

Spatial and Temporal Patterns in Fish Assemblages of the Lower Mokelumne River

Casey Del Real, Ed Rible, Jason Shillam, and Matt Saldate
East Bay Municipal Utility District, 1 Winemasters Way, Lodi, CA 95240

Abstract

In order to characterize the fish community of the lower Mokelumne River (LMR), fish community data from boat electrofishing surveys between 2001 and 2016 were examined. During this time period, thirty-seven fish species (12 native and 25 introduced) were identified. Fish species composition was found to be significantly different based on regional and reach scale analyses. Throughout the year, native species had greater abundance than introduced species from the base of Camanche Dam downstream to the Woodbridge Irrigation District Dam and were able to extend their range further downstream during the winter and spring when favorable conditions allowed. Chinook salmon and largemouth bass are the only species identified as indicator species for each reach within the LMR demonstrating their broad dispersal, overlapping distributions, and persistent presences throughout the Mokelumne River. Inclusion of Sacramento splittail, striped bass, and redeye bass as indicator species in Reach 2 represents both the potential for native species restoration within the LMR, but also predation and river management challenges. This study provides further evidence that a native fish community can thrive in the downstream reaches below a non-passable dam in the Central Valley of California. However, identified seasonal variables structuring the fish community (introduced species, river kilometer, and water temperature) interact to limit the overall downstream distribution of native species in the LMR.

Introduction

The Sacramento-San Joaquin Watershed has been substantially modified by dams, water diversions, and land conversion (Herren and Kawasaki 2001; Kimmerer 2002; Micheli et al. 2004). Most of the major east-side tributaries of the Sacramento and San Joaquin rivers are currently dammed, with terminal water impoundments located along the ecotone between the

Central Valley and western foothills of the Sierra Nevada. As water demands are likely to increase, water resource managers are faced with the complex challenges of balancing the competing interests of providing sustainable supplies of freshwater and hydropower and the need to protect and restore downstream aquatic ecosystems (Covich 1993; Postel 1996; Vitousek et al. 1997; Postel and Carpenter 1997; Postel 2000; Sala et al. 2000).

Changes in river regulation can lead to shifts in species diversity and community composition, with dramatic changes to overall native fish assemblages (Ward and Stanford 1983; Bain et al. 1988; Ligon et al. 1995; Poff et al. 1997; Aparico et al. 2000; Brown 2000; Brown and Ford 2002). Flow modification and in-stream habitat alteration often support introduced species (Marchetti and Moyle 2001; Brown and Ford 2002). Likewise, changes in the Delta's ecosystem have been accompanied by declines in native fish species and an increase in numerous non-native species, including introduced fishes (Cohen and Carlton 1998; Jassby et al. 2002; Moyle 2002; Brown and Moyle 2005). Introduced species may be better suited for these modified habitats which can negatively influence the abundance and/or survival of native fishes through competition and predation (Brown and Moyle 1997; Brown 2000; Brown and Michniuk 2007; Nobriga and Feyrer 2007).

Fish assemblages are key indicators of river condition and environmental quality as changes in species composition can reflect broad ecosystem changes in both freshwater environments and estuaries (Karr 1991; Moyle 1994; Brown 2000; Waite and Carpenter 2000; Whitfield and Elliot 2002; Matern et al. 2002; Hurst et al. 2004; O'Connell et al. 2004). Commitment to long-term ecological monitoring is critical to gain an in-depth understanding of spatial and temporal trends, biotic and abiotic factors structuring the fish community, and species responses to management decisions. For fisheries managers, the long-term monitoring of fish assemblages, based on standardized procedures, is vital as the opportunities and limitations of native fish restoration are still not entirely understood (Brown 2003). Fish community monitoring remains imperative if management decisions to preserve and restore fish populations and communities are to be based on scientifically defensible information (Walters and Martell 2004). Science-based decisions, without long-term datasets, are often just not plausible (Walters 2001; Walters et al. 2005).

This research examined fish community survey data between 2001 and 2016 in order to characterize the fish community structure of the lower Mokelumne River (LMR). The research

goal was to assess the status of native species in the LMR. Specific study objectives were to: 1) describe fish species richness and abundance in the LMR; 2) determine if persistent patterns of assemblage structure exist; 3) assess regional and seasonal variation in the species composition; and 4) investigate the influence of environmental variables on the fish community of the LMR. This research will provide an opportunity to evaluate the fish community of the LMR following the implementation of the Joint Settlement Agreement (JSA).

Methods

The following section describes the study area, the research methods for the fish community surveys, lower Mokelumne River management history, and data analysis.

Study Area

The Mokelumne River, a snow-fed system, drains approximately 1,624 square kilometers (km²) of the central Sierra Nevada. Its headwaters originate in the Eldorado National Forest, some 65 kilometers (km) south of Lake Tahoe, at approximately 3,050 meters (m) above mean sea level. The LMR stretches 103 river kilometers (rkm) from Camanche Dam, the lowest non-passable dam on the LMR, to its confluence with the San Joaquin River within the central Sacramento-San Joaquin Delta (Delta) (Figure 1). The main tributaries to the LMR are Murphy Creek, Dry Creek, and the Cosumnes River. Between Thornton (New Hope Landing) and the San Joaquin River confluence, the Mokelumne River is connected to the Sacramento River via the Delta Cross Channel (DCC) and Georgiana Slough and to the central Delta via Little Potato and Little Connection sloughs.

Lower Mokelumne River

The LMR is uniquely situated in that there is a tidally influenced portion that flows into the Central Delta and an upstream portion, above tidal influence, regulated by dam management. For this report, the LMR is separated into four river reaches starting in the Delta and ending at Camanche Dam (Figure 1). Reach 1 extends upstream from the confluence of the San Joaquin River to the confluence of the Cosumnes River, approximately 56.3 km (35 mi). Reach 2 continues from the confluence of the Cosumnes River upstream to Woodbridge Irrigation District Dam (WIDD), approximately 24.5 km (15.2 mi). Reach 3 starts at WIDD and continues

upstream to the Elliott Road Bridge, approximately 23.8 km (14.8 mi). Reach 4 extends from the Elliott Road Bridge upstream to the base of Camanche Dam, approximately 16.5 km (10.2 mi). The reaches were delineated based on instream habitat characteristics unique to each reach.

In 2004, the riverine habitat of the LMR was delineated using aerial photographs. The majority of the LMR's configuration, at the time of the survey, was straight channel (>67%), channel bend (28%), and split channel (4%). The lower river was mainly comprised of flatwater habitat (81%), followed by bar complex (15%), and finally off-channel habitat (4%). Glide habitat was the most common habitat type in the LMR. Riffle habitat accounted for 0.06% of the total habitat mapped in 2004. However, with the implementation of ongoing spawning gravel enhancement projects, riffle habitat has increased over time. Riffle habitat has increased by roughly 1.7 hectares to a total of 2.3 hectares representing 0.25% of total river area (R. Bilski, personal communication, March 15, 2018). Tidal influence can reach 3.2 to 4.8 km upstream of the Interstate 5 Bridge near Thornton, CA to WIDD depending on the water year type, discharge rates, and the severity of the tides (Merz and Setka 2004). For this research, the sample site at Feist is considered the upper extent of tidal influence and located at rkm 47.1.

Land Use Changes

Lower Mokelumne River

The pre-disturbance LMR consisted of anastomosing channels that joined in the Sacramento flood basin (Florsheim and Mount 2003). Geomorphic processes and sediment deposition near the confluences with the Cosumnes River and Dry Creek created heterogeneous topography that included multiple connected channels, islands, and floodplain lakes. Upstream, the LMR varied from a single incised meandering channel in confined reaches to multiple channels in open areas with varying floodplain widths. Prior to anthropogenic disturbances, the complex hydrogeomorphic system of the Mokelumne River supported thriving aquatic and terrestrial fauna and had an extensive riparian forest (Florsheim and Mount 2003; Dawdy 1989; The Bay Institute 1998).

The Mokelumne River system has experienced significant land use changes in the past 200 years. Following European settlement, intact riparian vegetation was cleared for fuel and agriculture use. Floodplain wetlands were drained and levee construction was initiated to reduce the occurrence of flooding. Additional land use changes were caused from logging, in-stream

woody debris removal, grazing, flood control dredging, continued deforestation of riparian forests, agricultural expansion, urbanization, and dams. Substantial changes also included loss of channel-floodplain connectivity, mining disturbances, and the reduction of shallow anastomosing channels and edge habitat (Florsheim and Mount 2003).

Flow reductions in the Mokelumne River began during California's gold rush in order to supply river water to hydraulic mining operations (CALFED 2001). As water diversion for mining operations declined, irrigation and municipal diversions have increased. The first irrigation diversion on the LMR occurred in 1890 (CVRWPCB 1952). Currently the river has 16 major water impoundments, including Salt Springs (0.175 km³; completed 1931), Pardee (0.244 km³; completed 1929) and Camanche (0.515 km³; completed 1963) reservoirs. The East Bay Municipal Utility District (EBMUD) operates Pardee and Camanche reservoirs for municipal, hydropower, irrigation, recreation, and fisheries uses, in addition to providing flood control protection.

Sacramento-San Joaquin Delta

The Sacramento-San Joaquin Delta was a highly productive environment, which exhibited seasonal variability and changes in annual runoff. There were abundant marshlands, shallow tidal wetlands, and an intricate network of sloughs with abundant food supplies. Prior to 1850, the Delta was composed of a diverse abundance of native fish and wildlife (The Bay Institute 1998).

Major physical modifications to Delta habitats have taken place since the latter half of the 19th century, resulting in substantial structural changes. The Delta has been transformed from a seasonal brackish marsh into the hub of California's water supply network. Habitat alterations include the draining and channelization of 95% of the Delta land for agricultural and urban uses, thus eliminating 95% of marsh habitats (Atwater et al. 1979). In addition, sloughs have been dredged in order to deepen the channels to accommodate shipping lanes and/or the transfer of water to the pumping facilities in the south Delta. The intricate, diverse marsh landscape of the Delta has largely been replaced by a network of rip-rapped banks designed to facilitate agricultural and urban needs (Atwater et al. 1979). Limited shallow water habitats that do remain have largely been invaded by submerged aquatic vegetation, most notably by invasive, non-native Brazilian waterweed (*Egeria densa*), which has been linked to increased abundance of non-native fish, particularly sunfish (Centrarchids) (Brown and Michniuk 2007).

