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Authors
Jacinto, Emily
Fangue, Nann A
Cocherell, Dennis E
et al.

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ARTICLE

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Increasing stability of a native freshwater fish assemblage following flow rehabilitation

Emily Jacinto[1] | **Nann A. Fangue**[1] | **Dennis E. Cocherell**[1] | **Joseph D. Kiernan**[2] | **Peter B. Moyle**[1,3] | **Andrew L. Rypel**[1,3]

[1]Department of Wildlife, Fish and Conservation Biology, University of California, Davis, Davis, California, USA

[2]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, University of California Santa Cruz, Santa Cruz, California, USA

[3]Center for Watershed Sciences, University of California, Davis, Davis, California, USA

Correspondence
Emily Jacinto
Email: eejacinto@outlook.com

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Abstract

Stream restorations are increasingly critical for managing and recovering freshwater biodiversity in human-dominated landscapes. However, few studies have quantified how rehabilitative actions promulgate through aquatic communities over decades. Here, a long-term dataset is analyzed for fish assemblage change, incorporating data pre- and post-restoration periods, and testing the extent to which native assemblage stability has increased over time. In the late 1950s, a large capacity dam was installed on Putah Creek (Solano County, CA, USA), which altered the natural flow regime, channel structure, geomorphic processes, and overall ecological function. Notably, downstream flows were reduced (especially during summer months) resulting in an aquatic assemblage dominated by warm-water nonnative species, while endemic native species subsisted at low levels as subordinates. A court-mediated Accord was ratified in 2000, providing a more natural flow regime, specifically for native and anadromous fishes in the stream. The richness of nonnative species decreased at every site following the Accord, while the richness of native species increased or stayed constant. At the three most upstream sites, native species richness increased over time and ultimately exceeded nonnative richness. Native assemblage recovery was strongest upriver, closer to flow releases and habitat restoration activities, and decreased longitudinally downstream. Rank–abundance curves through time revealed that, while species evenness was low throughout the study, dominance shifted from nonnative to native species in the upstream sites coincident with rehabilitation efforts. Mean rank shifts decreased following flow rehabilitation; thus the assemblage became increasingly stable over time following flow rehabilitation. Putah Creek's rehabilitation may represent a model for others interested in improving endemic freshwater communities in degraded ecosystems.

KEYWORDS

assemblage structure, ecosystem stability, fish conservation, reconciliation ecology, stream fishes, water management

INTRODUCTION

Native freshwater fish communities are experiencing severe declines across the globe (Dudgeon et al., 2006; Moyle & Williams, 1990; Ricciardi & Rasmussen, 1999). Climate change (Moyle et al., 2013; Sharma et al., 2011, 2019), fragmentation and regulation of rivers (Carlisle et al., 2010; Dynesius & Nilsson, 1994; Poff et al., 1997), pollution (Carpenter et al., 2011; Dudgeon et al., 2006), overharvest (Embke et al., 2019; Post et al., 2002), and invasive species (Marchetti, Light, et al., 2004; Marchetti et al., 2004b; Moyle & Marchetti, 2006) threaten freshwater ecosystems at all scales. Further, observed and predicted extinction rates are higher in aquatic than in terrestrial ecosystems, indicating that these environments are extremely sensitive to human activities (Moyle & Williams, 1990; Ricciardi & Rasmussen, 1999).

Understanding the ecological effects of humans on freshwater ecosystems can be challenging because of the high spatiotemporal heterogeneity in these environments (Cid et al., 2020; Rypel, 2021). Further, actual tracking of long-term habitat and community change is often highly limited (Bernhardt et al., 2005; Sass et al., 2017). In some cases, ecological consequences are not fully realized until decades or centuries later (Kuussaari et al., 2009; Tilman et al., 1994). Understanding the importance of managing freshwater habitats has generally lagged behind advances made in terrestrial ecosystems (Sass et al., 2017), sometimes leading to confusion and a lack of guidance on appropriate methods for monitoring ecosystem recovery (Palmer et al., 2005). Broader utilization of tools and approaches developed rigorously in other subdisciplines of ecology and environmental science have the potential to benefit freshwater conservation.

Ecological stability is one concept that has long been of interest to ecologists (Connell & Slatyer, 1977; Loucks, 1970; Paine, 1969). Community "stability" (i.e., reduced variance in species abundance) is a particularly critical concept in community ecology (Loreau & de Mazancourt, 2008; Luo et al., 2021; Walter et al., 2021). Collins et al. (2008) demonstrated how experimentally fertilized grassland plots experienced increased mean rank shifts (a measure of reduced community stability), and that rank shifts were higher in infrequently burned vs. annually burned plots. Furthermore, community ecology approaches have a rich history of addressing core intellectual challenges in terrestrial ecosystems (Hobbs et al., 2014; Leibold et al., 2004; Tilman, 1987; Whittaker, 1965), and have also been exceptionally effective in assessing restoration outcomes (Funk et al., 2008; Hallett et al., 2017). Many of these approaches have strong potential for application to aquatic ecology (Erős et al., 2020; Vasseur et al., 2014) but have rarely been used in this context. Expanded use of community ecology techniques, including stability approaches into highly invaded stream ecosystems could be useful (Bunn & Arthington, 2002; Marchetti, Light, et al., 2004; Marchetti et al., 2004b; Moyle & Marchetti, 2006). Stream restorations have long been criticized for lacking robust experimental designs and for tracking metrics that reflect the meaningful ecological change (Bernhardt et al., 2007). For example, it would be logical to expect stream rehabilitative actions would stabilize ecological communities over time; however, this important hypothesis has not been tested.

California provides a model landscape upon which to study the cumulative effects of habitat change and nonnative species in freshwater ecosystems. The region's human population has doubled since 1970 (from ~20 to ~40 million people, United States Census Bureau, https://www.census.gov/data/datasets.html), but also hosts a high degree of freshwater endemism (Moyle, 2002). This combination and overall dominance by humans over watersheds places intense pressure on an already fragile fauna. For example, 83% of freshwater fish in California are declining, at risk of decline, or are already extinct (Moyle et al., 2011). One of the largest threats to freshwater systems in California is water diversion and extraction (Carlisle et al., 2010; Grantham et al., 2010; Moyle et al., 2011; Moyle & Williams, 1990). Alongside human population growth, water needs for industrial and irrigation use are intense. For example, even though agricultural and urban water use has declined over time, total water use annually often ranges between 34.5 and 43.2 billion m^3 (Department of Water Resources, various years, https://water.ca.gov). Water demand drives the construction of dams, diversion channels, and intricate water projects that ultimately fragment rivers and further reduce biodiversity (Bunn & Arthington, 2002; Carpenter et al., 2011; Poff et al., 1997; Power et al., 1996).

