

RESEARCH

Abundance Trends, Distribution, and Habitat Associations of the Invasive Mississippi Silverside (*Menidia audens*) in the Sacramento–San Joaquin Delta, California, USA

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ABSTRACT

Although many alien fish species have colonized the Sacramento–San Joaquin Delta (Delta), few are as pervasive and abundant as Mississippi Silversides (*Menidia audens*). Moreover, Mississippi Silversides are hypothesized to be an intra-guild predator of the endangered Delta Smelt (*Hypomesus transpacificus*). Because of their prevalence in the Delta and potential predation on Delta Smelt, Mississippi Silversides may have far-reaching effects on both the aquatic ecosystem and conservation management policies of the region. Yet little is known about how Mississippi Silverside abundance and distribution have changed within the Delta, or how they respond to various habitat attributes such as temperature, turbidity, and flow. We examined 19 years of beach seine survey data to evaluate how the abundance and distribution of Mississippi Silversides has changed over the years, characterize their habitat associations, and determine

the environmental factors that predict their annual cohort strength. Concurrent with the decline of several pelagic fish species in the San Francisco Estuary in the early 2000s, we observed a significant increase in Mississippi Silverside catch that was accompanied by a moderate distributional shift in which densities increased in the western Delta region. We also found that the occurrence of this highly prolific alien species was associated with higher water temperature, higher turbidity, relatively low conductivity, and moderate to high levels of dissolved oxygen. Lastly, we demonstrated that freshwater input to the Sacramento–San Joaquin Delta during the summer and water exports during the spring months were both negatively correlated with the annual cohort size of Mississippi Silversides in the region. Our study identified the environmental variables deserving additional attention in future studies involving Mississippi Silverside and suggests that the species favors habitat conditions that are likely to be detrimental for pelagic species such as Delta Smelt.

KEY WORDS

Mississippi Silverside, invasive species biology, *Menidia audens*, littoral fish, life history

INTRODUCTION

The introduction of non-native species has commonly been identified as one of the major causes of global biodiversity loss (Vitousek et al. 1996; Sala et al. 2000). This is especially apparent in the highly invaded San Francisco Estuary (estuary), where large numbers of alien species have successfully colonized (Cohen and Carlton 1998; Winder et al. 2011) while populations of native species have either declined or become extirpated (Bennett and Moyle 1996; Moyle 2002). Among the many alien fish species found within the estuary, Mississippi Silversides (*Menidia audens*) are one of the most widely distributed and abundant (Moyle 2002; Nobriga et al. 2005). Mississippi Silversides were first introduced in California to the Blue Lakes and Clear Lake in 1967, and following subsequent introductions, they became well-established throughout the estuary by 1975 (Cook and Moore 1970; Moyle 2002).

Since 1975, Mississippi Silverside numbers appeared to increase dramatically within the Sacramento–San Joaquin Delta (Delta) portion of the estuary (Brown and May 2006; Brown and Michniuk 2007). The Delta is a complex network of interconnected channels, which forms the inland portion of the estuary (Whipple et al. 2012). This apparent increase of Mississippi Silverside abundance was concurrent with the severe declines of several pelagic fish species (Sommer et al. 2007) in the estuary. Within this group of declining pelagic fish species, Delta Smelt (*Hypomesus transpacificus*), a euryhaline pelagic fish species, are of particular interest. Low abundance indices in the past few decades led to the listing of Delta Smelt under both the California and United States Endangered Species Acts (USFWS 1993). Multiple interacting stressors are implicated in this species' precipitous decline (Baxter et al. 2010; MacNally et al. 2010), and predation by non-native species has been identified as a potential contributing factor (Sommer et al. 2007).

Mississippi Silversides have been hypothesized as intra-guild predators of Delta Smelt larvae because they share similar life histories (Moyle 2002) and their diets overlap considerably (Bennett and Moyle 1996). A recent investigation of the presence of Delta Smelt DNA in the stomach contents of Mississippi Silversides confirmed that they prey on early life-

stage Delta Smelt in the wild (Baerwald et al. 2012). To gain a better understanding of the extent of this ecological interaction between Delta Smelt and Mississippi Silversides, knowledge of the life history of both species is crucial. However, though multiple studies have described the biology and population dynamics of Delta Smelt (Moyle et al. 1992; Bennett 2005; Feyrer et al. 2007; Merz et al. 2011; Sommer et al. 2011; Sommer and Mejia 2013; Rose et al. 2013), little is known about the life history and habitat associations of Mississippi Silversides within the Delta. Characterizing the abundance and distribution of this invasive species with environmental factors may provide insight into what has allowed Mississippi Silverside to become so widespread and abundant in this system.

In this study, we describe the abundance and distribution patterns—as well as the short-term and long-term habitat associations—of Mississippi Silversides in the estuary using data available from a long-term Interagency Ecological Program (IEP) monitoring program. Our analyses focused on the Delta region, where the species is highly abundant and commonly captured in shallow-water habitat (Brown and May 2006; Brown and Michniuk 2007). Specifically, we aim to address the following questions: (1) How have the abundance and distribution of Mississippi Silversides changed over time? (2) How does the occurrence of Mississippi Silversides vary in relation to habitat parameters? (3) Which seasonal environmental variable(s) correlate well with the annual cohort strength of Mississippi Silversides?

METHODS

Study Area

The Sacramento–San Joaquin Delta is a complex, highly altered tidal channel network that forms the upstream-most portion of the San Francisco Estuary. Though it was once a dynamic system of tidal floodplains and marshes shaped by the flows of the Sacramento and San Joaquin rivers, the Delta's wetlands have been diked and filled extensively over the past two hundred years, turning it into a highly modified tidal freshwater ecosystem with over 1,000 miles of levees (Lund et al. 2008; Whipple et al. 2012). However, the 3,000 km² network of tidal channels within the Delta still contains a diversity of habitats,

from wide and deep shipping channels maintained by dredging to narrow dead-end sloughs. Several large expanses of open water also exist in the Delta from flooding of subsided agricultural islands. In addition to the freshwater input from rivers upstream, habitat within the Delta is also heavily influenced by thousands of small agricultural water diversions, and by two major water export facilities in the south which pump water from the Delta to agricultural and urban areas in the San Joaquin Valley and southern California.