The San Francisco Estuary is acknowledged as one of the most invaded ecosystems in North America (Cohen and Carlton 1998). The loss of shallow marsh habitats has eliminated most historical fish and wildlife habitats. Food web productivity has been substantially altered via changes in trophic linkages (Jassby et al. 2002; Feyrer et al. 2003). Water exports have substantially altered the hydrodynamics and water quality of the Delta, negatively impacting fisheries through reduced habitat diversity, changed species distribution, and increased mortality (Kimmerer 2002; Kimmerer 2004; Feyrer et al. 2007). On an evolutionary timeline, changes to the Delta ecosystem have taken place rapidly, resulting in vastly different conditions from which native species evolved, and which now support species not native to the region.

Fish Community Survey

Historical fish community surveys performed in the LMR identified such native species as California roach, hitch, Pacific lamprey, Sacramento blackfish, Sacramento squawfish, Sacramento sucker, tule perch, and white sturgeon (Turner and Kelley 1966; Moyle 1976). Several other introduced fish species also utilize the Delta portion of the Mokelumne River system, including American shad, bullhead, golden shiner, largemouth bass, mosquitofish, smallmouth bass, striped bass, and white catfish (Hatton 1940; Turner 1966a; CDFG 1991). General LMR fish community species surveys were also sporadically implemented during the late 1980s and identified 9 native and 19 introduced fish species (Envirosphere Company 1988; BioSystems Analysis, Inc. 1992). EBMUD has been conducting fish community surveys in the LMR since 1997. Since 2001, the sites in the Delta portion of the LMR fish community survey have been consistently sampled. Detailed survey methods described below.

Survey Techniques

Selected nonwadeable and swift water (velocities > 0.91m/s) habitats were sampled with a Smith-Root SR-18E electrofishing boat. Sampled sites were chosen to best represent the habitat diversity and fish community of each reach in the LMR with the intent of detecting all of the species present in numbers proportional to actual in-river abundance. Electrofishing is recognized as the most effective technique for sampling river fish communities (Bagenal 1978; Plafkin et al. 1989). However, it does have some limitations. Electrofishing is biased towards sampling larger sized fish (Wiley and Tsai 1983) and variability in catchability has the potential to misrepresent abundance trends. Reynolds (1983) recommended against using electrofishing as

the sole technique in determining fish community structure. However, increasing the number of years analyzed should improve statistical power and incorporating spatial and temporal trends when assessing catchability should improve study conclusions (Hangsleben et al. 2013). Due to its broad application and general effectiveness, boat electrofishing provides a starting point from which to assess the fish community of the LMR.

Methods used were based on original guidelines described by Meador et al. (1993). Boat electrofishing surveys were conducted using three passes in each designated habitat: one pass on each bank followed by a pass in the middle of the channel. The cycle frequency was set at 120 pulses per second (pps) of direct current (although 60 pps was used once and 90 pps was used twice). Voltage was adjusted between 4-100% with an amperage target of 5 ± 1 amps. An automatic timer was used to measure the total length of time a specific site was sampled.

During the study period, numerous sites were sampled, both historical sample sites and intermittent sample sites. Intermittent sampling sites addressed specific questions or were incorporated into the surveys when access allowed. In addition, sampling frequency and effort were variable during this time period due to flows, access issues, equipment failures, and weather. Due to the variability in sampled sites, only sites sampled on a regular, annual basis were included in the analysis.

Captured fish were placed in the boat live well and processed in the field with the intent to minimize stress and reduce the likelihood of mortality due to handling. An aerator was placed in the live well when needed. All fish were identified to species and enumerated. The first 50 specimens of each species were measured to fork length or standard length, weighed, and examined for external anomalies which included, but were not limited to, abrasions, bacterial infections, deformities, fungus, and parasites. Post processing, fish were released at the sample site.

Lower Mokelumne River Management

The Federal Energy Regulatory Commission's November 27, 1998 Order Approving Settlement Agreement and Amending License approved the Joint Settlement Agreement (JSA) submitted by EBMUD, United States Fish and Wildlife Service, and California Department of Fish and Wildlife. The JSA included flow and non-flow measures aimed at protecting and maintaining reliable, high quality water supplies and protecting all water rights on the LMR

while protecting and enhancing conditions in the LMR for anadromous fisheries. In order to ensure that protection of the fishery resources in the LMR is balanced with other water resource demands, the parties involved in the JSA agreed upon specific minimum flow releases from Camanche Dam and expected flow below Woodbridge Irrigation District Dam.

The minimum flow releases were established based on the time of year, water year type, and Chinook salmon life stage requirements. Designated water year types were established for the October – March period based on storage levels in Camanche Reservoir and for the April – September period based on runoff projections. Water year types included Normal & Above, Below Normal, Dry, and Critically Dry. During this study period, there were 7 Normal & Above, 4 Below Normal, 4 Dry, and 1 Critically Dry water year types for the October thru March period; and 3 Normal & Above, 5 Below Normal, 7 Dry, and 1 Critically Dry water year types for the April thru September period (Figure 2).

Data Analysis

Fish community data were examined for spatial and temporal differences to investigate fish species composition in the LMR over a sixteen year period. Since the goal of the study was to assess instream dynamics of the LMR fish community, hatchery releases of Chinook salmon and steelhead that were sampled by our efishing surveys were excluded from the analyses. Steelhead are known to residualize within the LMR (Del Real et al. 2012) and adclipped steelhead not associated with any hatchery release were included in the dataset. To obtain a comparable index of fish abundance, catch-per-unit-effort (CPUE) was calculated for each fish species captured at each sample site. Due to differences in sample sizes, an automatic timer was used to measure the total sample time (effort) for each site to calculate CPUE (number of fish per second). The CPUE provides a comparable estimate of abundance which assumes that the rate of catch per sample is proportional to the stock size (Thompson et al. 1998). Therefore, changes in the CPUE over time can indicate changes in the density or population size of sampled species. In order to compare trends in species abundance across all seasons, an abundance index was calculated as the sum of mean seasonal CPUEs. Simple linear regression and ANOVA were used to evaluate annual changes in abundance indices of three categories: all species, native species, and introduced species.

Due to the high frequency of low species abundances and presence of zeros within the dataset, the CPUE data were $\log_{10}(x+1)$ transformed to balance the relative importance of common and rare species (McCune and Grace 2002). Following data transformations, species CPUEs were entered into the statistical software program PCORD V.6 (McCune and Mefford 2011) for analysis. Data were organized by sample units which represent individual sampling events based on survey date and sample site location. A nonparametric multi-response permutation procedure (MRPP) was used to analyze the data. MRPP was used to test for differences in fish species composition by region (tidal vs. non-tidal) and reach, using all detected fish species. Distance matrices were rank transformed before the test statistic was calculated.

MRPP produces a test statistic (T), an agreement statistic (A), and a p -value. The test statistic describes the separation between groups of entities with stronger negative values representing greater separation. The A statistic (chance-correlation within-group agreement) is a measure of within-group compared to among-group homogeneity. A significant p -value denotes that analyzed groups were more different than expected by chance. However, with large datasets, small effect size can produce statistical significance. Therefore, with MRPP, it is important to assess the A statistic to quantify the effect size as it is independent of sample size. Large A -values indicate strong differences among groups. A -values <0.1 are common for ecological community analyses while values ≥ 0.3 are relatively high (McCune and Grace 2002). Therefore, it can be said that MRPP provides an evaluation of the statistical significance and ecological significance when assessing whether differences within groups are less variable than expected given the observed range of variability among all groups.

Indicator species analysis (ISA) was used to identify species indicative of the composition of the LMR fish community. Species CPUE data were used in order to assess both the abundance and frequency of individual species within each sample unit by reach and defined by season. Only species that accounted for 1% or more of the total abundance were included in the analysis to reduce the influence of rare species.

Nonmetric multidimensional scaling (NMS) was used (Mather 1976; Kruskal 1964) to explore trends in fish species composition of the LMR. In order to capture the greatest species diversity and interactions, species life stages that contributed to 1% or more of the overall abundance were analyzed by season for each sample unit from the upper extent of tidal influence

to the base of Camanche Dam. Sample units included for analysis were limited to sites that could be used to assess the influence of LMR water management and the implementation of the JSA. Therefore, sites influenced by Delta management were excluded from this analysis. In 2006 and 2011, spring surveys had mean seasonal flow which exceeded 2,000 cfs and, due to these high flow events, were excluded from the NMS analysis as a result of reduced catchability. Including these surveys would have resulted in diminished ability to draw correlations of species response to environmental variables. Although two high flow events were excluded from the analyses, research has shown that these events can be advantageous for native species while discouraging introduced species abundance and distribution (Ford and Brown 2001).

Eight environmental variables (survey water temperature, mean seasonal water temperature, previous summer water temperature, survey flow, mean seasonal flow, previous spring flow, dissolved oxygen, and river kilometer) and one biological variable (proportion of introduced species per sample unit) were overlaid onto the final NMS ordination to identify influential variables structuring the LMR fish community. A correlation coefficient (r^2) value of 0.20 was used to indicate the influential species and variables within the final ordinations. Inclusion of the different measures of temperature and flow allowed for assessment of instantaneous responses to these variables in addition to seasonal and annual variability which could structure the LMR fish community. River kilometer (rkm) measures the distance from the sample site to the confluence with the San Joaquin River. The proportion of introduced species was included to assess the influence of introduced species on the composition of the fish community.

The Sørensen (Bray-Curtis) distance measure was used to ordinate samples based on species CPUEs. Species and sample scores greater than two standard deviations above the mean average distance were investigated further as potential outliers. Upon investigation, all potential sample outliers were retained in the final dataset as they incorporate the diversity of catch during seasonal surveys.

A random starting configuration was used to assess the relationship between sample units. Fifty runs with the real data were initially used to identify the appropriate dimensionality of the data. A Monte Carlo test was used to evaluate stress obtained from the original dataset with stress from randomized data. For each seasonal analysis, a three-dimensional NMS ordination was selected as it best represented the multivariate solution. Two hundred and fifty

iterations were used to verify the final solution. The stability criterion was set at 0.000010 to evaluate the instability of the solution.

