into the Delta. *Points* represent partial residuals of the data after accounting for the effect of time. *Shading around the line* represents a 95% confidence interval around the mean (solid line). Significant ($\rho < 0.05$) trends determined by our multivariate linear regression model are highlighted by *red*. Overall percent change of the mean is indicated for each plot in the *top right*.

Three-spined Stickleback, Pacific Staghorn Sculpin, Western Mosquitofish [*Gambusia affinis*]) that had relatively large CPUE decreases in the West Delta. Like the temporal analysis, contrasting species trends that contributed to regional differentiation during high-inflow years were also seen, counteracting the overall homogenization trend. These species included Sacramento Splittail, which had relatively large increases of CPUE in the South and West Delta, higher CPUE of White Crappie in the lower Sacramento Region, and higher CPUE of Goldfish (*Carassius auratus*) and Common Carp (*Cyprinus carpio*) in the South Delta (Table 2).

## DISCUSSION

Biotic homogenization—the replacement of local species by cosmopolitan species that can better tolerate a broader range of environmental conditions and human activities—is occurring for various ecosystems worldwide (Olden and Poff 2003; Devictor et al. 2008; Magurran et al. 2015; Solar et al. 2015). But despite the pervasiveness and significant increase in abundance of cosmopolitan species (Mahardja et al. 2017), we found no evidence of biotic homogenization across the Delta over the last 25 years. In contrast, we observed a significant increase in regional differentiation over time, driven by increasing differences in the regional abundance of both native and non-native species. Despite the near extinction of certain native species (i.e., Delta Smelt), these results are encouraging because they indicate that the Delta has remained a regionally diverse environment, with the capacity to support a diversity of fish species, including native and endemic species. Here, we discuss potential regional environmental factors that drive species distributions and trophic interactions that could be contributing to these patterns, and how climate change and habitat restoration may affect the Delta's regional beta diversity in the future.

### Drivers of Beta Diversity

In this study, we found that balanced variation in species abundance contributed more to regional beta diversity than abundance gradients on a year-to-year basis. However, both balanced variation in species abundance and abundance gradients contributed to the significant increase in regional beta diversity over the 25-year study period. These results suggest that both spatial and environmental filtering processes are important in structuring regional fish assemblages and there are many abiotic and biotic factors that may contribute to these processes occurring within the Delta. For example, salinity is a significant factor in structuring estuarine fish communities around the world as a result of the variability in