Data Source

Because Mississippi Silversides are common and abundant in shallow, nearshore habitat (Matern et al. 2002; Nobriga et al. 2005; Cohen and Bollens 2008), we used the long-term beach seine survey data from the U.S. Fish and Wildlife Service's (USFWS) Delta Juvenile Fish Monitoring Program (DJFMP) to assess their abundance and distribution in the Delta (http://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm). In the late 1970s the USFWS initiated the DJFMP with the original goal of monitoring the abundance and distribution of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Delta (Kjelson et al. 1982). Currently, the DJFMP covers a total of 62 sites that are sampled either weekly or biweekly year-round, ranging from the Sacramento and San Joaquin rivers to the San Francisco Bay (Appendix A, Figure A-1). Sampling consists of one seine haul using a 15.2-m $\times$ 1.3-m net with 3-mm mesh and a 1.3-m $\times$ 1.3-m bag. Upon completion of each seine haul, all fish are identified to species, counted and measured (fork length, FL, in mm). Beginning in 1985, measurements of width, depth, and length (± 1 m) of area sampled are recorded to estimate the water volume (m^3) swept by the beach seine. Consistent measurements of electrical conductivity ($\mu\text{S cm}^{-1}$) and water temperature ($^{\circ}\text{C}$) began in 1999; while the measurements of turbidity (NTU) and dissolved oxygen (mg L^{-1}) started in 2010 or 2011, depending on the location. For this study, we analyzed only data since 1995 because this marked the first year that Delta sites were surveyed year-round.

Data Analysis

Q1: How have the abundance and distribution of Mississippi Silverside changed over the years?

To first confirm that Mississippi Silversides are largely an annual species in the Delta (Moyle 2002), we plotted fork length (FL) density histograms of each month using the full data set from calendar years 1995 to 2014. The resulting FL frequency histograms confirmed that Mississippi Silversides are an annual species with a new cohort appearing in June of every year (Appendix A, Figure A-2). We therefore designated the period between June of one year and May of the following year as a “cohort year” (with each cohort named after the year it was born).

We evaluated the overall long-term abundance trend of Mississippi Silversides over the study period (1995 to 2014) by first selecting beach seine sites within the Delta that have been consistently sampled year-round since 1995, resulting in 22 sites (hereafter referred to as “index sites”) that cover a broad range of locations across the Delta (Figure 1). Though the efficiency of beach seine sampling may vary spatiotemporally to a certain extent, it should depict Mississippi Silverside's general abundance trend in the Delta, because they are most commonly found in shallow-water, near-shore habitat (Matern et al. 2002; Nobriga et al. 2005; Cohen and Bollens 2008). To visually assess the trend of abundance over time, catch per unit effort (CPUE) data (in this case, in cubic meters) were collapsed to a monthly mean, averaged across all 22 index sites, and plotted against time (Wickham 2009). We then took the average CPUE for each cohort year and performed Kendall's tau rank correlation test using *R* (R Core Team 2014) to evaluate whether the species' abundance trend (if any) was statistically significant (see Appendix A, Table A-1 for a full summary on how the data was configured for each analysis).

We also investigated spatiotemporal patterns in Mississippi Silverside CPUE across sites within the Delta over the study period (1995–2014) through non-metric multidimensional scaling ordination (NMDS) and similarity profile (SIMPROF) permutation test in the Primer 7 software (Clarke 1993; Clarke et al. 2008, 2014). We calculated the average cohort-year CPUE for each index site and subse-

