Environ Biol Fish
DOI 10.1007/s10641-012-0037-y

Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss)*

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Received: 31 March 2011 / Accepted: 11 May 2012

Abstract The release of hatchery reared salmonid smolts is a common management tool aimed at enhancing depleted wild stocks and maintaining fisheries throughout Northern California and the Pacific Northwest. In the Sacramento River watershed, smolts must migrate through the river, delta and estuary in order to successfully reach the Pacific Ocean. Migration success (success defined as apparent survival from one monitor location to another) may vary between species, year and habitat. We released 500 late-fall run Chinook salmon and 500 steelhead smolts in 2009 and 2010 in the Sacramento River (river kilometer 207). Each smolt was implanted with a coded ultrasonic tag, which was detected by an array of over 300 underwater receiver stations deployed throughout the system. Less than 25 % of fish migrated successfully to the Pacific Ocean in both years. We found that reach specific success was greater in the Delta in 2009 (>60 %) than in 2010 (<33 %), whereas this pattern was reversed in the Bay (<57 % in 2009, >75 % in 2010). Identifying the location, timing and causes of smolt mortality can lead to improved management of the resource.

Keywords Steelhead trout · Chinook salmon · Telemetry · Sacramento River · Migratory success · San Francisco Estuary

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Introduction

Understanding the survival patterns of outmigrating salmonid smolts is a key issue for fisheries management, especially where hatcheries are used to artificially propagate and release smolts to supplement natural populations. The Sacramento River watershed in the California Central Valley (CV) is a particularly complex drainage system which includes a multitude of habitats – the more natural run-riffle-pool structure of the upper river, a channelized lower river, the heavily modified and intricate Sacramento-San Joaquin Delta, and the San Francisco Bay Estuary. Within the estuary, there are tidal marshes, tidally influenced river channels, shoals, shipping channels and marinas that are subject to dredging, and natural and modified shore areas. Several species of anadromous fish are native to

Published online: 22 May 2012

this system, including four runs of Chinook salmon (*Oncorhynchus tshawytscha*) and the anadromous form of rainbow trout – the steelhead (*O. mykiss*). As they migrate through each of these different habitats, smolts are exposed to different natural and anthropogenic sources of mortality. Studies of reach-specific mortality may help to identify and mitigate major threats to the outmigrating smolts.

Native salmon and steelhead stocks are in decline throughout California (Huntington et al. 1996). CV Chinook salmon stocks have been conservatively estimated to have peaked at 1–2 million active spawners (Yoshiyama et al. 1998, 2000). However, all runs in the CV have shown population declines, and late-fall run Chinook are federally listed as a “species of concern” (NMFS 2004) after numbers of returning fish declined drastically in the early 1990s (Moyle 2002). Central Valley steelhead were listed as “threatened” under the Endangered Species Act in 1998. Naturally reproducing steelhead and rainbow trout that support anadromy in the Sacramento River Watershed have been relegated to populations that spawn in the upper Sacramento, Feather, Yuba, Mokelumne, Calaveras, and Stanislaus rivers, and Butte, Deer, and Mill Creek (McEwan 2001).

Late-fall run Chinook salmon mainly display a stream-type juvenile life strategy – they may reside in the river for 7–13 months before migrating out to the ocean at a size of 150–170 mm fork length, where they remain along the coast of California until they return to spawn as 4–5 year olds (Moyle 2002).

Central Valley steelhead are classified as winter-run, with adults returning to fresh water during winter pulse flow events, even though some fish enter fresh-water as early as the summer and peak as late as September to October (Moyle 2002). Most juveniles rear in cool, clear, fast moving portions of rivers and tributaries for up to 2 years, before migrating to the ocean in spring (McEwan 2001). Others may residu-alize remaining in freshwater for their entire lives (Quinn 2005).

One of the main management responses to declin-ing salmon stocks has been to implement large scale hatchery release programs in most river basins along the Pacific coast of the USA, a practice that is not without controversy (e.g. see Meffe 1992; Brannon et al. 2004; Myers et al. 2004). Hatchery programs for salmonids in California began in the 1870 s, with the objective of increasing populations that were declining due to overfishing, the placement of dams and the resulting habitat loss (Moyle 2002). Hatchery pro-grams increase growth rates and size at release to enhance smolt to adult survival (Mahnken et al. 1982; Dickhoff et al. 1995). Currently, approximately 37 million fish (mostly Chinook, steelhead and Coho) are released by hatcheries in California each year (Kostow 2009).