The primary goal of this study was to assess whether long-term rehabilitation of the flow regime in Putah Creek, California, USA resulted in positive increases in the native fish assemblage over an extended period. Specifically, we evaluated (1) specific changes in the flow regime over time; (2) trends in assemblage richness, evenness and relative abundance of species; (3) temporal shifts in rank abundance and mean rank shifts at differing sites before and after initiation of restoration and reconciliation actions; and (4) we revisit several questions raised in a previous paper published a decade earlier (Kiernan et al., 2012), specifically (A) whether native species would be able to maintain populations over time, especially when faced with significant drought; and (B) if the creek would eventually be able to support anadromous salmon.

METHODS

Study location

Putah Creek occurs in the Mediterranean climate of the Central Valley of California where the natural flow regime is characterized by high seasonality of flows, including high flows in the winter and spring, and low summer base flows (Carlisle et al., 2010; Gasith & Resh, 1999). Putah Creek originates in the coast range of California (Mayacamas Mountains) and flows east ~130 km before reaching Berryessa Reservoir behind Monticello Dam (Kiernan et al., 2012; Marchetti & Moyle, 2001; Moyle et al., 1998). The outflow from Berryessa Reservoir flows ~13 km to a second, much smaller, dam, the Putah Diversion Dam (PDD), which creates Lake Solano. Any water released from PDD is either diverted into the Putah South Canal for water users in Solano County or released into lower Putah Creek. Below PDD, lower Putah Creek flows ~40 km where it enters channels in the Yolo Bypass (a managed floodplain of the Sacramento River) and then flows into the Sacramento River, which joins the San Francisco Estuary and the Pacific Ocean (Figure 1). The volume of water in lower Putah Creek is mostly regulated through the operation of the PDD, while water temperatures are largely driven by releases from Berryessa Reservoir. During high rainfall years, Monticello Dam overflows through a spillway and large volumes of water are periodically delivered to lower Putah Creek.

Study history

Similar to many western United States streams, water diversions and dams limit ecological activity in Putah Creek. The two dam installations in 1957 effectively reduced downstream water flows (Kiernan et al., 2012; Moyle et al., 1998), and contributed to incisement of the river channel and degradation of natural channel processes. These alterations changed the timing and reduced the magnitude of flows in Putah Creek, while also substantially increasing water temperatures. During the 1990s, areas of the creek regularly dried during summer periods (Figure 2). Ultimately, these modifications led to the extirpation of previously occurring anadromous fish, such as Chinook salmon (*Oncorhynchus tshawytscha*), Pacific lamprey (*Entosphenus tridentata*) and steelhead trout (*Oncorhynchus mykiss*), as well as marked declines in most other native fish (Kiernan et al., 2012; Moyle et al., 1998; Shapovalov, 1947). A lawsuit (Putah Creek Council vs. Solano Irrigation District and Solano County Water Agency, Sacramento Superior Court Number 515766) was filed to provide a more natural flow regime under a provision of California Fish and Game Code 5937 requiring that fish populations below a dam be kept in "good condition" (Börk et al., 2012; Moyle et al., 1998). At the time, legal issues focused on keeping the creek from drying, developing spring flows for native fish (which assist in the dispersal and survival of juveniles), creating fall attraction flows for spawning Chinook salmon, and generating high flows to displace nonnative fish and to promote natural channel processes. The Putah Creek Accord (the Accord) was ratified in 2000 and resulted in key changes in the quantity and timing of water flows. The changes included the maintenance of minimum flows in the creek, increased flows in fall and spring to support spawning and rearing, respectively, of native and anadromous fish, and a pulse flow in the fall to attract salmon (Kiernan et al., 2012; Moyle et al., 1998). Pulse flow events included 3 days of releases of 4.2, 2.8, and 2.3 cubic meters per second (CMS) in the spring and 5 days of 4.2 CMS in the fall followed by at least 1.4 CMS released daily through spring (Moyle et al., 1998). Overall, flows attempt to mimic critical timing elements of the natural flow regime, but not necessarily

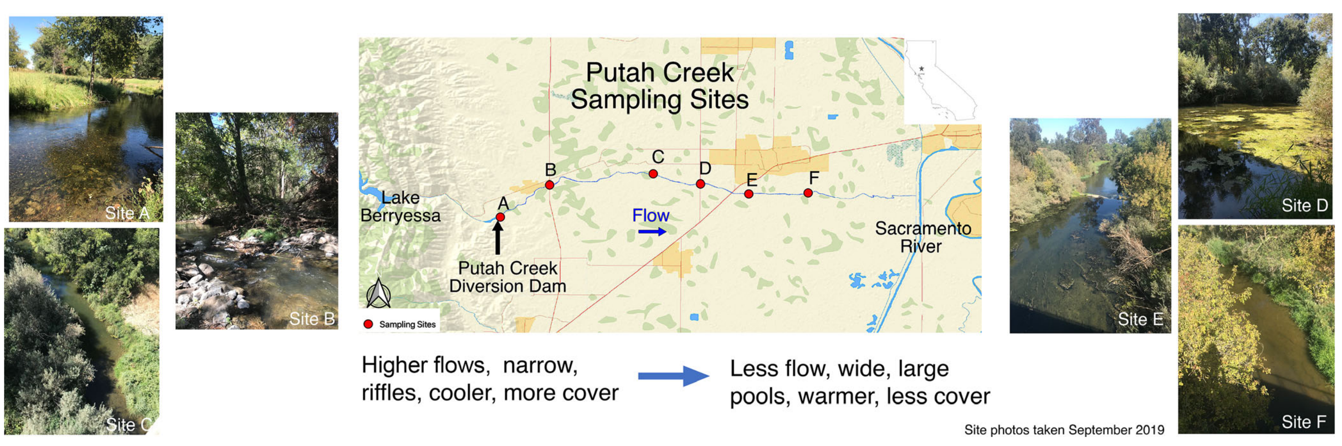

FIGURE 1 Map of sampling sites along lower Putah Creek, CA. All photographs by Emily Jacinto.

FIGURE 2 Images at two locations on lower Putah Creek, CA (Pedrick Road Bridge and Mace Boulevard) before and after the Accord. Photographs by Emily Jacinto with the exception of photographs prior to 2018 that were taken by Peter Moyle.

historical quantities of flow (Yarnell et al., 2015, 2020). Marchetti and Moyle (2001) documented that a cycle of wet years in the late 1990s resulted in a more natural flow regime downstream of PDD and increased abundance of larval native fish. Later, Kiernan et al. (2012) evaluated data from before and after the Accord (1993–2008) and found that some native fish species had returned to areas of the creek where they were previously absent. In the nine sampled years since Kiernan et al. (2012), Chinook salmon (*O. tshawytscha*) have begun returning and continue to actively colonize and spawn in the creek (Moyle et al., 2017; Willmes et al., 2020), even while the region experienced one of the most severe droughts on record (2012–2016, Moyle et al., 2017).

