

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/328086750>

Seasonal Movement Patterns of Striped Bass (*Morone saxatilis*) in Their Nonnative Range

Article in *Estuaries and Coasts* · October 2018

DOI: 10.1007/s12237-018-0467-7

CITATIONS

12

READS

460

5 authors, including:



Megan Sabal

University of California, Santa Cruz

11 PUBLICATIONS 114 CITATIONS

[SEE PROFILE](#)



Cyril Michel

University of California, Santa Cruz

31 PUBLICATIONS 652 CITATIONS

[SEE PROFILE](#)



Joseph M. Smith

Northwest Fisheries Science Center

44 PUBLICATIONS 600 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Freshwater survival of juvenile spring-run Chinook in California Central Valley [View project](#)



Seasonal Movement Patterns of Striped Bass (*Morone saxatilis*) in Their Nonnative Range

Megan C. Sabal¹ · Cyril J. Michel^{2,3} · Joseph M. Smith⁴ · Andrew Hampton⁵ · Sean A. Hayes⁶

Received: 14 August 2017 / Revised: 13 September 2018 / Accepted: 25 September 2018
© Coastal and Estuarine Research Federation 2018

Abstract

Movement dynamics of nonnative species can change in new environments and differ from native populations. It has been more than 100 years since striped bass (*Morone saxatilis*) were introduced to the Sacramento-San Joaquin River system in California from the US east coast. Acoustic telemetry from 2011 to 2015 was used to examine striped bass seasonal residence patterns in their nonnative range across three regions—bay, delta and rivers, and the effect of fish length and release river (Sacramento River [SR] vs. Feather River [FR]) on movement. In spring, SR striped bass ($n = 52$) increased travel speed by 39% and river residence by 63% relative to other seasons, which is consistent with spawning migrations. In summer, SR striped bass spent the most time in the bay (mean = 28.2 ± 30.9 days) relative to other seasons and across regions. In winter, 87% of striped bass were detected in the delta over 42% in the bay and 25% in the river. Release river also affected movement behaviors—FR striped bass ($n = 11$) spent more time in the river in all seasons compared to SR bass. Striped bass with sufficient tag life ($n = 17$) traveled farther distances in 365 days (mean = 1248 ± 405 km, range: 641–2212 km) with increasing fish length. Seasonal patterns observed appeared to follow seasonal prey sources throughout the San Francisco Estuary. Individual behaviors, however, were highly variable, and this flexibility may be an important trait that has allowed striped bass to persist in their nonnative range.

Keywords Striped bass · California · Movement · Migration · Seasonality · Tagging

Communicated by David G. Kimmel

✉ Megan C. Sabal
msabal@ucsc.edu

¹ Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 130 McAllister Way, Santa Cruz, CA 95060, USA

² Cooperative Institute for Marine Ecosystems and Climate (CIMEC) Award number: 22694-443861, University of California Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA

³ Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA

⁴ National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, Point Adams Research Station, 520 Heceta Place, Hammond, OR 97121, USA

⁵ Division Feather River Program, Pacific States Marine Fisheries Commission, 460 Glen Dr., Oroville, CA 95966, USA

⁶ Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration, 166 Water Street, Woods Hole, MA 02543, USA

Introduction

Local animal movements and larger-scale migrations may change as a nonnative species is introduced to a new environment. Species may extend their range to take advantage of newly available niches (Peterson 2003) or may lose a migratory life history strategy if it is no longer advantageous (Quinn et al. 2001). These potential changes in animal movements can have a suite of ecological effects (Nathan et al. 2008). Movement behavior affects fitness and consequently the dynamics of the population and demography (McIntyre and Wiens 1999; Morales et al. 2010), and is critical in determining spatial overlap of interacting species, such as predators, prey, and competitors (Winder et al. 2001; Lima 2002). Examining species movement behaviors in their nonnative ranges provides information on how nonnative species interact with their new environment.

One such species exhibiting complex movement behaviors residing in both a native and nonnative range is the striped bass (*Morone saxatilis*). Striped bass is a highly mobile species exhibiting complex local movements and seasonal migrations, both in their native range on the east coast of North America and nonnative range on the west coast. The east coast

range spans from the St. Lawrence River in Canada to St. John's River in Florida (Collette and Klein-MacPhee 2002) and the most productive spawning rivers are the major tributaries of Chesapeake Bay, Hudson River, and Delaware River. Humans first introduced striped bass to the San Francisco Estuary in 1879, and a mere 20 years later, commercial fisheries were harvesting well over a million pounds a year (Stevens et al. 1985). This is the only major population of anadromous striped bass outside of their native range. The California Department of Fish and Wildlife (CDFW) actively managed and stocked striped bass populations until 2001 when concern arose over nonnative striped bass consumption of native and endangered fish species (Lindley and Mohr 2002). Over the last century, anthropogenic changes such as diking, leveeing, flow manipulation, and invasions of introduced species have disrupted the San Francisco Estuary drastically (Nichols et al. 1986; Cloern and Jassby 2012). Furthermore, changes in salinity, water clarity, and food webs have led to the decline of many pelagic species starting around 2002 which includes striped bass (Feyrer et al. 2007; Mac Nally et al. 2010). With more than 100 years since the introduction of striped bass on the west coast, a comparison of movement dynamics between their native and nonnative ranges will provide knowledge on how a nonnative, mobile species has adapted to a new environment.

Striped bass exhibit strong seasonal movements that vary extensively over space. On the east coast, striped bass spawn from April to early June, their larvae develop as they move downstream until they are retained in the Estuarine Turbidity Maximum (North and Houde 2001), and juveniles (< 200 mm) are found in estuaries and inland coastal sounds (Able et al. 2012). Young striped bass remain in rearing waters up to 5 years before some enter the Atlantic Ocean and become coastal ocean migrants (Able et al. 2012). Some striped bass do not enter the ocean and instead become residents in their natal rivers and estuaries (Secor et al. 2001). Once striped bass leave their rearing location and enter the ocean, they migrate northward in the late spring, take up residence in summer feeding grounds, and migrate southward in the fall to over-wintering areas, and finally return to rivers to spawn in spring. Within this broader migration pattern, striped bass vary in fine-scale movements by location, populations, and individuals. A variety of environmental variables, such as salinity (Able et al. 2012), temperature (Nelson et al. 2010), dissolved oxygen (Kraus et al. 2015), age (Callihan et al. 2014), density (Callihan et al. 2014), and habitat structure (e.g., sandbars, channel networks) (Kennedy et al. 2016), can influence finer-scale movements. Furthermore, studies have widely documented migratory “contingents”, which are defined as groups of individuals belonging to the same population that adopt different migratory patterns (Secor 1999). Contingent groups can be observed at both small and large spatial scales and across life stages (Morissette et al. 2015). The extensive

knowledge on striped bass movements in their native range allows for the comparison of movement patterns between their native vs. nonnative range.

On both the east and west coasts, striped bass persist in large, shallow estuary systems with abundant forage fish and invertebrate prey. However, the San Francisco Estuary system differs in its highly seasonal hydrograph and narrow entrance into the Pacific Ocean with cool and productive upwelling. These ecological differences or founder effects from the initial invaders could influence genetic and behavioral change (Prentis et al. 2008). The limited studies that exist on California striped bass movements indicate that striped bass occupy the entire San Francisco Estuary including the Sacramento-San Joaquin Delta, nearby coastal Pacific Ocean, and major rivers entering the delta, including, but not limited to, the Sacramento, Feather, Mokelumne, and San Joaquin (Calhoun 1952; Chadwick 1967). Striped bass spawn in the spring: from April to early June on the San Joaquin, Sacramento, and Feather rivers (Turner 1976). Similar to populations on the east coast, striped bass lay eggs in rivers, where they hatch and develop as they are carried downstream with water flow to the western delta and bays where salinity gradients are important for many larval species (Stevens et al. 1985). By August, the juveniles are about 50 mm long and reside in the western delta and Suisun Bay where they rear in productive nursery habitats where fresh and salt water mix (Turner and Chadwick 1972). Sometime after this rearing stage, striped bass begin active movements within the delta. Striped bass reach sexual maturity at ages 4–5 (530–630 mm) in females and at ages 2–3 (280–400 mm) in males (Scofield 1931). In general, adult striped bass move upstream in the spring to spawn, migrate back downstream to the bays or ocean in the summer and fall, with some moving back upstream to the delta in winter (Calhoun 1952; Chadwick 1967; Le Doux-Bloom 2012). On the east coast, larger striped bass are more likely to become coastal ocean migrants; however, this pattern is highly variable (Secor and Piccoli 2007; Callihan et al. 2014). Despite knowledge on general movement patterns, a quantitative approach to characterizing striped bass movement dynamics in their nonnative range is lacking which is necessary to understand how movement behavior may have changed for this species in a new environment.