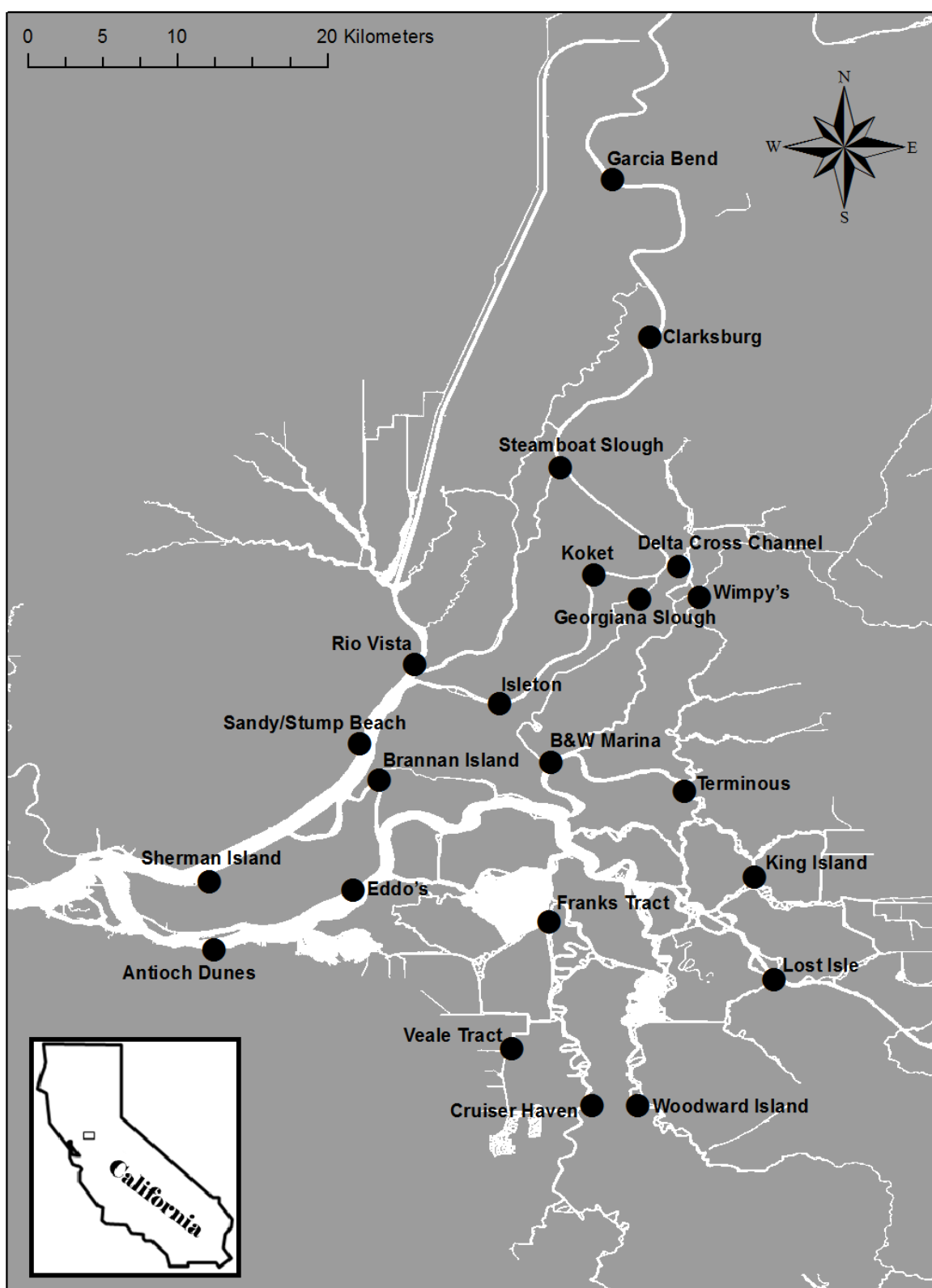


Figure 1 Overview map of the Sacramento–San Joaquin Delta with the 22 Mississippi silverside index beach seine sites (other non-index sites not shown)

quently square-root transformed the data to reduce the influence of sites with exceedingly high numbers of Mississippi Silverside. We then constructed a Euclidean distance matrix for the various cohorts and grouped them by using the SIMPROF permutation test (Clarke et al. 2008). The SIMPROF test searches for evidence of hierarchical clustering within the data by way of permutations. We performed 1,000 permutations with the significance threshold set at 0.01. We then visualized the resulting SIMPROF groups and resemblance matrix via NMDS (Field et al. 1982; Clarke 1993). To find which particular sites were driving the differences between the SIMPROF groups, we used the similarity percentage routine (SIMPER) analysis with a cutoff percentage of 70% (Clarke 1993; Clarke and Warwick 1994). We also calculated Pearson correlations between the square-root transformed data and the two NMDS axes and plotted them on the NMDS to view the directionality of select sites. To avoid excessive overlapping of correlation vectors and points, we only overlaid onto the NMDS vectors for sites or variables that correlated at >0.8 . Each Mississippi Silverside cohort plotted on the NMDS was color-coded by its associated California Department of Water Resources' (CDWR) Sacramento Valley water year index (<http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST>) to visualize how each cohort's distribution varied by water year type.

Q2: How does the occurrence of Mississippi Silversides vary in relation to habitat parameters?

The broad spatio-temporal coverage of the DJFMP beach seine survey data set allowed for the quantification of Mississippi Silverside occurrence in near-shore habitat relative to a variety of habitat parameters. We used generalized additive models (GAMs; smoother = cubic spline) with a binomial error structure to explore the relationships between Mississippi Silverside occurrence and measured water quality variables. GAMs are extensions of generalized linear models (GLM), which use a sum of smooth functions of covariates to depict potentially non-linear relationships between response and explanatory variables (Wood 2006). To cover a wider range of variation for these habitat variables, all DJFMP sites were used in this portion of the study. However, because GAM does not allow for any null value in the pre-

dictor variables, a smaller time-frame was covered (2011 to 2014) for this specific analysis (Appendix A, Table A-1). We performed analyses in R (R Core Team 2014) using the mgcv package (Wood 2011). Smoothing parameters were estimated by the unbiased risk estimator criterion, and gamma was set to 1.4 to limit over-fitting to the data (Wood 2006).

We converted Mississippi Silverside count data to occurrence (presence-absence) data to reduce the influence of outliers (i.e., extremely anomalous abundance values) and bias associated with year-to-year variation in abundance. Water quality data used were those measured concurrently with DJFMP fish sampling (water temperature, electrical conductivity, turbidity, and dissolved oxygen level). We removed outliers for certain variables (conductivity $\geq 45,00 \mu\text{S cm}^{-1}$, turbidity $\geq 200 \text{ NTU}$, and dissolved oxygen $\geq 20 \text{ mg L}^{-1}$) from this analysis. To reduce seasonal effects when elucidating the relationship between temperature and Mississippi Silverside occurrence, we used deviance from expected temperature in place of the measured temperature in our GAM analysis. We first constructed expected daily temperature model by fitting a quadratic regression model on water temperature by Julian day using the DJFMP data set. The resulting model has an adjusted R^2 of 0.79 and is as follows (where y is predicted temperature and x is Julian day):

$$y = -0.000433(x^2) + 0.168(x) + 4.63$$

We then calculated deviance from expected temperature by subtracting the measured temperature from the predicted/expected temperature (in $^{\circ}\text{C}$) based on the model. We constructed the final GAM using the backward stepwise approach of removing non-significant terms ($\alpha=0.01$) from the full model.

Q3: Does Mississippi Silverside cohort strength correlate with any seasonal environmental variable(s)?

Population level associations between Mississippi Silversides and biotic or abiotic habitat variables have yet to be described for the Sacramento-San Joaquin Delta. We used GLM in R (R Core Team 2014) with glmulti package (Calcagno 2013) to

determine if and which seasonal habitat metrics best predict Mississippi Silverside cohort strength in the Delta. We calculated the annual cohort strength of Mississippi Silverside by taking the mean CPUE across the previously described 22 index sites for each cohort year (beginning from June of one year and ending at May of the following year) within the study period (1995 to 2013; 19 cohorts in total). We then used these annual cohort strength indices as the response variable in our GLM model building process. We tested for the presence of temporal auto-correlation in our response variable by way of auto-correlation function plot, and found it to be non-significant ($\alpha = 0.05$).

Covariates tested in this analysis include total Delta inflow (cubic feet per second; cfs), combined south

Delta water exports (cfs), water temperature ($^{\circ}\text{C}$), Secchi depth (cm), cyclopoid copepod abundance (catch per m^3), and calanoid copepod abundance (catch per m^3) (Table 1). It has been previously shown that estuarine species respond strongly to interannual variability in freshwater flow (Jassby et al. 1995; Kimmerer 2002), though this has yet to be evaluated for Mississippi Silversides. Water diversion projects within the Delta can alter the hydrodynamics of the region and have been shown to entrain a sizeable number of Mississippi Silversides in certain years (Grimaldo et al. 2009). Water temperature and turbidity may be important for Mississippi Silversides on a longer time scale based on our GAM analysis results (Question 2 above) and previous studies (Moyle 2002). We selected the two classes of copepods as possible factors because of past studies that suggested

Table 1 Definition, data source, and range of values for the variables used in the GLM analysis

