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RESEARCH

# Seasonal and Size-Specific Occupancy of Striped Bass in the Stanislaus River, California

William Ware<sup>1,2</sup>, Matthew L. Peterson<sup>3</sup>, Tyler J. Pilger<sup>3\*</sup>

## ABSTRACT

Striped Bass (*Morone saxatilis*) monitoring and research in California's Central Valley primarily occurs in the Sacramento River basin and the Sacramento–San Joaquin Delta. A relatively under-studied contingent of the Striped Bass population is present in the San Joaquin River and its tributaries. One such tributary, the Stanislaus River, is an important source of natural production of native anadromous fishes, including fall-run Chinook Salmon (*Oncorhynchus tshawytscha*), Steelhead (*O. mykiss*), and Pacific Lamprey (*Entosphenus tridentatus*). Because Striped Bass are a non-native piscivore, characterizing when and where their distribution overlaps with native fishes is a first step to assessing the potential for negative inter-specific interactions. We compiled incidental observations of Striped Bass made during long-term (1996 to 2021) salmonid monitoring programs performed at different times of the year, and found that

Striped Bass were present at monitoring locations throughout most of the year, although not detected in every year. We also used data on Striped Bass captured during boat electrofishing surveys conducted during the 2019, 2020, and 2021 juvenile salmonid emigration season (February to June), for a more detailed evaluation of Striped Bass occupancy within the lower 65 kilometers of the Stanislaus River. Median fork length (FL) of Striped Bass captured from February to April was significantly larger than those captured in May and June ( $p < 0.001$ ). Using dynamic occupancy models, we showed that Striped Bass larger than 300 mm FL were present, and their occupancy increases earlier in the year than individuals under 300 mm FL. In all 3 years, occupancy estimates were greater than 80% of the lower Stanislaus River by May. Our results suggest a high degree of spatial and temporal overlap with native migratory fishes, which may have important implications for understanding and managing how predation affects juvenile salmon and other native species.

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## KEY WORDS

*Morone saxatilis*, dynamic occupancy models, differential migration, habitat overlap

## INTRODUCTION

Striped Bass (*Morone saxatilis*) were introduced to California in 1879 (Smith 1895), and by the following decade, a productive commercial fishery had been established which operated from 1885 to 1935 (Dill and Cordone 1997). Today, Striped Bass contribute to an economically important recreational fishery in California (American Sportfishing Association c2021). The same characteristics that make this species a valuable sport fish (i.e., large body size, strong swimmer, and pelagic piscivore), also contribute to the species being an effective predator, capable of exerting strong top-down control on populations of native fishes (Nobriga and Smith 2020; Nobriga et al. 2021). While not the only stressor to native fishes, Striped Bass can contribute to mortality of native fishes (e.g., Sabal et al. 2016; Stompe, Roberts, et al. 2020; Peterson et al. 2023) and may impede recovery efforts for listed species such as Delta Smelt (*Hypomesus transpacificus*; e.g., Nobriga et al. 2013) and winter- and spring-run Chinook Salmon (*Oncorhynchus tshawytscha*; e.g., Lindley and Mohr 2003). Striped Bass are highly mobile, roving predators that exhibit differential migration strategies related to size and maturity status (Callihan et al. 2015; Secor et al. 2001; 2020). Therefore, assessing the spatial and temporal overlap of Striped Bass with native species, especially threatened and endangered species, is needed to fully understand Striped Bass predation as a cause of native fish mortality.

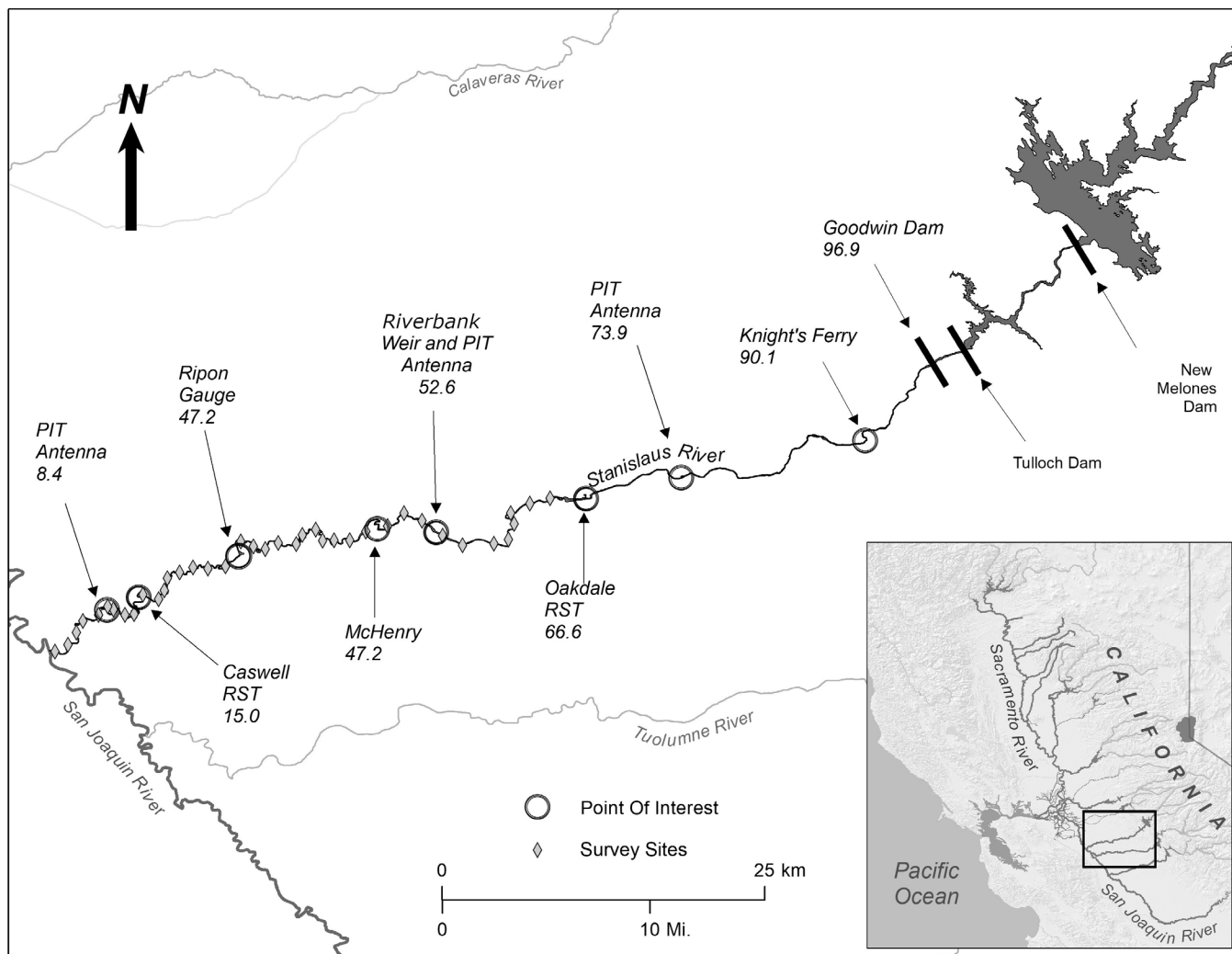
As a long-lived, highly mobile, iteroparous species, Striped Bass have a complex life history. They exhibit facultative anadromy, meaning that migrations to the ocean are not required to spawn or complete their life cycle (Secor et al. 2001). In California's Central Valley, there is a contingent of anadromous individuals that feed in the San Francisco Estuary and Pacific Ocean, then migrate into the Sacramento–San Joaquin Delta and up the Sacramento River between late March and early June to spawn, and then move back downstream to the estuary and ocean (Sabal et al. 2019; Goertler et al. 2021). However, there are landlocked populations of Striped Bass (Moyle 2002), as well as the potential for resident