Several studies have addressed the mortality of outmigrating hatchery-reared salmonid smolts on the Pacific coast of the USA (e.g. Welch et al. 2008; Melnychuk et al. 2010). Early studies in the Sacramento River focused on mass tagging of smolts with coded wire tags, release at specific locations, and recapture further downstream (Kjelson et al. 1981; Brandes and McLain 2001). More recently, Newman and Brandes (2010) used a similar approach to study the survival of outmigrating Chinook salmon through the Sacramento-San Joaquin Delta in relation to water pumping facili-ties. In recent years, ultrasonic telemetry has been used to study the survival and migratory pathways of salmo-nid smolts through river systems. This involves the placement of small internal tags within smolts that emit a unique ultrasonic code detected by an array of passive receivers placed along and across the river. Examples of such systems include the Pacific Shelf Ocean Tracking (POST) array (e.g. see Welch et al. 2008, 2009; Melnychuk 2009; Melnychuk et al. 2010), and the California Fish Tracking Consortium (CFTC) (e.g. Perry et al. 2010; Chapman et al. 2012; Sandstrom et al. 2012; Ammann et al. 2011).

The CFTC maintains ultrasonic receiver stations at locations from Redding (river km 559) down to the Golden Gate (river km 0) and including an offshore linear array at Point Reyes, 57.84 km to the north of San Francisco. Cross-river arrays have been placed at key sites to maximize the detection probability of fish passing through specific river reaches. Single-lined arrays are at Benicia, Carquinez, Richmond and Bay Bridges, and a double-lined array is maintained at the Golden Gate. A suite of receivers was deployed in the Delta in order to study the route selection of migrating smolts (Perry et al. 2010).

Here, we describe the reach-specific success of out-migrating hatchery-reared steelhead and late-fall run Chinook salmon smolts carrying these coded tags in 2009 and 2010, based on their detection by automated tag-detecting monitors from their release site near Sacramento to the Golden Gate Bridge – the entrance to the Pacific Ocean. Apparent survival and detection probabilities were estimated using Program Mark (White and Burnham 1999). We hypothesize several factors regarding survival estimates: (a) that smolts with higher condition factors will have higher apparent survival than those with lower condition factors, (b) fishes traveling through the east Delta will have lower survival when compared to fishes not selecting this route, due to a longer overall migration distance and possible entrainment in the pumping facilities in the Delta, (c) intraspecies apparent survival by reach across the 2 years of the study will be similar, and (d) Chinook will have higher overall apparent survival, as steelhead may residualize in fresh water.

Methods and materials

Surgical procedure

In 2009 and 2010 500 late-fall run Chinook salmon and 500 steelhead trout smolts were obtained from Coleman National Fish Hatchery (CNFH), located in Anderson, CA. The fish were transported from CNFH to the UC Davis campus and held for approximately 5 weeks prior to tagging and fed rations of feed at 1 % of their body weight per day. The fish were starved 48 h prior to the tagging procedure. The fish were anaesthetized with a dose of 90 mg/L tricaine methanesulphonate (MS222) in accordance with a UC Davis Animal Care Protocol (#15486). Once anesthetized, each individual was removed from the solution, photographed, and the fork length, weight and condition were recorded. Any fish whose tag to body weight ratio was greater than 5 % was not tagged and returned to the tanks. A 5 % tag to body weight ratio was a conservative cutoff based on previous research conducted by Lacroix and McCurdy (2004) and Martinelli et al. (1998) who reported tag burdens of 8 and 6 % respectively. Fish were then placed ventral-side up on a surgery cradle and kept sedated by flushing a lower concentration of 30 mg/L MS222 over the gills. A 10 mm incision was made beside the mid-ventral line, ending 3 mm anterior to the pelvic girdle. A sterilized, cylindrical ultrasonic tag was inserted into the peritoneal cavity of the fish and positioned so as to lay just under the incision. The incision was then closed using two simple interrupted sutures (Supramid, 3–0 extra nylon cable). Mean surgery time was 129(± 36 SD) seconds.