Improved understanding of striped bass movement dynamics has multiple advantages. In California, striped bass support a recreational fishery, and there is concern over recent population declines. Simultaneously, striped bass are predators with high energetic requirements and are considered a threat to native prey fishes (i.e., salmonids *Oncorhynchus* spp. and Delta smelt *Hypomesus transpacificus*) (Loboschewsky et al. 2012). This concern has prompted discussions about how to manage striped bass to increase native prey fish survival for example through predator removals. Therefore, it is important

to better understand California striped bass movements to inform our understanding of population life histories, interactions with the environment, and to better evaluate predation threats to native species.

This study addressed the question: how has a novel environment shaped striped bass life history patterns of movement? Five years of data from acoustically tagged striped bass that included bay, delta, and riverine habitats was used to quantify striped bass movements in California. Three metrics were used to describe striped bass movements over space and time including: residence days, percent of bass present, and speed. Movement patterns were also compared between striped bass tagged on the Sacramento and Feather Rivers where different spawning groups may exhibit distinct behaviors. The influence of size-related changes on striped bass movement was assessed by examining how fish length affected all movement metrics.

Methods

Study Site and Telemetry Network

California's two largest rivers, the Sacramento River and San Joaquin River join in the Sacramento-San Joaquin Delta, an expansive, tidally-influenced freshwater system comprised of a complex network of hundreds of kilometers of rivers and sloughs. The water flows west from the delta with increasing salinity, through the Suisun Bay, the Carquinez Strait, and finally, the San Francisco Bay, which connects to the Pacific Ocean at the Golden Gate Bridge. The San Francisco Bay and Sacramento-San Joaquin Delta together compose the San

Francisco Estuary, the largest estuary on the west coast of the Americas.

Due to the wide movement capabilities of striped bass, an extensive telemetry network was used to acoustically monitor the areas they inhabit. The network was available from 2011 to 2016 as part of the California Fish Tracking Consortium (CFTC), a collaboration between numerous state, federal, and academic institutions. The CFTC telemetry network used Vemco (Amirix Systems, Inc., Halifax, Nova Scotia, Canada) 69 kHz VR2/VR2W acoustic receivers positioned at various locations in the estuary and rivers. A total of 460 receivers were deployed from 2011 to 2016. Some receivers were only present for part of the study duration, but overall, there was good coverage across regions, seasons, and years (Table 1; Fig. 1). Major habitat regions (bay, delta, river) were distinguished by salinity and tidal influence. The bay region extended from the San Francisco Bay through Suisun Bay where the salinity gradient shifts from ~30 to 0 PSU. The delta region has low salinity values, but is highly influenced by tides, which affect river flows and water depth. The river region in this study starts where tidal effects in river flows are no longer seen: upstream of Freeport on the Sacramento River and the Cosumnes River confluence on the Mokelumne River. Striped bass are known to occupy all three of these regions. Of note, only one receiver was present on the Feather River in 2014, and none were present in 2015.

Capture, Tagging, and Release

Striped bass were captured, tagged, and released on the Sacramento River ($n = 81$, mean with SD fork length [FL] = 354 ± 83) and Feather River ($n = 20$, mean with SD

Table 1 Number of receivers present in each region across seasons and years

Year	Season	Total receivers in bay	Total receivers in delta	Total receivers in river
2011	fall	153	55	106
	spring	150	54	125
	summer	157	48	121
	winter	154	52	131
2012	fall	74	53	103
	spring	101	54	100
	summer	93	48	93
	winter	144	55	96
2013	fall	76	48	61
	spring	82	64	71
	summer	79	53	68
	winter	95	54	83
2014	fall	66	49	48
	spring	75	42	55
	summer	72	44	44
	winter	75	47	56
2015	fall	68	76	43
	spring	67	72	45
	summer	68	75	45
	winter	64	66	47

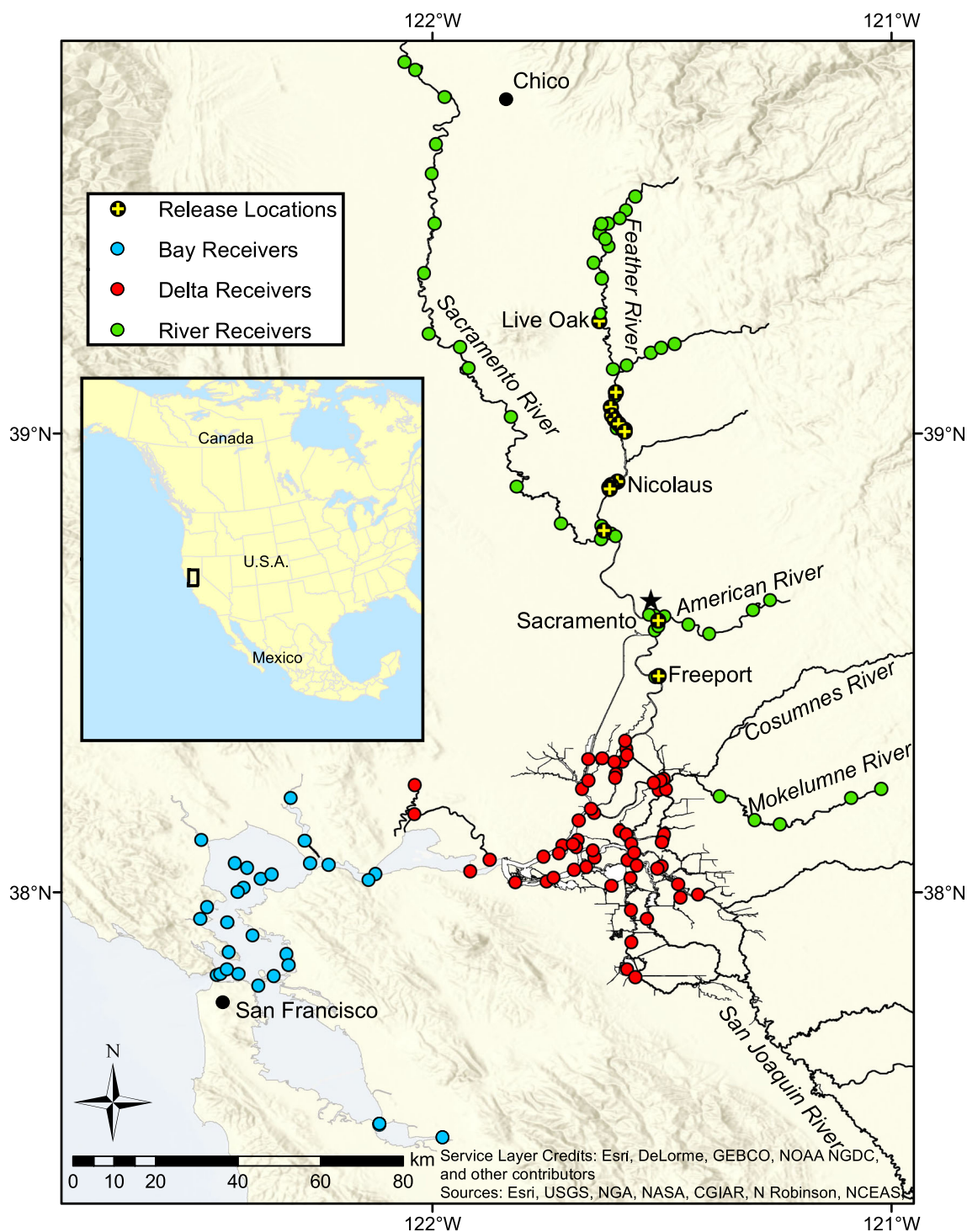


Fig. 1 Map showing locations of receivers throughout the study area color coded by region (blue = bay, red = delta, green = river). Black circles with yellow crosses represent release locations of tagged fish

FL = 622 ± 354), within which were multiple sampling locations (Fig. 1). Two sampling locations were on the mainstem Sacramento River, narrowly upstream of the boundary between the river and delta, one near Sacramento and the second near Freeport. The other major area of sampling was in

the mainstem Feather River with 13 sampling locations located between Live Oak and Nicolaus.