contingents to persist in anadromous waters year-round (Le Doux–Bloom 2012). A diverse life history and plastic habitat requirements helps to explain their widespread distribution in the Central Valley (Moyle 2002). This widespread distribution suggests high potential for spatial overlap with native fish species. Because Striped Bass can shift to piscivory in their first year (Nobriga and Feyrer 2007), and increasingly consume fish as they grow (Moyle 2002; Peterson et al. 2023), documenting the spatial and temporal overlap of different sizes of Striped Bass is needed to fully understand their potential to prey on native fishes.

Fisheries monitoring programs, operated by state and federal agencies, have captured Striped Bass throughout the estuary and the Delta (Stompe, Moyle, et al. 2020). Yet, gaps related to size and spatial coverage in Striped Bass monitoring have persisted. Larval and juvenile Striped Bass (i.e., individuals < 100 mm total length [TL]) have been captured in Summer Towntnet, 20-mm trawl, Fall Midwater Trawl, and Spring Kodiak Trawl surveys (Mahardja et al. 2017; Stompe, Moyele, et al. 2020). Adult Striped Bass, particularly individuals of legal size for harvest ( $\geq 457$  mm TL), have been captured in fyke traps and gill nets deployed in the estuary and Sacramento River (Goertler et al. 2021). Fyke traps and gill nets have predominantly captured Striped Bass > 350 mm TL. Striped Bass between 100 and 350 mm were less frequently captured by these monitoring programs, but this size range has been captured using boat electro-fishing (McKenzie and Mahardja 2021). Furthermore, these programs focus on the estuary, Delta, and Sacramento River, with little monitoring occurring in the San Joaquin River watershed upstream of the Delta, particularly in the tributaries (i.e., the Stanislaus, Tuolumne, and Merced rivers).

In this study, our goal was to document spatial and temporal occurrence patterns of Striped Bass in the Stanislaus River.

**First**, to identify when Striped Bass were present in the Stanislaus River, we compiled incidental observations of Striped Bass from multiple



**Figure 1** The Stanislaus River from the confluence with the San Joaquin River to New Melones Reservoir. Electrofishing surveys were performed at 39 fixed sites (gray diamonds) throughout the lower 65-km reach of the river. Juvenile salmon rotary screw trapping (RST) occurs at Caswell and Oakdale. A weir with a counting device for adult salmonid escapement monitoring occurs near the town of Riverbank at the downstream end of where spawning has been documented. Snorkel surveys occur in the reach between Goodwin Dam and the Oakdale RST, and surveys for spawning redds occurs from Goodwin Dam downstream to McHenry. Also included are the locations of passive integrated transponder (PIT) antennas.

Chinook Salmon and Steelhead/Rainbow Trout (*O. mykiss*) monitoring programs.

**Second**, to characterize the size distribution of the Striped Bass population present during the fall-run Chinook Salmon juvenile migration season (February through June), we used Striped Bass capture data from standardized electrofishing surveys that targeted Striped Bass.

**Lastly**, to investigate how Striped Bass occupancy varied by fish size across three juvenile Chinook

Salmon emigration seasons, we used multi-season dynamic occupancy models.

**METHODS**

**Study Area**

The Stanislaus River, a major tributary of the San Joaquin River (Figure 1), remains a stronghold for native fishes such as anadromous Chinook Salmon, Steelhead, and Pacific Lamprey (*Entosphenus tridentatus*). Because there is no hatchery on the river, the Stanislaus River is

also an important source of natural production of fall-run Chinook Salmon. Goodwin Dam is an upstream barrier for all anadromous species, so all salmon and Steelhead spawning occurs in the 45-km reach below the dam (Peterson et al. 2020). The lower 65 km of the Stanislaus River is the beginning of the migratory corridor for native anadromous fishes before they enter the San Joaquin River.

Five long-term monitoring programs have been implemented on the Stanislaus River to track populations of fall-run Chinook Salmon and Steelhead/Rainbow Trout. Although Striped Bass were not the focus of this monitoring, these programs provided a source of incidental Striped Bass observations. Since 1996, two programs have monitored emigrating juvenile salmon and Steelhead using rotary screw traps (RST) from January through June. The upstream trap, located near the city of Oakdale (Figure 1), captured juveniles leaving the spawning and rearing reach (Pilger et al. 2019). The downstream program has operated two RSTs in tandem and was located 15 km upstream of the confluence with the San Joaquin River (Sturrock et al. 2020). Adult Chinook Salmon and Steelhead have been monitored using a fish-counting weir located at the downstream end of the spawning reach since 2003 (Peterson et al. 2017; Eschenroeder et al. 2022). The weir has an infrared counting device that, when triggered, captures a silhouette and photograph of the passing fish. Since observed Striped Bass were not handled, TLs were estimated by using the body depths measured from the silhouettes and an empirically derived body depth to length ratio of 5.0 ( $n = 14$  individuals measured). The weir was typically operated from September through January, but occasionally for extended periods. During 2006–07, 2008–09, and 2009–10, the weir was operated from September through June, and in 2012–13 the weir was operated from September 2012 to August 2013. In 2009, a redd survey program began to track spatial and temporal distribution of fall-run Chinook Salmon spawning in October and November (Peterson et al. 2020). Lastly, a snorkel survey program began in 2009 to estimate the

abundance of resident and juvenile *O. mykiss* in July and August (Eschenroeder et al. 2022).