All fish were placed into a 284 L tank to recover from the anesthetic before being moved outside to larger holding tanks, where they were kept under observation before release. No mortalities or tag shedding were observed during this period.

The tags (Vemco V7-4 L) used on the steelhead were 22.5 mm length, 7 mm diameter, weighed 1.84 g in air, and had a power rating of 136 dB (1 μP @ 1 m). They had a 30–90 s random delay, and a battery life of 138 days. The tags (Vemco V7-2 L) used on the Chinook smolts were 20 mm long, 7 mm in diameter, weighed 1.6 g in air, and had a power rating of 136 dB (1 μP @ 1 m). They had a 15–45 s random delay, and a battery life of 52 days. The steelhead smolts, which are larger than the Chinook smolts at the time of release from the hatchery, were implanted with the V7-4 L tags. The V7-4Ls were programmed with a longer delay, so that we could take advantage of the longer battery life of the tag, because we anticipated a longer outmigration time for these fish.

Release site and procedure

The smolts were released at Elkhorn Boat Landing in Sacramento, CA 36.6227°N, 121.6248°W, approximately 18 km upstream from the first receiver they would be expected to encounter at the I80/50 junction (Fig. 1). Fish were released after dark, in batches of 500 (250 steelhead and 250 late-fall Chinook), on February 27th and March 6th 2009, and January 30th and February 5th 2010. Two fish transport tanks, one for each species, were used for transport to the release site at Elkhorn Boat Landing on the river above Sacramento. Oxygen was pumped from tanks mounted on the truck through hoses to oxygen diffusers placed in the bottom of each tank. Dissolved oxygen and temperature were monitored throughout transport. Upon arrival at the release site, we compared the temperatures in the tank and the river. When water temperature differed by greater than 1°C the fish were acclimated by bringing the tank temperature up to within 1°C of the river temperature in increments of 1°C every 45 min. The fish were released once the temperatures were within 1°C of each other.

Receivers and array maintenance

An array of underwater passive ultrasonic receiver stations (VR2/VR2W, VEMCO Ltd. Halifax, Canada)