In 2011–2013, striped bass were collected from the Sacramento River sampling area. Hook-and-line angling was used to collect bass and they were tagged in the spring (April–

June). Vemco V9-2L 69-kHz tags with an estimated tag life of 415 days, with a ping rate of every 50 to 130 s, and 145 dB level were used in this study (83% of striped bass in final analyses). In 2014–2015, striped bass were collected from the Feather River using hook-and-line angling and fyke traps (dimensions: 9 m long by 3 m high fyke net with wings that are 7.5 m long and 2.5 m high), and they were also tagged in spring (February–April). Vemco V13-1L 69 kHz acoustic tags with a 748-day tag life and 147-dB level were used in these years (17% of striped bass in final analyses). Once activated, the ping rate was relatively fast for the first 60 days, pinging once every 50 to 110 s, then slower for the next 305 days, pinging once every 120 to 240 s. This rate then repeated for 60 days in the fast mode, followed by 305 days in the slower mode. Both V9 and V13 tags have been used in other tagging studies with similar sized striped bass (Mather et al. 2010; Kennedy et al. 2016).

Acoustic tags were attached to striped bass using two methods. The majority (81%) of tags were surgically implanted into the peritoneal cavity. For this method, striped bass were anesthetized and the acoustic tag was implanted into the fish through a 2-cm incision made slightly off and parallel to the ventral line approximately 3–4 cm anterior to the pelvic fins, and the incision was closed with 2 to 3 interrupted sutures (Ethicon 2–0 and 3–0 Vicryl-coated braided synthetic absorbable). A smaller subset of tags (19%) were implanted using “backpack” tagging procedures, which consisted of securing tags with two sterile surgical pins that passed through the musculature 2 cm below the base of the dorsal fin and were secured with 1-cm diameter plastic washers on one end, and the acoustic tag on the other end. All surgical equipment, tags, and sutures were sterilized with chlorhexidine, and taggers wore synthetic surgical gloves while performing operations. In 2011–2012, CO₂ was used as an anesthetic at a concentration of 1 g per 45 L of water. In 2013–2015, fish were anesthetized with Aqui-S 20E (10% Eugenol), following protocols established in the Investigational New Animal Drugs (INAD) exemptions (USFWS 2011), at a concentration of 20 to 30 mg/L. Shifting tagging protocols across years could have affected tag retention or survival. After the surgery, striped bass recovered in a 170-L container filled with fresh water after which they were released in the river near the capture site. The CFTC telemetry array tracked striped bass movements through the watershed year-round for the duration of the study. All animal handling and tagging followed Institutional Animal Care and Use Committee procedures.

Analysis of Acoustic Data

Seasons were defined as winter (Jan, Feb, Mar), spring (Apr, May, Jun), summer (Jul, Aug, Sep), and fall (Oct, Nov, Dec). The RunResidenceExtraction function in the R package “VTrack” was used to calculate movement events defined as

each time a tag was detected at least twice and remained in the field of a given receiver until it was detected at a different receiver or when 1 h had passed between detections at the same receiver (Chamberlin et al. 2011; Campbell et al. 2012; Dwyer et al. 2012). The data were manually examined for quality control and no false detections were observed. The first 5 days post-tagging were excluded from the detection histories for each fish to avoid including tagging effects in movement analyses. The movement events at the last detection location were also excluded as a pre-cautionary step to remove dead striped bass, and analyses were limited to striped bass with tags that were active for at least 30 days to ensure enough temporal data to summarize movement patterns.

To evaluate residence time in each region by season, residence days was calculated as the total time elapsed between the first and last detection within a region (DeCelles and Cadrin 2010; Wingate et al. 2011; Daley et al. 2015; Arostegui et al. 2017). There was good receiver coverage at borders between regions minimizing the chance that a striped bass resided in a region for an extended amount of time before its first detection. When striped bass moved between regions, the percent of bass that were detected at the closest receiver sites to that border were 95.3% at the bay-delta border, 100% at the delta-Sacramento River border, and 100% at the delta-Mokelumne River border. For those few bass that were undetected at the border, residence in that region began when it was detected at the next receiver in that region. When striped bass used regions intermittently, the continuous time intervals were summed for the season to estimate total residence time in days (Wingate et al. 2011). To test if the right-skewed residence data differed by season, region, or release river, nonparametric statistical approaches were used, including Kruskal-Wallis one-way analysis of variance and post hoc Dunn’s test with the Bonferroni method for multiple comparisons. For striped bass with tag detections spanning longer than 365 days, movement metrics were calculated separately for each season of their first and second years and averaged values were used in analyses. This was done to include complete information for individual striped bass, while still standardizing for season.

Seasonal patterns were also examined using the percent of striped bass present. The number of unique striped bass that were detected in a given region and season was divided by the total number of striped bass with live tags at the time. Striped bass that were detected for longer than 1 year had multiple, independent opportunities to be present/absent in a given season and region. In those cases, first and second years were considered separately. Pearson’s Chi-squared tests with Monte Carlo simulated *p* values based on 2000 replicates were used to compare the percent of striped bass present within regions across seasons and separately, within seasons across regions. Both residence days and percent of striped bass present analyses were conducted for Sacramento and Feather Rivers separately.

Travel speed (m/s) for each striped bass was calculated as the distance between receiver sites divided by the time between detections (Chamberlin et al. 2011; Ajemian et al. 2018). If groups of receivers were less than 1 km apart, then we used general locations with a mean latitude and longitude (Rohde et al. 2013). The shortest distances between receiver sites were calculated following the river using ArcGIS 10.4 Network Analyst tools with the National Hydrography Dataset (USGS) (<https://nhd.usgs.gov/>) river layer linking receiver sites. Speeds for each river segment were averaged for individuals for each season. Kruskal-Wallis one-way analysis of variance and post hoc Dunn's test with Bonferroni adjustment were used to compare median speed across seasons. Mann-Whitney tests were used to compare seasonal speeds between release rivers.

The influence of striped bass length on movement was examined only for bass released on the Sacramento River due to the sufficient sample size. A series of hurdle models were used for each region and season combination to analyze movement by length. First, the effect of length on the probability of presence in a given region and season was examined with general linearized models (GLM) with a binomial distribution. All striped bass were included in these models. Second, the effect of length on amount of time (residence days) spent in a given region and season was examined using a GLM with a Gamma distribution for right skewed residence data. These models only included striped bass that were present in a given season and region. Bonferroni adjustments for multiple comparisons were used to adjust the *p* values for each set of models. For only those striped bass that were detected for one full year (*n* = 17), the total kilometers traveled (sum of distances between subsequent detection locations) for the first 365 days after tagging was related to striped bass size using linear regression.

To examine if striped bass excluded differed from those included in the analyses, a *t* test was used to compare log-transformed striped bass length for included fish versus excluded fish, and Chi-squared tests were used to evaluate if fish that were included and excluded from the data analyses were independent of tag type (V9 and V13) or tagging method (internal and external). The level of significance (α) for all statistical testing was 0.05. All data analyses were conducted using Program R (R Core Team 2017).

Results

In total, 101 striped bass were captured, tagged, and released on the Sacramento and Feather Rivers from 2011 to 2015. After excluding striped bass (< 30 active tag days), 63 bass were included in the final analysis (mean FL with SD: 425 ± 183 mm), 52 bass released on the Sacramento River and 11 on the Feather River (Table 2). Striped bass were detected a total of 1,150,511 times, and active tag days ranged from 32 to 676 days (mean with SD: 244 ± 158 days). There were no significant differences in mean length (*t* test: *t* = 1.49, *p* = 0.14), tag type (Chi-squared: χ^2 = 0.25, *p* = 0.62), or tagging method (Chi-squared: χ^2 = 0.30, *p* = 0.58) between striped bass that were included (*n* = 63) vs. excluded (*n* = 38) in the analysis.