Results

Twenty-eight electrofishing sample sites within four river reaches of the LMR were analyzed. A total of 53,421 fish were counted representing 1,107 sampling events during the sixteen year time period (Table 1). Thirty-seven fish species representing 15 taxa were collected. Families represented in electrofishing surveys include: silversides (Atherinopsidae), suckers (Catostomidae), sunfishes (Centrarchidae), herrings (Clupeidae), sculpins (Cottidae), minnows (Cyprinidae), surfperches (Embiotocidae), gobies (Gobiidae), bullhead catfishes (Ictaluridae), striped basses (Moronidae), smelts (Osmeridae), perches (Percidae), lampreys (Petromyzontidae), livebearers (Poeciliidae), and salmon and trout (Salmonidae). Hybrid *Lepomis* sunfish and unidentified juvenile black bass were excluded from species richness calculations, but included in abundance estimates.

Overall, 12 native species and 25 introduced species were identified in the LMR. Based on count, presence, and abundance data, the two most abundant fishes collected were native species: Sacramento sucker and prickly sculpin (Table 1; Figure 3). The next two most abundant fishes collected were: Chinook salmon and largemouth bass. Largemouth bass were detected in sample units more often than Chinook salmon and had a higher overall count (Figure 3). These four species accounted for 38% of the total catch. Native species represented 47% of total catch.

The tidally influenced portion of the LMR consistently had higher spring and summer temperatures than upstream sample sites. The highest average seasonal water temperatures, for both the tidal and non-tidal regions, were recorded during California's recent drought in the summers of 2014 and 2015. However, the third highest mean survey temperature recorded from the upper extent of tidal influence to the Camanche Dam occurred during elevated summer flows of the 2011 Normal & Above water year type which was also preceded by high spring flows. Seasonal peaks in flow on the LMR usually occurred during spring, except when water year class designation changed from Normal and Above in winter to Dry in spring (2001, 2007, and 2012) and during the critically dry water year of 2015 (Figure 2).

Annual

Abundance for all species in the entire study area increased significantly during the study period ($P < 0.0001$; $r^2 = 0.78$; $F = 41.99$; $df = 1$; Figure 4). Annual fish abundance indices within both the tidal ($P < 0.0001$; $r^2 = 0.83$; $F = 64.08$; $df = 1$) and non-tidal ($P = 0.011$; $r^2 = 0.43$; $F = 8.97$; $df = 1$) regions each also significantly increased. These trends were largely driven by the differences in native and introduced species abundances within the tidal and non-tidal regions.

For native fish species, annual abundance increased significantly ($P = 0.001$; $r^2 = 0.60$; $F = 18.02$; $df = 1$; Figure 4). This increase was a result of increases of native species abundance indices within the non-tidal region of the LMR ($P = 0.003$; $r^2 = 0.54$; $F = 14.22$; $df = 1$) as annual native fish abundance indices within the tidal region showed no significant change ($P = 0.676$; $r^2 = 0.01$; $F = 0.18$; $df = 1$). For introduced species, abundance also increased significantly during the study period ($P < 0.0001$; $r^2 = 0.85$; $F = 65.93$; $df = 1$; Figure 4) but this was a result of annual increases in the tidal region of the LMR ($P < 0.0001$; $r^2 = 0.83$; $F = 65.43$; $df = 1$). Introduced species abundance in the non-tidal region were not significantly different through time ($P = 0.118$; $r^2 = 0.19$; $F = 2.83$; $df = 1$).

Regional

Differences in the LMR fish community between the tidal and non-tidal regions were significant during the study period ($T = -463.334$; $A = 0.292$; $p < 0.0001$). Regional fish composition between the tidal and non-tidal regions of the LMR was also significantly different for each season (Table 2).

The tidally influenced portion of the LMR had greater overall species richness ($n = 36$) than the non-tidal portion ($n = 31$). The tidally influenced portion of the LMR also had both greater native species and introduced species richness than the non-tidal portion. Differences by region in native species richness were due to the detection of Delta smelt, Sacramento blackfish, and Sacramento splittail in the tidally influence portion of the LMR. Differences by region in introduced species richness were due to the detection of bigscale logperch, fathead minnow, and yellowfin goby in the tidal portion and kokanee in the non-tidal portion of the LMR. Kokanee are believed to be introduced to the LMR from water releases from Camanche Reservoir.

Categorical analysis of all species abundance determined that abundance was greater in the non-tidal portion of the LMR compared to the tidal portion. When analyzing native species, the abundance index was greater in the non-tidal portion (0.072) of the LMR compared to the tidal portion (0.021) while the abundance index of introduced species was greater in the tidal portion (0.052) of the LMR compared to the non-tidal portion (0.037). Seasonally, this trend is consistent and depicted in Figure 5. When the non-tidal portion of the LMR was assessed independently, native species abundance was greater than introduced species abundance. Conversely, introduced species abundance was greater in the tidal region of the LMR.

In the tidal region of the LMR, bluegill, redear sunfish, and largemouth bass were the most abundant and common species detected. In the non-tidal region, hitch, striped bass, and Chinook salmon were the three most abundant species. However, Sacramento sucker, prickly sculpin, and steelhead, followed by Chinook salmon and hitch, were encountered most frequently representing a broad distribution throughout the sample area (Figure 6). The elevated abundance of striped bass was primarily due to the concentration of striped bass in the basin below WIDD, although a few detections did occur upstream.

Reach

Fish species composition was significantly different between each sample reach ($T=324.974$; $A=0.355$; $p<0.0001$). In addition, species composition within designated river reaches remained significantly different when analyzed by season (Table 3). However, pairwise comparisons show some reaches have similar species composition. When season was not incorporated into the analysis, Reaches 4 and 3 and Reaches 1 and 2 shared similarities in overall species composition and were not distinctly different, based on their effect size ($A=0.050$; $A=0.093$, respectively). This demonstrates that WIDD represents a division in overall species composition as Reaches 1 and 2 are located downstream of WIDD and Reaches 3 and 4 are located upstream. However, when abundance data was analyzed separately for each season, the species compositions only within Reaches 4 and 3 were not significantly different (based on the low effect size).

Reach 4 had the greatest overall mean abundance when compared to downstream reaches. Differences in reach abundances were largely driven by differences in native and introduced species abundances (Figure 7). The upper reaches (Reach 4 and Reach 3) consistently

had greater mean abundance of native species during each seasonal survey. Within Reach 2, native species were more abundant during winter and spring while introduced species became dominant during the summer. Reach 1 had the lowest mean abundance of native species and the greatest abundance of introduced species each season.

Species abundance and distribution within survey reaches reinforce the trends described above. Within Reach 1, as within the tidal portion of the LMR, bluegill, redear sunfish, and largemouth bass are the most abundant and common species (Figure 8). Within Reach 2, threadfin shad, inland silverside, and gambusia are the most abundant species while Sacramento suckers, spotted bass, and redear sunfish are the most common (Figure 9). With the influence of Lodi Lake within Reach 3, carp had the highest abundance index. This is due to a relatively few large catches of carp within sample units inundated by Lodi Lake in the Spring and Summer. Overall, carp were encountered only 1% of the time in Reach 3. Prickly sculpin, Chinook salmon, and tule perch were also abundant within Reach 3 with native species representing 80% of all encountered species. In Reach 4, hitch, Chinook salmon, and prickly sculpin were the most abundant species while prickly sculpin, Sacramento suckers, and steelhead were the most common.

Indicator species analyses performed by reach and grouped by season reflect changes in the relative importance of different species throughout the LMR (Table 4). Within Reach 1, the majority of indicator species are introduced species. However, there are several native species including Chinook salmon, prickly sculpin, Sacramento pikeminnow, Sacramento Sucker, and Tule perch. Sacramento splittail, striped bass, and redeye bass are included as indicator species only within Reach 2. In Reach 3, more native species are included as indicator species than introduced species exhibiting the dominance of native species in sample units upstream of the influence of Lodi Lake. Pacific lamprey are only included as an indicator species within Reach 3. Within Reach 4, half of the indicator species are natives while the other half are introduced species. Chinook salmon and largemouth bass are the only species identified as indicator species for each reach within the LMR demonstrating their broad dispersal, overlapping distribution, and persistent presence throughout the Mokelumne River.

Spatial and Temporal Trends

The ordination correlation coefficients depict the seasonal shift in species abundance trends and their influence upon the fish assemblage within the LMR downstream to rkm 47. Correlation coefficients for winter express a final ordination influenced by the native species: parr and adult steelhead ($r^2=0.50$ and 0.21 , respectively) and adult Sacramento sucker ($r^2=0.34$). The spring and summer fish species assemblages were influenced by both native and introduced species. In spring, ordination was influenced by the abundance trends of Chinook salmon parr ($r^2=0.38$), juvenile hitch ($r^2=0.25$), and juvenile largemouth bass ($r^2=0.21$) while the summer ordination was influenced by adult Sacramento suckers ($r^2=0.36$), adult prickly sculpin ($r^2=0.30$), steelhead parr ($r^2=0.28$), juvenile largemouth bass ($r^2=0.28$), and juvenile and adult striped bass ($r^2=0.21$ and 0.20 , respectively).

Throughout the sampled seasons, river kilometer and the proportion of introduced species present within sampled sites were highly correlated with the fish species composition in the LMR (Table 5). Survey water temperature at sampled sites and previous summer temperatures were also identified as variables that are strongly correlated with the structure of the spring and summer LMR fish community. In addition, average seasonal river temperature was highly correlated with the abundance and distribution of fish species in the LMR, but only during summer.

Discussion

Stream fish assemblages may form distinct groups based on shared adaptations to environmental variables structured along a longitudinal gradient and influenced by temporal changes (Matthews 1998). Today the Mokelumne River fish assemblage is a mix of native and introduced species. Although spatial and temporal differences in species composition were observed due to both biotic and abiotic factors, a pattern of fish assemblage which follows a distinct seasonal progression was observed largely based on species life history strategies. This is not to say that the LMR fish community is in a stable state. Annual increases of introduced species abundance in the tidal region and increased abundance of native species within the non-tidal region could indicate a shifting fish species composition.

