

I. Long-term rehabilitation of a native freshwater fish assemblage in California

II. Acknowledgments

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III. Abstract

Stream restorations are increasingly important fisheries management tools; however, few studies have monitored fish assemblages over decades following restoration. 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) which resulted in the replacement of an endemic fish community with an assemblage dominated by resilient, warmwater nonnative species. In response to declines, a court-mediated Accord was ratified in 2000 providing a more natural flow regime, specifically for native and anadromous fishes. Here, a long-term dataset is analyzed for fish assemblage changes incorporating data from 8 sampling years pre- and 16 sampling years post-restoration. Richness of nonnative species decreased at every site following the Accord, while richness of native species increased or stayed constant. At the three most upstream sites, native species richness increased significantly over time and ultimately exceeded nonnative richness. Positive ecological effects were strongest upriver, closer to flow releases and habitat restoration activities, and decreased in a downstream direction. Rank-abundance curves through time revealed that while species evenness was low throughout

the study, species dominance shifted from nonnative to native species in the upstream sites coinciding with rehabilitation efforts. Putah Creek's reconciliation and rehabilitation activities may represent a model for recovering endemic freshwater communities in similarly degraded stream ecosystems.

Key words: assemblage structure; flow regime; fish assemblage; fish conservation; freshwater fishes; native and nonnative fish species; Putah Creek, California, USA; rank abundance; reconciliation ecology; stream fishes; water management

IV. Introduction

Native freshwater fish communities across the globe are experiencing severe declines (Moyle and Williams 1990, Ricciardi and Rasmussen 1999, Dudgeon et al. 2006, Moyle et al. 2011). Climate change (Sharma et al. 2011, 2019, Moyle et al. 2013, Till et al. 2019), fragmentation and regulation of rivers (Dynesius and Nilsson 1994, Power et al. 1996, Poff et al. 1997, Carlisle et al. 2010, Grantham et al. 2010), pollution (Dudgeon et al. 2006, Carpenter et al. 2011), overharvest (Post et al. 2002, Embke et al. 2019), and invasive species (Marchetti et al. 2004a, 2004c, Moyle and Marchetti 2006) threaten freshwater ecosystems at all scales. Further, observed and predicted extinction rates are higher in aquatic than terrestrial ecosystems indicating high sensitivities of these ecosystems to human activities (Moyle and Williams 1990, Ricciardi and Rasmussen 1999). Beginning in the 19th century human disturbance on the environment was largely unregulated (Moyle 2002, Moyle et al. 2011). Yet understanding the importance of habitat loss and management of freshwater habitats has generally lagged behind advances made in terrestrial ecosystems such that cumulative understanding of freshwater

47 fisheries habitat is currently at the same point as terrestrial wildlife ecology during the 1970s
48 (Sass et al. 2017). For example, activities impacting freshwater habitats such as mining, logging,
49 and damming were once extremely common, but only later were the ecological consequences
50 fully realized (Tilman et al. 1994, Kuussaari et al. 2009).

51 Negative impacts from habitat change are often amplified through cumulative effects of
52 nonnative species (Moyle 2002, Bunn and Arthington 2002, Marchetti et al. 2004a, 2004c,
53 Moyle and Marchetti 2006, Carpenter et al. 2011). In many cases, altered habitats facilitate
54 dynamics that allow nonnative fish species to not only invade these changed habitats, but then
55 severely alter the native fish populations and ecosystem function (Matsuzaki et al. 2009, Weber
56 and Brown 2009). In the western United States, resilient warmwater nonnative species often
57 appear well-adapted to novel ecosystem conditions, which has allowed them to invade and
58 reduce or eliminate the native species population through competition or predation (Baltz and
59 Moyle 1993, Moyle 2002, Marchetti et al. 2004a, 2004c, Moyle and Marchetti 2006). Combined
60 effects quicken the rate of population collapse, presenting yet another conservation challenge.

61 California provides a model landscape upon which to study cumulative effects of habitat change
62 and nonnative species in freshwater ecosystems. The human population has effectively doubled
63 in California since 1970 from ~20 million to ~40 million people. California hosts a high degree
64 of species endemism and this diversity is greatly threatened by human activities. For example,
65 83% of freshwater fishes are declining, at risk of decline, or are already extinct (Moyle et al.
66 2011). Furthermore, from 1989 to 2011, rates of fish species imperilment increased 21%
67 signaling the growing intensity in modern ecosystem alterations. One of the largest threats to
68 freshwater systems in California is diversions and extractions (Moyle and Williams 1990, Power
69 et al. 1996, Poff et al. 1997, Moyle 2002, Carlisle et al. 2010, Grantham et al. 2010, Moyle et al.

2011). Alongside human population growth, water needs for potability and irrigation have increased rapidly. Water demand in turn drives construction of additional dams, dikes, and water projects that ultimately fragment rivers and further reduce biodiversity (Poff and Ward 1989, Power et al. 1996, Poff et al. 1997, Bunn and Arthington 2002, Carpenter et al. 2011). The primary goal of this study was to assess whether a rehabilitated flow regime in Putah Creek resulted in positive changes to the native fish assemblage over an extended period. Specifically, changes were evaluated in (1) key aspects of the flow regime over time (2) assemblage diversity, richness and abundance change and (3) rank-abundance (i.e., species dominance and evenness) and rank shift (MRS) change at differing sites before and after the Accord.

V. Paper/Chapter

Methods

Study Location

Long-term standardized monitoring occurs annually in lower Putah Creek, located in northern California bordering Yolo and Solano counties. The present study used monitoring data from 1993-2017, with major flow restorations beginning in 2000. Putah Creek occurs in the Mediterranean climate of the Central Valley where the natural flow regime includes predictable high flows from fall to spring, and low summer flows (Gasith and Resh 1999, Carlisle et al. 2010, Kiernan et al. 2012). Starting in the Coast Range, Putah Creek flows east ~130 km before reaching Monticello Dam which forms the Berryessa Reservoir (Moyle et al. 1998, Marchetti and Moyle 2001, Kiernan et al. 2012). Below the Berryessa Reservoir, Putah Creek flows to a second much smaller dam, the Putah Diversion Dam (PDD), which creates Lake Solano. Flows are then either diverted into the Putah South Canal for Solano County or released into lower Putah Creek. Lower Putah Creek flows from PDD nearly 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). Flows and temperatures in Putah Creek are primarily regulated through releases from PDD and Monticello Dam. Flows are mostly regulated through operation of the PDD, while temperatures are regulated mostly through releases from Berryessa Reservoir. During high rainfall years, Monticello dam overflows through a spillway at times causing massive surges of water into Putah Creek.