### Fish Capture Methods

Our standardized electrofishing surveys targeting Striped Bass occurred in the lower 65 km of the Stanislaus River from March to June in 2019; in February to March and May to June in 2020; and in February to May in 2021. We delineated the entire reach into 384 potential sample sites, each approximately 300 m long. We randomly selected the first downstream site and every fifth site thereafter, alternating between the left or right bank, for a total of 39 sites. The up- and downstream boundaries of each site were marked with flagging and recorded as GPS waypoints for repeated visits. Our surveys followed Pollock's robust design (Pollock 1982), whereby visits to each site consisted of a primary event with two secondary events. For each primary event, sites were surveyed on 2 consecutive days, and we assumed that sites were closed to changes in the occupancy state (i.e., occupied or unoccupied) during secondary events on back-to-back visits. Primary events were repeated semi-monthly (every 3 to 4 weeks) from February through June, depending on year. Between primary events, the occupancy state of each site could change or remain the same.

We used boat electrofishing to capture Striped Bass. Electrofishing boats had a 5.0-watt generator-powered pulsator (GPP), and initial settings at each site were typically 60 Hertz and 30% duty cycle at either high or low range with direct current only. We held captured fish in a re-circulating tank until the entire site was fished. We measured TL and fork length (FL) to the nearest millimeter (mm). Before release, we implanted a 12-mm, half-duplex, passive integrated transponder (PIT; Oregon RFID [Portland, OR] or Biomark [Boise, ID]) tag into the peritoneal cavity of each Striped Bass as part of a concurrent mark-recapture study. We then released the fish in the middle of the site.

## Data Analyses

### ***When Do Striped Bass Occur in the Stanislaus River?***

We compiled incidental observations of Striped Bass from the five long-term salmonid monitoring programs to identify which months of the year Striped Bass were present in the Stanislaus River. Because Striped Bass life history is vastly different from the species targeted by these monitoring programs, these observations only provided a coarse depiction of when and where Striped Bass have occurred. Observations from each program were grouped by month, and when length data were available, we noted the size range observed. Given the lack of information on Striped Bass in the Stanislaus River, monthly presence served as a first step in identifying seasonal occurrence patterns.

### ***What is the Size Distribution of Striped Bass During Juvenile Salmonid Migration Season?***

To characterize Striped Bass size distribution from February to June, we used fish captured during the standardized electrofishing surveys and supplemented these with fish captured during additional electrofishing surveys at different sites related to the mark–recapture study. First, we grouped fish by month to examine fork length (FL) distributions in each month. We also used catch per unit effort (CPUE) in electrofishing hours to quantify Striped Bass catch each month. Due to uneven numbers of individuals captured across months in a year, we pooled data into an early period (February, March, and April surveys) and a late period (May and June surveys) to test for temporal differences in fork length. Results from Shapiro–Wilk normality tests (Royston 1982) indicated that fork lengths from both time-periods in each year were not normally distributed and had unequal variances. Therefore, we used non-parametric Mann–Whitney U tests (Hollander and Wolfe 1999) to evaluate differences in median FL between the early and late periods for each year. We considered tests to be statistically significant at the  $\alpha = 0.05$  level. Analyses were performed using functions from package “stats” for R software (R Core Team 2021).

### ***Does Striped Bass Occupancy Vary by Body Size Within and Among Years?***

We used dynamic, multi-season occupancy modeling (MacKenzie et al. 2003) to evaluate occupancy patterns within and among years, and to assess whether occupancy varied by body size. Based on visual assessment of annual length-frequency distributions for the early and late survey periods, we chose a 300-mm FL cut-off for grouping Striped Bass into two size classes. Detection/non-detection data from each site visit within and among semi-monthly surveys were stratified by year and size class for analysis. Within each year, the proportion of occupied sites was estimated for each semi-monthly survey (i.e., seasons). The robust design allowed detection probability ( $p$ ) to be estimated using information from site visits across consecutive days where occupancy state was assumed closed. Estimates of the proportion of occupied sites were derived from modeling initial occupancy ( $\psi$ , the probability a site was occupied before sampling), colonization ( $\gamma$ , the conditional probability that a site became occupied given it was previously unoccupied), and extinction ( $\epsilon$ , the conditional probability that an occupied site became unoccupied given it was previously occupied). Modeling was performed using the R package “unmarked” (Fiske and Chandler 2011).

We modeled heterogeneity in the four model parameters using continuous and discrete covariates. In the vernacular of Fiske and Chandler (2011), observation covariates corresponded to variables for each site visit, and we used these for modeling  $p$ . Our observation covariates were electrofishing effort (seconds) and river discharge (cubic feet per second [cfs]; downloaded from the USGS Gauging Station at Ripon; #11303000) on the day of the site visit because we expected these two factors to affect detection of Striped Bass. We assessed collinearity of these variables using Pearson’s correlation coefficient. For each site, the distance in kilometers upstream of the confluence with the San Joaquin River was used to account for spatial effects on  $\psi$  and  $\gamma$ . Specifically, if Striped Bass migrate into and upstream each year, we predicted that downstream sites would have

higher initial occupancy probability and higher colonization probabilities than upstream sites. We also included survey event number (E; 1 to 5) as a discrete time covariate for  $\gamma$  and  $\epsilon$ . We scaled (mean-centered) the continuous covariates effort (e), discharge (f), and river kilometer (r), to assist with numerical convergence of the models. Lastly, we included year (Y) and size group (S) as discrete covariates to evaluate if  $\psi$ ,  $\gamma$ , and  $\epsilon$  varied across years and size groups. Rather than evaluate all possible model combinations, we used a multi-step approach to assess *a priori* hypotheses about model parameters and covariates (Williams and Fabrizio 2011). First, we compared a series of univariate and additive detection models using effort, discharge, size group, year, and event, while holding the three occupancy parameters constant. Second, we used the parametrization from the most supported detection model(s) in a candidate set of models to identify covariates for  $\psi$ . Third, we then used the most supported covariate(s) for  $p$  and  $\psi$  in a candidate set for  $\gamma$  covariates. And lastly, we used the most supported covariates from the first three parameters in a candidate set for assessing  $\epsilon$  covariates. We used Akaike Information Criterion (Akaike 1973) corrected for sample size (AICc), to evaluate model support, and we considered