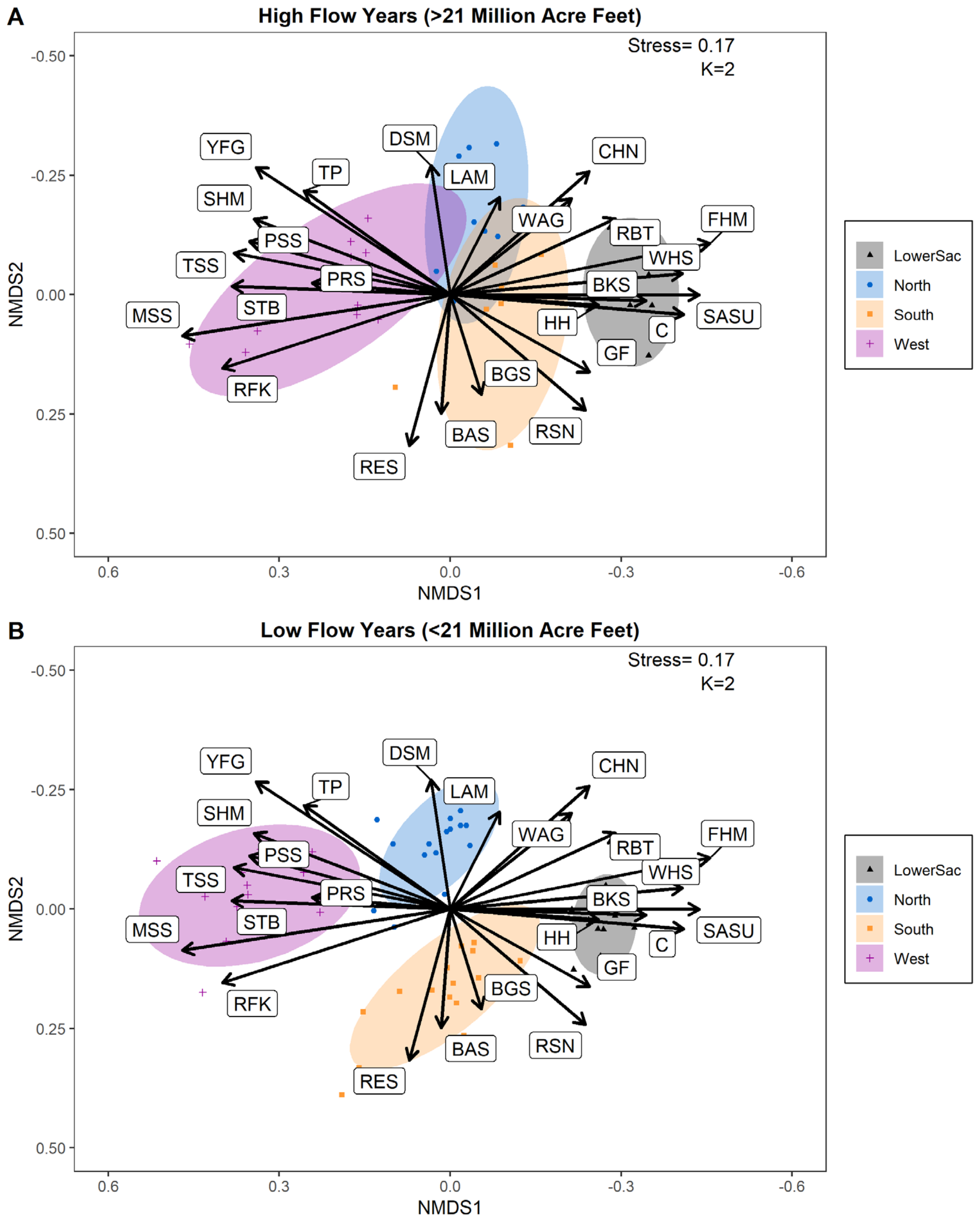

**Figure 7** Non-metric dimensional scaling ordinations based on Bray–Curtis dissimilarity of beach seine regions' species compositions in the Sacramento–San Joaquin River Delta during (**A**) high-inflow (> 21 million acre feet) and (**B**) low-inflow (< 21 million acre feet) conditions. *Labeled vectors* represent increasing catch-per-unit effort of species. Species code definitions can be found in Table 1. *Dots* represent annual species assemblages, and *colored polygons* represent a 95% confidence ellipses.

salinity tolerances across fish species and their preferred biological resources (Martino and Able 2003; Nicolas et al. 2010; Borgnis and Boyer 2016; Kimmerer and Slaughter 2016). Salinity fluctuations in the Delta are highest in the West Delta region because of its downstream location (Hutton et al. 2016), and our results showed that this region was differentiated by higher densities of native and non-native salt-tolerant species, and many of these species contributed to the significant increase in regional differentiation over time (Table 2). For example, Mississippi Silversides, Rainwater Killifish, Three-spined Stickleback, and Western Mosquitofish showed a clear upstream density gradient over time, with the highest increases occurring in the most downstream West Delta region, moderate increases in the interior North and South Delta regions, and the smallest increases in the most upstream non-tidally-influenced lower Sacramento River region. We also observed the largest density increases for the salt-tolerant Tule Perch and Pacific Staghorn Sculpin in the West Delta; however, there was no clear upstream density gradient for these species. These regionally variable density increases contributed to the increasing species density gradients observed over time (Figure 3C), and suggest that salinity conditions have been an important contributor to the spatial and environmental filtering processes that have structured the Delta's nearshore fish assemblages and that changes over time have led to an increase in habitat suitability and upstream dispersal and colonization of salt-tolerant species (Young et al. 2018).