Study History

Putah Creek, much like many other western United States river systems, has been severely impacted by water diversions and dams. The two dam installations in 1957 effectively reduced downstream flows (Moyle et al. 1998, Kiernan et al. 2012), while also contributing to ongoing 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. For example, during the 1990s, areas of the creek regularly dried during summer months (Figure 2). Ultimately, these modifications led to a greatly altered channel structure and extirpation of previously occurring anadromous fishes, such as Chinook salmon (*Oncorhynchus tshawytscha*), Pacific lamprey (*Entosphenus tridentata*) and steelhead trout (*Oncorhynchus mykiss*), as well as massive declines in most other native fishes (Shapovalov 1947, Moyle et al. 1998, Kiernan et al. 2012). A lawsuit (Putah Creek Council vs. Solano Irrigation District and Solano County Water Agency, Sacramento Superior Court Number 515 766) was filed to provide a more natural flow regime under a provision of California Fish and Game Code 5937 that requires the provision of good conditions for fish below dams (Moyle et al. 1998, B rk et al. 2012). At the time, legal issues focused on keeping the creek from drying,

developing spring flows for native fishes, creating fall attraction flows for salmon, generating high flows to push out non-native fishes and to promote more natural channel processes. In 1996, the court required part of the requested additional flows to be implemented. The Putah Creek Accord (the Accord) was ratified in 2000 and implemented the remainder of requested changes in flow quantity and timing. Litigation included specific flow requirements to simulate the natural flow regime (based on Poff et al. 1997), such that there must be water throughout the creek all year and two seasons of “pulse flows”, increased flow release events, that would occur in the spring and fall to support spawning and migration of native and anadromous fishes (Moyle et al. 1998, Kiernan et al. 2012). These flow events included 3 days of releases of 150, 100, and 80 cubic feet per second (CFS) in spring and 5 days of 150 CFS in fall followed by at least 50 CFS released daily through spring (Moyle et al. 1998). Overall, flows are intended to mimic critical timing elements of the natural flow regime, but not necessarily historic quantities of flow (Yarnell et al. 2015, 2020).

Following 2000, seasonally increased flows have occurred in the system and appear to have improve ecological conditions. Marchetti and Moyle (2001) documented that only a few wet years in the late 1990s, which created a more natural flow regime, resulted in positive responses in the Putah Creek fish assemblage. Later, Kiernan et al. (2012) evaluated data from both before-and-after the Accord (until 2008) and found that native fish were returning to areas of the creek where they were previously absent. In the nine sampled years since Kiernan et al. (2012), Chinook salmon (*Oncorhynchus 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 (from 2012-2016, Moyle et al. 2017).

Sites

Six sites were selected from annual, standardized fish sampling beginning in 1993 and continuing until present day. All sites are located in a 30 km reach between PDD and the Yolo Bypass Wildlife Area (Figure 1). Sites are labeled A-F and occur sequentially downstream from the PDD approximately at river kilometers 0, 6, 16, 20, 25, 30, and replicate sites presented in Kiernan et al. (2012). Only fall fish sampling during October was analyzed. Data were analyzed during two discrete time periods, 1993-2000 (pre-flow restoration), and 2001-2017 (post-flow restoration). 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 and 2001.

Sampling Methods

Standardized tote barge electrofishing methods were used to capture and evaluate species presence and relative abundance (Reynolds and Kolz 2012). All data used for this study were collected by Normandeau Associates and TRPA Fish Biologists (TRPA fish biologists sampled from 1991-2010). Fish were collected using a Smith-Root 2.5 Generator Powered Pulsator (GPP) electrofishing tote barge set up (Smith-Root, Vancouver, Washington, USA). Electrofishing was single pass, and all stunned fish were captured by net, held in a bucket or a net pen in creek until identified, enumerated and a subset measured for size, and then released. Sampling of equivalent distance occurred at each site during each year (Kiernan et al. 2012); thus data are presented more simply at catch totals rather than catch-per-unit-effort (effort is essentially the same each year. Sculpins were identified as a single species (prickly sculpin, *Cottus asper*) even though some debate exists over the existence and classification of two species in the ecosystem (P.B. Moyle, unpublished data¹). Nonnative sunfish hybrids and unidentified sunfish were classified as

¹ Some sculpins sampled have been identified as *Cottus gulosus*. However, genomic and other analyses indicate that all sculpins in Putah Creek are *Cottus asper* (P.B. Moyle, pers. comm).

a single species, sunfish (*Lepomis spp.*) hybrids. Resident and anadromous forms of rainbow trout (*Oncorhynchus mykiss*) have the potential to occur in Putah Creek but are not differentiated in this analysis.

Flow Change

Long-term discharge data were obtained from PDD where a gage is operated by the Solano County Irrigation District in combination with the USA Bureau of Reclamation. Discharge data 1978-Present were available; thus full pre/post comparative analysis of the effect of dams on the natural flow regime of Putah Creek (e.g., Lytle and Poff 2004) was not completed. Nonetheless, elements of Lytle and Poff (2004) were replicated by generating 3-dimensional plots of daily discharge versus month versus year on an annual time frame from 1978-2017 (Figure 3), and for only the low flow summer months (days 180-304 or June-October) which is the period during which Putah Creek flows are known to have changed greatly. A full analysis of how the natural flow regime in Putah Creek has changed following the Accord is important, but ultimately beyond the scope of this study.