The Sacramento-San Joaquin Delta is one of, if not the most studied aquatic systems in the world. Many studies have been completed in describing the fish species composition within this region (Mahardja et al. 2017). Our study is unique in that it describes the fish community throughout the year of a freshwater river system that flows directly into the central Delta. As a result, the LMR is comprised of two distinct fish communities with distinct population structures above and below WIDD. Above WIDD, the river is managed largely by operations of upstream reservoirs and supports the dominance of native species. Downstream of WIDD, the LMR is influenced more by Delta management and consists predominantly of introduced species. Since we were not looking to duplicate work completed in the Delta and interested in how reservoir management and the JSA influence the fish community of the LMR, analyses of the influential variables structuring the fish community of the LMR were limited to upstream of tidal influence.

Even with the establishment of introduced species above WIDD, native species remain dominant and, at times, mimic historical distributions structured along rkm and instream temperature, albeit on a smaller scale. However, the establishment of introduced species poses a continual risk to native species populations through competition and predation, which could be intensified if California experiences increased or prolonged drought conditions in the future. In addition, the establishment of introduced species could represent a change in habitat conditions which could contribute to limiting native species distributions. The importance of rkm represents a mix of factors including temperature, flow, and habitat availability and complexity. Temperature also proved to be an important variable structuring the fish community of the LMR. Results indicate that species are not just reacting to instantaneous responses to spring and summer daily temperatures, but are structured by seasonal and annual fluctuations.

Flow was not identified as an influential variable structuring the LMR fish community. This study was conducted following the implementation of JSA minimum flow requirements to support Chinook salmon life stages. While the current flow regime appears adequate, flow can influence such variables as temperature and habitat availability and, as such, should remain an important variable to consider. With limited critically dry water year designations, further analyses will need to be completed if and when the Mokelumne River is operated under additional critically dry water year types.

Management goals for the LMR should be focused on sustainable supplies of water while restoring and maintaining diverse migratory and resident native fish and wildlife populations.

Dam management can be used as a tool to preserve and restore native species. In the Cosumnes River, a tributary to the LMR, introduced species dominated the majority of the river with predatory redeye bass widely distributed throughout the study area (Moyle et al. 2003). Unlike the LMR, the Cosumnes River does not have a major dam which can alter the effects of water diversions and the invasion of introduced species.

The study results indicate that management actions designed around Chinook salmon life stage requirements support native fishes and can create the conditions for them to remain dominant, even with the annual presence of introduced species. However, the fish community in the non-tidal portion of the LMR above WIDD is particularly vulnerable to further introduced species invasion. For example, in the spring following the only critically dry water year designations on the LMR, the first redeye bass were detected upstream of WIDD. The coldwater pool in Camanche Reservoir, is utilized to support cold-water native species, and can also discourage warm-water introduced species. As this pool can be a finite resource, it needs to be managed annually to meet specific fisheries objectives.

Successful native fish species conservation in the Central Valley necessitates integrated management of rivers, not solely as water supplies or conveyance channels, but also as dynamic ecosystems (Nehlsen et al. 1992; Bottom 1995; Yoshiyama et al. 1998). Essential to this goal is a comprehensive monitoring and applied research program which informs and guides adaptive management to strike a balance between water and power supply operations, flood control, hatchery operations, and ecosystem restoration efforts.

Acknowledgements

We would like to thank Charles Hunter, Steve Boyd, Robyn Bilski, and James Jones for their hard work and field support. We would also like to thank Terry Cummings for her data entry and data verification assistance and Michelle Workman and Jose Setka for their ongoing support and technical expertise. In addition, we would like to acknowledge all of the assistance we have received over the years, from numerous individuals too many to name here, which has enabled this study to continue.

Literature Cited

Aparico, E., M.J. Vargas, J.M. Olmo, and A. de Sostoa. 2000. Decline of native freshwater fishes in a Mediterranean watershed on the Iberian Peninsula: A quantitative assessment.

Environmental Biology of Fishes 59: 11–19.

Atwater, B.F., S.G. Conard, J.N. Dowden, C.W. Hedel, R.L. MacDonald, and W. Savage 1979. History, landforms, and vegetation of the estuary's tidal marshes. In: T.J. Conomos, editor. *San Francisco Bay: the urbanized estuary*. San Francisco (CA): Pacific Division of the American Association for the Advancement of Science. p 347–385.

Bagenal, T. 1978. *Methods for assessment of fish production in fresh waters*. Oxford, Blackwell Scientific Publications. p 365.

Bain, M.B., J.T. Finn, and H.E. Brooke. 1988. Stream flow regulation and fish community structure. *Ecology* 69: 382–392.

BioSystems Analysis, Inc. 1992. *Lower Mokelumne River Management Plan*. Tiburon, California.

Bottom, D.L. 1995. Restoring salmon ecosystems, myth and reality. *Restoration and Management Notes*: 64: 37–40.

Brown, L.R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* 57:251–269.

Brown, L.R. 2003. Will tidal wetland restoration enhance populations of native fishes? In: Brown LR, editor. *Issues in San Francisco Estuary Tidal Wetlands Restoration*. San Francisco Estuary and Watershed Science 1 (1). Article 2. Available: <http://repositories.cdlib.org/jmie/sfew/vol1/iss1/art2> (November 2003).

Brown, L.R., and T.J. Ford. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. *River Research and Applications* 18:331–342.

Brown, L.R., and D. Michniuk. 2007. Littoral fish assemblages of the alien-dominated Sacramento–San Joaquin Delta, California, 1980–1983 and 2001–2003. *Estuaries and Coasts* 30:186–200.

Brown, L.R., and P.B. Moyle. 1997. Invading species in the Eel River, California: Successes, failures, and relationships with resident species. *Environmental Biology of Fishes* 49: 271–291.

Brown, L.R., and P.B. Moyle. 2005. Native fish communities of the Sacramento-San Joaquin watershed, California: a history of decline. In: F. Rinne, R. Hughes, R. Calamusso, editors. *Fish communities of large rivers of the United States*. American Fisheries Society, Bethesda, Maryland. p 75-98.

CALFED Bay Delta Program. 2001. CALFED Ecosystem Restoration Program Draft Stage 1 Implementation Plan. p 173.

California Department of Fish and Game (CDFG). 1991. Lower Mokelumne River Fisheries Management Plan. Department of Fish and Game, Streamflow Requirements Program, Sacramento, California.

Central Valley Regional Water Pollution Control Board (CVRWPCB). 1952. Pollution study: Mokelumne River, San Joaquin River watershed. Sacramento, California. p 38.

Cohen, A.N., and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555-558.

Covich, A. 1993. Water and ecosystems. Pages 40–55. In: P.H. Gleick, editor. *Water in Crisis: A guide to the world's fresh water resources*. Oxford University Press, New York.

Dawdy, D.R. 1998. Feasibility of mapping riparian forests under natural conditions in California. In: California Riparian Systems Conference Proceedings. Davis, CA, September 22-24, 1988. Technical Report PSW-110:194-203.

Del Real, S.C., M. Workman M, and J. Merz. 2012. Migration characteristics of hatchery and natural-origin *Oncorhynchus mykiss* from the lower Mokelumne River, CA. Environ Biol Fish. 94:363. doi:[10.1007/s10641-011-9967-z](https://doi.org/10.1007/s10641-011-9967-z)

Envirosphere Company. 1988. Lower Mokelumne River Fisheries Study. Draft report prepared for the California Department of Fish and Game, Region II, Rancho Cordova.

Feyrer, F., B. Herbold, S.A. Matern, and P.B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67:277-288.

Feyrer, F., M. Nobriga, and T. Sommer. 2007. Multi-decadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 136:1393–1405.

Florsheim, J.L., and J.F. Mount. 2003. Floodplain restoration potential on the lower Mokelumne River, California. Center for Integrated Watershed Science and Management, Davis, California. p 31.

Ford, T. J., and L. R. Brown. 2001. Distribution and abundance of Chinook salmon and resident fishes of the lower Tuolumne River, California. Pages 253–304. In: R.L. Brown, editor. Contributions to the biology of Central Valley salmonids, Volume 2. California Department of Fish and Game, Fishery Bulletin 179.

Hangsleben, M.A., M.S. Allen, and D.C. Gwinn. 2013. Evaluation of Electrofishing Catch per Unit Effort for Indexing Fish Abundance in Florida Lakes. *Transactions of the American Fisheries Society*, 142:1, 247-256.

Hatton, R.S. 1940. Progress report on the Central Valley Fisheries Investigations, 1939. *California Fish and Game* 26(4) 334-373.

Herren, J.R., and S.S. Kawasaki. 2001. Inventory of water diversions in four geographic areas in California's Central Valley. Pages 343–355. In: R.L. Brown, editor. *Contributions to the Biology of Central Valley Salmonids, Volume 2*. California Department of Fish and Game, Fish Bulletin 179.

Hurst, T.P., K.A. McKown, and D.O. Conover. 2004. Interannual and long-term variation in the nearshore fish community of the mesohaline Hudson River Estuary. *Estuaries* 27:659-669.

Jassby, A.D., J.E. Cloern, and B.E. Cole. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography* 47:698-712.

Karr, J.R. 1991. Biological integrity – a long-neglected aspect of water resource management. *Ecological Applications* 1:66-84.

Kimmerer, W.J. 2002. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. *Estuaries* Vol. 25, No. 6B. p. 1275–1290.

Kimmerer, W.J. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological response. *San Francisco Estuary and Watershed Science*. Vol. 2, Issue 1 (February 2004), Article 1. Available: <http://repositories.cdlib.org/jmie/sfews/vol2/iss1/art1>.

Kruskal, J.B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1-27.

Kruskal, J.B. 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115-129.

Ligon, F.K., W.E. Dietrich, and W.J. Trush. 1995. Downstream ecological effects of dams. A geomorphic perspective. *Bioscience* 45:183-192.

Mahardja B., M.J. Farruggia, B. Schreier, T. Sommer. 2017. Evidence of a Shift in the Littoral Fish Community of the Sacramento-San Joaquin Delta. *PLoS ONE* 12(1): e0170683.

Marchetti, M.P., and P.B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. *Ecological Applications* 11: 530–539.

Matern, S.A., P.B. Moyle, and L.C. Pierce. 2002. Native and alien fishes in a California estuarine marsh: twentyone years of changing assemblages. *Transactions of the American Fisheries Society* 131:797-816.

Mather, P.M. 1976. *Computational methods of multivariate analysis in physical geography*. J. Wiley & Sons, London. p 532.