Fish sampling

Beginning in 1993, fish assemblage composition was quantified each fall (October) at six permanent sites located in the 30 km stream segment between PDD and the Yolo Bypass Wildlife Area (Figure 1). The six sites (designated A, B, C, D, E, and F) were located ~0, 6, 16, 20, 25, and 30 km, respectively, downstream of PDD (Kiernan et al., 2012) and continue the use of the same sites analyzed in Kiernan et al. (2012). No sampling occurred at any sites in 2009 or for the following situations: Sites A–D in 2011, Site A in 2013, Site B in 2017, and Site E in 2000 or 2001.

Standardized tote barge electrofishing was used to capture and evaluate species presence and relative abundance (Reynolds & Kolz, 2012). During each sampling event, fish were collected via single-pass electrofishing using a Smith-Root model 2.5 Generator Powered Pulsator electrofisher operated from a tote barge (Smith-Root, Inc., Vancouver, Washington, USA). Stunned fish were captured using dip nets, held in a bucket or a net pen in the creek until identified, enumerated, a subset measured for length and weight, and then released. Sculpins were identified as a single species (prickly sculpin, *Cottus asper*) although some debate exists over the existence and classification of two species (*C. gulosus* or *C. asper*) in the watershed (P. B. Moyle, personal communication, 28 October, 2020). Nonnative sunfish hybrids and unidentified sunfishes were classified as a single species, sunfish (*Lepomis* spp.). Both resident and anadromous forms of rainbow trout (*O. mykiss*) occur in Putah Creek but were not differentiated in this analysis. Sampling protocols aimed for equivalent stream-length distances sampled at each site during each year (Kiernan et al., 2012), however in some cases (e.g., in the upper creek) parts of the creek can become inaccessible or dry during very flow flows, as might occur during droughts. Nonetheless, catch data are effectively considered standardized for effort, and thus presented as catch totals rather than catch-per-unit-effort. All data used for this analysis were collected by Normandeau Associates and TRPA Fish Biologists (TRPA fish biologists sampled from 1991 to 2010, Arcata, CA USA; Jacinto et al., 2022).

Flow change

To examine long-term changes in discharge and flow in lower Putah Creek, we obtained daily discharge data for the period 1978–2017 collected at PDD by a gauge operated by the Solano County Water Agency and the US Bureau of Reclamation. Three-dimensional plots were generated of daily discharge versus day of the year versus year on an annual time frame from 1978 to 2017 (Soetaert, 2019). Flow differences between periods can be difficult to distinguish when examining patterns across a full year; thus an additional plot of only summer flows (days 180–304, approximately July through October) is also presented (Figure 3).

Fish assemblage structure

Similar to Collins et al. (2008), we examined changes in fish assemblage diversity and evenness at each of the six sites over time. Assemblage metrics (Shannon diversity index and Pielou's index) were calculated using the *vegan* package (Oksanen et al., 2019) in R statistical computing software (R Core Team, 2020). For each site, Spearman correlations were calculated to assess directional associations between diversity indices and year (Table 1). To control against type 1 errors arising from multiple comparisons, a Bonferroni correction was applied to the original threshold *p*-value (0.05). We also highlight correlation coefficients >0.60 as showing an important relationship. Furthermore, species were classified as either native or nonnative species and changes in the dynamics of fish communities were examined in this context in relation to species richness over time (Figure 4).

Analysis of covariance (ANCOVA) was used to compare changes in species richness over time (Table 2). A separate ANCOVA was developed for each site with

TABLE 1 Spearman and Pearson correlations between fish species diversity indices and year in Putah Creek, 1993–2017.

Site	Species richness[a]	Shannon's index[b]	Pielou's index[b]
A	−0.48	−0.32	0.10
B	**−0.72***	−0.35	0.14
C	**−0.84***	**−0.70***	−0.36
D	−0.35	−0.53	−0.39
E	−0.36	0.11	0.28
F	−0.24	0.31	0.50

Note: Correlation coefficients >0.60 are indicated in bold and regarded as showing an important relationship. Significant correlations following a Bonferroni correction are indicated with an asterisk.
[a]Pearson index.
[b]Spearman index.

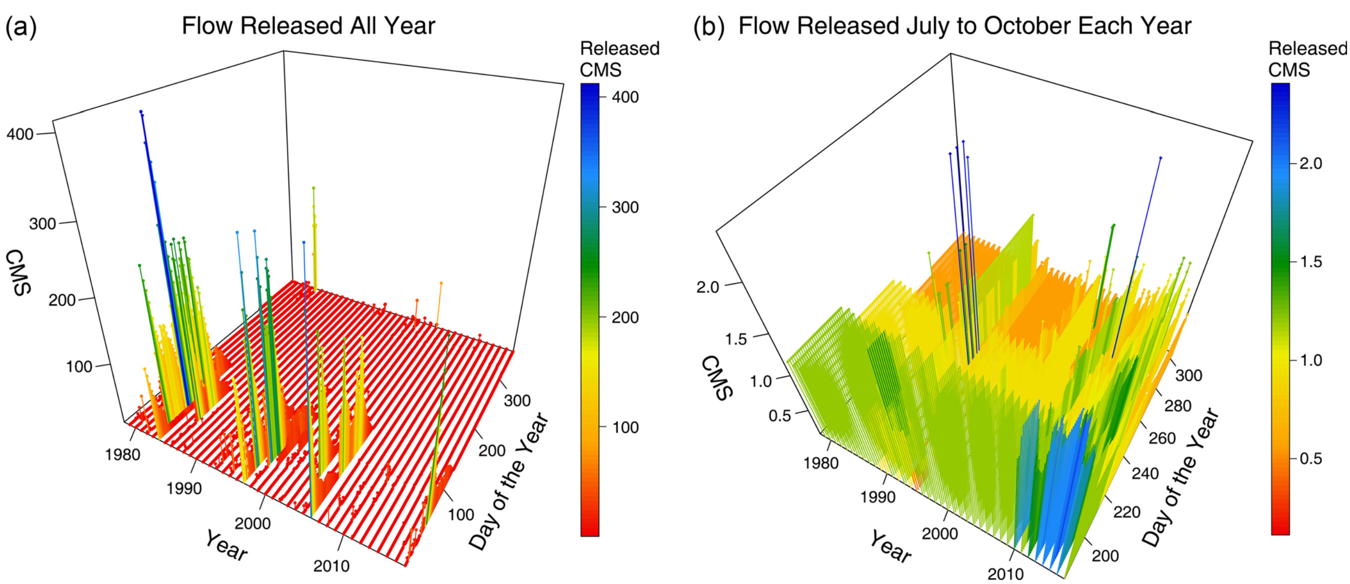

FIGURE 3 Three-dimensional plots of discharge, year, and day of year for flows released from Putah Diversion Dam (PDD), October 1978 through 2017. Data are presented for (a) calendar year and (b) calendar days 180–304 (July through October).