Fish Assemblage

Parallel to Collins et al. (2008), changes were examined in fish assemblage diversity and evenness at each of the study 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 conducted to assess directional correlations between diversity indices and time (year) (Table 1). 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). Analyses of covariance (ANCOVA) were used to compare the change in

richness of species over time (Table 2). For each site, an ANCOVA was developed where $\log_{10}(\text{species richness} + 1)$ was the dependent variable, year was the independent variable, and species type (native or nonnative) was a categorical variable. Directional changes in the diversity of native and nonnative species were assessed by examining the coefficients (i.e., slopes) of the model, and differences in slopes between native and nonnative species assessed by way of the year x native/nonnative interaction term in each model. It is recognized that differences in slopes would ideally be examined in this way, but 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 pre data precluded such an analysis, especially given the lifespan and turnover rates of focal species (Marchetti et al. 2004b, Rypel and David 2017).

Fish Abundance

Pearson's correlations (R) were used to assess directional change (correlation) in the abundance of individual species at each site over time. For each correlation, abundance data were \log_{10} -transformed to meet assumptions of normality (Table 3). Furthermore, to counteract the potential of type errors arising from multiple comparisons a Bonferroni correction was also performed to the threshold P-value for these specific correlations and present this information as supplementary results (Supplementary Table 1).

Changes in the dominance and evenness of fish assemblages were examined by constructing and comparing rank-abundance curves (Figure 5) over time (Whittaker 1965, Collins et al. 2008, Avolio et al. 2019). Rank-abundance curves combine elements of 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 along on the x-axis. Parallel to Collins et al. (2008), species points in these plots were identified as native and nonnative species. Combined, these

plots illustrate most of the key aspects of assemblage dynamics that have occurred over time in Putah Creek and in response to rehabilitation of flows. To test for changes in assemblage stability over time (Collins 2008, White 2020), mean rank shifts (MRS) for the assemblage were calculated at each sampling sites using the R package Codyn (Hallett et al. 2016). Thus sites with a high MRS value indicate increased instability of the fish assemblage whereas reduced values indicate enhanced assemblage stability. A mixed effects regression model was developed in the lmer package in R (Bates et al. 2014) to test whether MRS changed directionally over time (Figure 6). 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 considered significant if $P < 0.05$, unless otherwise specified.

Results

Flow Change

Discharge data from PDD were analyzed from October 1978 through December 2017. Beginning in 2000, major flow alterations were made to Putah Creek that resulted in additional flow deliveries. Furthermore, as the water originates from deep limnetic habitats in Lake Berryessa, cool (generally $< 22^{\circ}\text{C}$) water has been provided to the creek (Kiernan et al. 2012). 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 to 304, approximately July through October) was also presented (Figure 3). Prior to the Accord, there were regular and extended periods of zero flow resulting in the creek drying. Post-restoration, there were no known experiences of Putah Creek experiencing zero flows and streambed drying has never been reported.

Fish Assemblage

A total of 35 fish species were captured as a part of standardized sampling described above from 1993 to 2017, including 11 native and 24 nonnative species. Richness of nonnative species decreased at every site following ratification of the Accord in 2000 (Figure 4), while the number of native species increased or stayed relatively constant. Increases in native species and decreases in nonnative species were strongest upriver, closer to the PDD and decreased as sites progressed downstream. Sites A, B, and C all expressed a trend where richness of native species increased over time and assumed a dominant position compared to nonnative species which became subordinate. However, richness of native species was highest at upstream sites and decreased as sites progressed downstream. Species richness decreased significantly at the three upstream sites, A-C (Table 1), and Shannon Diversity Index declined significantly at two sites (C and D). Only the downstream most site, site F, had a significant positive increase in Pielou's Index. At four sites (A, B, C, D), there was a significant difference in the richness x year interaction term (ANCOVA model, Table 2). Only the two downstream sites (E and F) failed to show significant trends in native versus nonnative species over time.

Fish Abundance

Many fish species shifted in relative abundance over time in Putah Creek. Out of 66 potential abundance-time correlations for native fishes, 15 were significant: 12 of these correlations were positive and 3 were negative (Table 3). Thus, 80% of native species that showed significant abundance trends over time expressed positive trends in abundance. Effects of stream rehabilitation were stronger in upstream reaches. For example, rainbow trout increased significantly in abundances over time at both of the upper most sites, A and B. Sacramento pikeminnow (*Ptychocheilus grandis*) increased in abundance in all sites, and significantly in half

of them (C, D, and F). At a more downstream site D, four native fishes all increased in abundance over time: prickly sculpin, Sacramento pikeminnow, Sacramento sucker (*Catostomus occidentalis*) and tule perch (*Hysterocarpus traskii*). A notable exception, Sacramento blackfish (*Orthodon microlepidotus*) decreased significantly in abundance over time at both of the lower most sites in the creek.

For nonnative species, 46 of 144 correlations were significant. A total of 38 of these significant correlations (83%) were negative. The 8 significant positive correlations for nonnative species occurred at the most downstream sites E and F; thus all sites upstream of that only had significantly decreasing abundance over time. Notable examples included bluegill (*Lepomis macrochirus*), which decreased significantly in abundance over time at every site, green sunfish (*Lepomis cyanellus*) which decreased significantly in abundance over time at 5 of 6 sites, and common carp which decreased significantly at 4 of 6 sites. At both sites B and C (mid-upstream habitats), nine nonnative species declined significantly in relative abundance over time.

Rank-abundance curves revealed additional aspects of assemblage change in Putah Creek over time (Figure 5). For example, the Putah Creek assemblage showed high unevenness in rank-abundances (i.e., steep slopes) overall. Thus, the fish assemblage is dominated by only a few species, and this dynamic does not appear to have changed appreciably over time. Nonetheless, the identity of the dominant and subordinate species has changed. While nonnative species like bluegill and green sunfish once dominated the fish assemblage in Putah Creek, now native species like tule perch, suckers and pikeminnow now dominate. These patterns appear to be site specific as in the upstream most sites (A, B and C) with rainbow trout, Sacramento sucker and prickly sculpin emerged as dominant species following rehabilitation, while in contrast,

largemouth bass (*Micropterus salmoides*) decreased in rank to a subordinate position at these sites.

Assemblage stability also appears to have changed and become more stable over time (Collins 2008, White 2020). MRS (i.e., amount of species changing rank between years) declined overall at all sites over time (Figure 6). Furthermore, all sites showed a similar pattern of decline in MRS as noted by a similarity in random effects coefficients. Overall, the parent regression suggested mean rank shift declined by 0.03 per year and the mixed effect model was highly significant (Mixed Effect Model, t-value = -3.85, P = 0.0002).