models with  $\Delta\text{AICc}$  values  $< 2$  and Akaike weights ( $w_i$ )  $> 0.20$  to be plausible competing models (Burnham and Anderson 2002). We used non-parametric bootstrapping with 1,000 iterations to derive 95% confidence for occupancy estimates (Kéry and Royle 2021). To assess goodness-of-fit of the occupancy models to the data, we used the MacKenzie and Bailey (2004) test implemented in the package “AICcmodavg” (Mazerolle 2023). The estimated  $\hat{c}$  from the test was 3.9, which indicated a moderate amount of over-dispersion. Therefore, we used quasi-AICc (QAICc) in the final model selection to account for the additional uncertainty (Burnham and Anderson 2002)

## RESULTS

### When Do Striped Bass Occur in the Stanislaus River?

Through monitoring efforts targeting salmonids, Striped Bass have been incidentally observed or captured in the Stanislaus River during every month of the year (Table 1). Rotary screw trap programs that operated from January through June have captured Striped Bass in January, March, April, May, and June. The size (FL) of Striped Bass that have been observed at the rotary screw traps ranged from 73 to 501 mm. Since 2003, a mean of 12 (range: 0–51) Striped Bass per year

**Table 1** Summary of Striped Bass observations from four salmonid monitoring programs in the Stanislaus River. In the month columns, a *Y* indicates that at least one Striped Bass was observed or captured, *N* indicates no observation or catch, and a *dash* indicates no monitoring occurred during that month. Locations of monitoring programs correspond to locations in Figure 1.

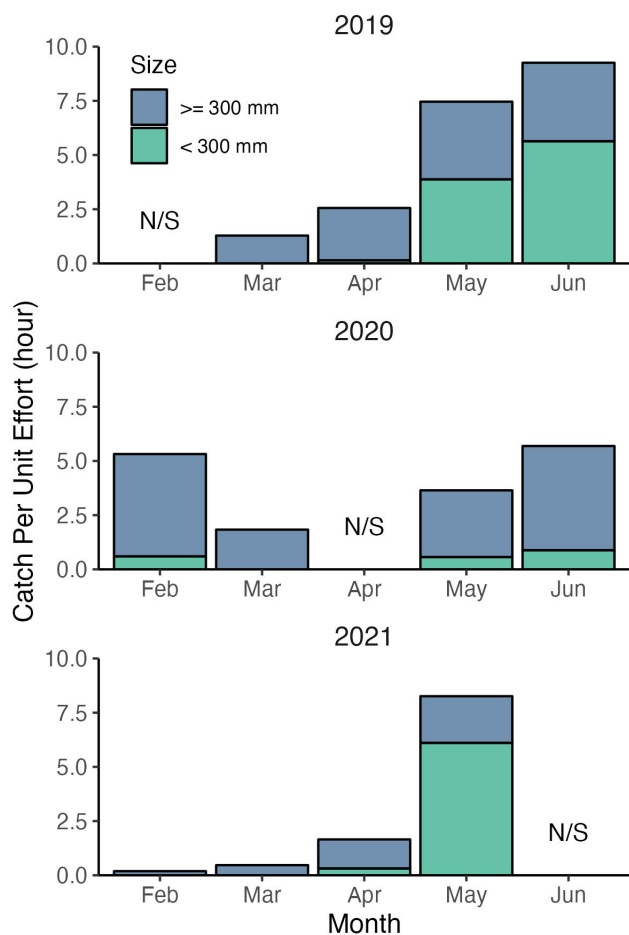
Program	Gear(s)	Location	Years	Month												Average observed (Range)
				J	F	M	A	M	J	J	A	S	O	N	D	
Juvenile monitoring	Rotary Screw Trap	Caswell	1996, 1998–2022	Y	N	Y	N	Y	Y	–	–	–	–	–	–	1 (0–4) <sup>a</sup>
		Oakdale	1996, 1998–2022	Y	N	N	Y	Y	Y	–	–	–	–	–	–	1 (0–3) <sup>b</sup>
Adult monitoring	Weir and VAKI river-watcher	Riverbank	2003–2021	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	12 (0–51) <sup>c</sup>
<i>O. mykiss</i> abundance	Snorkel	Oakdale–Goodwin Dam	2009–2021	–	–	–	–	–	–	Y	Y	–	–	–	–	39 (4–86)
Chinook Salmon redd surveys	Visual observations	McHenry–Goodwin Dam	2009–2019	–	–	–	–	–	–	–	–	–	Y	Y	–	N/A <sup>d</sup>

a. Mean fork length (FL, mm) = 287 mm; range = 148–510 mm.

b. Mean fork length (FL, mm) = 233 mm; range = 73–500 mm.

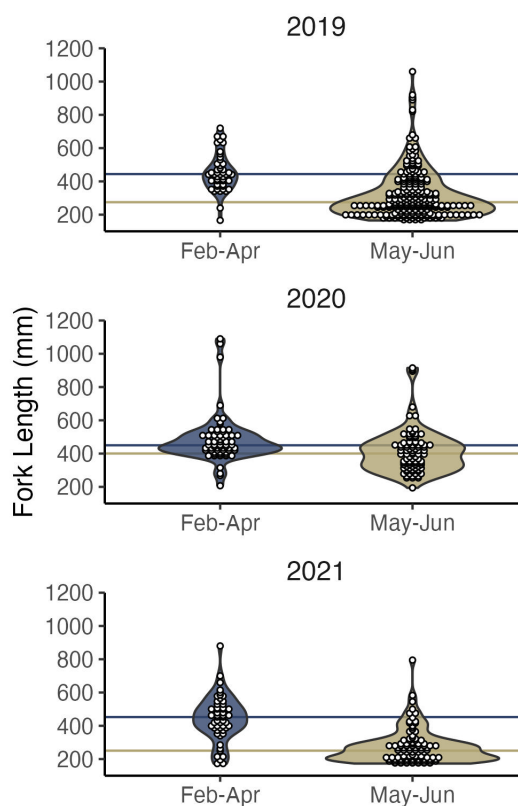
c. Mean total length (TL; mm) = 438 mm; range = 175–1,130 mm TL.

d. Data insufficient to estimate annual mean and range.