Variable	Definition	Data Source	Range of values
Response variable			
Mississippi Silverside (<i>Menidia audens</i>) cohort strength	Mean catch per m^3 across 22 index sites (as seen in Figure 1) for the cohort year (June of one year to May of following year)	USFWS Delta Juvenile Fish Monitoring Program	0.42–2.13 per m^3
Covariates			
Spring inflow	Spring (Mar–May) total Delta inflow	California DWR Dayflow Program	14,485–132,467 cfs
Summer inflow	Summer (Jun–Sep) total Delta inflow		12,992–47,113 cfs
Spring export	Spring (Mar–May) total Delta exports and diversions/transfers		2,525–6,150 cfs
Summer export	Summer (Jun–Sep) total Delta exports and diversions/transfers		4,895–11,468 cfs
Spring water temperature	Spring (Mar–May) mean Delta water temperature	IEP Discrete Water Quality Monitoring Program. Delta stations: D10, D12, D16, D22, D28A, D4, MD10A, P8	13.4–18.3 $^{\circ}\text{C}$
Summer water temperature	Summer (Jun–Sep) mean Delta water temperature		21.3–23.1 $^{\circ}\text{C}$
Spring Secchi depth	Spring (Mar–May) mean Delta Secchi depth		42.6–100.4 cm
Summer Secchi depth	Spring (Mar–May) mean Delta Secchi depth		44.5–105.8 cm
Spring calanoid	Spring (Mar–May) mean catch per m^3 for all calanoid adults and copepods	IEP Bay–Delta Monitoring and Analysis Section Zooplankton Monitoring Program. Delta stations: NZ054, NZ060, NZ064, NZ074, NZ086, NZ092, NZD16, NZD28, NZM10.	92–1,916 per m^3
Summer calanoid	Summer (Jun–Sep) mean catch per m^3 for all calanoid adults and copepods		1,823–4,001 per m^3
Spring cyclopoid	Spring (Mar–May) mean catch per m^3 for all cyclopoid adults and copepods		110–1,528 per m^3
Summer cyclopoid	Summer (Jun–Sep) mean catch per m^3 for all cyclopoid adults and copepods		1,157–2,850 per m^3

Mississippi Silversides primarily feed on zooplanktons (Elston and Bachen 1976; Wurtsbaugh and Li 1985) and the high relative efficiencies for which these copepods are sampled.

Each covariate was partitioned into spring season (March to May) and summer season (June to September) to assess the relative importance of the two time periods for the various habitat variables. We acquired inflow and export data from the CDWR Dayflow data set (<http://www.water.ca.gov/dayflow/>). Water temperature and Secchi depth data were compiled from the IEP Discrete Water Quality Monitoring Program using nine stations covering the Delta region (Table 1; Appendix A, Figure A-1). Although electric conductivity data was available, we precluded it from the list of covariates as it was strongly correlated with Delta inflow (Jassby et al. 1995). We acquired calanoid and cyclopoid catch data from the IEP Zooplankton Monitoring Program from nine stations within the Delta (Table 1; Appendix A, Figure A-1).

We evaluated collinearity between covariates by using variance inflation factor (VIF). We sequentially dropped any covariate with the highest VIF starting from the full model as suggested by Montgomery and Peck (1992) and Zuur et al. (2010) until VIF values for covariates were below 10. We removed spring calanoid abundance, summer cyclopoid abundance, and summer water export as predictor variables because of the presence of collinearity (Appendix A, Table A-2). We constructed GLMs with all possible subsets of the nine remaining predictor variables using the identity link and Gaussian error distribution. To avoid overfitting given the relatively small sample size and to simplify the interpretation of the GLM results, we did not include interaction effects. All possible models were ranked with Akaike's Information Criterion corrected for small sample size (AICc), subsampled for the best 100 models. Resulting AICc weights from the top 100 models were used to calculate model-averaged estimates and the relative importance of terms (Burnham and Anderson 2002; Johnson and Omland 2004).

RESULTS

Q1: How have the abundance and distribution of Mississippi Silversides changed over the years?

Based on the minimal CPUE in the spring months (Figure 2), and the appearance of a new cohort in the June fork length density histogram, as well as the scarcity of adults in the following July fork length density histogram (Appendix A, Figure A-2), it appears that most Mississippi Silverside adults in the Delta do not survive to a second year (in other words, the species is largely annual). On average, Mississippi Silverside CPUE appears to be the lowest in May and highest in the fall and winter months (Figure 2). Mean fork length of each new Mississippi Silverside cohort increased fairly quickly, starting at roughly 30 mm FL in June, on average, and plateauing at around 60 mm FL from November through the following April (Appendix A, Figure A-2). Mississippi Silversides rarely exceed 110 mm FL in the estuary; only 21 fish larger than 110 mm FL have been captured by the DJFMP since 1995.

Kendall's tau rank correlation test for yearly average Mississippi Silverside CPUE was significant at $p < 0.001$ with a correlation coefficient of 0.672, indicating that CPUE for Mississippi Silversides has been increasing over the study period at the 22 index sites. The SIMPROF test split the 19 Mississippi Silverside cohorts into three groups: the first comprising cohorts from 1995 to 2003, the second just the 2011 cohort, and the third containing the 2004–2013 cohorts, excluding the 2011 cohort (Appendix A, Figure A-3; Figure 3). The 2011 cohort of Mississippi Silversides appears to be more similar to the early years (1995–2003) than to the latter years (2004–2013) based on SIMPROF results (Appendix A, Figure A-3) and their relative distance from one another along the two NMDS axes. Both the overlaid vectors for the NMDS (Figure 3B) and results from the SIMPER analysis demonstrated that two sites in the western Delta (Eddo's and Sherman Island) were highly influential in differentiating between the early years (1995 to 2003) and the latter years (2004 to 2013), contributing 36.8% and 21.0% to the difference between the groups, respectively (see Figure 3A). The next three highly influential sites in differentiating the two main SIMPROF groups were Antioch Dunes, Frank's Tract, and Clarksburg, contributing 6.7%, 4.1%, and 3.3%