Discussion

Rehabilitation of the natural flow regime in Putah Creek has assisted in long-term recovery of the native fish assemblage. In this study, increased seasonal flows resulted in decreased nonnative species richness and abundance through much of Putah Creek, while native species recovered and regained dominance at numerous sites. Native fish communities in Putah Creek and California are generally cool water fishes adapted to the Mediterranean climate of the region (Moyle et al. 1998, Gasith and Resh 1999, Moyle 2002, Kiernan et al. 2012). Summer flows, while reduced often to pools, historically originated from stored rainfall where springs were present prior to increased groundwater pumping. A return of predictable flow releases, and flow pulses during spring and fall are important dynamics for native California fishes (Poff et al. 1997, Gasith and Resh 1999, Moyle 2002). In contrast, many nonnative species thrive in warm, deep, stagnant waters and are often resilient in human altered environments (Carpenter 2011, Moyle 2002, Bunn and Arthington 2002, Marchetti et al. 2004a, 2004c, Moyle 2002, Moyle and Marchetti 2006). Additionally, since temperature is a critical ecological resource (Magnuson et al. 1979, Rypel 2014) it should not be surprising that many warmwater species were impacted by

297 restoration of cold summer flow releases into Putah Creek. For example, largemouth bass was
298 once one of the dominant species in the upper sites in Putah Creek but has since flow restoration
299 declined to the point that it is almost extirpated. In contrast, native species like prickly sculpin,
300 Sacramento sucker, rainbow trout, and Sacramento pikeminnow increased dramatically,
301 especially in the 3 upstream sites. All these species require cold water and have better survival in
302 high flows (Moyle 2002).

303 This study highlights further ecological changes to Putah Creek since prior reporting by
304 Kiernan et al. (2012). One major fish change to the ecosystem in recent years has been the return
305 of spawning adult Chinook salmon in Putah Creek (Moyle et al. 2017, Willmes et al. 2020).
306 While spawning salmon are primarily straying adults from hatcheries, the development of a self-
307 sustaining salmon run in Putah Creek is of increasing interest (Willmes et al. 2020). Recent
308 unpublished screw trap data suggests a large number of smolts are being produced in the upper
309 reaches of the creek (>30,000 smolts annually, and potentially up to 60,000, UC Davis
310 unpublished data). Therefore recovery of Chinook salmon is ongoing and future contributions of
311 Putah Creek and the broader Central Valley salmon population could be large. However, data
312 also reveal how reconciliation activities have been highly successful in rehabilitating fish
313 communities in the upstream portions of the study area, but less so in the downstream most
314 reaches. For example, in the most downstream sites (E and F), nonnative species richness is still
315 higher than native and abundances are still above most natives. Future restoration efforts in
316 Putah Creek will need to address some substantial habitat issues in the lower portions of the
317 system, including large pools, slow moving water, and the presence of a check dam that diverts
318 water and prevents fish from entering and exiting the system during summers. Addressing these

issues will be important for supplying improved migration paths for Chinook salmon in the ecosystem.

Using the natural flow regime concept as the basis for rehabilitation of flows in regulated rivers is an important conservation management tool for declining freshwater taxa, especially in the western United States. California Department of Water Resources (DWR) classified the 8 sampling years prior to the Accord as wet for 5 of the years, 2 above normal years and 1 critically dry year, and during the 16 sampling years after the Accord as wet for 3 of the years, 2 above normal years, 4 below normal years, 4 dry years, and 3 critically dry years (DWR Water Year Hydrologic Classification Indices of the Sacramento Valley, <http://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>). Showing that even though a majority of years before the Accord were above average water years and after the Accord being below average water years, the additional water released from the dam provided the flow needed to recover native species and depress nonnatives. Augmenting flow of coldwater from dams is an increasingly common and effective approach to recovering native fish species, especially in Western USA rivers (Poff et al. 1997, Richter and Thomas 2007, Watts et al. 2011). Other systems have used similar management tools for restoration of freshwater species. For example, in the Owens River Gorge (in California) and the San Juan River (originating in Colorado) where with the use of environmental flows that were based on the natural flow regime abundances of native fish and prized recreational fisheries have increased (Hill and Platts 1998, Propst and Gido 2004). Altered flows and yearlong connectivity through Putah Creek provided the necessary flows and temperatures for native California fishes to sustain and expand (Bunn and Arthington 2002). Even though it may not be possible to replicate all the ways these systems previously operated, an ability to approximate system dynamics using manipulated flows out of reservoirs is

important (Poff et al. 1997, Richter and Thomas 2007, Watts et al. 2011, Yarnell et al. 2015, 2020).

Few studies have examined long-term changes in fish communities over time in highly altered and incised western USA streams. Often restoration projects have little-to-no long-term ecological monitoring; thus ecological effects are rarely quantified even after significant time and money expenditures, and are instead more or less anecdotal (Palmer et al. 1997, 2005, Bernhardt 2005, Wortley et al. 2013). One important lesson from this work is that while positive changes ultimately occurred, they did not happen overnight. Chinook salmon did not return to Putah Creek until 14 years after the flow restoration, and then it took another 3 years to build salmon numbers (Moyle et al. 2017, Willmes et al. 2020, UC Davis unpublished data). Many endemic fish species in Putah Creek are notably long-lived including tule perch (~5 years), prickly sculpin (~ 5 years), Sacramento sucker (10+ years) and pikeminnow (15+ years) (Moyle 2002). Therefore, replacement rates of some species can be correspondingly slow and populations require time, often many years, to rebuild (Rypel and David 2017). However, some native species (e.g., Sacramento pikeminnows) have high fecundities with individuals maturing in as little as 3 years and populations can often recover more quickly, sometimes in only 10-12 years (Moyle et al. 1983). This study provides another example of the value of long-term ecological research, including how slow change can allude ecologists and lead to miss understanding (Magnuson 1990, Turner et al. 2003).

Community ecology approaches are useful and powerful for understanding the dynamics of ecosystem restoration using long-term data. Community ecology has a long and rich history of addressing such questions such as diversity, competition, disturbance, patch dynamics, and terrestrial management (Whittaker 1965, Tilman 1987, Leibold et al. 2004, Hobbs et al. 2014).