Matthews, W.J. 1998. *Patterns in Freshwater Fish Ecology*, Chapman & Hall, New York. p 756.

McCune, B., and M.J. Mefford. 2011. *PC-ORD. Multivariate Analysis of Ecological Data. Version 6*. MjM Software, Gleneden Beach, Oregon.

McCune, B., and J.B. Grace. 2002. *MjM Software Design*. Gleneden Beach, Oregon.

Meador, M.R., T.F. Cuffney, and M.E. Gurtz. 1993. *Methods for sampling fish communities as a part of the National Water-Quality Assessment Program: U.S. Geological Survey Open-File Report 93-104*. p 40.

- Merz, J.E., and J.D. Setka. 2004. Riverine habitat characterization of the lower Mokelumne River, California. East Bay Municipal Utility District, Lodi, California.
- Micheli, E.R., J.W. Kirchner, and E.W. Larsen. 2004. Quantifying the effect of riparian forest versus agricultural vegetation on river meander migration rates, central Sacramento River, California, USA. *River Research and Applications* 20(5):537 – 548.
- Moyle, P.B. 1976. *Inland fishes of California*. University of California Press, Berkeley. p 405.
- Moyle, P.B. 1994. Biodiversity, biomonitoring, and the structure of stream fish communities. Pages 171–186. In: S.L. Loeb, A. Spacie, editors. *Biological Monitoring of Aquatic Systems*, Lewis Publishers, Boca Raton.
- Moyle, P.B. 2002. *Inland fishes of California, revised and expanded*. University of California Press, Berkeley. p 502.
- Moyle, P.B., P.K. Crain, K. Whitener, and J.F. Mount. 2003. Alien fishes in natural streams: Fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A. *Environmental Biology of Fishes* 68:143–162.
- Nehlsen, W., J.A. Lichatowich, and J.E. Williams. 1992. Pacific salmon and the search for sustainability. *Renewable Resources* 10: 20–26.
- Nobriga, M., and F. Feyrer. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science*. Available from: <http://escholarship.org/uc/item/387603c0>.
- O'Connell, M.T., R.C. Cashner, and C.S. Schieble. 2004. Fish assemblage stability over fifty years in the Lake Ponchartrain Estuary: comparisons among habitats using canonical correspondence analysis. *Estuaries* 27:807-817.

Plafkin, J.L., M.T. Barbour, K.D. Porter, S.K. Gross, and R.M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: U.S. Environmental Protection Agency, EPA/444/4-89-001.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow paradigm. *BioScience* 47:769–784.

Postel, S. 1996. *Dividing the waters: food security, ecosystem health, and the new politics of scarcity*. Worldwatch Institute, Washington, D.C.

Postel, S. 2000. Entering an era of water scarcity: the challenges ahead. *Ecological Applications* 10:941-948.

Postel, S.L., and S. Carpenter. 1997. Freshwater ecosystem services. Pages 195–214. In: G.C. Daily, editor. *Nature's Services: Societal dependence on natural ecosystems*. Island Press, Washington D.C.

Reynolds, J.B. 1983. Electrofishing. In: L.A. Nielsen, D.L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland. p.147–163.

Sala, O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.

The Bay Institute. 1998. *From the sierra to the sea*. The Bay Institute, San Rafael, California.

Thompson, W.L., G.C. White, and C. Gowan. 1998. *Monitoring vertebrate populations*. Academic Press, Inc., San Diego, California.

Turner, J.L. 1966a. Distribution of food habitats of ictalurid fishes in the Sacramento-San Joaquin Delta. Pages 154-159. In: J L. Turner, D.W. Kelley, editors. Ecological studies of the Sacramento-San Joaquin Delta, Part II. California Department of Fish and Game, Fish Bulletin 136.

Turner, J.L., and D.W. Kelley, editors. 1966. Ecological studies of the Sacramento-San Joaquin Delta, Part II. California Department of Fish and Game, Fish Bulletin 136.

Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo. 1997. Human domination of the earth's ecosystems. *Science* 277:494-499.

Walters, C. J. 2001. Adaptive management of renewable resources. The Blackburn Press, Caldwell, New Jersey.

Walters, C. J., and S.J.D. Martell. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.

Walters, C.J., V. Christensen, S.J. Martell, and J.F. Kitchell. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES Journal of Marine Science* 62:558-568.

Ward, J.V., and J.A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29-42. In: T.D. Fontaine, S.M. Bartell, editors. Dynamics of Lotic Ecosystems, Ann Arbor Science Publications, Ann Arbor, MI.

Waite, I.R., and K.D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. *Transactions of the American Fisheries Society* 129: 754-770.

Wiley, M.L., and C. Tsai. 1983. The relative efficiencies of electrofishing vs. seines in Piedmont streams of Maryland. *North American Journal of Fisheries Management*, v. 3. p 243-253.

Whitfield, A.K., and M. Elliott. 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. *Journal of Fish Biology* 61 (Supplement A):229-250.

Yoshiyama, R.M., F.W. Fisher, and P.B. Moyle. 1998. Historical abundance and decline of Chinook salmon in the central valley region of California. *North American Journal of Fisheries Management* 18: 487–521.

Table 1 Origin, total catch, total presence in sample units, and overall abundance based on CPUE for all species captured during LMR fish sampling between January 2001 and May 2016.

Species	Species Code	Scientific Name	Origin	Total Count	Sample Units Presence	Overall Abundance
American Shad	AMS	<i>Alosa sapidissima</i>	Introduced	497	70	1.244
Bigscale Logperch	BSLP	<i>Percina macrolepida</i>	Introduced	77	39	0.145
Black Bass	BBAS	<i>Micropterus</i>	Introduced	71	24	0.156
Black Bullhead	BLBH	<i>Ameiurus melas</i>	Introduced	12	7	0.032
Black Crappie	BCP	<i>Pomoxis nigromaculatus</i>	Introduced	230	151	0.629
Bluegill	BG	<i>Lepomis macrochirus</i>	Introduced	4534	511	11.176
Brown Bullhead	BBH	<i>Ameiurus nebulosus</i>	Introduced	63	48	0.139
Channel Catfish	CCAT	<i>Ictalurus punctatus</i>	Introduced	43	32	0.078
Chinook Salmon	CS	<i>Oncorhynchus tshawytscha</i>	Native	4243	468	13.197
Common Carp	CARP	<i>Cyprinus carpio</i>	Introduced	647	217	1.435
Delta Smelt	DS	<i>Hypomesus transpacificus</i>	Native	4	4	0.011
Fathead Minnow	FHM	<i>Pimephales promelas</i>	Introduced	1	1	0.002
Gambusia	GAM	<i>Gambusia affinis</i>	Introduced	278	41	1.127
Golden Shiner	GS	<i>Notemigonus crysoleucas</i>	Introduced	1702	325	4.973
Goldfish	GF	<i>Carassius auratus</i>	Introduced	230	93	0.806
Green Sunfish	GSF	<i>Lepomis cyanellus</i>	Introduced	328	175	1.027
Hitch	HTC	<i>Lavinia exilicauda</i>	Native	2555	301	10.990
Inland Silverside	ISS	<i>Menidia beryllina</i>	Introduced	2576	177	5.032
Kokanee	KOK	<i>Oncorhynchus nerka</i>	Introduced	18	12	0.034
Largemouth Bass	LMB	<i>Micropterus salmoides</i>	Introduced	5193	607	12.808
Lepomis hybrid	LAPX	<i>Lepomis</i>	Introduced	119	78	0.264
Pacific Lamprey	PLAM	<i>Lampetra tridentata</i>	Native	542	141	1.210
Pacific Staghorn Sculpin	PSS	<i>Leptocottus armatus</i>	Native	11	7	0.033
Prickly Sculpin	PSCLP	<i>Cottus asper</i>	Native	5430	704	14.810
Redear Sunfish	RSF	<i>Lepomis microlophus</i>	Introduced	4804	480	11.481
Redeye bass	RDEB	<i>Micropterus coosae</i>	Introduced	693	168	1.496
Sac. Pikeminnow	SPKMW	<i>Ptychocheilus grandis</i>	Native	1089	331	2.722
Sacramento Blackfish	SCB	<i>Orthodon microlepidotus</i>	Native	59	24	0.130
Sacramento Splittail	SPT	<i>Pogonichthys macrolepidotus</i>	Native	95	23	0.195
Sacramento Sucker	SSKR	<i>Catostomus occidentalis</i>	Native	5700	833	14.821
Smallmouth Bass	SMB	<i>Micropterus dolomieu</i>	Introduced	27	16	0.046
Spotted Bass	SPB	<i>Micropterus punctulatus</i>	Introduced	3224	494	7.403
Steelhead	STH	<i>Oncorhynchus mykiss</i>	Native	3485	487	9.011
Striped Bass	STB	<i>Morone saxatilis</i>	Introduced	971	159	2.078
Threadfin Shad	TFS	<i>Dorosoma petenense</i>	Introduced	1484	85	3.055
Tule Perch	TP	<i>Hysteroecarpus traski</i>	Native	1983	344	5.631
Warmouth	WAR	<i>Lepomis gulosus</i>	Introduced	248	87	0.711
White Catfish	WCAT	<i>Ameiurus catus</i>	Introduced	30	28	0.067
Yellowfin Goby	YFG	<i>Acanthogobius flavimanus</i>	Introduced	125	55	0.255

Table 2 Regional MRPP analysis of the LMR seasonal fish species composition.

Season	T	A	p
Winter	-159.725	0.305	<0.001
Spring	-164.122	0.302	<0.001
Summer	-152.545	0.318	<0.001

Table 3 Reach MRPP analysis by season.

Season	T	A	p
Winter	-105.737	0.351	<0.001
Spring	-117.634	0.376	<0.001
Summer	-116.019	0.421	<0.001

Table 4 Indicator species analysis results. Dashes (-) indicate that a species was not included in reach analysis. Bold p-values denote indicator species. P-values included in the table were derived using randomization (Monte Carlo) technique.