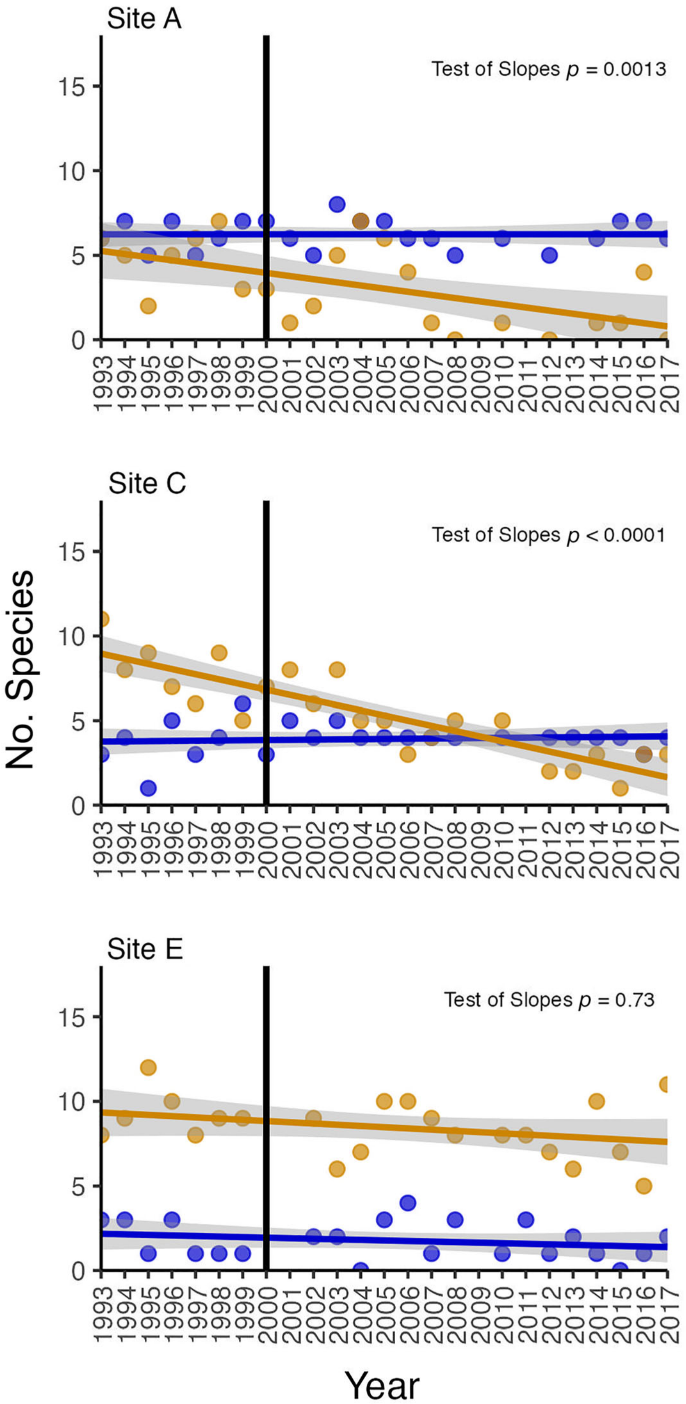

FIGURE 4 Changes in richness of native (blue) and nonnative (orange) taxa at sampling sites along Putah Creek CA, 1993–2017. Vertical black line denotes the ratification of the Putah Creek Accord in 2000, and subsequent restoration of flows in the ecosystem. Regressions represent ANCOVA models as described in the methods, and "test of slopes" refers to the significance level of the site × year interaction term in the ANCOVA models. Shaded areas of the regressions represent 95% CIs.

$\log_{10}$(species richness +1) as the dependent variable, year as the independent variable, and species type (i.e., native or nonnative) as a categorical variable. Directional changes in the diversity of native and nonnative species were assessed by examining coefficients (i.e., slopes) of the model, and differences in slopes between native and nonnative species assessed by way of the year × native/nonnative interaction term in each model across the entire study period. It is recognized that differences in slopes would ideally be examined while also accounting for a before/after term. However, there were only 8 data points before the Accord versus 16 data points after; thus lack of sufficient

TABLE 2 Results of the analysis of covariance (ANCOVA) examining the effects of time (year) and type of species (native vs. nonnative) on species richness in Putah Creek, 1993–2017.

	Site A	Site B	Site C	Site D	Site E	Site F
Year	0.0014	0.0005	<0.0001	0.2618	0.1130	0.5240
Native/Nonnative	<0.0001	<0.0001	0.0059	<0.0001	<0.0001	<0.0001
Year:Native/Nonnative	0.0013	<0.0001	<0.0001	0.0277	0.7340	0.6560

Note: Numbers indicate p-values and all richness data were $\log_{10}(x + 1)$ transformed prior to analysis.

pre-data precluded such an analysis, especially given the lifespan and turnover rates of focal species (Marchetti et al., 2004a; Rypel & David, 2017). Therefore, we emphasize that, in this study, we focused more on the trends of fish communities over long-term periods in Putah Creek.

Fish abundance

Pearson's correlations (R) were used to assess directional change (correlation) in the abundance of individual species at each site over time (Table 3). For each correlation, abundance data were $\log_{10}$ transformed prior to analysis to meet assumptions of normality. To control against type 1 errors arising from multiple comparisons, a Bonferroni correction was applied to the original threshold p-value (0.05). This produced a new threshold p-value for each species and a more stringent bar for significance that is conservative in guarding against the potential for type 1 errors. We also highlight correlation coefficients >0.60 as showing an important relationship.

Rank–abundance curves were used to assess temporal changes in the dominance and evenness of the fish assemblages at each site over time (Avolio et al., 2019; Collins et al., 2008; Whittaker, 1965). Rank–abundance curves combine elements of numerical dominance (height of the curve) and species richness (number of points), with evenness (slope of the curve), and in this case also a time dimension on the x-axis. Parallel to Collins et al. (2008), species points in these plots were identified as native and nonnative species overall, and other contrasting patterns of species native and nonnative species trends were highlighted (Figure 5).