Unfortunately, similar studies in aquatic ecosystems, and in fish communities more specifically, have been rarer (Sass et al. 2017). Other long-term studies of freshwater communities could benefit by developing parallel analyses as those in plant ecology (Collins et al. 2008, 2018). Assemblage ‘stability’ is a fundamental and frequently studied aspect of ecosystems (MacArthur 1955, Connell and Slatyer 1977, Lhomme and Winkel 2002). Putah Creek developed increased ecological assemblage stability following stream and flow rehabilitation as indexed by reduced mean rank shifts over time. Other metrics and measures exist to quantify assemblage stability. For example, synchrony of populations and communities, can also be quantified and compared as a measure of ‘stability’ (Loreau and de Mazancourt 2008, Vasseur et al. 2014, Zhao et al. 2020, Walter et al. 2020). Future studies on the synchrony of populations and sub-communities (spatial communities) could further elucidate change in assemblage stability dynamics in Putah Creek and similarly degraded aquatic ecosystems over time. However, here we show how assemblage stability can also be viewed by examining changes in species ranks over time. MRS has been studied in other ecosystems and taxa. For example, species invasions caused an increase in MRS values (i.e., the inverse patterns as this study) in grassland ecosystems over time (Jones et al. 2017). Further, fish communities suffering from habitat degradation have also experienced increased MRS values (Robinson and Yakimishyn 2013, Obaza et al. 2015). In Putah Creek, a reduction in mean rank shift coincided with the recovery of native species as dominants provides compelling evidence that the stream ecosystem became more stable following managed flows that have caused more predictable conditions.

Putah Creek as a Novel Ecosystem

Often systems cannot be restored to their historic state due to the scale of changes that have occurred and continued need for human use (Miller 2006, Hobbs et al. 2014, Moyle 2014).

This reality does not mean that these altered systems should not still be managed and improved to provide a better system for both human use and biodiversity of native wildlife. “Reconciliation ecology” is an emerging ecological philosophy devoted to exploring management of highly modified ecosystems in a human-dominated world (Rosenzweig 2003). Human-dominated systems no longer look or function like they previously did, and most likely never will, but this does not mean that they cannot be managed to a new and productive, or novel, system (Miller 2006, Hobbs et al. 2014, Moyle 2014). Indeed, Putah Creek is an excellent example of a novel ecosystem that has gone under significant reconciliation and rehabilitation. With only small seasonal water releases from Monticello Dam, Putah Creek has been able to reestablish much of its unique native fish assemblage, yet nonnative species remain present and other human threats (water diversions, landscape modification, channel incisement and fishing) remain pervasive.

Putah Creek, although highly agriculturalized and urbanized, still provides countless benefits to the surrounding area. Many values still exist such as, aesthetic, scientific, and educational value (Moyle et al. 1998, Dudgeon et al. 2006, Miller 2006, Moyle 2014). Having a place of enjoyment of wildlife and nature in people’s backyards is important to and provides an educational classroom to all ages (Dybala et al. 2018). Having ‘wild’ national parks nearby is not always attainable, so having an ecosystem nearby that is accessible to the public and managed towards desired ecological endpoints is still beneficial. Even if an ecosystem is not pristine, which is becoming rare as human impacts spread, there is still value in improving it for multiple benefits, starting with native fishes.

Conclusion

Recovery was observed in a native fish fauna following stream rehabilitation activities in a human-dominated freshwater ecosystem. Highlights of the recovery included increased

richness and abundance of native fishes, decreased richness and abundance of nonnative fishes, increased stability of the fish assemblage, and the eventual return of an iconic, potentially keystone, species Chinook salmon. Similarly degraded and managed stream ecosystems could apply methods of seasonal and continuous flows to recover at risk fish populations and remove nonnative species. It is unlikely that human impacts will subside in the near future and indeed will only intensify. Thus, reconciliation approaches that incorporate flow rehabilitation could be particularly useful and only require minimal additional water releases (Moyle et al. 1998, Kiernan et al. 2012). In an era when freshwater fish are declining rapidly (Moyle and Williams 1990, Ricciardi and Rasmussen 1999, Dudgeon et al. 2006, Moyle et al. 2011), resource relatively small management changes can yield major conservation wins.

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Tables:

Table 1: Spearman and Pearson correlations between diversity indices and year in Putah Creek 1993-2017.

Site	Species Richness*	Shannon's Index**	Pielou's Index**
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

*= Pearson Index

**= Spearman Index

Significant correlations are indicated in bold.

Table 2. Results of Analysis of Covariance (ANCOVA) examining effects of time/year and type of species on species richness in Putah Creek. Species richness data were $\log_{10}(x + 1)$ -transformed prior to analysis.

	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

Numbers indicate *P*-values, significant values indicated in bold.

All richness data were $\log_{10}(x + 1)$ -transformed.

Table 3. Pearson correlations (R) examining the correlation between fish abundances and year in Putah Creek, 1993-2017. All abundance data were $\log_{10}(x + 1)$ -transformed to meet assumptions for normality.

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
Threespine stickleback	-0.02	0.54	NA	NA	NA	NA
Nonnative Species						
Bigscale 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

Significant correlations are indicated in bold.

All abundance data were $\log_{10}(x + 1)$ -transformed.

NA values indicate species was not captured at site.

Supplementary Table 1. Pearson correlations (R) examining the correlation between fish abundances and year in Putah Creek, 1993-2017 following a Bonferroni correction. All abundance data were $\log_{10}(x + 1)$ -transformed to meet assumptions for normality. Significant correlations following the Bonferroni correction are highlighted in bold.

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
Threespine stickleback	-0.02	0.54	NA	NA	NA	NA
Nonnative Species						
Bigscale 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

Significant correlations are indicated in bold.

All abundance data were $\log_{10}(x + 1)$ -transformed.

NA values indicate species was not captured at site.

677 **Figure Legends:**

678 Figure 1: Map of sampling sites along Lower Putah Creek, CA.

679 Figure 2: Images at two locations on Putah Creek, CA (Pedrick Road Bridge and Mace
680 Boulevard) before and after the Accord.