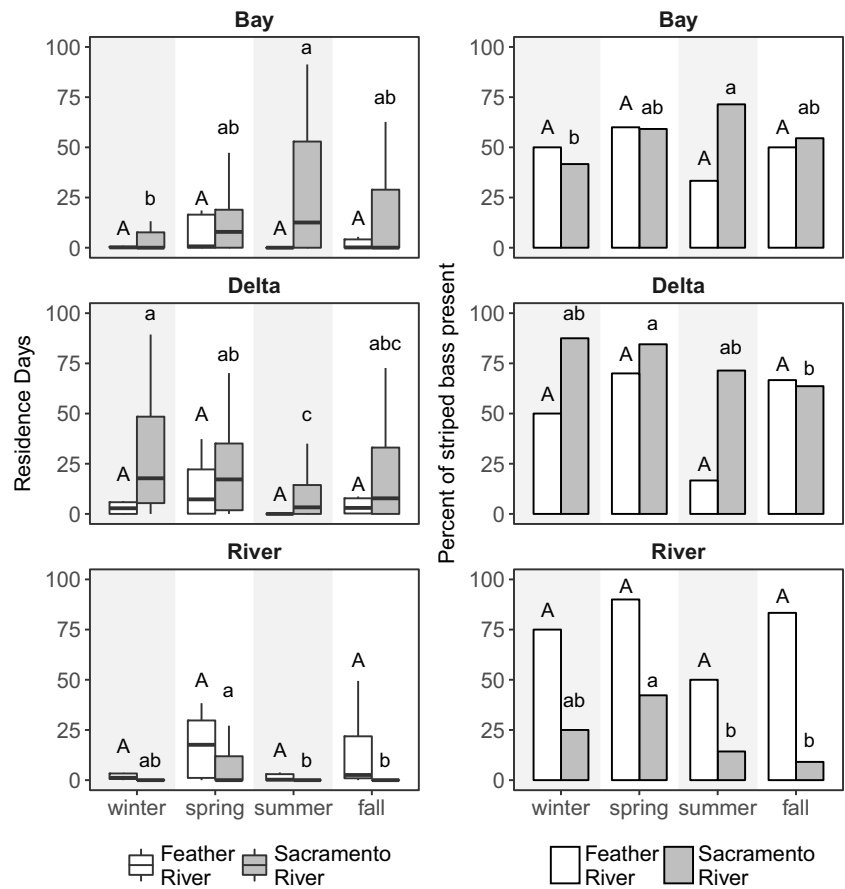
Striped bass seasonal residence patterns were observed using both residence days of individual fish and percent of striped bass present. These residence metrics provided similar information on seasonal use of regions. Striped bass released on the Sacramento River spent significantly more time in the bay in the summer (28.2 ± 30.9 days; 71.43%) compared to winter (10.8 ± 22.8 days; 41.67%) based on both residence metrics (Fig. 2; Tables 3 and 4). In the delta across seasons, SR striped bass spent fewer residence days in the summer (11.7 ± 17 days) compared to winter (29.8 ± 30.2 days) and spring (21.6 ± 20.8 days) (Fig. 2; Tables 3 and 4). These patterns significantly differed using the percent of bass present—84.51% of striped bass were present in the delta in spring compared to 63.64% in fall (Fig. 2; Tables 3 and 4). River residence varied across seasons for SR striped bass with the highest residence (both metrics) in spring (8.7 ± 14.2 days; 42.25%), which was significantly greater compared to summer (5.7 ± 20.5 days; 14.29%) and fall (2 ± 8 days; 9.09%) (Fig. 2; Tables 3 and 4). FR striped bass did not exhibit significant seasonal residence differences, except for a marginally significant difference in residence days in the delta where there was higher residence in spring (14.7 ± 19.1 days) over summer (0.003 ± 0.008 days) (Table 4).

Patterns in regional residence days and percent of striped bass present were consistent when comparing residence within seasons. In winter and spring, SR striped bass exhibited higher residence in the delta (winter: 29.8 ± 30.2 days, 87.50%, spring: 21.6 days ± 20.8, 84.51%) relative to time

Table 2 Summary of the striped bass included in the analyses: number of fish, dates and river released, and mean size (±SE)

Year tagged	Fish in analyses	Dates released	Mean FL (mm)	Release river
2011	9	5/5–6/8	343 ± 26	Sacramento River
2012	23	4/11–6/6	349 ± 13	Sacramento River
2013	20	4/3–5/31	378 ± 17	Sacramento River
2014	2	3/11–4/24	1065 ± 15	Feather River
2015	9	2/9–4/14	664 ± 62	Feather River

Fig. 2 Striped bass residence days (left column) and percent of striped bass present (right column) in each region by season. Significant differences ($p < 0.05$) in residence across regions are noted by lowercase letters (Sacramento River) and uppercase letters (Feather River)



spent in the bay (winter: 10.8 ± 22.8 days, 41.67%; spring: 12 ± 15.6 days; 59.15%) and river (winter: 2 ± 4.7 days, 25.00%; spring: 8.7 ± 14.2 , 42.25%) (Fig. 2; Table 5). In the summer

and fall, SR bass spent less time in the river (summer: 5.7 ± 20.5 days, 14.29%; fall: 2 ± 8 days, 9.09%) compared to the bay (summer: 28.2 ± 30.9 days, 71.43%, fall: 16.3 ± 24 days,

Table 3 Summary of residence days and percent of striped bass present by release river, region, and season

Release River	Region	Season	Mean \pm SD residence days	Range residence days	Percent present
Sacramento River	bay	winter	10.8 ± 22.8	0–83.26	41.67
		spring	12 ± 15.6	0–64.98	59.15
		summer	28.2 ± 30.9	0–91.29	71.43
		fall	16.3 ± 24	0–90.60	54.55
	delta	winter	29.8 ± 30.2	0–89.36	87.50
		spring	21.6 ± 20.8	0–85.35	84.51
		summer	11.7 ± 17	0–67.46	71.43
		fall	18.6 ± 25.5	0–91.87	63.64
	river	winter	2 ± 4.7	0–17.03	25.00
		spring	8.7 ± 14.2	0–62.16	42.25
		summer	5.7 ± 20.5	0–84.75	14.29
		fall	2 ± 8	0–39.90	9.09
Feather River	bay	winter	0.3 ± 0.5	0–0.99	50.00
		spring	12.9 ± 20.4	0–53.64	60.00
		summer	1.5 ± 3.7	0–9.07	33.33
		fall	3.1 ± 5.2	0–12.68	50.00
	delta	winter	3 ± 3.5	0–6.42	50.00
		spring	14.7 ± 19.1	0–55.84	70.00
		summer	0.003 ± 0.008	0–0.02	16.67
		fall	8.6 ± 14.4	0–37.18	66.67
	river	winter	2.7 ± 3.9	0–8.41	75.00
		spring	17.1 ± 15.6	0–38.34	90.00
		summer	5.3 ± 10.9	0–27.29	50.00
		fall	13.9 ± 20.4	0–49.44	83.33

Table 4 Statistical results from Kruskal-Wallis, Dunn's, and Chi-square tests on how residence days and percent of striped bass present vary within region across seasons. † $p < 0.1$, * $p < 0.05$