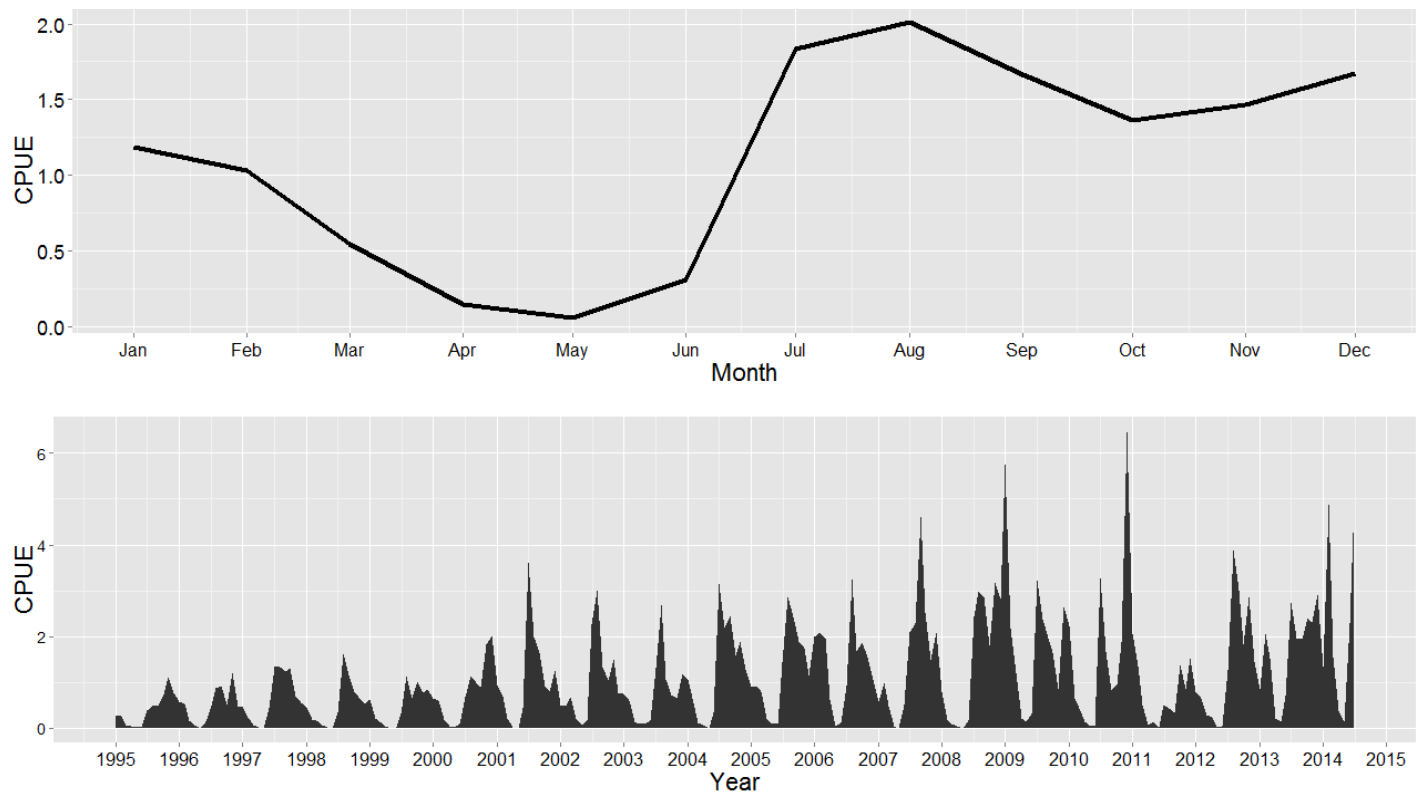


Figure 2 Plot of average CPUE (catch per m³) for the study period (1995–2014) at the 22 index sites collapsed by month (top) and plotted across time (bottom). Year in the *x*-axis of bottom graph indicates the start of each calendar year (January 1).

to the total difference, respectively. These top five sites cumulatively make up 71.9% of the difference between the two large SIMPROF groups.

Q2: How does the occurrence of Mississippi Silversides vary in relation to habitat parameters?

We found all four environmental variables (water temperature, electric conductivity, turbidity, and dissolved oxygen) to be statistically significant predictors of nearshore Mississippi Silverside occurrence at $p < 0.001$. Thus, no habitat variable was removed from the multi-term model. The full model with all four variables accounted for 17.3% of the deviance in the model. The relationship between occurrence of Mississippi Silversides and deviance from expected daily water temperature appeared to be largely linear, with increasing occurrence as temperature becomes higher than normal (Figure 4). Predicted occurrence was generally higher at lower values of conductivity ($< 10,000 \mu\text{S cm}^{-1}$) and declined at higher end of the conductivity range. Predicted occurrence of

Mississippi Silversides mostly increased as turbidity increased, reaching its highest at around 20 to 30 NTU with estimates becoming more variable at higher NTUs. Lastly, predicted occurrence based on dissolved oxygen level peaked around 10 mg L^{-1} and was highly variable at both extremes.

Q3: Does Mississippi Silverside cohort strength correlate with any seasonal environmental variable(s)?

Our model selection process produced 512 GLMs, and we kept the 100 best models ranked by their AICc values for model averaging. The top model included summer Delta inflow, spring water export, and spring Secchi depth as covariates (all terms significant at $p < 0.05$) with an adjusted R^2 of 0.59 (Table 2). The next two highest-ranked models within 2 AICc units