Further, to assess changes in assemblage stability over time, we calculated mean rank shift (MRS; Collins et al., 2008; White et al., 2020) values using the entire time series for each sampling site (Figure 6). MRS provides a measure of dissimilarity in species rank abundance between consecutive years in a time series. Higher MRS values indicate increased instability of the fish assemblage, whereas low values indicate enhanced assemblage stability. MRS is only one measure of stability and there has long been a debate over metrics and definitions in the ecological literature. MRS values were calculated using the R package *codyn* (Hallett et al., 2016). Last, we developed a mixed effect regression model using the *lmer* [2] package in R (Bates et al., 2014) to test whether MRS changed directionally over time. In the model, MRS was the dependent variable, year was the independent variable and site was a random effect. All analyses were conducted using R statistical software (R Core Team, 2020). Effects and models were regarded as showing an important relationship if $p < 0.05$, unless otherwise specified.

RESULTS

Flow change

Beginning in 2000, major flow alterations were made to Putah Creek that resulted in increased water flow through the ecosystem. Prior to the Accord, there were regular and extended periods of zero flow resulting in the creek drying. Following the Accord, there were no known periods of zero flow in Putah Creek and full streambed drying has not been reported (Figure 3). In general, a pattern is apparent whereby summer base flows have greatly increased post-Accord versus pre-Accord. However, winter flows have largely remained unchanged.

Fish assemblage structure

In total, 35 fish species (11 native and 24 nonnative species) were captured in lower Putah Creek between 1993 and 2017. Richness of nonnative species decreased at every site over time (Figure 4), while the number of native species increased or stayed relatively constant. Increases in native species and decreases in nonnative species richness were significant upriver, closer to the PDD and decreased as sites progressed downstream. Native species at Sites A, B, and C all exhibited significant increases in richness with time

TABLE 3 Pearson correlations (*R*) examining trends in fish abundance over time in Putah Creek, 1993–2017.

Species	Site A	Site B	Site C	Site D	Site E	Site F
Native species						
California roach	−0.31	NA	NA	NA	−0.30	−0.28
Chinook salmon	0.29	NA	NA	NA	NA	NA
Pacific lamprey	0.07	−0.29	−0.36	−0.23	−0.09	−0.11
Prickly sculpin	0.17	0.33	**0.65**	0.58	0.03	−0.05
Rainbow trout	0.59	**0.81***	−0.16	NA	NA	NA
Sacramento blackfish	NA	NA	−0.46	−0.28	−0.56	−0.59
Sacramento perch	NA	NA	−0.25	−0.28	NA	NA
Sacramento pikeminnow	0.23	0.06	**0.74***	**0.68***	0.27	0.53
Sacramento sucker	−0.35	0.24	0.43	0.56	−0.35	0.30
Sacramento tule perch	−0.41	0.37	**0.81***	**0.65**	0.01	0.20
Three spine stickleback	−0.02	0.54	NA	NA	NA	NA
Nonnative species						
Big scale logperch	−0.39	**−0.71***	−0.52	−0.22	0.31	0.40
Black bullhead	−0.12	NA	−0.34	−0.56	−0.20	−0.53
Black crappie	−0.01	NA	−0.25	−0.30	−0.56	−0.59
Bluegill	−0.55	−0.47	**−0.78***	−0.61	−0.47	−0.44
Brown bullhead	NA	NA	−0.46	−0.31	NA	NA
Channel catfish	NA	NA	−0.43	−0.33	0.14	−0.21
Common carp	−0.48	−0.53	−0.51	−0.25	−0.57	−0.39
Fathead minnow	NA	NA	−0.19	0.36	−0.44	**−0.71***
Golden shiner	NA	NA	NA	NA	NA	0.33
Goldfish	−0.49	−0.44	−0.35	−0.12	−0.39	−0.32
Green sunfish	−0.54	−0.57	**−0.78***	−0.42	0.15	**−0.66**
Inland silverside	0.03	NA	−0.07	0.08	0.35	0.41
Largemouth bass	−0.23	**−0.63**	−0.46	0.00	**0.77***	**0.64**
Pumpkinseed	NA	NA	0.01	−0.13	−0.01	0.02
Red shiner	NA	NA	−0.13	−0.22	−0.22	−0.08
Redear sunfish	NA	−0.55	−0.28	0.04	0.10	**0.62**
Smallmouth bass	−0.19	**−0.74***	**−0.63**	0.26	0.44	0.11
Spotted bass	0.35	NA	0.21	0.29	**0.63**	0.49
Striped bass	NA	NA	NA	NA	0.25	−0.27
Sunfish hybrids	−0.16	−0.22	−0.52	**−0.62**	**−0.63**	−0.24
Warmouth	NA	NA	NA	NA	−0.42	−0.07
Western mosquitofish	−0.22	−0.43	−0.38	−0.44	−0.51	−0.34
White catfish	NA	−0.25	−0.24	−0.02	0.22	0.44
Yellowfin goby	NA	NA	NA	NA	NA	−0.11

Note: Correlation coefficients >0.60 are indicated in bold and regarded as showing an important relationship. Significant correlations following a Bonferroni correction are indicated with an asterisk. All abundance data were $\log_{10}(x + 1)$ transformed prior to analysis. NA values denote species not captured at a given site.

(Figure 4). By the end of the study, native species richness superseded nonnative species richness at Sites A, B, and C.

While few new native species arrived over the study period, many nonnative species dropped in rank and abundance, or were extirpated from sites altogether