Release River	Region	Season	Residence days				Percent present									
			Kruskal-Wallis		Dunn's test		Chi-sq		Chi-sq							
			χ^2	p	Z	p	χ^2	p	χ^2	p						
SR $n = 52$	bay	w-sp	9.4	0.03*	1.5	0.44	6.4	0.09†	1.6	0.21						
		w-su			2.9	0.01*			4.8	0.03*						
		w-f			1.1	0.78			0.5	0.49						
		sp-su			-2	0.14			1.4	0.24						
		sp-f			-0.2	1			0.05	0.82						
	delta	su-f	-1.9	0.19	1.8	0.18										
		w-sp	11.7	< 0.01*	-0.7	1.00	8	0.05*	0	0.98						
		w-su			-2.8	0.02*			1.5	0.22						
		w-f			-2.0	0.12			2.9	0.09†						
		sp-su			2.7	0.02*			2.3	0.13						
	sp-f	-1.7			0.25	4.6			0.03*							
	river	su-f	22.6	< 0.01*	0.6	1.00	18.2	< 0.01*	0.3	0.62						
		w-sp			2.3	0.06†			1.6	0.21						
		w-su			-0.7	1.00			0.6	0.42						
		w-f			-1.1	0.84			1.6	0.21						
sp-su		3.9			< 0.01*	9.4			0.002*							
FR $n = 11$	bay	sp-f	2.3	0.51	-4	< 0.01*	1.1	0.79	9.9	0.001*						
		su-f			-0.5	1.00			0.13	0.72						
		w-sp			6.5	0.09†			1.1	0.78	4.8	0.19	3.6	0.31		
		w-su													-0.9	1.00
		w-f													0.6	1.00
	sp-su	2.5	0.04*													
	sp-f	-0.5	1.00													
	delta	su-f	4.4	0.22	1.7	0.25										
		w-sp			4.4	0.22	3.6	0.31								
		w-su														
		w-f														
		sp-su														
	sp-f															
	river	su-f														
		w-sp														
w-su																
w-f																
sp-su																

54.55%) and delta (summer: 11.7 ± 17 days, 71.43%, fall: 18.6 ± 25.5 days, 63.64%) (Fig. 2; Table 5). There were no statistically significant differences in residence within seasons for FR striped bass likely due to a small sample size or because FR striped bass were larger sizes (Table 5); however, there were significant residence differences between release rivers.

Sacramento River striped bass residence varied by region (Kruskal-Wallis: $\chi^2 = 82.2$, $p < 0.001$) and was highest in the delta compared to the bay (Dunn's test: $z = -2.6$, $p = 0.01$) and river ($z = 8.8$, $p < 0.001$), while bay residence was higher than the river ($z = 6.2$, $p < 0.001$; Fig. 3). No significant regional residence differences were detected for FR striped bass (Kruskal-Wallis: $\chi^2 = 4.5$, $p = 0.11$); however, all pair-wise comparisons between SR and FR striped bass were highly significant (Fig. 3). SR bass had higher residence in the bay (17.3 ± 24.3 days) compared to FR bass (6.1 ± 13.7 days) (Mann-Whitney: $w = 2744$, $p = 0.05$) as well as in the delta (SR: 19.3 ± 22.9 days, FR: 8.1 ± 14.5 days) ($w = 3002$, $p = 0.004$), but lower river residence (SR: 5.6 ± 14.8 days, FR: 11.4 ± 15.2 days)

($w = 1187$, $p < 0.001$; Fig. 3). FR striped bass were present in the river across seasons ranging from 50 to 90%, while SR striped bass presence ranged from 9 to 42%.

Striped bass speed varied across seasons for SR striped bass (mean: 0.65 ± 0.52 m/s, range: 0.0008–3.83 m/s; Kruskal-Wallis: $\chi^2 = 24.4$, $p < 0.001$) and for FR striped bass (mean: 0.55 ± 0.39 m/s, range: 0.001–1.60 m/s; Chi-squared: $\chi^2 = 12.1$, $p = 0.007$; Fig. 4). SR striped bass traveled faster during the spring relative to all other seasons: winter (Dunn's test: $z = 3.8$, $p < 0.001$), summer ($z = 4.2$, $p = 0.001$), and fall ($z = -2.6$, $p = 0.03$). Mean travel speed of SR striped bass in the spring was 0.86 m/s ± 0.6 , which was 39% faster than the mean of all other seasons. FR striped bass traveled faster in the spring (0.78 ± 0.38 m/s) compared to summer (0.18 ± 0.24 m/s; Dunn's test: $z = 3.2$, $p = 0.004$). In pair-wise comparisons between release rivers within seasons, speed only differed in summer where SR fish traveled at 0.48 ± 0.28 m/s, which was faster than FR bass that traveled at 0.17 ± 0.24 m/s (Mann-Whitney: $w = 151$, $p = 0.01$; Fig. 4).

Table 5 Statistical results from Kruskal-Wallis, Dunn's, and Chi-square tests on how residence days and percent of striped bass present vary within seasons across regions. † $p < 0.1$, * $p < 0.05$

Release River	Season	Region	Residence days				Percent present			
			K-W		Dunn's test		Chi-sq		Chi-sq	
			χ^2	p	z	p	χ^2	p	χ^2	p
SR n = 52	winter	b-d	24.3	< 0.001*	-3.5	0.007*	20.1	< 0.001*	9.1	0.003*
		b-r			1.2	0.33			0.8	0.36
		d-r			4.8	< 0.001*			16.6	< 0.001*
	spring	b-d	23.8	< 0.001*	-3.2	0.002*	27.3	< 0.001*	10.1	0.002*
		b-r			1.7	0.15			3.4	0.06†
		d-r			4.8	< 0.001*			25.5	< 0.001*
	summer	b-d	35.2	< 0.001*	1.2	0.37	42.8	< 0.001*	0	1
		b-r			5.6	< 0.001*			30.4	< 0.001*
		d-r			4.5	< 0.001*			30.4	< 0.001*
	fall	b-d	21.2	< 0.001*	-0.7	0.72	23.1	< 0.001*	0.3	0.62
		b-r			3.6	0.005*			13.7	< 0.001*
		d-r			4.3	< 0.001*			18.9	< 0.001*
FR n = 11	winter	b-d	1.3	0.53			0.69	0.71		
		b-r								
		d-r								
	spring	b-d	1.3	0.52			2.4	0.3		
		b-r								
		d-r								
	summer	b-d	2	0.36			1.5	0.47		
		b-r								
		d-r								
	fall	b-d	1.4	0.5			1.5	0.47		
		b-r								
		d-r								

Striped bass length influenced few aspects of movement or regional use. Length differed between striped bass released on the Sacramento and Feather Rivers (SR: mean: 359 ± 71 mm; FR: mean: 737 ± 232 mm; Mann-Whitney: $w = 560$, $p < 0.001$). Within SR striped bass, larger striped bass were marginally more likely to occur in the bay in the summer (GLM: $z = 2.74$, $adj.p = 0.06$) and spring (GLM: $z = 2.74$, $adj.p = 0.07$; Fig. 5). For all other season-region combinations, presence of striped bass was not influenced by striped

bass length (Table 6). Furthermore, length did not explain any variation in the amount of time spent in each season-region combination (Table 6). Travel speed was also unaffected by length (GLM: $t = -0.54$, $p = 0.59$). Considering only the striped bass with tag life > 365 days ($n = 17$), larger striped bass traveled farther (km) during their first year since tagging (mean with SD = 1248 ± 405 km, range: 641–2212 km) than did small fish (linear regression: $t = 4.18$, $r^2 = 0.52$, $p < 0.01$; Fig. 6).