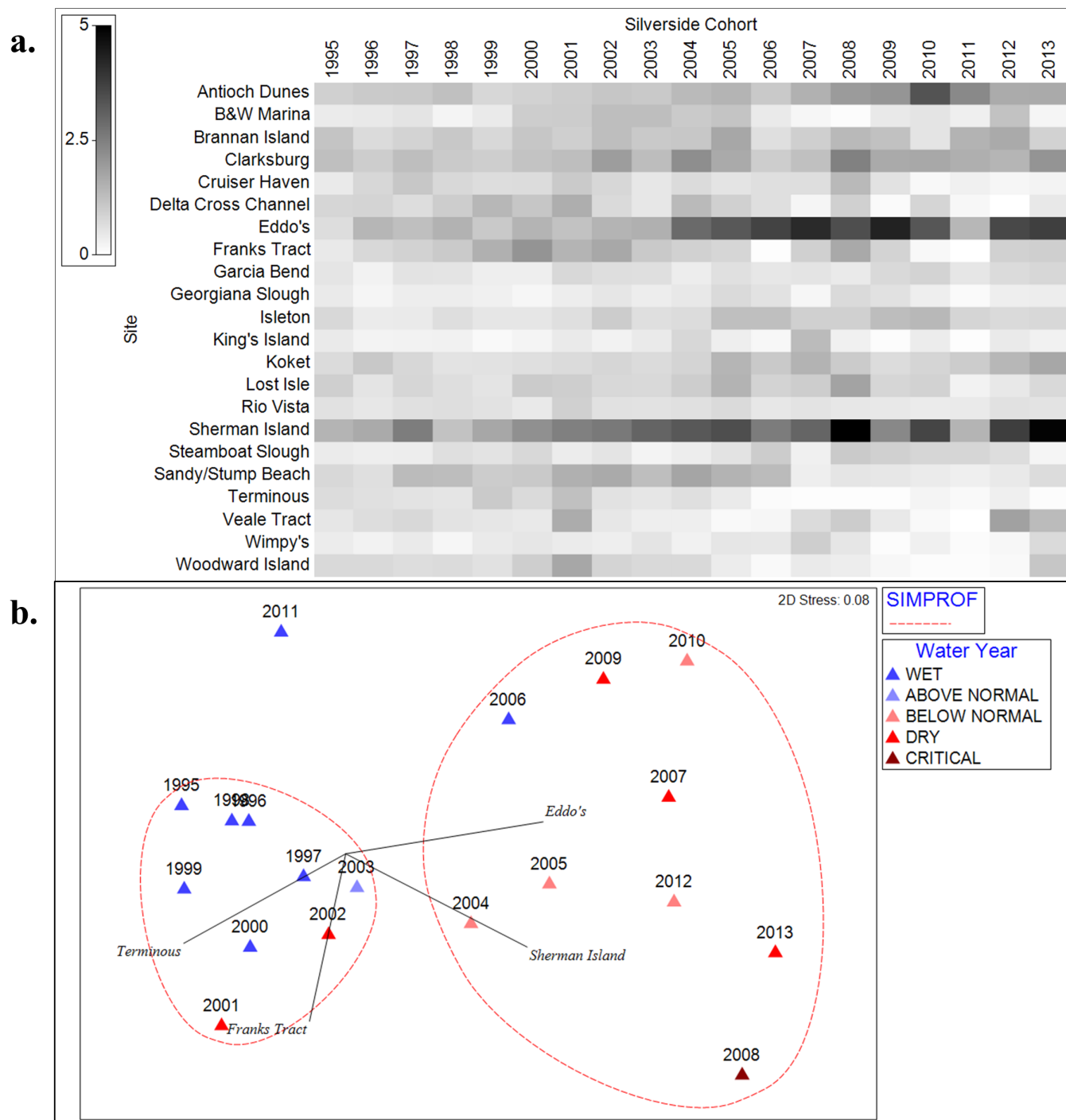


Figure 3 (A) Shade plot of the square-root transformed average CPUE for the 22 index stations ordered by Mississippi Silverside cohort years. (B) The nMDS plot of the 19 Mississippi Silverside cohorts based on the Euclidian distance matrix with Pearson correlation vectors of >0.8 shown. Dotted red circles represent statistically significant SIMPROF grouping, while color for each cohort indicates their associated water year index.

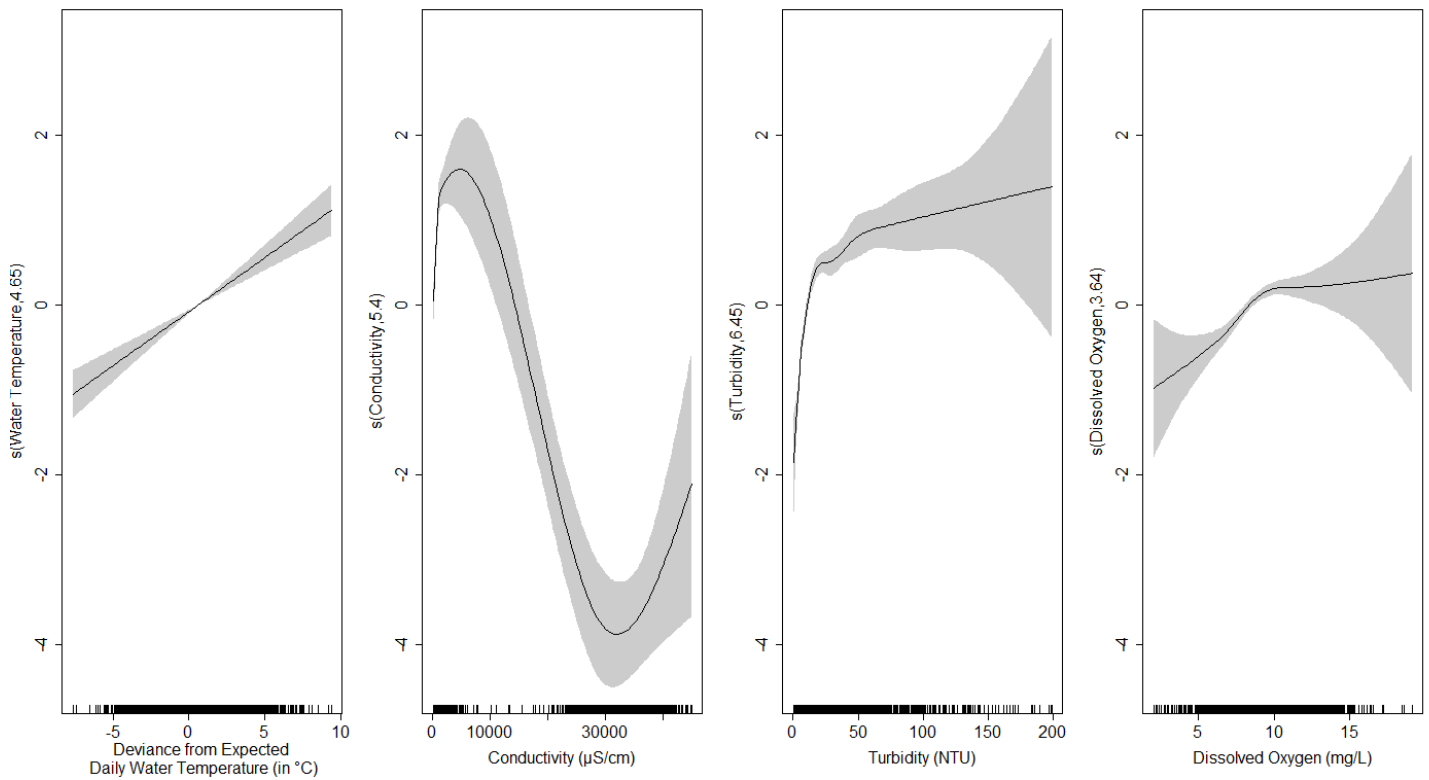


Figure 4 Partial GAM plots showing associations between habitat variables with Mississippi Silverside occurrence. Plots are fitted smooths with 95% confidence intervals in grey. The y-axis units are logit transformed, so that value of 0 represents occurrence probability of 0.5. Tick marks along the x-axis represent observations and numbers within y-axis title represent the estimated degrees of freedom for each smooth.