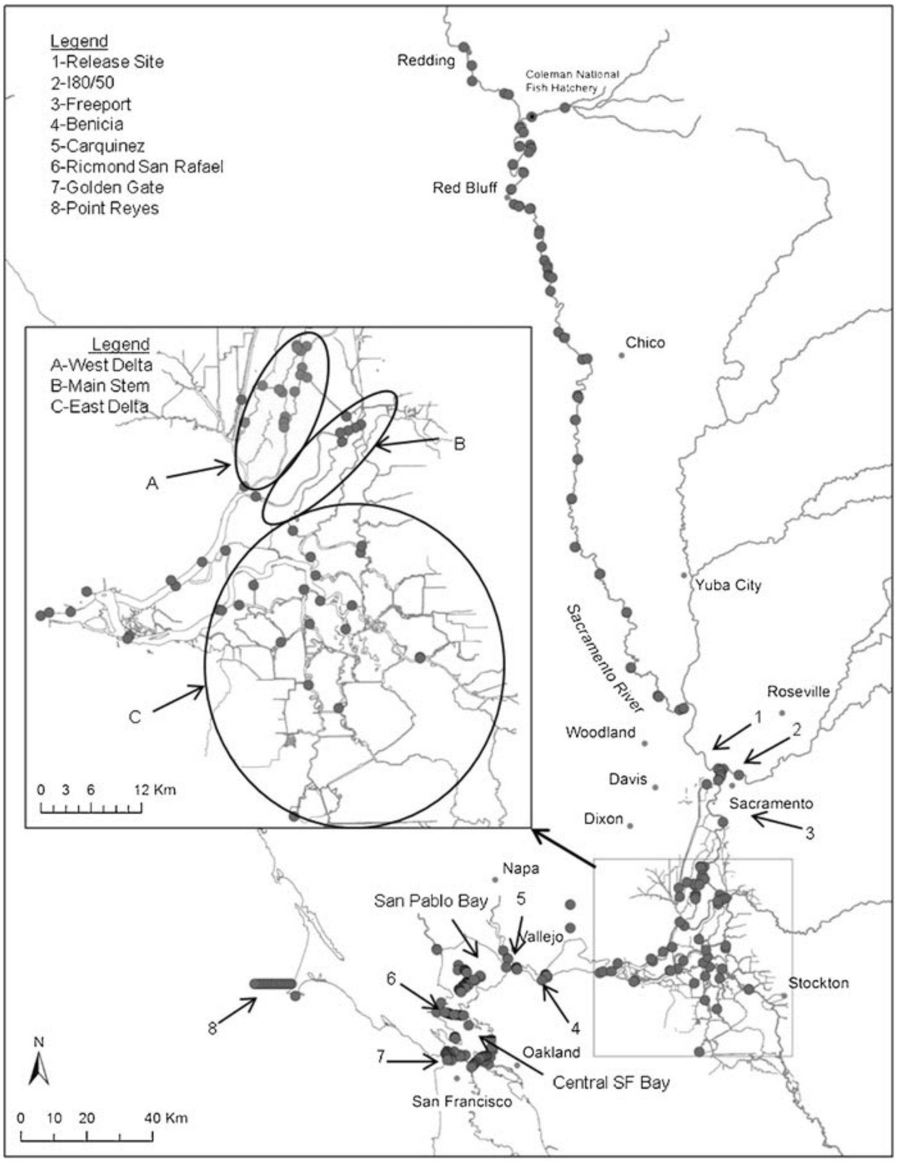

Fig. 1 Map of study area. Inset is the Delta with three routes highlighted. Numbers indicate locations of various checkpoints used in study, and letters indicate the different routes. Circles on the map indicate the location of tag detecting monitors maintained by the California Fish Tracking Consortium, including the monitors used in this study

was deployed throughout the Sacramento River system. Along the river and delta, the receivers were mostly deployed on weighted moorings (9–41 kg mass), attached to steel cables running from onshore manmade or natural structures. Cross section arrays at major bridges (Benicia, Carquinez, Richmond and Bay Bridge) involved direct attachment of receivers to weighted steel cables at bridge abutments. Other receivers were deployed on acoustic releases for ease of recovery in deepwater and mid-channel locations (such as the Golden Gate, or arrays in San Pablo Bay) where no structure was available for mooring the receivers. Receivers were interrogated and maintained every 3–4 months. Receiver locations that define the reaches and their corresponding river kilometers (rkm) can be found in Table 1. The files of tag detections were entered into the CFTC shared database, maintained by the National Marine Fisheries Service.

We carried out a range test to determine the ideal spacing of receivers within cross section arrays. A range test tag, similar in characteristics to the tags used in the fish, except that the pulse interval was fixed, was placed on a mooring with a receiver. This was followed by a line of receivers each spaced 30 m apart to a distance of 330 m, followed by a final receiver at 410 m from the tag. After 24 h we

Table 1 Reaches used to create encounter histories by name, river km, and reach length

Location	River km	Reach length (km)
Elk Landing	207.7	
I-80/50	189.0	18.77
Freeport	168.5	20.46
Benicia Bridge	51.69	116.8
Carquinez Bridge	41.47	10.22
Richmond Bridge	14.72	26.76
Golden Gate East Line	1.717	13.0
Golden Gate West Line	0.798	0.919
Point Reyes	−57.84	58.64

recovered the array and calculated the detection probability of the range test tag with increasing distance. Range tests were conducted in three locations that were representative of the different environments expected to be encountered in our study area. Range testing was conducted at Knights Landing, the San Francisco Bay, and Comanche Reservoir. We found that the tag had a detection probability of a value of 0.75 at a distance of 75 m from a receiver, in a less than ideal acoustic environment. Therefore, a conservative spacing of 150 m was used between receivers at cross section arrays.

In order to gain information on the amount of water the fish encountered as they migrated through our array, we obtained river discharge (in cubic feet per second, which were then converted to cubic meters per second) at Freeport from the California Data Exchange Center (http://cdec.water.ca.gov/cgi-progs/staSearch).