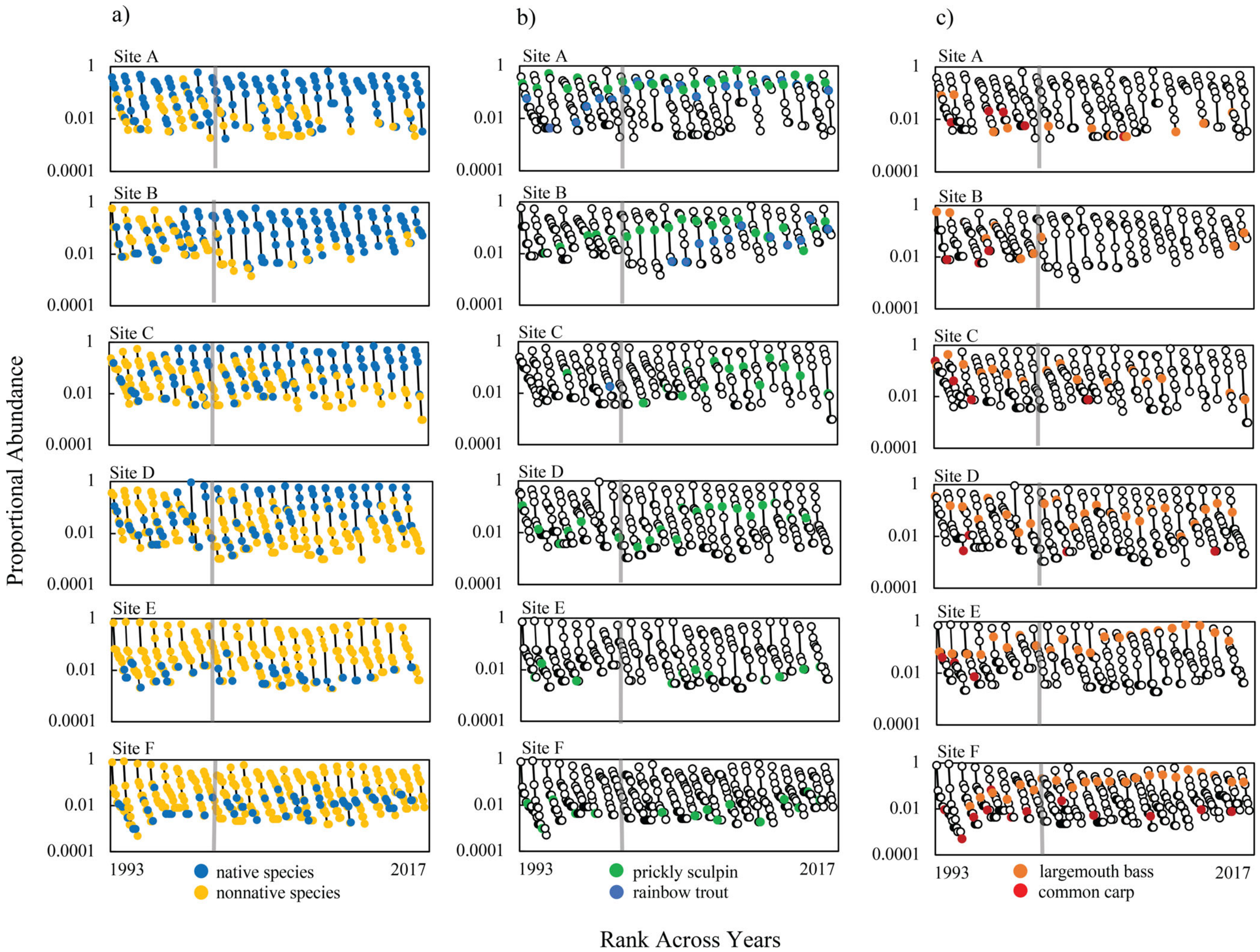

FIGURE 5 Annual rank–abundance curves for sites showing proportional abundance changes in native (solid blue circles) and nonnative (solid orange circles) species in panel (a) (left). The center (b) and right (c) panels show the same curves, but highlight two native (rainbow trout = solid blue circles and prickly sculpin = solid green circles), and two nonnative (largemouth bass = solid orange circles and common carp = solid red circles) species. Each curve represents 1 year of data; thus curves move from the earliest (1993) to more recent years along the *x*-axis. Initiation of restorative flows from the Accord is indicated by a gray vertical line.

(Figure 5 and Table 3). This is perhaps most apparent at Sites A–C (Figure 4) where a significant decrease in species richness is driven largely by the extirpation of nonnative species (Table 1). Only the most downstream site (Site F) had a significant positive increase in a diversity measure (Pielou's index). At four sites (A, B, C, D), there were significant (p-value = 0.0013, <0.001, <0.001, 0.03, correspondingly) differences in the richness × year interaction term (ANCOVA model, Table 2); thus diversity metrics were changing differently for native versus nonnative species over time. However, the two downstream sites (E and F) did not exhibit significant differences in native versus nonnative diversity trends (ANCOVA, $p > 0.65$ in both cases; Table 2).

Fish abundance

Many fish species shifted in relative abundance over time, 56% (25/45) of possible native species correlations showed positive correlations overall. For example, rainbow trout increased in abundance at both of the uppermost sites. Out of the 45 abundance–time correlations for native fish, 6 (13%) with correlations greater than 0.6, and all of these were positive indicating positive trends in abundance across the study period (Table 3). Sacramento pikeminnow (*Ptychocheilus grandis*) increased in abundance in all sites, with significance at two of them (C, D). Mid-watershed (Site C), two native fish increased significantly in abundance: Sacramento pikeminnow, and tule perch (*Hysterocarpus traskii*).

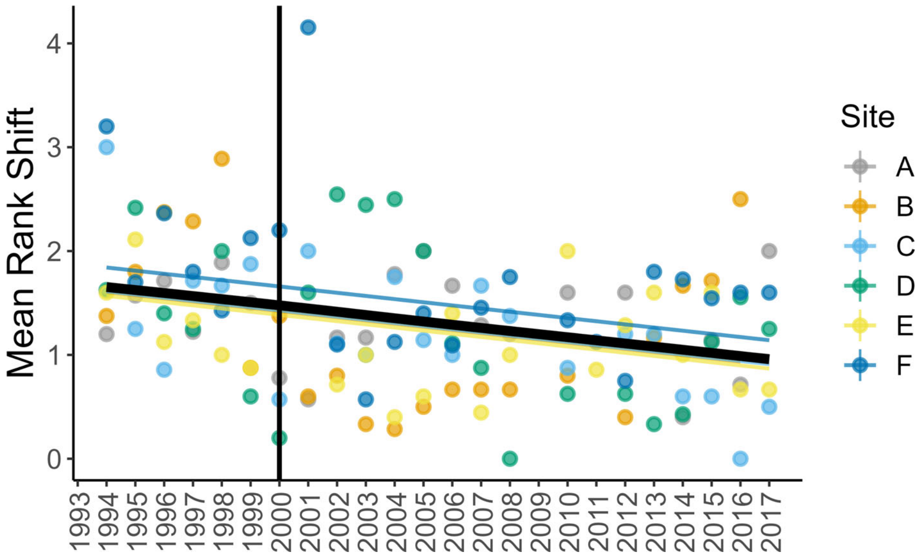

FIGURE 6 Changes in stability mean rank shift (MRS) in the Putah Creek fish assemblage, 1993–2017. Vertical black line denotes ratification of the Accord in 2000 and subsequent restoration of flows. Light colored points represent MRS data for the fish assemblage at each site. The thick solid black line shows the overall trend in MRS across all sites as defined by the mixed effects model. Light colored lines denote random (site-level) effects.

For nonnative species, 14 of 108 correlations coefficients exceeded 0.6; and 10 of these correlations (71%) were negative. Overall, 79 of 108 (73%) possible correlations for nonnative species were negative. Notable examples included bluegill (*Lepomis macrochirus*), which decreased in abundance over time at every site (significantly at C), green sunfish (*Lepomis cyanellus*), which decreased in abundance over time at five of six sites (significantly at C and F), and common carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), sunfish hybrids, and western mosquitofish (*Gambusia affinis*) decreased at all six sites. Black bullhead and black crappie decreased at all sites where they were sampled (five of six sites).