Water temperature, flow, and turbidity are important spatial and environmental filters for fish assemblages (Taylor and Warren 2001; Reyjol et al. 2008; Henriques et al. 2017) and likely play important roles in the Delta. For example, the lower Sacramento and North Delta experience higher flows, lower water temperatures, and higher turbidity compared to the South Delta (Wright and Schoellhamer 2005; Vroom et al. 2017), and past studies have attributed this regional variation in water-quality parameters to the higher densities of native fishes and lower densities of non-native fishes observed in the lower Sacramento River and North Delta compared to the South Delta (Feyrer and Healy 2003; Brown and Michniuk 2007; Moyle et al. 2016; Goertler et al. 2020). The lower water temperatures, higher flows, and turbidity in the lower Sacramento and North Delta regions may support native species by reducing metabolic costs and predation rates, increasing access to floodplains, and increasing visual acuity and feeding efficiency (Feyrer et al. 2006; Hasenbein et al. 2016; Goertler et al. 2018), whereas, the warm, slower-moving clear waters of the South Delta may promote the proliferation of non-native centrarchids by increasing cover of submerged aquatic vegetation, extending optimal reproductive windows, and increasing the survival and growth of juveniles (Nobriga et al. 2005; Cooke and Philipp 2009; Bae et al. 2018). Results from our study concur with these past studies because the lower Sacramento River and North Delta were differentiated by higher densities of native species, and the South Delta was primarily differentiated by non-native species. Results from our temporal analysis also revealed that the density distributions of many native species (Sacramento Sucker, Sacramento Splittail, Sacramento Pikeminnow, Chinook Salmon) had large decreases in the South Delta and increases—or smaller decreases—in the lower Sacramento River and North Delta. Warm-water centrarchids conversely had the highest density increases in the South Delta. These results suggest that conditions for native species in the lower Sacramento River and North Delta remain supportive, whereas conditions in the South Delta continue to deteriorate for native fishes. In addition to these abiotic factors, interspecific competition and predation may also be an important biological factor that contributes to the environmental filtering observed between these regions. Past studies have suggested that competition and predation by non-native centrarchids may reduce habitat quality for native species (Marchetti 1999; Nobriga et al. 2005; Grossman 2016; Michel et al. 2018), so the increased density of non-native centrarchids in the South Delta may add to the mechanisms that limit native species in this region.

Freshwater inflow is one major environmental factor that can affect many abiotic and biotic factors regulating fish beta diversity in estuarine systems. Past studies have documented that high inflow can increase hydrological connectivity, enhance dispersal, homogenize environmental conditions, and often results in decreased fish beta diversity (De Macedo–Soares et al. 2010; Rolls et al. 2022). Results from our study concur with these findings as because regional beta diversity significantly declined as inflow levels increased, and was primarily driven by decreases in balanced variation in species abundance, suggesting that a reduction in environmental filtering processes was the primary driver. The homogenization of the West Delta was a large contributor to the trend due to increased densities of freshwater species and decreased densities of salt-tolerant species. This pattern is commonly observed in estuarine fish assemblages during high inflow because regional salinity gradients are significantly reduced, thereby improving habitat suitability and increasing the distributions of freshwater species (Garcia et al. 2003; Whitfield and Harrison 2003; Baptista et al. 2010; Norris et al. 2010; França et al. 2011; Molina et al. 2020).

Therefore, it is likely that the decrease in densities of salt-tolerant species we observed during high inflows were due to the displacement of these species downstream of the western Delta sampling boundary. Significant homogenization also occurred between the North and South Delta regions and contributed to the overall trend. Increased densities of native Chinook Salmon, Sacramento Sucker, and Sacramento Splittail in the South Delta during high inflows were a large contributor to the homogenization trends between these regions and consistent with past studies (Feyrer and Healey 2003), suggesting that environmental conditions in the South Delta become more suitable for native species during high-inflow periods. These results demonstrate that water inflow has significantly affected regional fish diversity within the Delta over the recent past, and suggest that factors regulating freshwater inflow to the system—such as climate change and water- management activities—will continue to play critical roles in the future.

### Climate Change

Climate change is intensifying the California water cycle, and models predict an increased severity of rapid weather shifts, longer periods of drought, and shorter, more intense flooding events (Dettinger et al. 2016). In California, there is an estimated 25% to 100% increase in extreme dry-to-wet precipitation events by the end of the century (Neelin et al. 2013; Berg and Hall 2015; Yoon et al. 2015; Swain et al. 2018). For example, 2007 to 2023 was a period of intense drought punctuated by extended high flows only in 2011, 2017, 2019, and 2023 (*https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST*). In response to these changes, water infrastructure projects are being developed to mitigate flood risks and increase water security under these future water regimes (ICF International 2015; Sites and USBR 2021; ICF International 2022). The extreme shifts in water-cycle patterns, the frequency in which they occur, and the development of water infrastructure projects to mitigate their effects on human populations will likely pose challenges to some species living within the Delta and are major stressors to ecosystem resiliency, increasing the potential for large changes to regional fish assemblages (Mahardja et al. 2021).