Species Name	Origin	Reach 1	Reach 2	Reach 3	Reach 4
American Shad	Introduced	0.0002	0.0002	-	-
Black Crappie	Introduced	0.0022	-	-	-
Bluegill	Introduced	0.0256	0.8218	0.7463	0.0332
Common Carp	Introduced	0.0002	0.3731	0.0274	-
Chinook Salmon	Native	0.0002	0.0002	0.0002	0.0002
Gambusia	Introduced	-	0.0028	-	0.3885
Goldfish	Introduced	-	-	-	0.0846
Golden Shiner	Introduced	0.0002	0.3655	0.074	0.2785
Green Sunfish	Introduced	0.2358	-	-	0.2062
Hitch	Native	-	-	0.0832	0.118
Inland Silverside	Introduced	0.0002	0.5247	-	-
Largemouth Bass	Introduced	0.0002	0.0442	0.0002	0.016
Pacific Lamprey	Native	-	0.1276	0.0154	0.8058
Prickly Sculpin	Native	0.0288	0.937	0.053	0.0002
Redeye bass	Introduced	0.128	0.0236	-	-
Redear Sunfish	Introduced	0.023	0.0168	-	0.6541
Spotted Bass	Introduced	0.0002	0.0562	0.0002	0.0002
Sac. Pikeminnow	Native	0.0004	0.0794	0.0346	0.1224
Sacramento Splittail	Native	-	0.0004	-	-
Sacramento Sucker	Native	0.0002	0.2096	0.0152	0.2346
Striped Bass	Introduced	0.2082	0.0002	-	-
Steelhead	Native	-	0.012	0.001	0.0012
Threadfin Shad	Introduced	0.0002	0.0004	-	-
Tule Perch	Native	0.0004	0.9592	0.0002	0.1508
Warmouth	Introduced	0.0598	-	-	-

Table 5 Pearson's r-sq correlations from the non-metric multidimensional scaling analysis. Values represent combined correlation coefficients of biotic and abiotic variables for each ordination.

Variables	Winter			Spring			Summer		
	Axis 1 & 2	Axis 2 & 3	Axis 1 & 3	Axis 1 & 2	Axis 2 & 3	Axis 1 & 3	Axis 1 & 2	Axis 2 & 3	Axis 1 & 3
Dissolved Oxygen	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00
Introduced Species (%)	0.31	0.31	0.01	0.31	0.21	0.07	0.57	0.02	0.57
Mean Seasonal Flow	0.02	0.02	0.02	0.04	0.02	0.00	0.03	0.01	0.02
Mean Seasonal Temperature	0.11	0.01	0.11	0.13	0.15	0.03	0.21	0.03	0.21
Previous Spring Flow	0.01	0.01	0.00	0.01	0.02	0.00	0.01	0.01	0.01
Previous Summer Temperature	0.16	0.07	0.16	0.14	0.20	0.05	0.20	0.06	0.21
RKM	0.35	0.18	0.31	0.15	0.24	0.04	0.44	0.13	0.42
Survey Flow	0.03	0.02	0.03	0.04	0.01	0.00	0.04	0.03	0.03
Survey Temperature	0.02	0.03	0.04	0.21	0.21	0.00	0.45	0.01	0.45

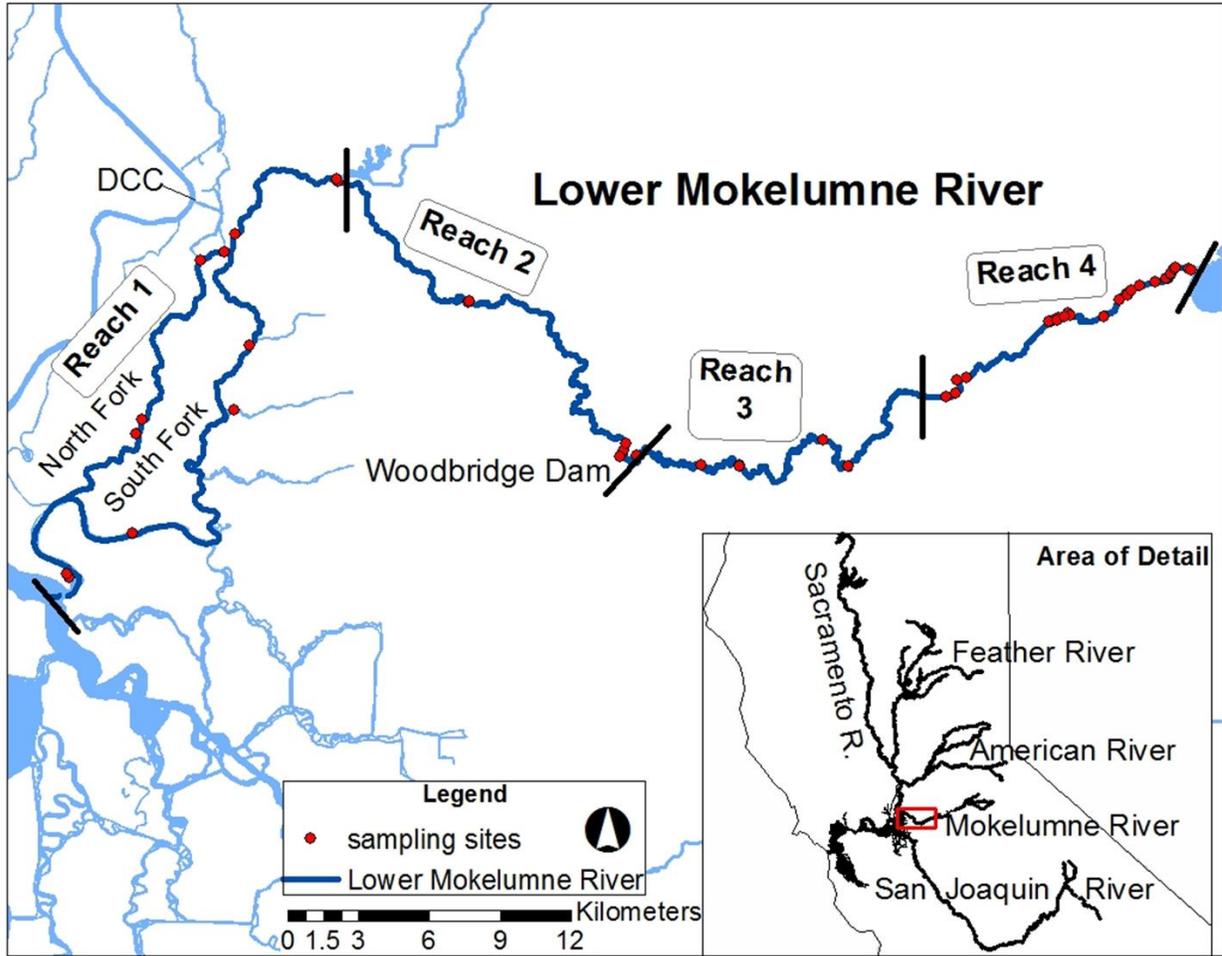


Figure 1 Lower Mokelumne River fish community survey reaches and sampled sites.

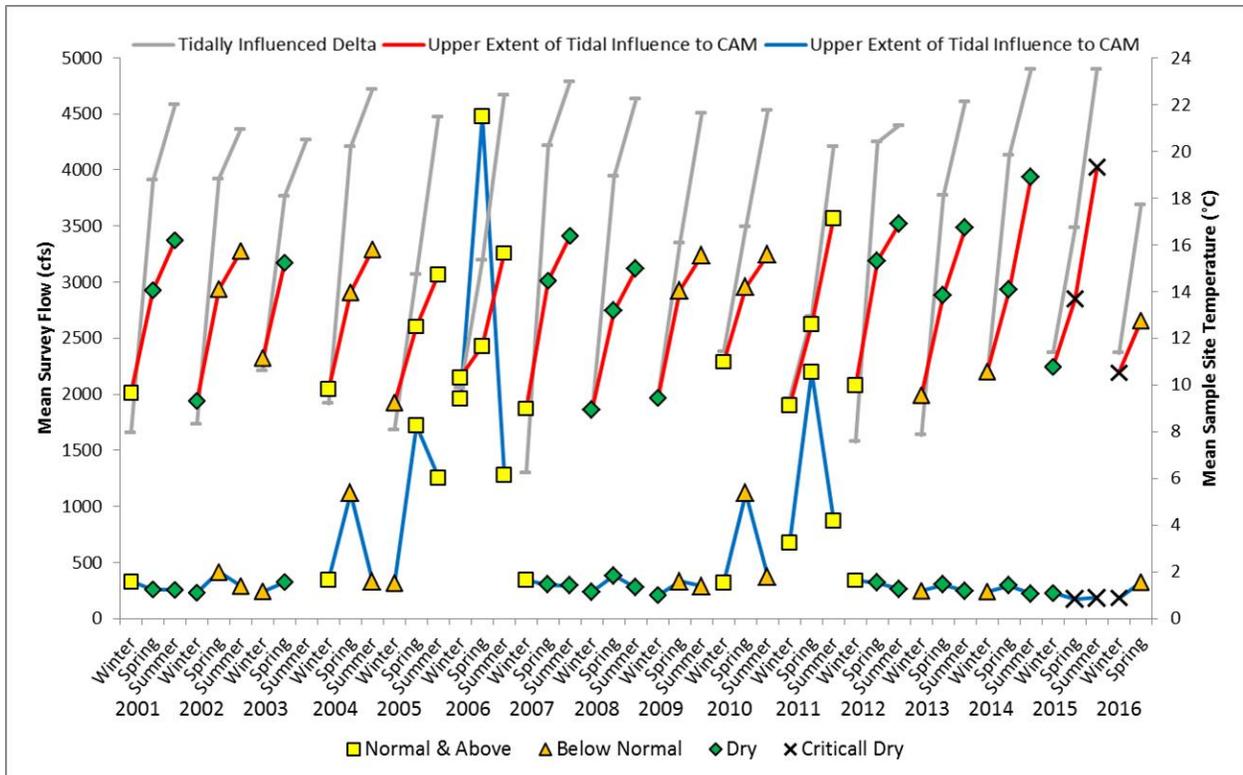


Figure 2 Data marks represent sampling event mean flow and temperature conditions. Flow data was acquired from below WIDD and Camanche Dam gauges while temperatures were recorded at each site on the day of the survey. Blue lines represent seasonal LMR flow trend. Grey and red lines represent seasonal temperature trend. JSA water year type designations are overlaid onto data marks from sample sites included in the NMS analyses from the Feist Ranch (rkm 47.1) upstream to Camanche Dam.