**Figure 2** Catch per unit effort of Striped Bass by month from electrofishing surveys on the Stanislaus River from 2019 to 2021. Bars are color-coded by size group, and N/S indicates unsampled months.

have been observed during weir monitoring. The Stanislaus River weir was primarily operated during the months of September through January; however, it has been intermittently operated for longer time-periods. Striped Bass ranging in size from 175 to 1,130 mm TL have been observed during every month of operation. During *O. mykiss* snorkel surveys in July and August, which started in 2009, a mean of 39 (range: 4–86) Striped Bass were observed each year and were seen as far upstream as Knight’s Ferry (Figure 1). Striped Bass were also incidentally observed during surveys for Chinook Salmon redds in October and November; however, the numbers observed per year were not recorded. Because no fish were captured during the snorkel and redd surveys, no data on sizes were collected.



**Figure 3** Individual fork lengths (white dots) and distributions of fork lengths for Striped Bass captured during electrofishing surveys on the Stanislaus River 2019–2021. Individuals were grouped depending on if they were captured during early (Feb–Apr) or late (May–Jun) periods. Horizontal lines indicate the median fork lengths and line colors correspond to early and late periods.

**What is the Size Distribution of Striped Bass During Juvenile Salmonid Migration Season?**

Across 3 years, we captured and measured a total of 580 Striped Bass during the standardized surveys for occupancy modeling and additional electrofishing efforts. The greatest number of Striped Bass were captured in 2019 (n = 278), with fewer numbers captured in 2020 (n = 154) and 2021 (n = 148). In 2019 and 2021, CPUE of Striped Bass increased from March to June and February to May, respectively (Figure 2). In February 2020, CPUE was substantially higher than March 2019 or February 2021, but CPUE in June 2020 was lower than June 2019 or May 2021. Captured Striped Bass exhibited a wide range of sizes, from 165 to 1,090 mm FL (Figure 3). In all years, the median FL of Striped Bass captured during the



early survey period (February through April) was larger than the median FL during late surveys (May through June). In 2019, the median FL during the early period was 444 mm (1st–3rd quartile range [QR]: 395–503 mm), which was 70 mm greater than during the late period (314 mm; QR = 275–392 mm;  $U = 8,523$ ,  $p < 0.001$ ). In 2020, the median FL during early surveys (450 mm; QR = 418–510 mm) was 50 mm greater than late surveys (400 mm; QR = 326–464 mm;  $U = 3,916$ ,  $p < 0.001$ ). In 2021, early median FL (452 mm; QR = 383–511 mm) was 202 mm greater than during the late period (250 mm; QR = 203–302 mm;  $U = 4,183$ ,  $p < 0.001$ ), a greater difference than observed in either 2019 or 2020. The decrease in median size reflects a relatively consistent catch of larger individuals in all months, in combination with increasing catch of smaller fish beginning in April (Figure 2).

### Does Striped Bass Occupancy Vary by Body Size within and Among Years?

Flow conditions were very different across the 3 years of this study, with 2019 having the highest flows and 2021 having the lowest flows. According to the San Joaquin Valley Water Year Index, 2019 was a wet year, 2020 was a dry year, and 2021 was a critical year (California Department of Water Resources; <http://cdec4gov.water.ca.gov/reportapp/javareports?name=WSIHIST>; accessed 12/15/23). The average daily discharge across all survey dates in 2019 was 3,349 cfs (SD = 1,387 cfs), in 2020 average discharge was 1,630 cfs (SD = 392 cfs), and in 2021 average discharge was 622 cfs (SD = 371 cfs). Average effort per site and survey (i.e., robust design primary event) in 2019 was 1,001 seconds (SD = 407 seconds). In 2020, average effort per site and survey was 933 seconds (SD = 264 seconds). In 2021, average effort per site and survey was 1,180 seconds (SD = 403 seconds). Pearson's correlation coefficient between flow and electrofishing effort was small ( $r = -0.24$ ); therefore, we considered these variables to not be correlated.

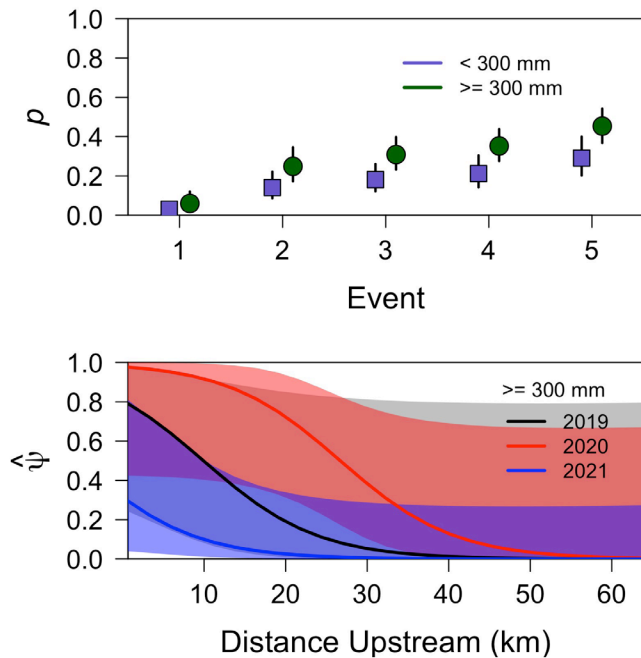
Our detection candidate set included 16 models to identify the most supported covariates for detection. The model with the lowest QAICc had detection probability varying by size group and survey event (Table 2). The QAICc of this model

**Table 2** Multi-season occupancy models for selecting covariates to detect the probability of Striped Bass in the Stanislaus River 2019–2021. Parameter covariates were size group (S), year (Y), survey event (E), electrofishing effort (e), and mean daily flow (f). Model summary statistics include the number of estimated parameters (K), difference in QAICc value from the model with the lowest QAICc ( $\Delta$ QAICc) and Akaike model weight ( $w_i$ ). Only models with a weight of 0.01 or greater are included.