Rank–abundance curves revealed additional aspects of assemblage change in Putah Creek over time (Figure 5). Overall, the Putah Creek fish assemblage showed low evenness in rank abundance overall (i.e., steep slopes). This pattern was consistent before and after the Accord, and highlights that the fish assemblage was numerically dominated by just a few dominant species regardless of its flow state. However, the dominant species at each site has changed dramatically. While nonnative species once dominated the fish assemblage in many sections of Putah Creek (Figure 5), native species now dominate. Channel catfish have almost been completely eliminated from the creek. Patterns also appear to be highly site specific: the uppermost sites, which now have ample cold water (Sites A and B), became increasingly dominated (higher rank abundance) by rainbow trout and prickly sculpin following rehabilitation (Figure 5b). In contrast, largemouth bass (*Micropterus salmoides*) decreased in rank from the dominant species to a subordinate (lower rank abundance) position at these same sites (Figure 5c). However, this same species retained dominance in the lower sites (D, E and F) where the effects of stream restoration and water releases are weaker.

The Putah Creek fish assemblage became more stable over time. MRS (i.e., the amount of species changing rank between years) declined overall at all sites over time (Figure 6). Furthermore, all sites showed a similar pattern in the decline of MRS as noted by a similarity in random effects coefficients (mixed effects model, t-value $= -3.85$, $p = 0.0002$). Thus sites not only trended toward more native species over time, but species compositional abundance became less volatile, indicated by enhanced persistence and stable ranks.

DISCUSSION

This study provides one of the first examples of how the rehabilitation of a natural flow regime resulted in enhanced stability and recovery of a highly endemic freshwater assemblage. In community ecology, many of the more well studied community structure metrics (e.g., richness, evenness, etc.) are static in that they usually represent just snapshots at any point in time, and are strongly affected by sampling effort (Collins et al., 2008; Roswell et al., 2021). While useful, static measures lack the dynamics that are often of most interest to many ecologists. Changing community metrics over time, such as in dominance, mean rank shifts, and rank change by species add novel insight and context of how freshwater ecosystems respond to ecological change, including stream restoration activities.

There is an expansive and growing body of literature on stream restoration (Barrett et al., 2021; Levi & McIntyre, 2020; Reisinger et al., 2019), however the idiosyncratic nature of each restoration limits generalizations across many efforts (Hiers et al., 2016; Lake et al., 2007). Furthermore, there is frequently a mismatch between restoration goals and ecological measures monitored over time (dos Reis Oliveira et al., 2020). Restorations of freshwater streams are conducted for a host of reasons ranging from urban area benefits (Bolund & Hunhammar, 1999) to protection of infrastructure and real estate (Kenney et al., 2012), public enjoyment and environmental justice (Lave, 2016), and protection of fisheries and ecological services (Layman & Rypel, 2020; Palmer & Filoso, 2009; Pierce et al., 2013). In Putah Creek, the driving motivation behind initiating rehabilitation of the natural flow regime was California Fish and Game Code 5937, stipulating that fish populations below dams be kept in "good condition" (Börk et al., 2012; Moyle et al., 1998). While it may seem unconventional that community ecological metrics such as mean rank shifts be applied to document legal responsibilities for water users, it nonetheless has a high potential for such use. These data and analyses provide actionable information to agencies charged with managing the stream and ensuring the sustainability of a fragile endemic freshwater fish community that includes threatened anadromous salmonids.

In this study, increased seasonal flows resulted in decreased nonnative species richness (Table 1) and abundance through much of Putah Creek (Table 3), while native species recovered and regained dominance at numerous sites (Figure 5). However, not all species demonstrated directional changes (see text below on study limitations). Native fish communities in Putah Creek and elsewhere in California are adapted to the Mediterranean climate of the region (Gasith & Resh, 1999; Moyle, 2002; Moyle et al., 1998). Historically, low summer flows in Putah Creek would reduce the stream to pools (Shapovalov, 1947); thus summer water supplies originated from stored precipitation (groundwater) representing cold-water releases from previous wet seasons. Consistent baseflows from Berryessa Dam now prevent stream drying, and may even be enhanced relative to the historical flow regime. Nonetheless, continuous flows of cold water throughout the summer better approximate the historical conditions of Putah Creek versus, for example, stagnant pools or full streambed drying (Figure 2). A return of predictable flow releases, and flow pulses during spring and fall are also important dynamics for native California fish as they cue spawning runs and allow juveniles habitat conditions that promote survivorship (Gasith & Resh, 1999; Moyle, 2002; Poff et al., 1997). In contrast, many nonnative species thrive in warm, deep, lacustrine waters and are often resilient in human-altered environments (Marchetti, Light, et al., 2004; Marchetti et al., 2004b; Moyle & Marchetti, 2006). Many nonnative fish are nesting species that recruit best under stable hydrodynamic conditions (Moyle, 2002) such as those that occurred before the Accord. Additionally, as temperature is a critical ecological parameter (Magnuson et al., 1979; Rypel, 2014), it is not surprising that many warm-water nonnatives were impacted by the restoration of cold summer flow releases into Putah Creek. For example, largemouth bass was once one of the dominant species in the upper sites in Putah Creek but has declined since flow restoration, to the point that it is nearly extirpated in upper sites. Channel catfish (another warm-water nonnative) has nearly been virtually eradicated throughout the entire ecosystem. In contrast, native species, such as prickly sculpin and rainbow trout, have increased especially at upstream sites. Our rank abundance analyses highlighted these shifts for a few select species, however this approach could be applied to any ecosystem where the community and composition of dominants changed in response to management actions, disturbance, or climate change. Future research might explore the extent to which changes to specific components of the natural flow regime and natural thermal regime (Willis et al., 2021) have catalyzed abundance trends for focal taxa.

This study also highlights further ecological changes to Putah Creek since reporting by Kiernan et al. (2012). Since 2008, one notable shift to the ecosystem in recent years has been the return of spawning adult Chinook salmon in Putah Creek (Willmes et al., 2020). While spawning salmon derive primarily from straying hatchery origin adults, the development of a self-sustaining salmon run in Putah Creek is of increasing interest (Willmes et al., 2020). Recent screw trap surveys (located between sites B and C) indicate that a large number of Chinook salmon smolts can be produced annually in the upper reaches of the creek (>30,000 smolts annually, and potentially up to 60,000; UC Davis, unpublished data). Therefore, the recovery of Chinook salmon is ongoing, and future contributions of wild fish in Putah Creek to the broader Central Valley salmon population could be large. However, while our study revealed how reconciliation activities (Rosenzweig, 2003) have been highly successful in rehabilitating fish communities in the upstream portions of the study area, these efforts have been much less successful in downstream reaches. Elevated temperatures remain common in the lowermost portions of Putah Creek (E, F), there are large lacustrine and warm-water areas, and deep incisement of streambanks; all of these impact the ability to better recover native species. Further, much of the riparian land in lower Putah Creek is privately owned, which also limits management options, to a degree. Future restoration efforts will need to address habitat issues in the lower portions of the system. This includes the presence of a check dam that diverts water and prevents the ingress and egress of fish during the late spring and summer months.