Table 2 Summary of regression coefficients and fit for the top 15 GLMs for predicting Mississippi Silverside cohort size

Model	Spring inflow	Summer inflow	Spring export	Spring water temperature	Spring Secchi depth	Summer Secchi depth	Summer calanoid	Spring cyclopoid	Intercept	AICc	$\Delta AICc$ from best model	wi	Adjusted R^2
1	—	-3.53×10^{-5b}	-1.82×10^{-4a}	—	9.54×10^{-3a}	—	—	—	2.09	21.0	0.00	0.140	0.59
2	—	-3.44×10^{-5b}	-1.62×10^{-4a}	—	—	8.07×10^{-3}	—	—	2.04	22.4	1.35	0.071	0.56
3	—	-3.85×10^{-5b}	-1.99×10^{-4a}	—	—	—	—	—	2.86	22.5	1.43	0.068	0.50
4	—	-3.08×10^{-5b}	—	—	—	1.07×10^{-2a}	—	—	1.06	23.9	2.83	0.034	0.46
5	-8.34×10^{-5b}	—	—	—	—	—	-3.65×10^{-4}	—	2.54	23.9	2.84	0.034	0.46
6	—	-4.63×10^{-5b}	-2.15×10^{-4a}	—	—	—	—	-3.50×10^{-4}	3.37	24.4	3.39	0.026	0.51
7	—	-3.22×10^{-5b}	—	—	1.08×10^{-2a}	—	—	—	1.12	24.5	3.43	0.026	0.44
8	—	-3.20×10^{-5b}	-1.89×10^{-4a}	5.65×10^{-2}	8.97×10^{-3}	—	—	—	1.17	24.6	3.60	0.023	0.58
9	—	-4.02×10^{-5b}	-1.94×10^{-4a}	—	8.56×10^{-3}	—	—	-2.01×10^{-4}	2.46	24.7	3.69	0.022	0.58
10	—	-3.35×10^{-5b}	-2.07×10^{-4a}	8.02×10^{-2}	—	—	—	—	1.48	25.0	3.93	0.020	0.50
11	-7.40×10^{-6b}	—	—	—	7.51×10^{-3}	—	-3.26×10^{-4a}	—	1.89	25.0	3.97	0.019	0.50
12	-7.31×10^{-6b}	—	—	—	—	7.08×10^{-3}	-2.98×10^{-4}	—	1.80	25.1	4.09	0.018	0.50
13	—	-3.43×10^{-5b}	-1.67×10^{-4}	—	9.33×10^{-3}	—	-7.02×10^{-5}	—	2.21	25.1	4.11	0.018	0.57
14	-5.39×10^{-7}	-3.35×10^{-5}	-1.81×10^{-4a}	—	9.39×10^{-3}	—	—	—	2.07	25.4	4.36	0.016	0.57
15	—	-3.55×10^{-5b}	-1.85×10^{-4a}	—	1.04×10^{-2}	-9.81×10^{-4}	—	—	2.12	25.4	4.37	0.016	0.57

a. $p < 0.05$

b. $p < 0.01$

Table 3 Model-averaged estimates and term importance based on AICc weights of top 100 GLMs

Variable	Estimated coefficient	Model-averaged term importance
Summer inflow	-2.59×10^{-5}	0.752
Spring export	-1.19×10^{-4}	0.660
Spring Secchi depth	3.59×10^{-3}	0.391
Spring inflow	-2.02×10^{-6}	0.314
Summer Secchi depth	2.43×10^{-3}	0.299
Summer calanoid	-5.77×10^{-5}	0.228
Spring temperature	1.05×10^{-2}	0.141
Spring cyclopoid	-3.13×10^{-5}	0.128
Summer temperature	-1.07×10^{-3}	0.079

of the best model also contain summer Delta inflow and spring water export, and the two terms were significant at $p < 0.05$ in both models. Model-averaged ranking of terms by AICc weights deemed summer inflow as the most important term for predicting Mississippi Silverside cohort strength, followed closely by spring export (Table 3). Both summer inflow and spring export were negatively correlated with Mississippi Silverside cohort strength. There was also some support for the positive relationship between Mississippi Silverside cohort strength and the spring Secchi depth (Table 3). The largest gap between two terms was between the spring water export (ranked as second most important) and spring Secchi depth (ranked as third most important) with a 0.269 drop in relative importance value.

DISCUSSION

Our analyses of the DJFMP indicated that Mississippi Silversides have become more abundant within the Delta, and have shifted their distribution to a certain extent in recent years. Notably, the abundance of Mississippi Silversides increased in 2004, especially within the western Delta region near the confluence of the Sacramento and San Joaquin rivers. This shift in 2004 occurred in conjunction with the collapse of multiple pelagic fishes in the estuary (Sommer et al. 2007), suggesting that the shift in the Delta ecosystem thought to cause of these pelagic species' decline may have simultaneously favored littoral alien species such as Mississippi Silversides. Our results further

suggest that higher water temperature, higher turbidity, relatively low conductivity, and moderate to high dissolved oxygen level all predicted the species' presence. And last, we found that, in a given year, higher summer freshwater flow into the Delta and higher spring water exports out of the Delta corresponded to a smaller overall cohort size of Mississippi Silverside within the region.

The first objective of our study was to evaluate the life history, abundance, and distribution patterns of Mississippi Silversides in the Delta. Consistent with the previous understanding of the species (Moyle 2002), we found Mississippi Silversides within the Delta to be a prolific annual species with virtually no second-year survivorship. The number of spawnings per individual is not known, but most adults seem to spawn and die in the late spring between April and June. Over the period examined in this study, Mississippi Silversides seemed to have experienced a dramatic increase in density (Kendall's tau rank correlation of average density was significant at $p < 0.001$). During this period of presumed population growth, we detected a noticeable change in their abundance and distribution; specifically in 2004 when the overall density appeared to have increased considerably and became much more heavily concentrated in the western Delta region (Figure 2; Figure 3A).