Model	K	$\Delta$ QAICc	QAICc $w_i$
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(SE)$	10	0.00	0.60
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(E)$	9	2.94	0.14
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(SYE)$	12	4.25	0.07
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(Ef)$	10	5.02	0.05
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(Ee)$	10	5.06	0.05
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(S)$	6	6.81	0.02
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(YE)$	11	7.00	0.02
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(EfE)$	11	7.17	0.01
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(Se)$	7	8.02	0.01
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(Sf)$	7	8.63	0.01
$\Psi(\cdot)\gamma(\cdot)\epsilon(\cdot)p(\cdot)$	5	9.13	0.01

was lower than the next model by a value of 2.94, and it had a model weight of 0.60. Size had a strong effect on detection, with the smaller-sized group having lower detection probability than the larger-sized group (Figure 4). For both size groups, estimates of detection probability were lowest during the first event each year, and increased during subsequent events. Increasing CPUE across survey events likely increased the probability of detecting individuals.

Our final occupancy candidate set included 30 models with different univariate and additive combinations of covariates for the occupancy parameters. The first set of seven models identified the best covariates for initial occupancy while holding colonization and extinction constant. The model that allowed initial occupancy to vary by size group (S), year (Y) and upstream distance ( $r$ ) –  $\Psi(SYr)$  – had the lowest QAICc by 5.18 compared to the model with the second lowest QAICc and had a model weight of 0.93. We carried this combination of covariates for initial occupancy over to the candidate set for probability of colonization. Two of the 11 colonization models that included combinations



**Figure 4** Estimates of occupancy model parameters for Striped Bass in the Stanislaus River from 2019 to 2021 based on the most supported model  $\Psi(SYr)\gamma(\cdot)\epsilon(\cdot)p(SE)$  in Table 3. The top panel shows detection probability varying by size group and survey event. The bottom panel shows the effect of distance upstream from the San Joaquin River (kilometers) by year on initial occupancy probabilities for the largest size group.

of size group, survey event, year, and distance upstream had  $\Delta QAICc$  values under 2.0 and model weights of 0.20 or greater. These were models that either held colonization constant or allowed it to vary by size group –  $\gamma(\cdot)$  or  $\gamma(S)$ . Lastly, our candidate set for probability of extinction consisted of 12 models using size group, year, and survey event as covariates, while keeping the best covariates for initial occupancy and the two alternatives for colonization. Comparing all 30 models, the model with constant colonization and constant extinction had the lowest QAICc and was the only model with weight greater than 0.20 (Table 3).

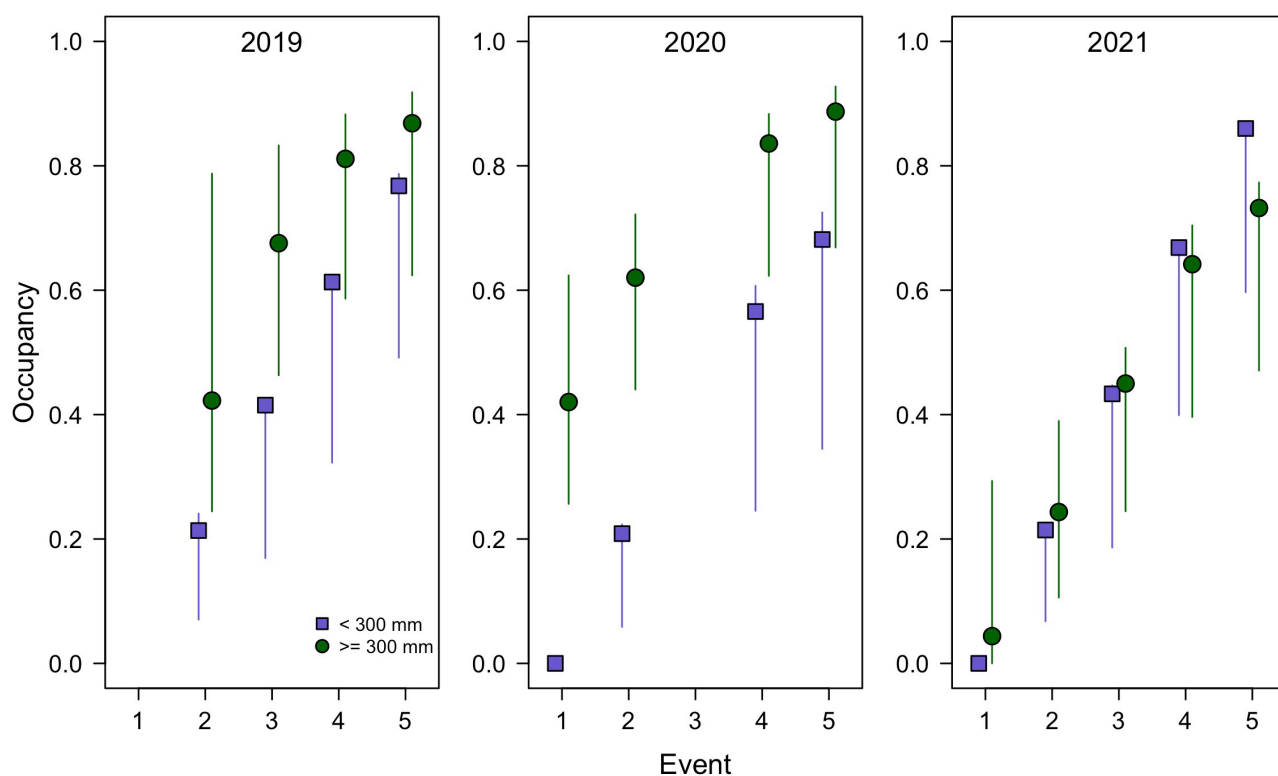
Because Striped Bass smaller than 300 mm FL were rarely captured at the beginning of each year, the estimates of initial colonization for this group had large standard errors relative to the estimates. For the larger size group, estimates of initial occupancy were greater at downstream

**Table 3** Multi-season occupancy models to estimate occupancy of Striped Bass in the Stanislaus River 2019–2021. Parameter covariates were size group (S), year (Y), distance upstream from the San Joaquin River (r), and survey event (E). Model summary statistics include the number of parameters (K), difference in QAICc value from the model with the lowest QAICc ( $\Delta QAICc$ ) and Akaike model weight ( $w_i$ ). Only models with a weight of 0.01 or greater are included.