Routes

We subdivided the Delta into the major routes which fish might select, based on Perry et al. (2010), but excluded the Delta Cross Channel (DCC) as this remained closed throughout the migration of our fish during both years. The estuary was subdivided into several regions, each bordered by receivers or receiver arrays at bridges. At the head of the estuary, the Sacramento and San Joaquin rivers flow into Suisun Bay (upstream of location 4 Fig. 1). This is largely brackish and is separated from San Pablo Bay by the Carquinez Strait (the area between locations 4 and 5 Fig. 1), an area between the Benicia and Carquinez Bridges. South of the Richmond-San Rafael Bridge (Location 6 in Fig. 1) lies the Central Bay, bordered on the west by the Golden Gate Bridge (Location 7 in Fig. 1), and to the south by the Bay Bridge and the South Bay (Fig. 1).

Successful migration

Successful migration through a particular reach by an individual fish was defined by that individual being detected at the end cross-section array of that reach or at any receiver located downstream from that array. For example, a fish was assumed to have successfully migrated through San Pablo Bay if it was detected at Richmond Bridge or below. Successful migration to the ocean was defined as those fish detected at the Golden Gate plus those detected at Point Reyes which were not detected at the Golden Gate. Values for the Golden Gate were corrected to include those fish detected at the Point Reyes array. However the results may be underestimations of the overall success rate, given that once fish arrive at the ocean they may potentially take a wide number of routes.

Data analysis

The body condition factor (K) was calculated by incorporating the weights and fork lengths (Figs. 2 and 3) of the fish recorded during the surgeries into the equation developed by Fulton (1902):

$$K = \left(10^5 \times W\right)/L^3$$

Where W is the mass of the fish (measured in grams) and L is the fork length of the fish (measured in mm). The value of K is then used an index for body condition, with higher K values indicating a better body condition. We compared fork lengths and K factor between species and years using a Kruskal-Wallis One Way Analysis of Variance on Ranks.

We divided the Delta into routes (see Fig. 1) similar to those described by Perry et al. (2010). We estimated the number of fish moving through each route by analysis of the detection sequence in the Delta array. For each route, we compared the numbers and proportions (with 95 % confidence intervals) of fish that successfully migrated through successive river reaches to the Golden Gate. A Pearson's Chi-Squared test was