The increase in Mississippi Silverside density partially coincided with the Pelagic Organism Decline (POD) that occurred in the estuary around 2002, in which four pelagic fish species (including Delta Smelt) dramatically decreased in relative abundance (Sommer et al. 2007; MacNally et al. 2010). Interestingly, our results also indicated that the 2011 Mississippi Silverside cohort was unique; resembling the early, pre-POD (1995 to 2003) cohorts more than the latter, post-POD cohorts (2004 to 2013), presumably because of their overall reduced density (Figure 3A). In contrast to Mississippi Silversides, a few pelagic fish species in the estuary (Delta Smelt; Longfin Smelt, *Spirinchus thaleichthys*; and Striped Bass, *Morone saxatilis*) saw an increase in recruitment during the wet year of 2011 relative to recent years (Brown et al. 2014).

The POD is considered one of the most important ecological regime shifts to have taken place in

the estuary ecosystem in recent times (Moyle and Bennett 2008; MacNally et al. 2010), and the apparent opposite responses between Mississippi Silversides and pelagic fish species highlights the potential of Mississippi Silversides to be an indicator species for the system. We recognize that we cannot fully distinguish whether the difference between the two SIMPROF groups was truly from the same factors that caused the POD regime shift or simply from the differences between wet and dry years, because most of the pre-POD years covered in our study period (1995 to 2002) were wet years. Nevertheless, this observation underscores the importance of analyzing the abundance trends for non-listed, commercially unimportant fish species in the estuary (e.g., Feyrer et al. 2009).

Our second objective was to relate fish occurrence to water quality variables to evaluate the habitat associations of Mississippi Silversides. We found through our GAM analysis that water temperature, specific conductance, turbidity, and dissolved oxygen were all important in predicting the presence of Mississippi Silversides. Specifically, Mississippi Silverside occurrence probability was higher at temperatures that are warmer than expected, at greater turbidity (> 20 to 30 NTU), and at a moderate to high level of dissolved oxygen (~ 10 mg L⁻¹) (Figure 4). Predicted occurrence also increased as conductivity increased, but declined rapidly as conductivity level exceeded $5,000 \mu\text{S cm}^{-1}$ (Figure 4). Our results were consistent with the presumption that Mississippi Silversides are associated with warm water and low-salinity conditions (Moyle 2002); however, the optimal salinity level for Mississippi Silversides in the Delta may be lower than previously thought. Moyle (2002) noted that Mississippi Silversides are commonly found at salinities of 10 to 15 parts per thousand (ppt) and Middaugh et al. (1986) found optimal salinity level for larval Mississippi Silverside to be around 15 ppt. In contrast, our GAM plot indicated that an optimal salinity level may be closer to ~ 3 ppt ($5,000 \mu\text{S cm}^{-1}$ is 3.4 ppt at 15°C), though we note that sampling frequency for our data set was lower at conductivities between 10,000 and $20,000 \mu\text{S cm}^{-1}$ (Figure 4). Aside from their association with higher temperature, Mississippi Silversides shares fairly similar habitat requirements with their presumed intra-guild prey, the Delta Smelt. A GAM of Delta Smelt occurrence

in their pelagic habitat during the fall season showed that Delta Smelt are more likely to be present at locations with higher turbidity and a conductivity of $< 10,000 \mu\text{S cm}^{-1}$ (Feyrer et al. 2007). The relationship between Mississippi Silversides and higher turbidity may need to be examined further, because net avoidance can occur with increased water clarity.

For our third objective, we assessed if and how Mississippi Silverside cohort strength correlates with seasonal environmental variables. Of the variables we tested in our analysis, we found summer Delta inflow (from June to September) and spring export (from March to May) to be the best predictors of Mississippi Silverside cohort strength, where higher summer inflow and spring water export are followed by lower abundance of Mississippi Silversides. Both variables ranked as the top two most important terms from model averaging (Table 3), and were the only two covariates consistently found in models within 2 AICc points of the top-ranking model (Table 2). The best model by AICc had a relatively good fit (adjusted $R^2=0.59$), which suggests that this model can be useful for predicting future Mississippi Silverside abundance. This result also demonstrated that freshwater flow and water export have a relatively large negative effect on the Mississippi Silverside population. However, we stress that these analyses are not meant to imply causality, but rather to identify ecological factors whose relationships with Mississippi Silverside productivity in the Delta merit further investigation into. As such, we were unable to describe the underlying mechanism(s) of how seasonal flow conditions affect the overall abundance of this invasive species.

The near absence of Mississippi Silversides in swift-flowing waters and their prevalence in reservoir pools within California and the southeastern United States (Moyle 2002; Strongin et al. 2011; Simmons 2013) seems to suggest that the species' low tolerance for higher current velocities may contribute to their lower abundance in wet years. However, the inherent negative correlation between Delta freshwater inflow and salinity prevented us from separating their relative effects (although the conductivity GAM plot in Figure 4 seemed to indicate that near-zero salinity does not adversely affect Mississippi Silverside any more than high salinity). We also cannot exclude the possibility of lower capture efficiency for Mississippi Silverside during high flow conditions or that the

center of distribution for the species simply moved further downstream (e.g., the Suisun Bay region) in seasons of high flow.

Non-native species not only frequently become novel sources of predation for native species, but they also often out-compete natives for limited resources (Sax et al. 2007). As the management agencies of Sacramento–San Joaquin Delta are tasked with restoring the habitat of multiple declining native fish species, information on the predicted responses by abundant invasive species such as Mississippi Silverside to future restoration projects would be highly valuable. We were able to detect substantial changes in Mississippi Silverside catch patterns between years before and after the POD ecological regime shift that occurred in the Delta around 2002 (Sommer et al. 2007; Baxter et al. 2010; MacNally et al. 2010). We also demonstrated that both discrete water quality parameters and seasonal flow on a large time-scale influence the distribution and abundance of Mississippi Silversides. Nevertheless, while our study provides some new insights into how this highly prolific annual species may respond to future changes to the Delta, it also demonstrates the need for a mechanistic understanding of their habitat associations and response to ecosystem drivers.

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