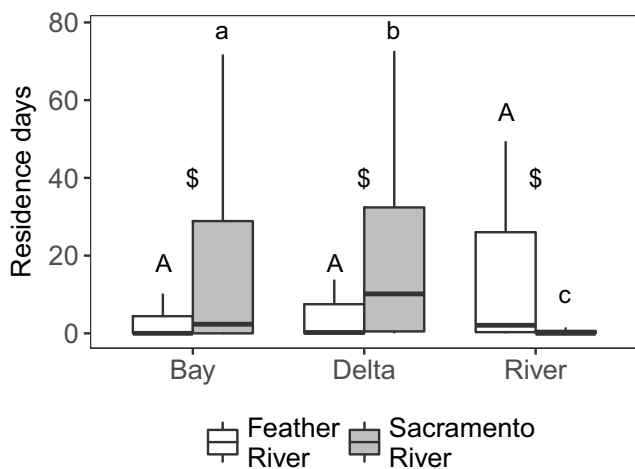


Fig. 3 Striped bass residence days by region and release river. Significant differences ($p < 0.05$) in residence across regions are noted by lowercase letters (Sacramento River) and uppercase letters (Feather River). Significant differences from Mann-Whitney pairwise comparisons are noted with the \$ symbol

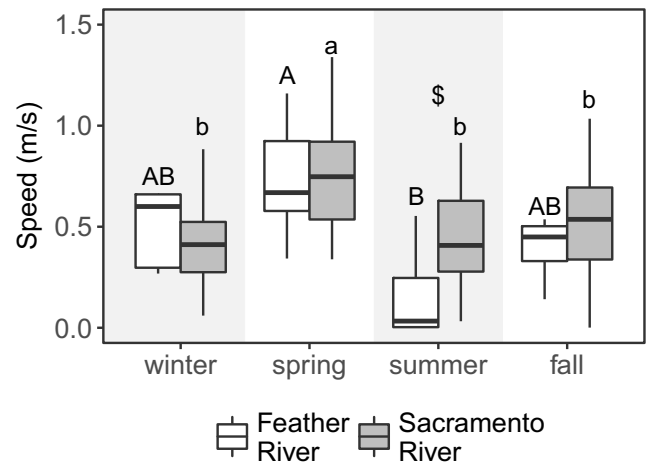
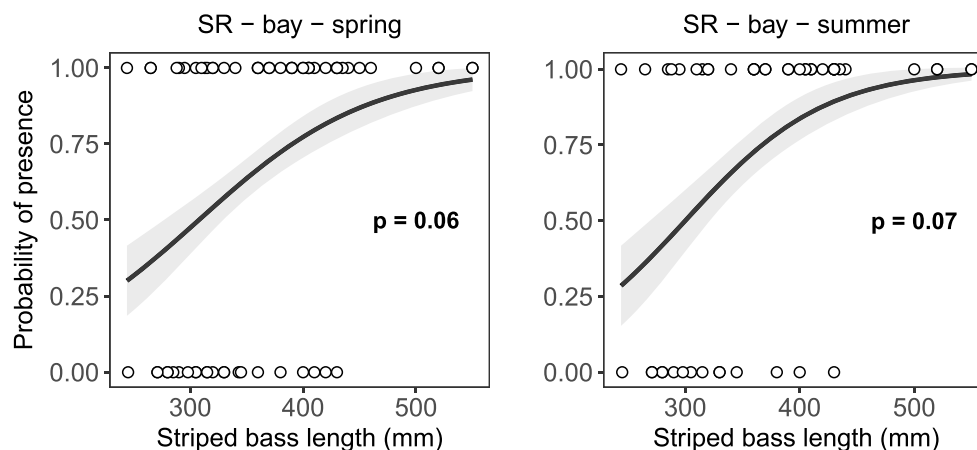


Fig. 4 Mean speed (m/s) calculated between each receiver detection for each striped bass by season with 95% confidence intervals. Significant differences ($p < 0.05$) in residence across regions are noted by lowercase letters (Sacramento River) and uppercase letters (Feather River). Significant differences from Mann-Whitney pairwise comparisons are noted with the \$ symbol

Fig. 5 Relationship between striped bass length (mm) and probability of presence for SR striped bass in the bay in summer (left) and spring (right). Predictions (solid lines) are from binomial generalized linear models. Raw data are in open circles



Discussion

California striped bass seasonal movements were diverse. Striped bass released on both the Sacramento and Feather Rivers were detected in every region and season as evidence through both residence days and percent of bass detected. Within this variation, however, SR striped bass exhibited distinct seasonal patterns. In spring, SR striped bass primarily resided in the delta over the river and bay. They also, however, exhibited the highest river detection (42%) relative to river detection in summer (14%) and fall (9%). SR striped bass also traveled at 39% faster speeds during spring compared to all other seasons. High river residence and fast travel speeds in spring are consistent with previous descriptions of the spawning migration from early April–June into the Sacramento and San Joaquin Rivers (Turner 1976). This also coincides with emigration of native, juvenile fall-run Chinook

salmon (*Oncorhynchus tshawytscha*), ESA threatened spring-run Chinook salmon, and ESA threatened Central Valley steelhead (*O. mykiss*) from the same rivers, which striped bass consume (Kjelson et al. 1982; Sabal et al. 2016).

In summer and fall, SR striped bass spent more time in the bay and delta over the river—although delta residence was relatively low for that region compared to other seasons. Increased bay residence occurs perhaps to take advantage of abundant prey driven by prior blooms of productivity and coastal upwelling that occurs the previous spring (Cloern 1996; Croll et al. 2005). Northern anchovies (*Engraulis mordax*) are an abundant forage fish in the bay, while young threadfin (*Dorosoma petenense*) and American shad (*Alosa sapidissima*) recruit to the delta in late summer and fall, therefore presenting striped bass with abundant prey resources across space (Feyrer et al. 2015). Delta summer residence was the only instance where statistical patterns varied between residence days and percent of bass present. Striped bass spent fewer residence days, but a relatively higher percent of bass was detected in the delta in the summer. This could result from

Table 6 Statistical results from hurdle models on how striped bass length (mm) influences the probability of presence and residence days in each region-season combination. † $p < 0.1$, * $p < 0.05$

Region	Season	Probability of presence		Residence days	
		z	Adjusted p	t	Adjusted p
bay	Winter	0.05	1.0	-0.31	1.0
	Spring	2.8	0.06†	-1.6	1.0
	Summer	2.74	0.07†	0.96	1.0
	Fall	0.34	1.0	1.93	0.86
delta	Winter	1.27	1.0	0.79	1.0
	Spring	-1.04	1.0	0.63	1.0
	Summer	1.42	1.0	0.24	1.0
	Fall	1.44	1.0	-2	0.66
river	Winter	-0.08	1.0	0.82	1.0
	Spring	1.22	1.0	2.08	0.56
	Summer	1.34	1.0	1.01	1.0
	Fall	-1.03	1.0	-0.6	1.0

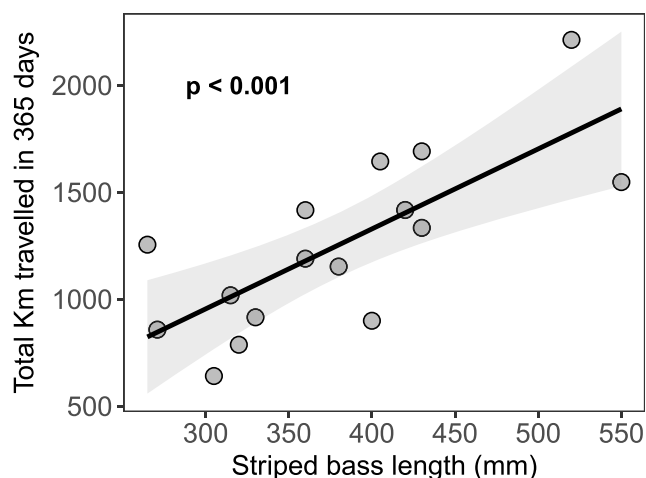


Fig. 6 Total km traveled in the first 365 days since the SR striped bass release date by fork length (mm). The black line indicates the best fit line from a linear regression where $p < 0.05$ and $R^2 = 0.52$

many, short visits, if striped bass were highly mobile or present at the edges of regional boundaries.

In winter, a higher percent of SR striped bass were detected in the delta (87%) compared to the bay (42%) and river (25%). Also, bay residence in the winter was significantly lower than bay residence in the summer. Reduced movements in winter may be influenced by reduced metabolic activity when water temperatures are cold (Keyser et al. 2016), although regions of overwintering may include fresh or marine environments (Andrews et al. 2018). On a broad scale, a spring spawning migration into the river, summer residence in the bay and delta, and winter residence in the delta are consistent with patterns observed in east coast populations. Although east coast striped bass frequently reside in marine habitats in summer and winter, we observed these behaviors to occur in the San Francisco Bay and delta, respectively.