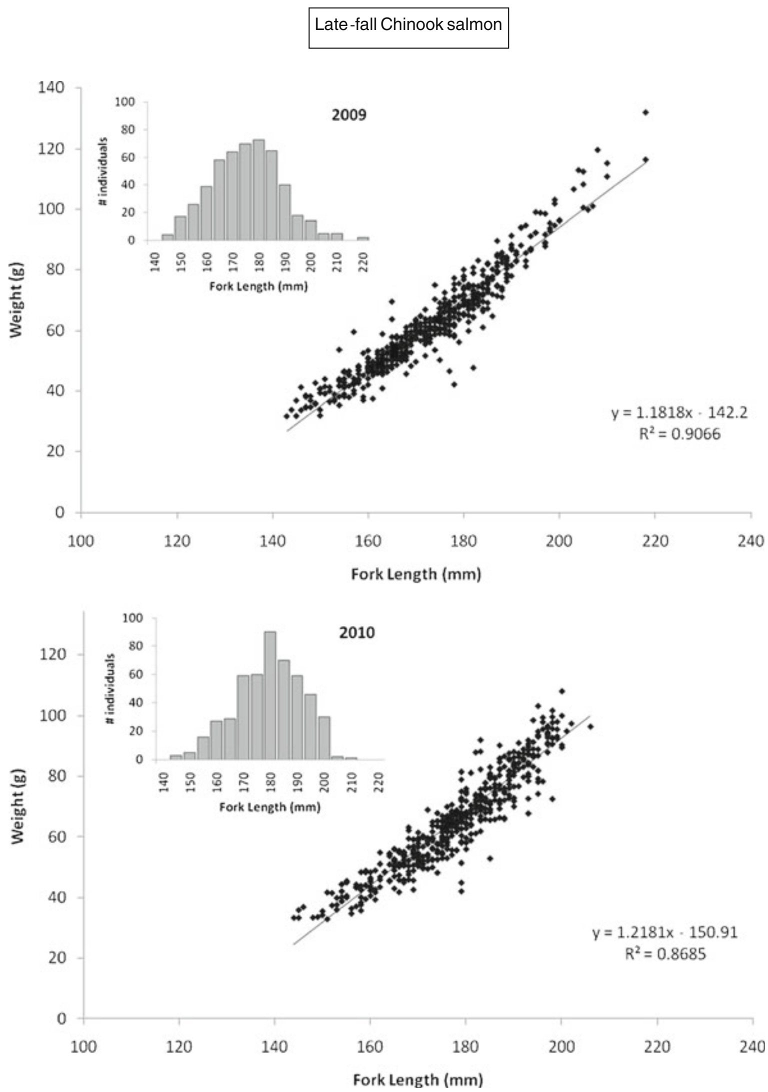

Fig. 2 Size structure for juvenile late-fall run Chinook salmon in 2009 (top) and 2010 (bottom). Fork Length in mm along the x-axis and weight in grams along the y-axis. The inset histogram shows the length distributions

run to compare survival by species and year across reaches.

Encounter histories were created for each fish based on the detection data from our array of monitors. The fish were then placed into one of 12 groups based on release timing, route selected through the Delta, and the year in which the fish was released. All of the data were incorporated into several models in Program Mark (White and Burnham 1999) in order to estimate apparent survival and detection probabilities. The candidate models were then ranked using Akaike's Information Criterion (AIC), and the top performing models were used to report the results of this study (Akaike 1973). The same models were run with data from both steelhead and late-fall run Chinook.

Results

Size and body condition

The size range of Chinook salmon was similar in both years. The fork lengths varied between 140 and 220 mm, although a Kruskal-Wallis One Way Analysis of Variance on Ranks revealed that the median length of 178 mm was significantly greater ($P<0.001$) in 2010 than the median length of 174 mm in 2009. Steelhead were larger than Chinook, but there was a greater difference in fork length range between years ($P<0.001$). The median length in 2009 was 260 mm, whereas in 2010, median length was 223 mm (Figs. 2 and 3). The