The functional flows concept (a conceptual extension of the natural flow regime; Poff et al., 1997) is an important conservation management tool for declining freshwater taxa in regulated rivers, especially in the western USA (Grantham et al., 2022; Yarnell et al., 2022). Augmenting the flow of cold water from dams specifically is increasingly common and effective for recovering native fish (Poff et al., 1997; Richter & Thomas, 2007; Watts et al., 2011; Willis et al., 2021). Environmental flow frameworks are useful for managing ecosystem function, mimicking natural variations in flow, and coupling flows to desired improvements in physical habitat and water quality benchmarks (Yarnell et al., 2015, 2020). In the Owens River Gorge (California) and the San Juan River (originating in Colorado), the utilization of an environmental flow framework increased the abundance of native and recreationally important fisheries (Hill & Platts, 1998; Propst & Gido, 2004). In this study, augmented flows and permanent wetted connectivity throughout the creek provided conditions that approximated the essential habitats of many endemic fish. While the management cannot replicate all elements of ecosystem function, attempts to recover some critical elements of the historical hydrologics are important and represent a significant step forward (Poff et al., 1997; Yarnell et al., 2015, 2020). Future research might explore the extent to which the managed flow regime of Putah Creek, which has now been in place for >20 years, in fact accurately approximates the historical pre-dam natural flow regime, and whether any differences in such might be useful in a reconciliation context.

It is worth noting some of the limitations of our work. For example, one of the main results (e.g., temporal trends in species diversity and relative abundance; Tables 1 and 3) are based on a small proportion of significant correlations. While 1993–2017 represents a relatively long record of ecological data (25 years), this is a relatively small sample size for many statistical models. The ability to detect more correlations will increase with additional time and data. For example, once data are available for 40 years in duration, and assuming the same alpha, and 80% power using a two-tailed test, a correlation of 0.34 might result in significance. These kinds of statistical realities point toward the difficulty and importance of obtaining long-term ecological data more generally. Putah Creek is also unique in having a flow management intervention that bifurcates the time series, but further cuts into statistical power because at least the first 7 years of data represent the initial (pre-Accord) conditions. However, for some of the nonsignificant correlations, there may simply be no substantial changes over time using these methods. Identifying species that do not respond positively to management change is equally as important as identifying those that respond positively. For example, inland silversides and pumpkinseed sunfish appear to have been recalcitrant to stream rehabilitation actions because they had low correlation coefficients at all sites. This may also be resultant of low abundance or rarity of certain species, thus significant changes may not be visible if few numbers of certain species were seen throughout the study. We again also note that the lowest sites (E and F) did not respond strongly to the flow alteration. Furthermore, these sites do not actually represent the lowermost portions of the stream, in fact, these habitats may be even further degraded than Sites E and F. Monitoring the quality of these habitats may be important for migratory fish such as Chinook salmon, Sacramento pikeminnow and Sacramento sucker that must navigate and use these habitats during portions of their life cycle. Combined, these limitations suggest that additional data, collected over even long periods, will be useful, and that additional information on responses of the lowermost portions of the stream ecosystem will be helpful for managers.

Community ecology tools for analyzing and visualizing data appear to be powerful methods for understanding the aggregate effects of ecosystem restoration. Assemblage stability, in particular, represents a fundamental aspect of ecosystems (Connell & Slatyer, 1977; Lhomme & Winkel, 2002; MacArthur, 1955), including how multiple dynamic ecological factors are jointly impacted by human activity (Collins et al., 2008). In grassland ecosystems, species invasions generated a significant increase in MRS values (Jones et al., 2017), indicating a decrease in ecological stability. In other aquatic studies, fish communities experiencing habitat degradation also express increased MRS values (Obaza et al., 2015; Robinson & Yakimishyn, 2013). This study complements prior work by demonstrating that fish community instability is linked to habitat degradation (i.e., Figure 6). However, our results substantially expand on this work by showing that restoration activities, including the implementation of a functional flows approach, substantially improve community dynamics, principally by increasing community stability. In response to restoration, Putah Creek MRS decreased across the board, coincident with a transition to an assemblage dominated by native species. Furthermore, an interesting pattern was that the trend toward enhanced stability was observed at all sites, including the downstream sites, which showed a lack of positive trends in the abundance of native species (discussed above). This finding highlights that these analyses are potentially revealing new ecological dynamics not observable by analyzing trends in abundance alone. It remains unclear whether this change is foreshadowing additional positive future changes to populations in the lower portions of the stream, or if it is simply a step in the right direction revealed through a community-level approach. Regardless, these findings provide empirical support that the ecosystem has been managed toward native species, and in favor of assemblage stability overall.

Conclusions

We document recovery and increased stability in native fish fauna following stream rehabilitation activities in a human-dominated freshwater ecosystem. The recovery included increased richness and abundance of native fish, decreased richness and abundance of nonnative fish, changing ranks of native and nonnative species, and the eventual return of an iconic, keystone species, Chinook salmon. Similarly degraded and managed stream ecosystems could apply methods of functional flow methodologies combined with community ecology approaches to recover at-risk fish populations and reduce or eradicate nonnatives. One of the surprising aspects of the Putah Creek story has been how strong the assemblage response was from relatively minor changes in the flow regime, perhaps notably from increased cold-water base flows during summer. This research therefore provides an intriguing case study into the potential for broader restorations of freshwater communities with perhaps just small tweaks to functional flow regimes. Furthermore, we provide an example of how community ecology approaches can be valuable for tracking the efficacy of restoration initiatives over long periods. In some cases, the metrics examined (e.g., community stability) are otherwise hidden, and therefore represent novel information that is likely to be of widespread interest to managers and decision-makers. While each restoration project necessarily has fundamentally unique goals and socioecological motives, the underlying response of the assemblage will probably align with many of the principal metrics of interest to diverse stakeholders. In our case, documenting the increased abundance and dominance of native versus nonnative fish, along with increased stability of the assemblage overall, was important for on-the-ground management. We anticipate that parallel analyses would be similarly powerful in many other restoration contexts, both in streams and other ecological realms.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Jacinto et al., 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.7822308. PDD gage data owned by the Solano County Water Agency are available by contacting the United States Bureau of Reclamation Area Office Manager.

ORCID

Andrew L. Rypel https://orcid.org/0000-0002-9812-8306

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