In this study, there were no statistically significant seasonal patterns observed for striped bass released on the Feather River likely due to a small sample size. There were, however, differences between overall residence patterns between release rivers. FR striped bass had significantly lower residence days in the bay and delta, and higher residence days in the river compared to SR striped bass. The percent of FR striped bass present in the river region across seasons ranged from 50 to 90%, while SR striped bass ranged from 9 to 42%. FR striped bass also traveled 35% slower in the summer compared to SR bass. SR and FR striped bass may comprise a separate spawning population with distinct behaviors. FR striped bass were significantly larger than SR striped bass; thus, some of the behavioral differences between release river may be due to size differences.

Within Sacramento River striped bass, however, length had little influence on seasonal movement patterns. Larger striped bass were marginally more likely to occur in the bay in the spring and summer, but length did not influence any other seasonal residence patterns. On the east coast, size-related patterns of movements farther into coastal waters have been documented (Secor and Piccoli 2007); however, sometimes, movement behaviors are independent of size (Gahagan et al. 2015). SR striped bass did increase their distance traveled in 365 days with increasing length. Larger striped bass are usually more likely to exit estuaries and engage in coastal ocean migrations, although the size at which this occurs is variable (Dorazio et al. 1994; Mather et al. 2010; Callihan et al. 2014). Striped bass may need to reach larger sizes before entering the ocean to better take advantage of productive marine waters. Larger striped bass may have needed to be tagged in this study to observe more size-related behaviors such as increased marine residence. FR striped bass were, however, much larger than SR striped bass and they spent significantly less time in the bay. Therefore, size-related behaviors may truly be weak or context dependent based on release river.

Some potential limitations in these analyses warrant discussion. First, movement and residence patterns were of acoustically tagged striped bass only and may not be completely representative of untagged individuals. It is possible that minor behavioral changes could occur in the short-term due to the capture, handling, and tag implantation, or in the longer-term due to the presence of the tag. Striped bass were also only captured and tagged from three sampling locations during limited sampling seasons, potentially resulting in the capture of fish from a subset of potential life history types. Thus, movement behavior, particularly for FR fish, may be more variable than described here. Furthermore, while the Sacramento River (and its tributary the Feather River) is considered the major spawning river of California striped bass, some fish are known to spawn in other Central Valley rivers, such as the San Joaquin River (Turner 1976). The level of interbreeding, and hence genetic similarity, between fish from different spawning areas is currently unknown, and some movement behaviors might have been missed which are representative of smaller spawning populations.

The diverse movement patterns of California striped bass across space and time may have important ecological and management implications. Striped bass are a key species in the San Francisco Estuary ecosystem because they are nonnative, have a high energetic demand (Loboschewsky et al. 2012), prey upon native and nonnative species (Nobriga and Feyrer 2008; Zeug et al. 2017), and can impact communities across salinity gradients. In this study, striped bass seasonal movements appeared to follow ephemeral prey—juvenile Chinook salmon are abundant in rivers in the spring while forage fish are abundant in the bay in the summer. Except, these patterns are variable. Striped bass may exhibit the flexible movement behaviors of nomadic migrants to exploit rich patches of prey over a wide area (Jonzén et al. 2011). Patterns of striped bass residence—general seasonal patterns, distinct behaviors in sub-populations, and highly variable behaviors—fall within the diverse patterns observed in east coast populations. Striped bass behavioral flexibility may be one important characteristic that has allowed them to persist in their nonnative range.

Acknowledgements We thank the many biologists and technicians who assisted with field work maintaining acoustic receivers and tagging striped bass, including but not limited to: Zach Amidon, Arnold Ammann, Julie Day, Nick Demetras, Allison Jehly, Ryon Kurth, Brendan Lehman, Jeremy Notch, Nicolas Retford, and Andrew Sobieraj. We also thank all the scientists who have contributed to the California Fish Tracking Consortium. We would also like to thank NMFS-SWFSC for logistical support and staff time. The constructive comments from two anonymous reviewers greatly improved the quality of the manuscript.

Funding Information The California Department of Water Resources and US Bureau of Reclamation funded this work.

References

- Able, K.W., T.M. Grothues, J. Turnure, D.M. Byrne, and P. Clerkin. 2012. Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales. *Fishery Bulletin* 2: 176–192.
- Ajemian, M.J., K.S. Mendenhall, J.B. Pollack, M.S. Wetz, and G.W. Stunz. 2018. Moving forward in a reverse estuary: Habitat use and movement patterns of black drum (*Pogonias cromis*) under distinct hydrological regimes. *Estuaries and Coasts*. Estuaries and coasts: 1–12. <https://doi.org/10.1007/s12237-017-0363-6>.
- Andrews, S.N., B. Wallace, M. Gautreau, T. Linnansaari, and R.A. Curry. 2018. Seasonal movements of striped bass *Morone saxatilis* in a large tidal and hydropower regulated river. *Environmental Biology of Fishes* 1957. *Environmental Biology of Fishes*: 1549–1558. <https://doi.org/10.1007/s10641-018-0799-y>.
- Arostegui, M.C., J.M. Smith, A.N. Kagley, D. Spilsbury-Pucci, K.L. Fresh, and T.P. Quinn. 2017. Spatially clustered movement patterns and segregation of subadult Chinook salmon within the Salish Sea. *Marine and Coastal Fisheries* 9. Taylor & Francis: 1–12. <https://doi.org/10.1080/19425120.2016.1249580>.
- Calhoun, A.J. 1952. Annual migrations of California striped bass. *California Department of Fish and Game*: 391–403.
- Callihan, J.L., C.H. Godwin, and J.A. Buckel. 2014. Effect of demography on spatial distribution: Movement patterns of the Albemarle sound-Roanoke river stock of striped bass (*Morone saxatilis*) in relation to their recovery. *Fishery Bulletin* 112 (2-3): 131–143.
- Campbell, H.A., M.E. Watts, R.G. Dwyer, and C.E. Franklin. 2012. V-track: Software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research* 63 (9): 815–820. <https://doi.org/10.1071/MF12194>.
- Chadwick, H.K. 1967. Recent migrations of the Sacramento-San Joaquin River striped bass population. *Transactions of the American Fisheries Society* 96 (3): 327–342.
- Chamberlin, J.W., A.N. Kagley, K.L. Fresh, and T.P. Quinn. 2011. Movements of yearling Chinook Salmon during the first summer in marine waters of hood canal, Washington. *Transactions of the American Fisheries Society* 140 (2): 429–439. <https://doi.org/10.1080/00028487.2011.572006>.
- Cloern, J.E. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* 34 (2): 127–168.
- Cloern, J.E., and A.D. Jassby. 2012. Drivers of change in estuarine - coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. *Reviews in Geophysics* 50: 1–33.
- Collette, B.B., and G. Klein-MacPhee (eds.) 2002. Bigelow and Schroeder's fishes of the gulf of Maine, 3rd ed. Washington, DC: Smithsonian Inst. Press. 748 p.
- Croll, D.A., B. Marinovic, S. Benson, F.P. Chavez, N. Black, R. Temullo, and B.R. Tershy. 2005. From wind to whales: Trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289: 117–130.
- Daley, R.K., A. Williams, M. Green, B. Barker, and P. Brodie. 2015. Can marine reserves conserve vulnerable sharks in the deep sea? A case study of *Centrophorus zeehaani* (Centrophoridae), examined with acoustic telemetry. *Deep-Sea Research Part II* 115. Elsevier: 127–136. <https://doi.org/10.1016/j.dsr2.2014.05.017>.
- DeCelles, G.R., and S.X. Cadrin. 2010. Movement patterns of winter flounder (*Pseudopleuronectes americanus*) in the southern gulf of Maine: Observations with the use of passive acoustic telemetry. *Fishery Bulletin* 108: 408–419.
- Dorazio, R.M., K.A. Hattala, C.B. McCollough, and J.E. Skjveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. *Transactions of the American Fisheries Society* 123 (6): 950–963. [https://doi.org/10.1577/1548-8659\(1994\)123<0950:TREOMO>2.3.CO;2](https://doi.org/10.1577/1548-8659(1994)123<0950:TREOMO>2.3.CO;2).
- Dwyer, R.G., M.E. Watts, H.A. Campbell, and C.E. Franklin. 2012. Package 'VTrack'. R package.
- Feyrer, F., M.L. Nobriga, and T.R. Sommer. 2007. Multidecadal trends for three declining fish species: Habitat patterns and mechanisms in the San Francisco estuary, California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 734: 723–734.
- Feyrer, F., J.E. Cloern, M.A. Fish, K.A. Hieb, and R.D. Baxter. 2015. Estuarine fish communities respond to climate variability over both river and ocean basins. *Global Change Biology* 21 (10): 3608–3619.
- Gahagan, B.I., D.A. Fox, and D.H. Secor. 2015. Partial migration of striped bass: Revisiting the contingent hypothesis. *Marine Ecology Progress Series* 525: 185–197. <https://doi.org/10.3354/meps11152>.
- Jonzén, N., E. Knudsen, R.D. Holt, and B. Saether. 2011. Chapter 7: Uncertainty and predictability: The niches of migrants and nomads. In *Animal migration: A synthesis*, ed. E.J. Milner-Gulland, J.M. Fryxell, and A.R.E. Sinclair, 91–109. Oxford: Oxford University Press.
- Kennedy, C.G., M.E. Mather, J.M. Smith, J.T. Finn, and L.A. Deegan. 2016. Discontinuities concentrate mobile predators: Quantifying organism – Environment interactions at a seascape scale. *Ecosphere* 7: 1–17.
- Keyser, F.M., J.E. Broome, R.G. Bradford, B. Sanderson, and A.M. Redden. 2016. Winter presence and temperature-related diel vertical migration of striped bass (*Morone saxatilis*) in an extreme high-flow passage in the inner bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 1786: 1–10.
- Kjelson, M.A., P.F. Raquel, and F.W. Fisher. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California. *Estuarine Comparisons*: 393–411.
- Kraus, R.T., D.H. Secor, and R.L. Wingate. 2015. Testing the thermal-niche oxygen-squeeze hypothesis for estuarine striped bass. *Environmental Biology of Fishes* 98 (10): 2083–2092.
- Le Doux-Bloom, C.M. 2012. *Distribution, habitat use, and movement patterns of sub-adult striped bass*. University of California Davis.
- Lima, S.L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends in Ecology & Evolution* 17 (2): 70–75.
- Lindley, S.T., and M.S. Mohr. 2002. Modeling the effect of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*). *Fishery Bulletin* 101: 321–331.
- Loboschewsky, E., G. Benigno, T.R. Sommer, K. Rose, T. Ginn, A. Massoudieh, and F. Loge. 2012. Individual-level and population-level historical prey demand of San Francisco estuary striped bass using a bioenergetics model. *San Francisco Estuary and Watershed Science* 10: 1–23.
- Mac Nally, R., J.R. Thomson, W.J. Kimmerer, F. Feyrer, K.B. Newman, A. Sih, W.A. Bennett, et al. 2010. Analysis of pelagic species decline in the upper San Francisco estuary using multivariate autoregressive modeling (MAR). *Ecological Applications* 20: 1417–1430.
- Mather, M.E., J.T. Finn, S.M. Pautzke, D. Fox, T. Savoy, H.M. Brundage, L.A. Deegan, and R.M. Muth. 2010. Diversity in destinations, routes and timing of small adult and sub-adult striped bass *Morone saxatilis* on their southward autumn migration. *Journal of Fish Biology* 77 (10): 2326–2337.
- McIntyre, N.E., and J.A. Wiens. 1999. Interactions between landscape structure and animal behavior: The roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* 14 (5): 437–447.
- Morales, J.M., P.R. Moorcroft, J. Matthiopoulos, J.L. Frair, J.G. Kie, R.A. Powell, E.H. Merrill, and D.T. Haydon. 2010. Building the bridge between animal movement and population dynamics. *Philosophical*