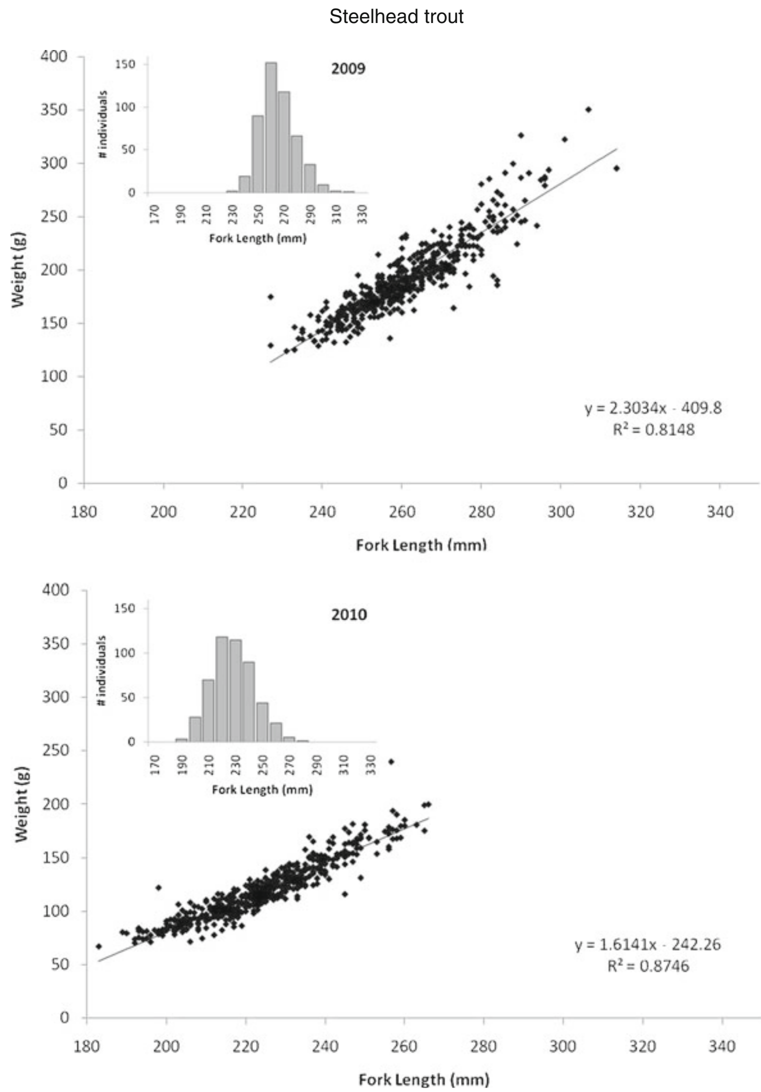

Fig. 3 Size structure for juvenile steelhead trout in 2009 (top) and 2010 (bottom). Fork Length in mm along the x-axis and weight in grams along the y-axis. The inset histogram shows the length distributions

mean condition factor was slightly greater in the 2009 fish for both species. However, there was no significant difference in condition factor within years between fish which successfully migrated to the Golden Gate and those which did not (Fig. 4). The relatively low K values for the fish used in this study were expected, and are indicative of the smoltification process. MacFarlane and Norton (2002) reported mean condition factors for juvenile Chinook salmon sampled at different points within the estuary ranging from 1.0 to 1.1. Campos and Massa (2010) reported mean condition factors for juvenile steelhead captured in rotary screw traps ranging from 0.9 to 1.1. These data are similar to our calculations for condition factor (Fig. 4).

Release site conditions

2009 smolts were released from Elkhorn Landing (river km 207.7) when the flows registered 1,125 $m^3\ s^{-1}$ and 961 $m^3\ s^{-1}$ and in-river temperatures were 12.3°C and 11.3°C respectively. In 2010, the first release coincided with a flow of 1,454 $m^3\ s^{-1}$ and a temperature of 9.7°C, while the second release occurred at 836 $m^3 s^{-1}$ and temperature of 10.9°C (Fig. 5), resulting in a much larger range of observed discharge.

Route selection

More than half of the fish migrating through the delta remained in the main stem Sacramento. A total of

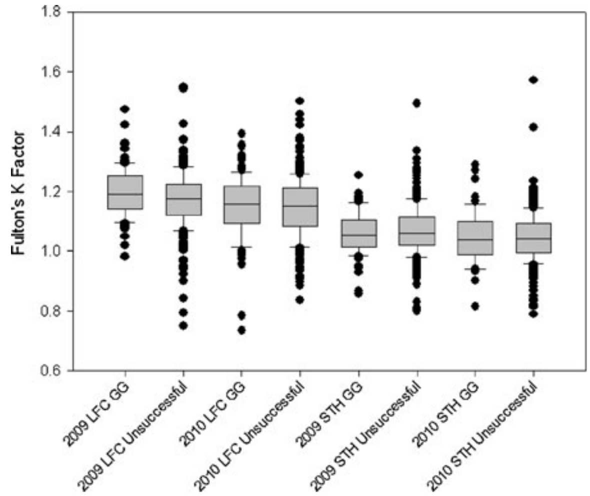

Fig. 4 Box plot comparing Fulton's condition factor of fish that successfully migrated to the Golden Gate Bridge to those that were unsuccessful. Late-fall Chinook (LFC) Steelhead (STH)

63.6 % (n=281) of Chinook that traveled far enough to encounter a junction that required a route selection, remained in the mainstem in 2009 and 54 % (n=234) remained in the mainstem in 2010. A total of 59.9 % (n=187) of the steelhead passed through the mainstem in 2009, while 52.4 % (n=109) passed through the same reach in 2010. Of these smolts, a greater percentage of Chinook, 26 %, and steelhead, 33 %, reached the Golden Gate in 2010, compared with 20 % and 25 % for both species, respectively in 2009. A similar percentage of each species were entrained into the East Delta each year, each of which displayed lower (9–19 %) success to the Golden Gate than for the other routes. Those fish which migrated through the West Delta had the highest survival rates of 30 % to the Golden Gate, with the exception of the 2009 batch of steelhead that had only a 10 % survival rate (Table 2).