Severe, prolonged, and frequent drought conditions create cascading ecological effects throughout the Delta that are driven by elevated temperatures, changes to water residence time and primary productivity, and facilitation and establishment of invasive aquatic vegetation that can all detrimentally affect native species (Winder and Jassby 2011; Kimmerer et al. 2019; Boyer et al. 2023). These effects may affect environmental filtering processes and trophic interactions that limit the distribution and abundance of some species while allowing others to proliferate. For example, while Mississippi Silverside density increased over time and under low-inflow conditions throughout the Delta, the highest increases occurred within the West Delta (Tables 2 and 3). This trend could result from a combination of increased immigration from areas downstream of our sampling regions (e.g., Suisun Marsh) and increased production in response to favorable water conditions (e.g., increased water temperature, moderate salinity) during low-inflow years (Mahardja et al. 2016). Whatever the cause, this trend is concerning because the western Delta overlaps with the rearing habitat of two native species in decline: the Longfin Smelt (*Spirinchus thaleichthys*) and the Delta Smelt (Stompe et al. 2023). Increased density of Mississippi Silversides during low-inflow years can has the potential to exacerbate the negative effects of drought on native smelts (Jeffries et al. 2016; Kurobe et al. 2022) by increasing larval smelt predation rates (Baerwald et al. 2012; Schreier et al. 2016) in the shallow-water habitats of the West Delta. Potential synergistic interactions between climate change and non-native fish species are a major concern for fish biodiversity around the globe (Carosi et al. 2023) and may represent an important avenue of research to help inform the Delta's native fish conservation and management strategies in the future.

### Habitat Restoration

Historically, the Delta was composed of a few mainstem river reaches interconnected by an intricate network of side- and backwater channels dominated by fluctuations in hydrologic regimes, which created seasonally flooded areas throughout the system (Robinson et al. 2014). These habitats, combined with historical unimpeded flow regimes, provided critical spawning, nursery, refuge, and feeding areas for native species in which they evolved and adapted to exploit (Moyle 2002). In modern times, there has been large-scale modifications to the hydrograph resulting from the construction of numerous water-control structures and an almost complete loss of wetland and floodplain habitats throughout the system. The historical fish habitat has been replaced by leveed agricultural islands, deepwater channels, and perennial open-water habitat, favoring non-native species (Atwater et al. 1979; Cloern et al. 2021). These changes to the Delta ecosystem have resulted in the historical native fish population becoming a minor element of the overall fish community (Feyrer and Healy 2003; Brown and Michniuk 2007; Mahardja et al. 2017). To help recover native fish species, conservation actions are ongoing to improve water-quality parameters by altering the management of water-control infrastructure and restoring native fish habitat throughout the Delta (DSC 2022). Habitat-restoration projects completed to date include the Decker Island Habitat Restoration Project, Dutch Slough (Phase 1), Winter Island Tidal Restoration Project, and Lookout Slough Tidal Habitat and Flood Improvement Project (California EcoRestore Program, *https://water.ca.gov/Programs/All-Programs/EcoRestore*). Much of this restoration work has focused on the Delta Arc, which includes the lower Sacramento River, and the North Delta, and West Delta regions of this study (Sloop et al. 2018). This area has been targeted because it is posited as a refuge for native and endemic species within the system (Moyle et al. 2018). Consistent with this idea, we found that the increasing beta diversity pattern over time in our study was partially driven by the increased density of some native species within the Delta Arc (increase of Sacramento Sucker and Splittail in the North Delta and lower Sacramento River regions, increase of Tule Perch in the West Delta). Thus, our results lend support to the idea that the Delta Arc continues to support native fishes across time and water-inflow regimes, whereas native species continue to be increasingly excluded from the South Delta. In particular, native fish presence in the Delta Arc even during low-inflow periods suggests that native fish habitat-restoration efforts targeting this area may offer long-term benefits to native species even during the prolonged drought periods associated with climate change in the future.