Model	K	$\Delta QAICc$	QAICc $w_i$
$\Psi(SYr)\gamma(\cdot)\epsilon(\cdot)p(SE)$	14	0.00	0.37
$\Psi(SYr)\gamma(S)\epsilon(\cdot)p(SE)$	15	1.70	0.16
$\Psi(SYr)\gamma(r)\epsilon(\cdot)p(SE)$	15	1.91	0.14
$\Psi(SYr)\gamma(\cdot)\epsilon(S)p(SE)$	15	2.11	0.13
$\Psi(SYr)\gamma(S)\epsilon(S)p(SE)$	16	3.82	0.05
$\Psi(SYr)\gamma(Sr)\epsilon(\cdot)p(SE)$	16	3.83	0.05
$\Psi(SYr)\gamma(SY)\epsilon(\cdot)p(SE)$	17	5.89	0.02
$\Psi(SYr)\gamma(Yr)\epsilon(\cdot)p(SE)$	17	5.95	0.02
$\Psi(SYr)\gamma(\cdot)\epsilon(SY)p(SE)$	17	6.56	0.01
$\Psi(SYr)\gamma(E)\epsilon(\cdot)p(SE)$	18	6.97	0.01
$\Psi(SYr)\gamma(SYr)\epsilon(\cdot)p(SE)$	18	7.98	0.01
$\Psi(SYr)\gamma(S)\epsilon(SY)p(SE)$	18	8.37	0.01

sites and decreased with upstream distance (Figure 4), suggesting these larger Striped Bass had recently entered the Stanislaus River. Estimates of initial occupancy were higher in 2020 than in the other 2 years. The constant colonization probability estimate was 0.29 (95% confidence intervals [CI] = 0.22–0.36); thus, any unoccupied site had approximately a 30% chance of becoming colonized by Striped Bass of any size at any location in the study area on any given survey event. In all years, observations of sites going from colonized to uncolonized were rare during the survey season; therefore, the model produced a very imprecise extinction estimate (i.e., a large SE relative to the estimate).

Occupancy estimates increased winter to spring for both small and large Striped Bass in all years (Figure 5). The greatest estimates were for the large size group on survey event 5 in 2019 (0.87; 95% CI = 0.62–0.92) and 2020 (0.89; 95% CI = 0.67–0.93), and the small size group in 2021 (0.86; 95% CI = 0.60–0.87). For the first 2 years, occupancy estimates for larger Striped Bass were substantially greater than estimates for the small



**Figure 5** Seasonal occupancy estimates for two size groups of Striped Bass in the lower Stanislaus River during electrofishing survey events that occurred during the late winter and spring of 2019, 2020, and 2021. Occupancy estimates were derived from the most supported model  $\Psi(SYr)\gamma(\cdot)\epsilon(\cdot)p(SE)$  in Table 3. Vertical lines show bootstrapped 95% confidence intervals of the estimate.

size group. In 2021, estimates tended to be more similar between size groups. After accounting for imperfect detection, Striped Bass were present in over 80% of the survey sites by the end of May each year.

## DISCUSSION

Understanding spatial and temporal occurrence of Striped Bass in the Stanislaus River is needed to characterize habitat overlap with native fish species and the potential for increased predation pressure. Based on incidental observations of Striped Bass that occurred in multiple long-term salmonid monitoring programs, some Striped Bass that were large enough to be piscivorous have been present in the Stanislaus River at any given time throughout the year. Furthermore, they have been observed upstream in reaches where Chinook Salmon and Steelhead/Rainbow Trout spawn and rear. To better document spatial and temporal overlap, we designed our

electrofishing surveys to target Striped Bass in the Chinook Salmon and Steelhead migratory corridor during the juvenile emigration season. We found that the Striped Bass most likely to be present at the beginning of the emigration season were 300 mm FL or greater. In all 3 years, Striped Bass shorter than 300 mm FL arrived later in the season. We also found that occupancy for both size groups increased throughout the salmon emigration season, reaching over 80% of the migratory corridor in both high- and low-flow years. These results, in conjunction with results from a concurrent diet study that found Striped Bass consumed Chinook Salmon at the highest frequency of any other predatory fish species examined (Peterson et al. 2023), suggest that Striped Bass may be capable of exerting strong top-down control on populations of Chinook Salmon, limiting the overall production from the Stanislaus River.

Before the initiation of our electrofishing surveys on the Stanislaus River, there was little information about Striped Bass in the San Joaquin basin. Because the monitoring programs on the Stanislaus River were designed around the life history of fall-run Chinook Salmon, Rainbow Trout, and Steelhead, historical data on Striped Bass were sparse. However, based on incidental observations, a broad range of sizes of Striped Bass have been present in the river during all months of the year. From these observations, it was unknown whether these individuals were exhibiting a resident life history or were temporarily using the Stanislaus River. The only size of Striped Bass that has not been observed was that corresponding to age-0 (< 50 mm FL). Larval and age-0 Striped Bass have been captured by trownet and seining monitoring programs in the lower San Joaquin River and Delta (Bashevkin et al. 2022; Mahardja et al. 2017). Since these gears are not deployed in the Stanislaus River, these fish may be present but undetectable by existing monitoring programs.

In all 3 years, we found that the median length of Striped Bass captured in the Stanislaus River was significantly longer in February through April compared to May through June. Striped Bass 300 mm FL and larger were consistently captured throughout each year of sampling, and were noticeably the only size group present at the start of sampling each year. Based on our occupancy modeling, large Striped Bass were more likely to be present at sites closer to the mouth of the river in February and March, suggesting that they were entering from the San Joaquin River or were aggregating near the mouth. In 2020 for example, the estimated probability that sites closest to the confluence with the San Joaquin River were occupied by large Striped Bass was 0.98 (CI = 0.42–1.00). The decrease in median length during May and June was caused by an influx of individuals that were under 300 mm FL that started in April and continued into June. Given that smaller Striped Bass appeared later, it is surprising that the most supported model had a constant colonization probability, although there was moderate support for size-specific colonization probabilities (i.e.,  $\Delta\text{QAICc} < 2.0$  but  $w_i < 0.2$ ). There

was also moderate support for colonization increasing with distance upstream. This would be expected because there would be fewer opportunities for downstream sites to become colonized since they were already occupied. The constant colonization, however, is supported by the high mobility of Striped Bass, and suggests that once they are present in the Stanislaus, they can move throughout the study reach within the time between our surveys (i.e., 3 to 4 weeks).