681 Figure 3: Three-dimensional plots of discharge, year, and day of year for flows released from
682 PDD, October 1978 to the end of 2017. Data are presented for (a) calendar year and (b) calendar
683 days 180 to 304 (July through October).

684 Figure 4. Changes in richness of native (blue) and nonnative (orange) taxa at all sampling sites
685 along Putah Creek CA, 1993-2017. Vertical black line denotes the ratification of the Putah Creek
686 Accord in 2000, and subsequent restoration of flows in the ecosystem. Regressions represent
687 ANCOVA models as described in the methods, and “test of slopes” refers to the significance
688 level of the site x year interaction term in the ANCOVA models. Shaded areas of the regressions
689 represent 95% confidence intervals.

690 Figure 5. Annual rank-abundance curves for sites on Putah Creek showing proportional
691 abundance changes in native (solid blue circles) and nonnative (solid orange circles) species.
692 Each curve represents one year of data; thus curves move from the earliest (1993) to more recent
693 years along the x-axis. Initiation of restorative flows from the Accord is indicated by an asterisk
694 symbol.

695 Figure 6: Changes in mean rank shift (stability) in the fish assemblage in Putah Creek CA, 1993-
696 2017. The vertical black line denotes ratification of the Putah Creek Accord in 2000 and
697 subsequent restoration of flows in the ecosystem. Light colored points represent MRS data for
698 the fish assemblage at individual sites. The thick solid black line shows the overall trend in MRS

699 across all sites as defined by the mixed effect model. Light colored lines denote random (site-
700 level) effects.

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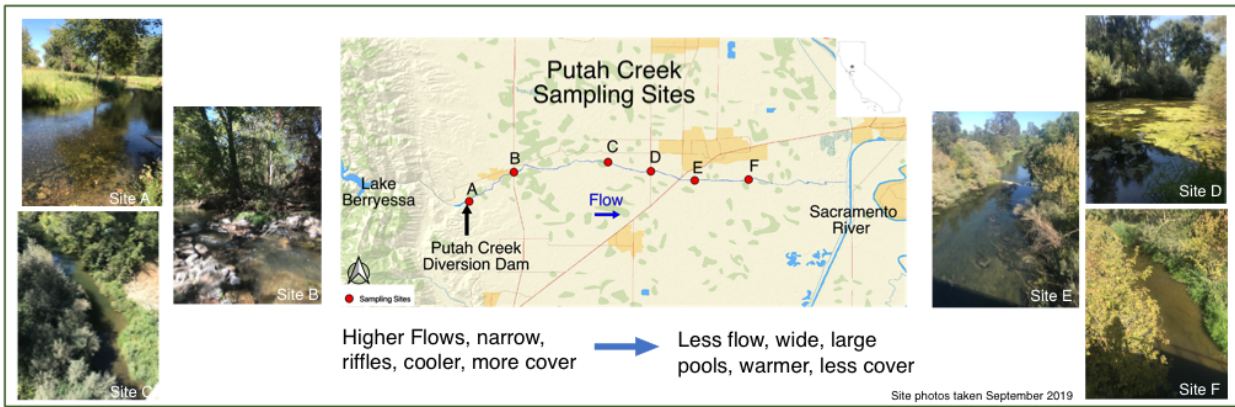
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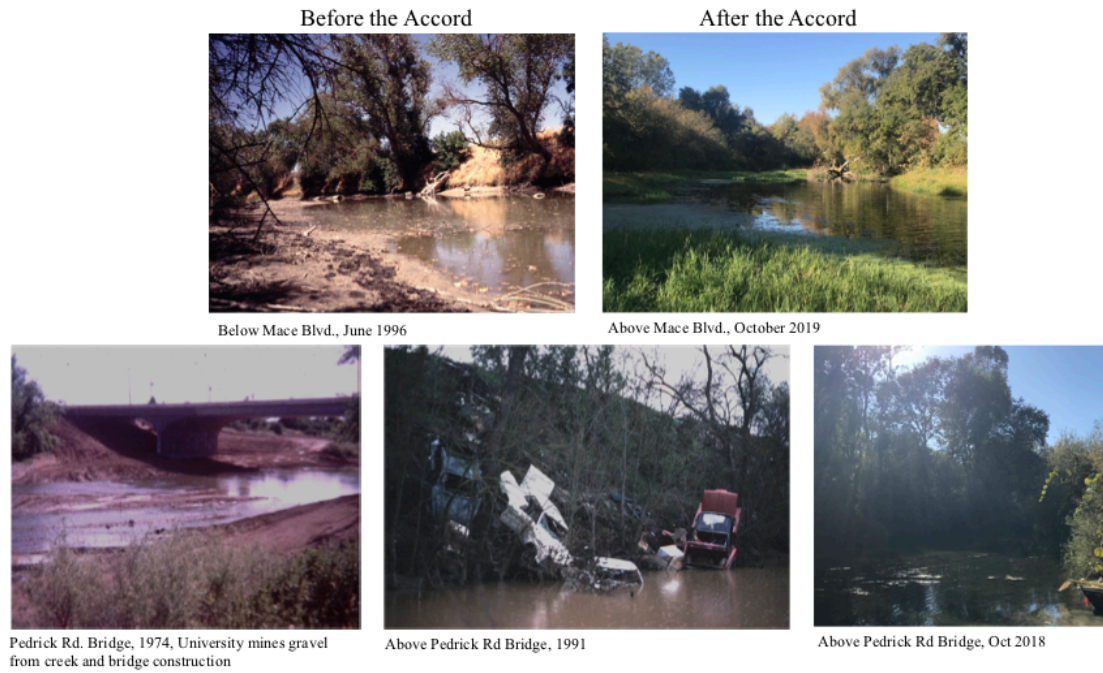
Figures:

Figure 1:



All photos by Emily Jacinto.