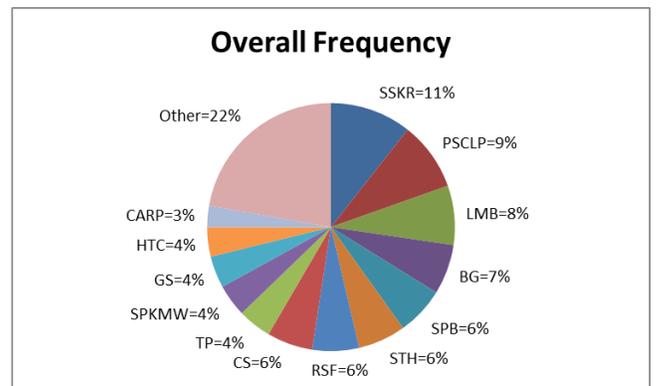
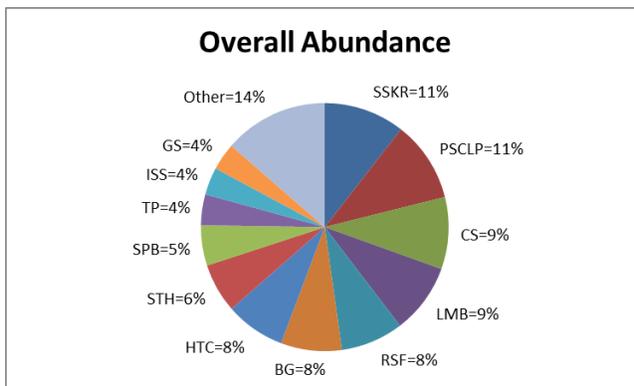


Figure 3 Species overall abundance and sample site frequency. “Other” includes species which make up 2% or less of the overall species composition.

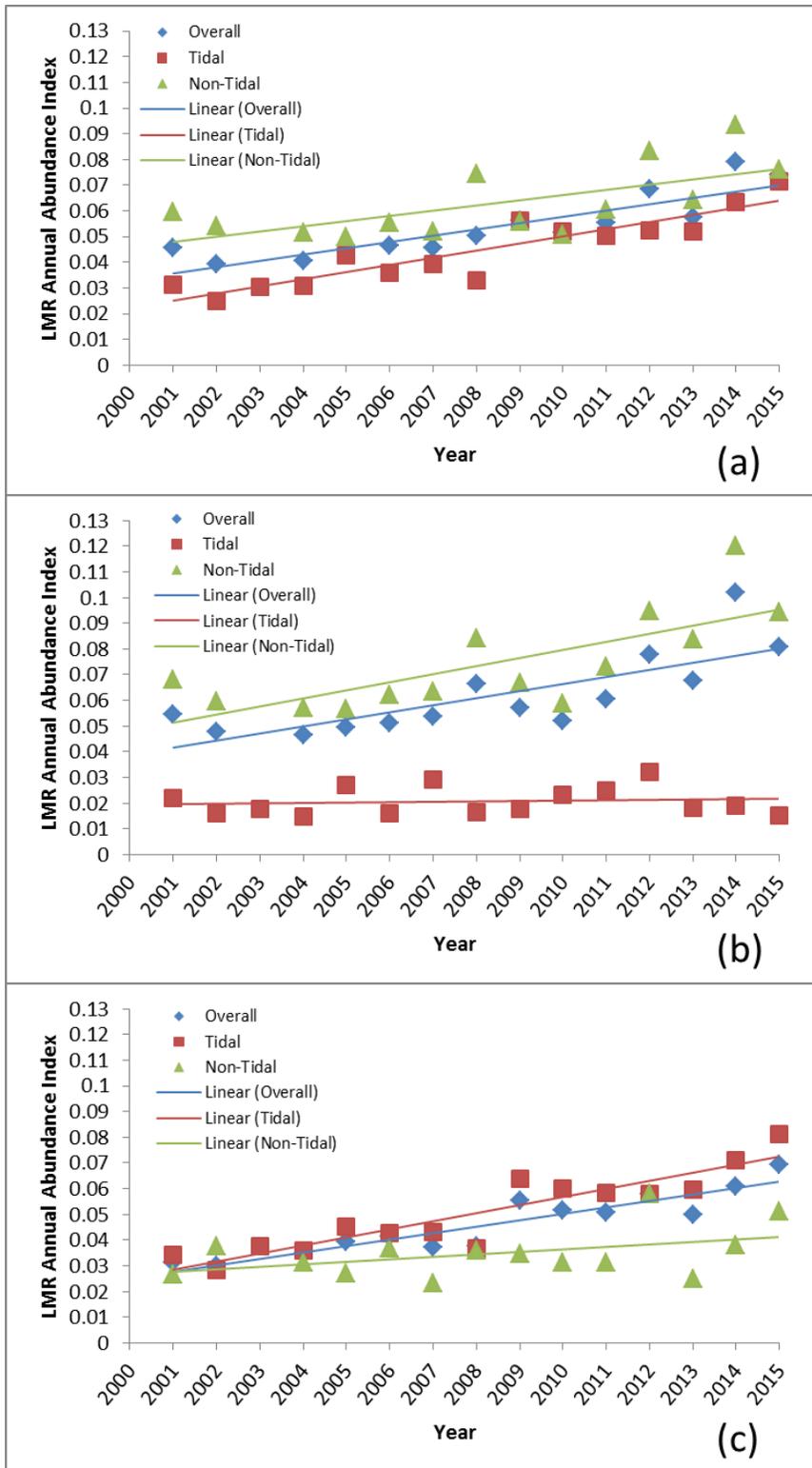


Figure 4 Annual abundance index trends for (a) all species, (b) native species, and (c) introduced species in the LMR between 2001 and 2015. In 2003, the non-tidal portion of the river was not sampled. An abundance index was not calculated for 2016 as the summer survey was not included in this report.

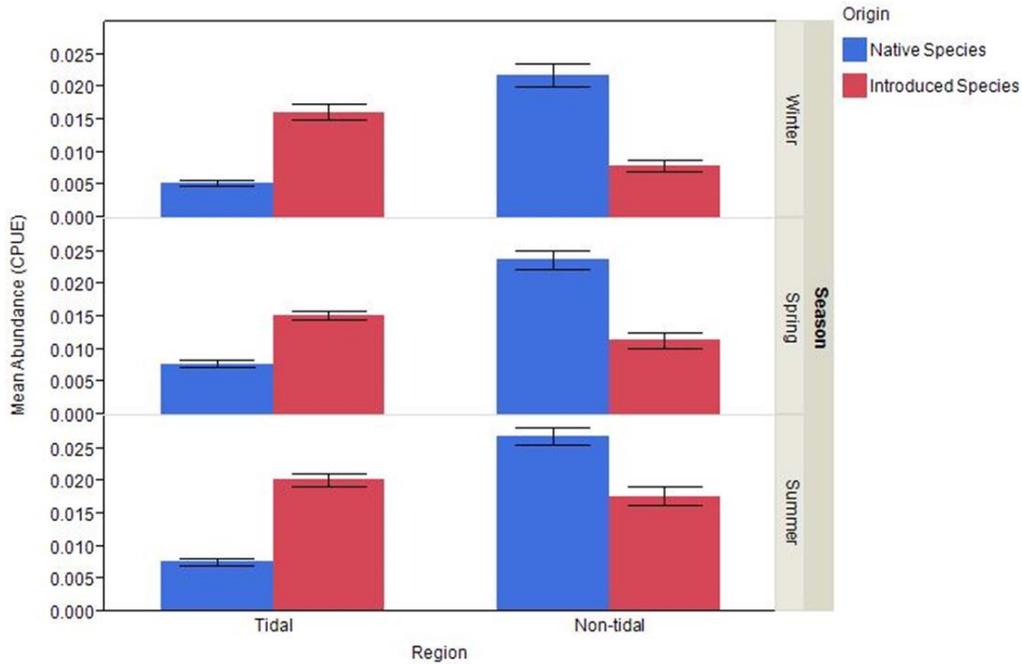


Figure 5 Mean abundance ± 1 SE of native and introduced species by region.

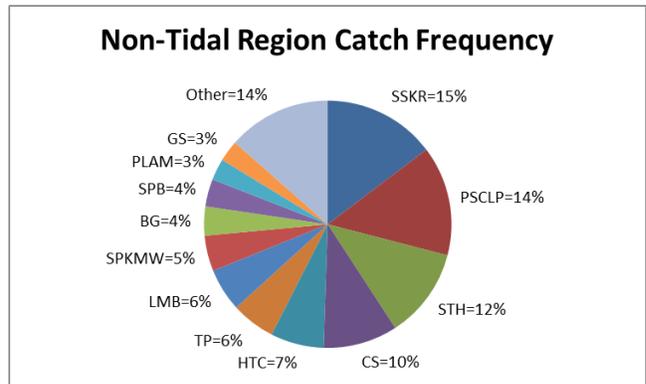
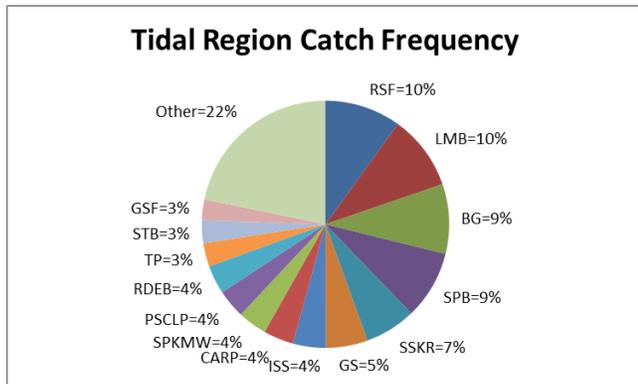
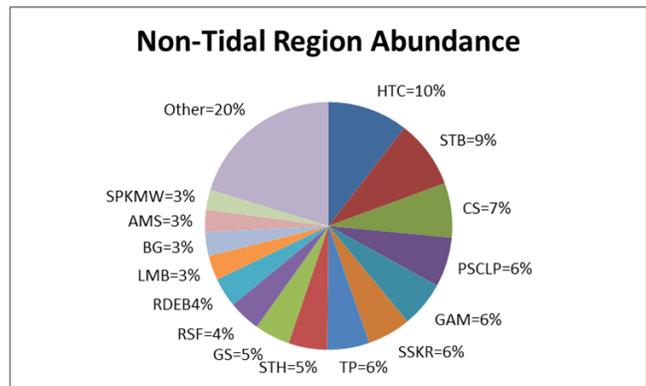
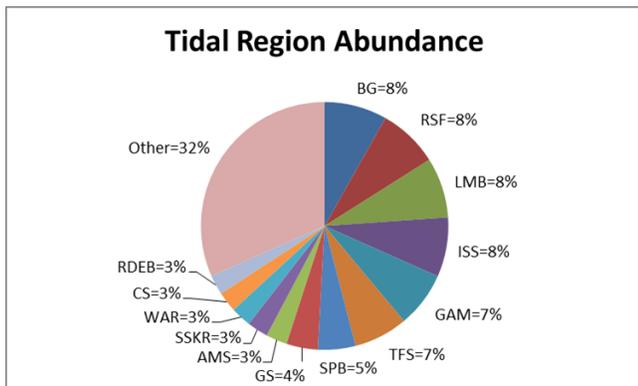


Figure 6 Regional species abundance indices and sample site frequencies. "Other" includes species which make up 2% or less of the overall species composition.