In the Stanislaus River, large, presumably mature Striped Bass were present in February and March. Because Striped Bass in the Sacramento River basin are known to winter in the Delta and migrate upstream starting in March (Sabal et al. 2019; Goertler et al. 2021), the fish we observed could be a resident contingent in the San Joaquin basin or have migrated from the Delta in January and February. These adults could be aggregating in habitats that support seasonally abundant prey (e.g., Nobriga and Feyrer 2007), holding until water temperatures are warm enough to spawn, or both. While we observed some male Striped Bass exhibiting signs of maturity (i.e., releasing milt upon capture), we did not observe ripe females. Based on catch from the two RSTs at Oakdale and Caswell, which occasionally captured age-1+ individuals (73 to 510 mm FL), there was no evidence of Striped Bass spawning in the Stanislaus River. However, these programs ceased operating in June, which may limit the ability to detect age-0 individuals (< 50 mm FL) dispersing downstream. Age-0 Striped Bass are captured in beach seine surveys and RSTs on the Yolo Bypass in June, July, and August (IEP et al. 2023). They have also been captured as part of beach seine surveys during the early summer in some years in the San Joaquin River around the confluence of the Stanislaus River (Bashevkin et al. 2022). This may indicate occasional successful spawning of adult Striped Bass in the San Joaquin watershed. Some individuals of Atlantic coastal migratory populations are known to move into rivers that do not support spawning, sometimes repeatedly over several spawning seasons, suggesting that movement into non-natal streams may be a behavior inherent to Striped Bass that allows for colonization of new areas or

re-colonization of streams where the population has been extirpated (Grothues et al. 2009).

We also observed a contingent of sub-adult Striped Bass enter the Stanislaus River beginning in April. Studies on Striped Bass have documented variable migratory behaviors related to size (Sabal et al. 2019; Le Doux–Bloom et al. 2021). Because these individuals are not mature, they were most likely migrating into the river to feed. Striped Bass in the Delta responded to seasonal changes in prey availability, and Nobriga and Feyrer (2007) suggested that they may aggregate in habitats that support seasonally abundant prey, such as emigrating juvenile salmonids. Le Doux–Bloom et al. (2021) suggested that movements of sub-adult Striped Bass (225 to 340 mm TL) into the Sacramento River in the spring could be the result of warming water temperatures, high abundance of prey, or that the sub-adults were following pheromone cues left by adults.

Across the 3 years, patterns of seasonal occupancy were similar in that occupancy estimates increased from February to June, to over 80% of sample sites in the lower Stanislaus River. Although our electrofishing surveys did not occur during January, some Striped Bass were likely present in all 3 years, based on past observations at the Stanislaus weir and captures at both the Caswell and Oakdale RSTs. In the Stanislaus River, the period from January through June encompasses nearly the entire emigration period for juvenile fall-run Chinook Salmon. Unpublished data on juvenile Chinook Salmon captured in the Oakdale RST during our surveys (February to June) in 2019, 2020, and 2021 show that 93%, 83%, and 80% of the total catch occurred in these months for each year, respectively (FISHBIO, unpublished data, see “Notes”). Based on long-term data at the Caswell RST (1996, 1998–2014), the mean date of peak fry (<55 mm FL) migration was February 15, and the peak of smolt (> 75 mm FL) migration was May 5 (Sturrock et al. 2020). Based on an optimal prey-to-predator size ratio of 0.12 for Striped Bass (Hartman 2000), a 500-mm-FL individual maximizes foraging profitability by targeting prey that are approximately 60 mm. A concurrent

diet study from the Stanislaus River showed that Striped Bass as small as 173 mm TL had consumed juvenile Chinook Salmon and juvenile Pacific Lamprey (Peterson et al. 2023). The high degree of spatial and temporal overlap between these native species and Striped Bass could result in substantial predation pressure. Thus, predation by Striped Bass could be limiting production of native anadromous fish species (Nobriga and Smith 2020; Nobriga et al. 2021).

Here, we presented the first formal evaluation of Striped Bass occupancy and occurrence patterns in the Stanislaus River using standardized electrofishing surveys. However, limitations to our study warrant some discussion.

**First**, our study was set up according to Pollock's (1982) robust design, which assumed that the occupancy states did not change between surveys on back-to-back days. Even though we implanted individuals with PIT tags, we never recaptured an individual at the same site on back-to-back days, and over the course of 3 years, very few Striped Bass were ever recaptured. The transient nature and high mobility of the species raised the possibility that our assumption of closure was not met. Violating the closure assumption could result in biased detection probabilities; however, estimates of detection probability can still be unbiased if movement into and out of the site was random during the period (Kendall 1999).

**Second**, our sampling focused on the juvenile salmon emigration period, and surveys ended in May or June (when water temperature reached 18 °C as required by our permit). Therefore, we were unable to determine when Striped Bass occupancy in the river declined each year. Extending the surveys into later months would help to identify when and under what conditions Striped Bass emigrated from the Stanislaus River.

**Lastly**, we suspect that some Striped Bass may be utilizing the river outside of the salmon emigration period based on the year-round incidental observations. How frequently this occurs and where those individuals come from are important questions that cannot be answered

with presence/absence data and occupancy modeling. There are now three PIT tag antennas operating on the Stanislaus River as part of a Steelhead monitoring program (Figure 1). Future detections of the individuals we tagged during this study could help answer these questions. In addition, acoustic telemetry studies in the San Joaquin watershed are needed to gain a better understanding of the diversity of individual movement patterns and habitat utilization, as has been done in the Sacramento River watershed (Sabal et al. 2019; Le Doux–Bloom et al. 2021).

## CONCLUSIONS

After their introduction, it took Striped Bass less than 2 decades to be widespread throughout California's Central Valley (Scofield and Bryant 1926). Their ability to thrive and persist outside of their native range can be attributed, in part, to a complex life history that includes partial migration and differential migration behaviors (Secor et al. 2001; 2020). As a popular and economically important sport fish, it is critical that the needs of the fishery are balanced against negative effects on sensitive native fishes. A full accounting of Striped Bass life history diversity and size-specific movement behaviors is needed to inform monitoring efforts aimed at assessing changes in population demographics and abundance. Furthermore, robust data on the occurrence of Striped Bass can be used to understand how the population overlaps in space and time with sensitive native fishes.

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