725 **Figure 2:**



726 Photos by Emily Jacinto with the exception of photos prior to 2018 which were taken by Peter Moyle.

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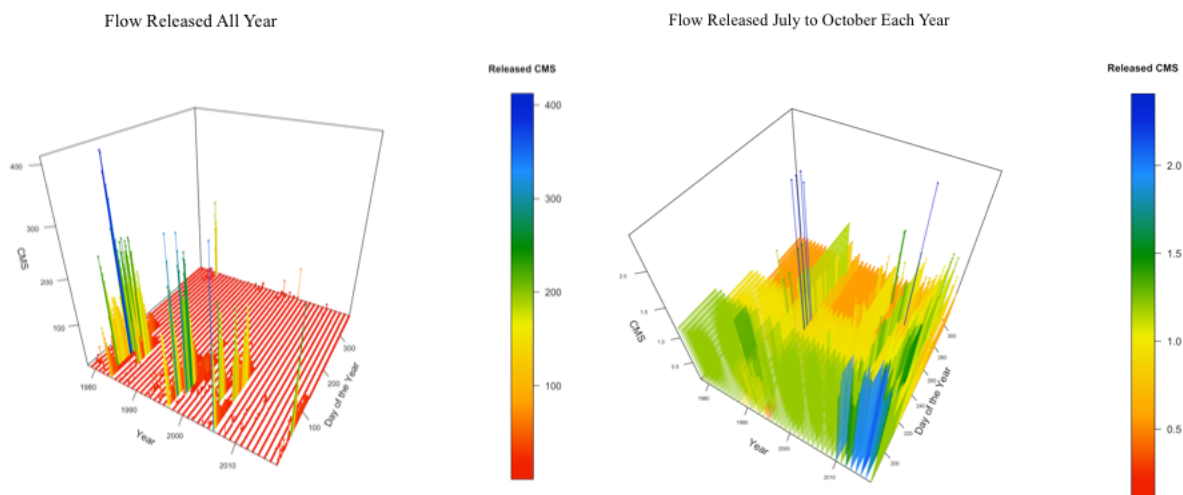
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735 **Figure 3:**



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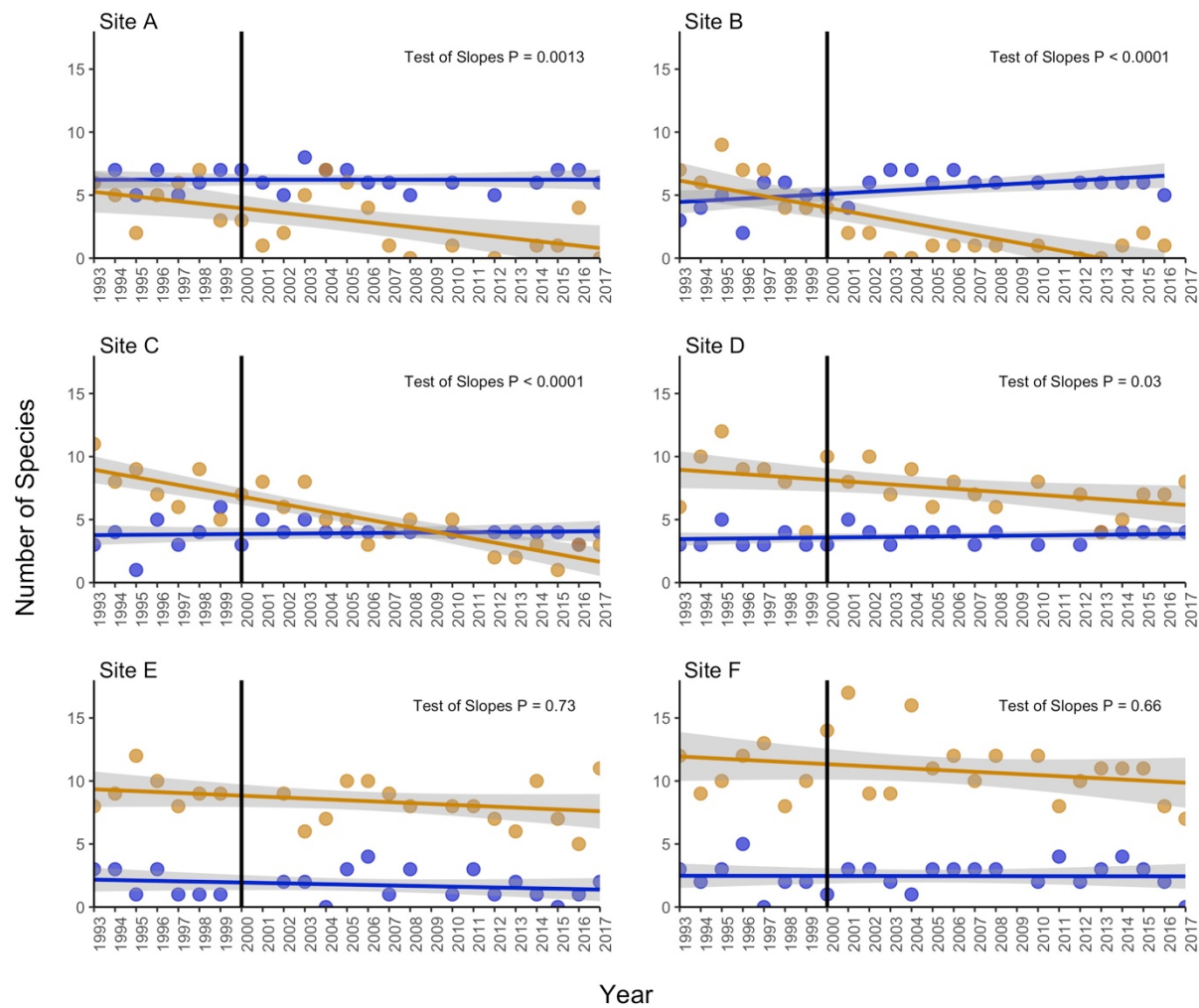
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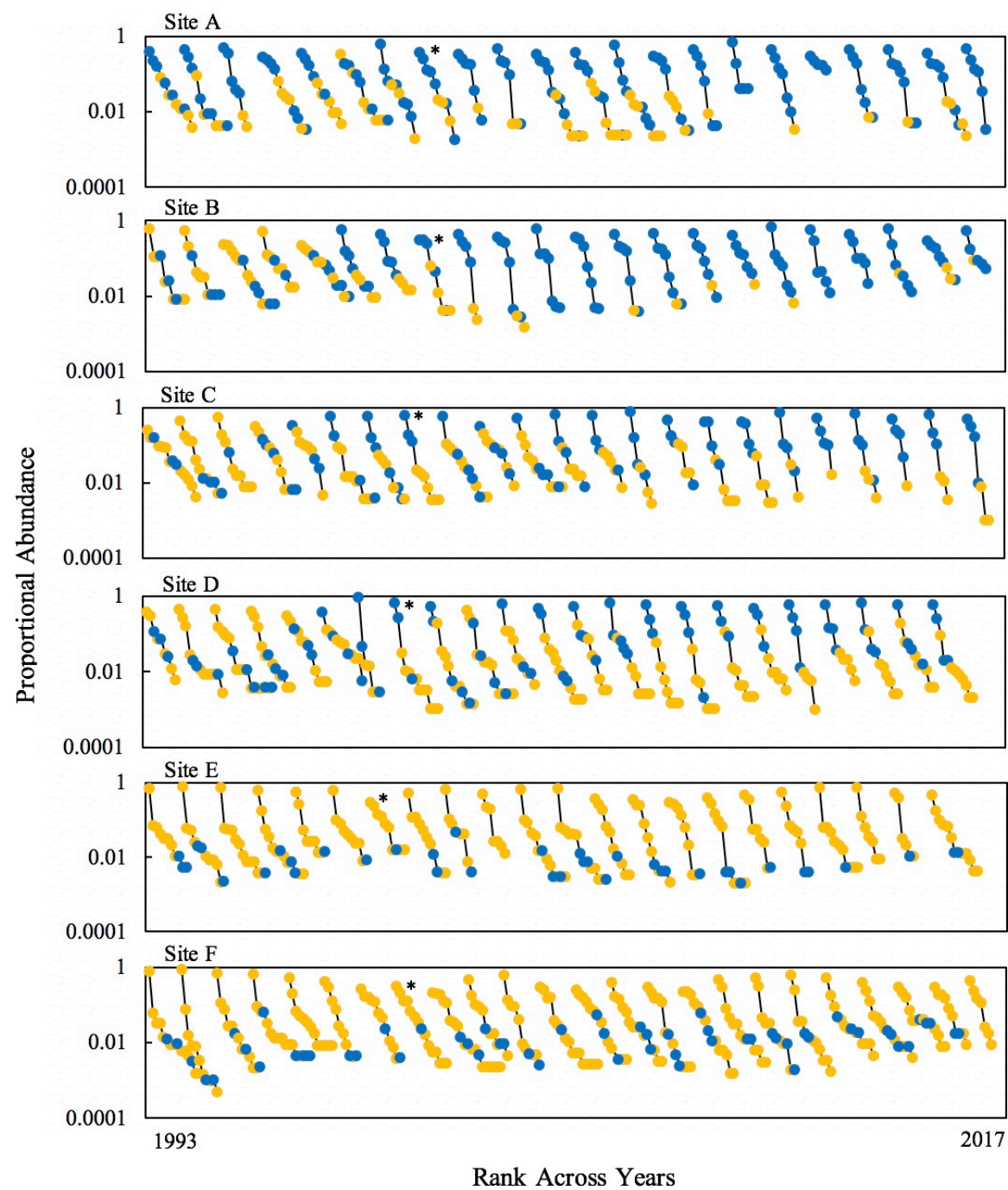
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746 **Figure 4:**