- Transactions of the Royal Society B Biological Sciences* 365 (1550): 2289–2301.
- Morissette, O., F. Lecomte, G. Verreault, M. Legault, and P. Sirois. 2015. Fully equipped to succeed: Migratory contingents seen as an intrinsic potential for striped bass to exploit a heterogeneous environment early in life. *Estuaries and Coasts*: 571–582.
- Nathan, R., W.M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P.E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* 105 (49): 19052–19059.
- Nelson, G.A., M.P. Armstrong, J. Stritzel-Thomson, and K.D. Friedland. 2010. Thermal habitat of striped bass (*Morone saxatilis*) in coastal waters of northern Massachusetts, USA, during summer. *Fisheries Oceanography* 19 (5): 370–381.
- Nichols, F.H., J.E. Cloern, S.N. Luoma, and D.H. Peterson. 1986. The modification of an estuary. *Science* 231 (4738): 567–573.
- Nobriga, M.L., and F. Feyrer. 2008. Diet composition in San Francisco estuary striped bass: Does trophic adaptability have its limits? *Environmental Biology of Fishes* 83 (4): 495–503. <https://doi.org/10.1007/s10641-008-9376-0>.
- North, E.W., and E.D. Houde. 2001. Retention of white perch and striped bass larvae biological- physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries* 24 (5): 756–769.
- Peterson, A.T. 2003. Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78 (4): 419–433.
- Prentis, P.J., J.R.U. Wilson, E.E. Dormontt, D.M. Richardson, and A.J. Lowe. 2008. Adaptive evolution in invasive species. *Trends in Plant Science* 13 (6): 288–294.
- Quinn, T.P., M.T. Kinnison, and M.J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: Pattern, rate, and process. *Genetica* 112–113: 493–513.
- R Development Core Team. 2017. *R: A language and environment for statistical computing*. Vienna, Austria.
- Rohde, J., A.N. Kagley, K.L. Fresh, F.A. Goetz, and T.P. Quinn. 2013. Partial migration and diel movement patterns in Puget Sound Coho salmon. *Transactions of the American Fisheries Society* 142 (6): 1615–1628. <https://doi.org/10.1080/00028487.2013.822421>.
- Sabal, M., S. Hayes, J. Merz, and J. Setka. 2016. Habitat alterations and a nonnative predator, the striped bass, increase native Chinook Salmon mortality in the central valley, California. *North American Journal of Fisheries Management* 36 (2): 309–320.
- Scofield, E.C. 1931. The striped bass of California (*Roccus lineatus*). *Division of Fish and Game of California Report: Fish Bulletin No. 29*.
- Secor, D.H. 1999. Specifying divergent migrations in the concept of stock: The contingent hypothesis. *Fisheries Research* 43 (1-3): 13–34.
- Secor, D.H., and P.M. Piccoli. 2007. Oceanic migration rates of upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. *Fishery Bulletin* 105: 62–73.
- Secor, D.H., J.R. Rooker, E. Zlokovitz, and V.S. Zdanowicz. 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Marine Ecology Progress Series* 211: 245–253.
- Stevens, D.E., D.W. Kohlhorst, L.W. Miller, and W. Kelley. 1985. The decline of striped bass in the Sacramento-San Joaquin estuary, California. *Transactions of the American Fisheries Society* 114 (1): 12–30. [https://doi.org/10.1577/1548-8659\(1985\)114<12](https://doi.org/10.1577/1548-8659(1985)114<12).
- Turner, J.L. 1976. Striped bass spawning in the Sacramento and San Joaquin Rivers in Central California from 1963 to 1972. *California Fish and Game* 62: 106–118.
- Turner, Jerry L., and Harold K. Chadwick. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin estuary. *Transactions of the American Fisheries Society* 101 (3): 442–452.
- USFWS. 2011. *Standards for the U.S. Fish and Wildlife Service's National INAD Program*. Bozeman, MT 59715.
- Winder, L., C.J. Alexander, J.M. Holland, C. Woolley, and J.N. Perry. 2001. Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field. *Ecology Letters* 4 (6): 568–576.
- Wingate, R.L., D.H. Secor, and R.T. Kraus. 2011. Seasonal patterns of movement and residency by striped bass within a subestuary of the Chesapeake Bay. *Transactions of the American Fisheries Society* 140 (6): 1441–1450. <https://doi.org/10.1080/00028487.2011.630279>.
- Zeug, S.C., F.V. Feyrer, A. Brodsky, and J. Melgo. 2017. Piscivore diet response to a collapse in pelagic prey populations. *Environmental Biology of Fishes* 100: 947–958.