However, previous research has shown that without active management or under certain conditions, restoration efforts may unintentionally favor non-native species and promote native species declines (Grimaldo et al. 2012; Williamshen et al. 2021). For example, the reintroduction of tidal exchange followed by passive restoration at Blacklock Marsh, located west of the West Delta, was found to provide extensive habitat for Mississippi Silverside, and this species dominated the fish assemblage (Williamshen et al. 2021). Additionally, fish assemblages within three restored marshes in the South Delta were found to be dominated by non-native species, specifically centrarchids, Mississippi Silversides, and Threadfin Shad (Grimaldo et al. 2012). The high density of Mississippi Silversides throughout the Delta and dominance of centrarchids in the South Delta observed in our study are likely to continue and highlight the need for additional research on habitat-restoration designs and management strategies to mitigate these biological risks and improve the efficacy of native fish habitat restoration.

### Study Limitations and Considerations

The following should be considered when interpreting our study results. First, as with many fish monitoring surveys (Huntsman et al. 2022), beach seine gear does not capture all available fish or sample all available habitats. Therefore, our results are biased to a subset of the Delta's fish community that are susceptible to beach seine gear, namely small bodied and young-of-year individuals that occupy nearshore habitats (McKenzie and Mahardja 2021). Despite these limitations, this study offers important insights into the nearshore fish community of the

Delta, which represent most fish species within the system (Nobriga et al. 2005; McKenzie and Mahardja 2021).

Another important aspect to consider when interpreting the results is the different types of diversity metrics used in the analysis (Jost et al. 2011; Gotelli and Chao 2013; Schroeder and Jenkins 2018). In this study, different trends were observed between the main analysis, using the Bray–Curtis dissimilarity index on fourth-root-transformed CPUE data, and the supplementary analyses using different dissimilarity indices (Figure 2). No significant temporal trend in regional beta diversity was found using the Jaccard's dissimilarity index, and a highly significant increase in regional beta diversity was found using the Bray–Curtis dissimilarity index using untransformed CPUE data. When looking at the components of the dissimilarity indices, the increase in regional beta diversity over time was largely driven by increasing differences in species abundance gradients between regions (Figure B3; Figure 3). Therefore, the variable beta diversity trends between all three analyses can be explained by the sensitivity of each index to changes in abundance, with the Jaccard index being the least sensitive, the Bray–Curtis index with fourth-root-transformed CPUE data being moderately sensitive, and the Bray–Curtis index with raw CPUE data being the most sensitive. These variable results across diversity indices are common in many studies (Cassey et al. 2008; Barwell et al. 2015; Schroeder and Jenkins 2018) and demonstrate the value of using multiple indices to provide a more comprehensive picture of beta diversity trends within a system.

In terms of future beta diversity trends in the Delta, our results suggest that under the current environmental conditions, the short intense flooding events and prolonged periods of drought associated with climate change will likely result in a continued increase in regional differentiation over the near-term future. In addition, continued decline of native fish populations in the South Delta and persistence of native fish in the Delta Arc aided by native-fish habitat-restoration efforts could contribute to the increasing differentiation of Delta regions. However, beta diversity trends are often cyclical in nature because of changing environmental conditions that give rise to the local establishment of new species, extirpation of existing species, and shifts in species abundance. For example, we can envision periods of biotic homogenization occurring within the Delta if Mississippi Silverside abundance equalizes across regions in the future and leads to local extirpations of existing species caused by shifts in the environmental filtering mechanisms previously discussed. It may be prudent to continue tracking the status of the Delta's fish assemblage, because it can help explain the success or failure of management actions.

The extensive modifications to the Delta over the past 150 years have led to the decline of native fishes in the system, and climate change may further inhibit the recovery of these species. Yet this has often been framed under the lens of species listed under federal or state Endangered Species Acts that may face different stressors than the rest of the California native fish community. Here, we show that unlike many other ecosystems around the world, we did not observe biotic homogenization in the Delta fish assemblage over the past 25 years. Instead, we found a moderate increase in beta diversity over time, which was significantly influenced by the high interannual variability of freshwater inflow. These beta diversity patterns were driven by Mississippi Silverside, that have proliferated in the system in recent years, but also by a handful of native fish species such as the Sacramento Sucker, Tule Perch, and Splittail. Overall, our study results suggest that despite the near extinction of some endangered fish species, there remain in the system pockets of habitat suitable for some native fish species. Although the outcomes of habitat restoration can be difficult to predict, opportunities seem to exist to improve habitat for native fishes in the Delta and assist in their adaptation to climate change.

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