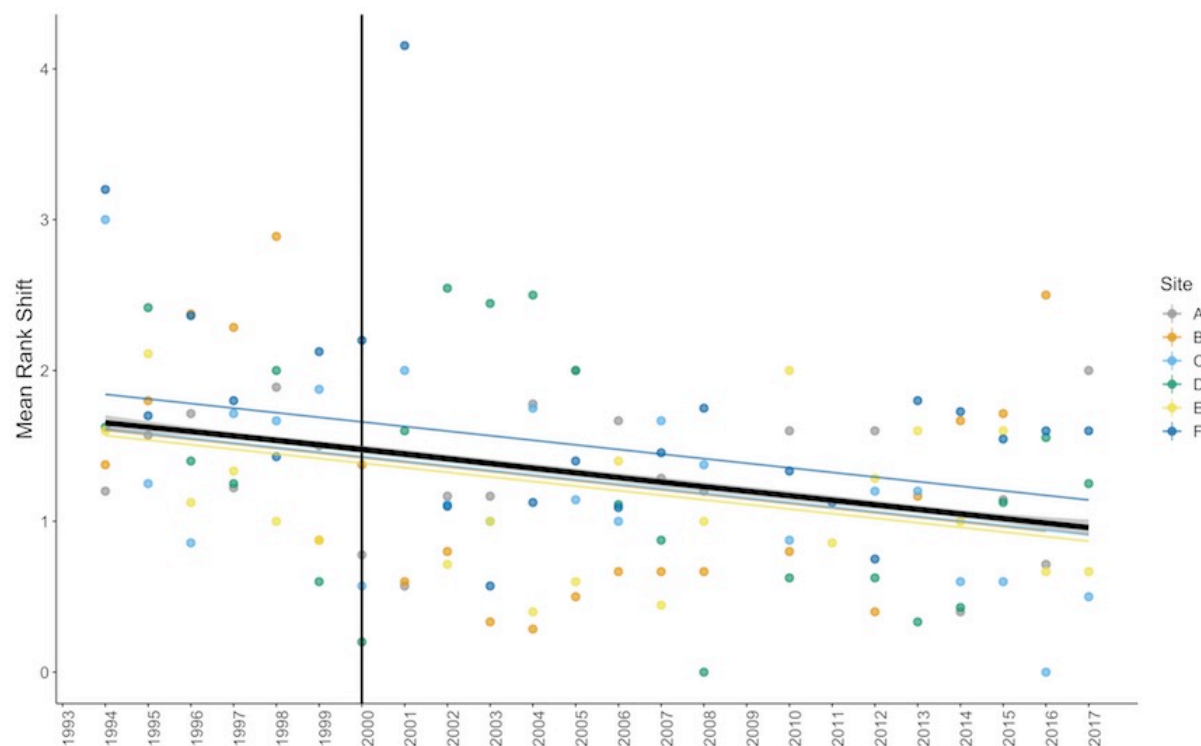
753 **Figure 5:**



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756 **Figure 6:**



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