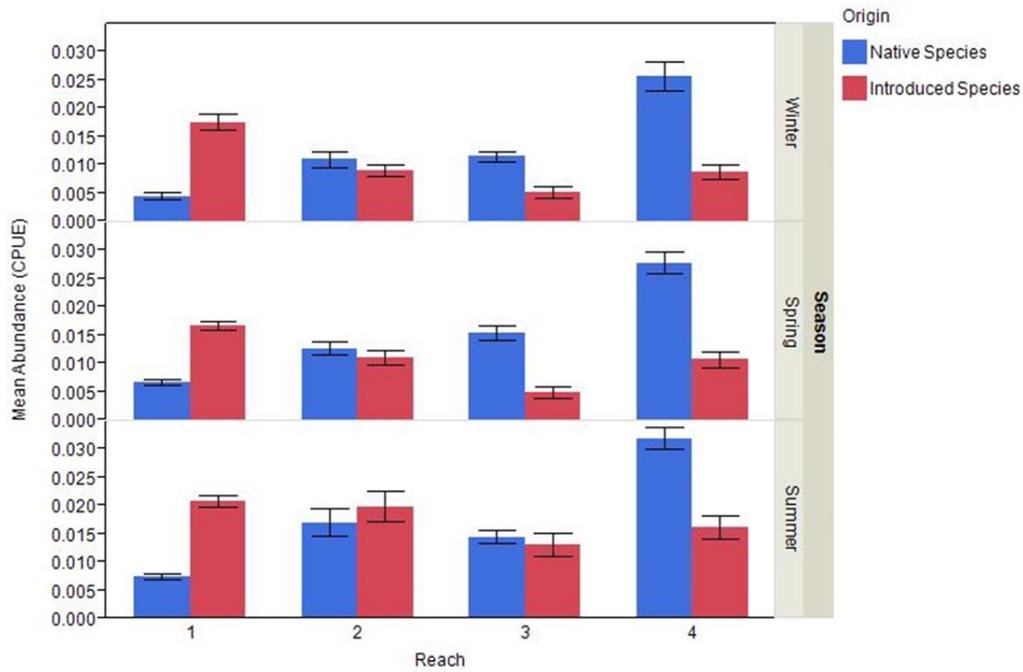


Figure 7 Mean abundance \pm 1 SE of native and introduced species by reach.

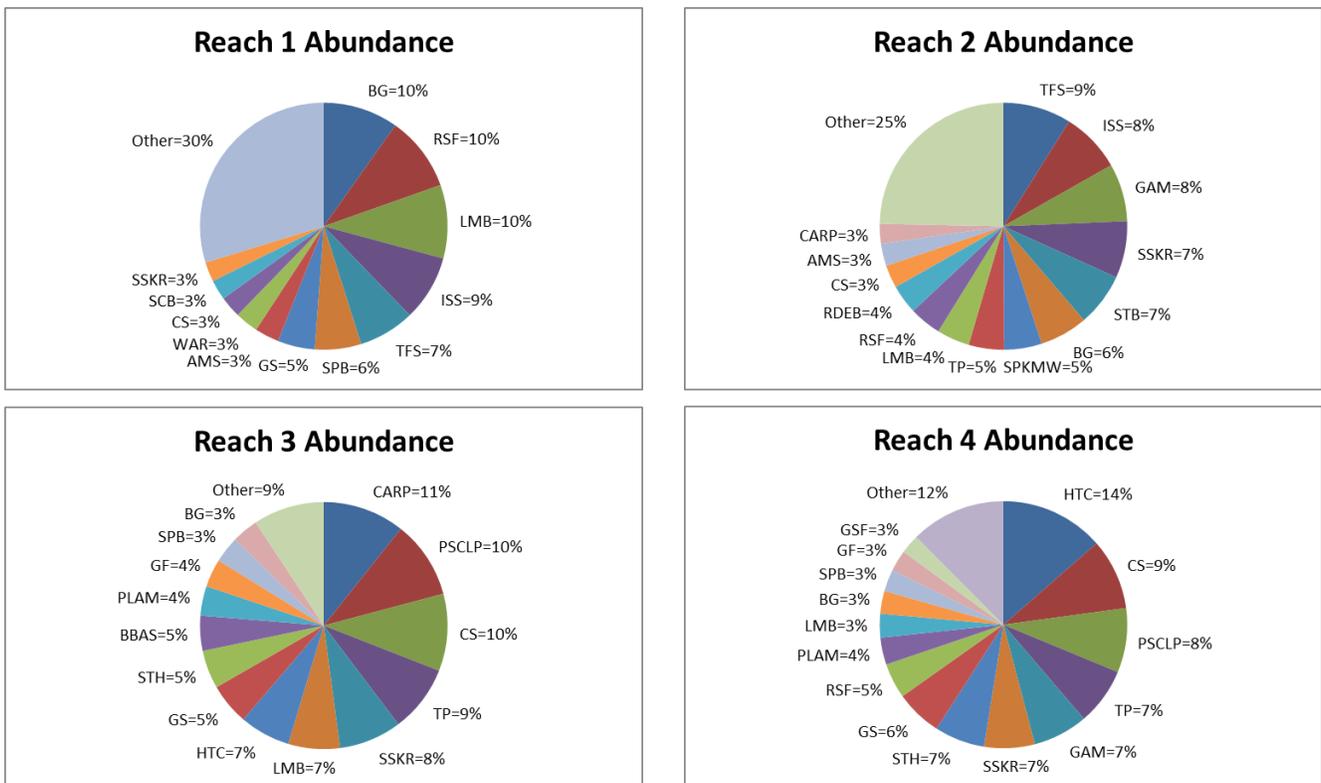


Figure 8 Species abundance indices by reach. "Other" includes species which make up 2% or less of the overall species composition.

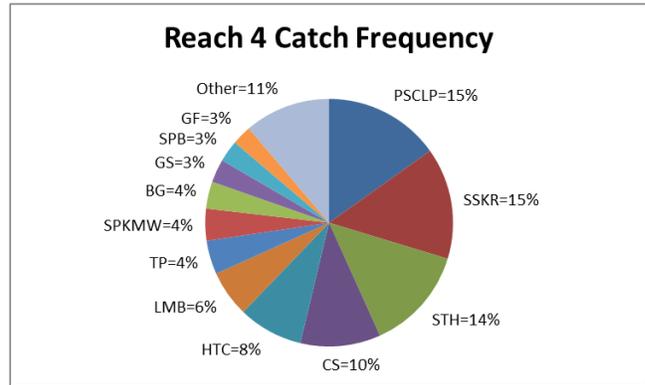
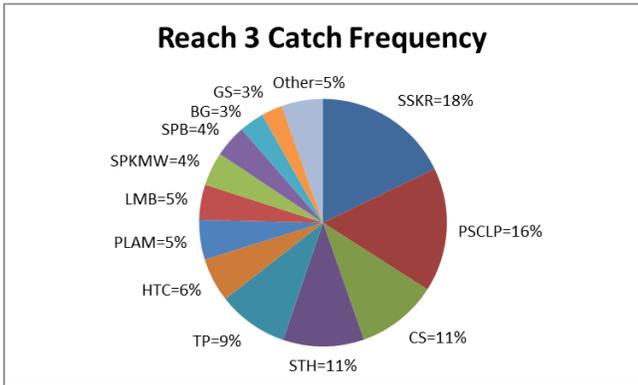
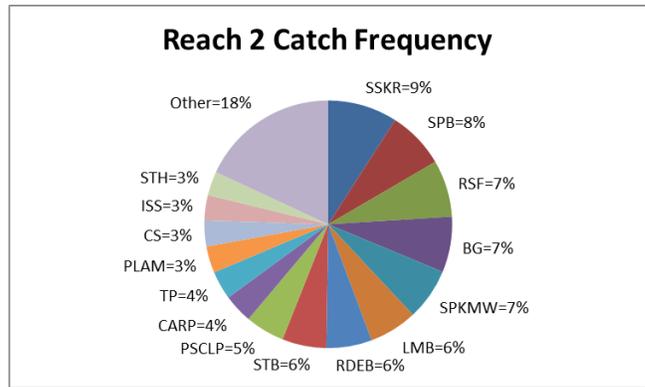
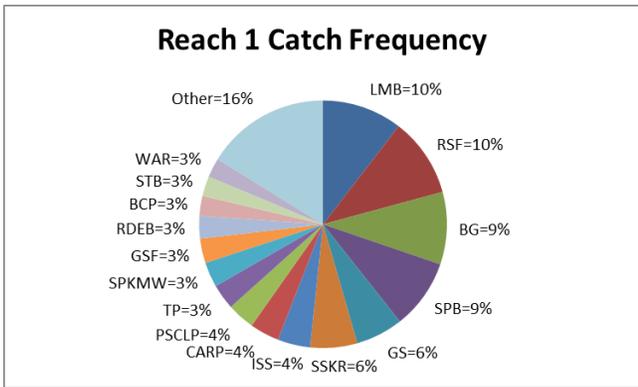


Figure 9 Species sample site frequency by reach. “Other” includes species which make up 2% or less of the overall species composition.