Reach specific success

Chinook numbers declined only slightly (500 to 487 in 2009 and 500 to 471 in 2010) between the release site and Freeport (the start of the Delta). This is in stark

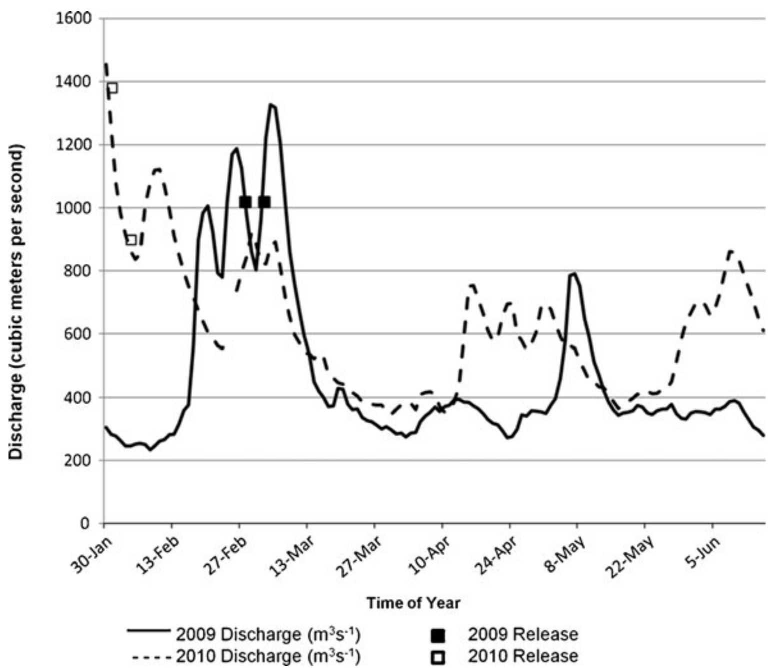

Fig. 5 Discharge by date as recorded at the CDEC station located at Freeport on the Sacramento River. Discharge is recorded in cubic meters per second. Dates of releases are indicated with squares

Table 2 Number and proportion of fish that used each route though the Delta, and their success to the Golden Gate Bridge

		Chinook		Steelhead	
		2009	2010	2009	2010
West Delta	# of fish	93	137	72	60
	Prop utilizing route	0.21	0.316	0.231	0.288
	# to Golden Gate	28	42	7	18
	Prop. Success to ocean	0.30	0.31	0.10	0.30
East Delta	# of fish	68	62	53	59
	Prop utilizing route	0.154	0.143	0.17	0.188
	# to Golden Gate	6	10	10	6
	Prop. Success to ocean	0.09	0.16	0.19	0.10
Mainstem	# of fish	281	234	187	109
	Prop utilizing route	0.636	0.54	0.599	0.524
	# to Golden Gate	55	61	46	36
	Prop. Success to ocean	0.20	0.26	0.25	0.33
Total fish in delta		442	433	312	208

contrast with steelhead, where over 20 % of the fish released each year were never detected. These fish probably did not migrate as far as the first receiver, I80/50, 20 km downstream from the release site - in 2009 only 357 of the 500 steelhead released were detected at Freeport or below, and in 2010 only 310 fish were detected here or below.

In the reach between Freeport and Benicia, both species exhibited similar rates of apparent survival. In 2009, the survival in the aforementioned reach was nearly identical at 66.7 % for steelhead and 63.0 % for Chinook (p=0.3098). In 2010, in the same reach survival across species was similar (35.8 % for steelhead and 43.5 % for Chinook), however and intraspecies comparison of survival differed significantly between years (p=0.0169).

Survival in the reach between Benicia and Carquinez differed little between species and years, and indicated little mortality for both species in this reach, although it is important to note that this was the shortest reach in the study site. In the Carquinez Straits success for Chinook ranged from 86.6 % (2009) to 94.6 % (2010), and 89.9 % (2009) to 90.1 % (2010) for steelhead. Success continued to decline as fish migrated through San Pablo Bay and Central San Francisco Bay. The Richmond to the Golden Gate Bridge reach had the lowest reach specific success for both species in 2009. In that reach, the final one before entry into the Pacific Ocean, success ranged from 56.5 % (2009) to 78.1 % (2010) for Chinook, and 45.6 % (2009) to 75.0 % (2010) for steelhead (Table 3).

Although overall migratory success to the Golden Gate was similar between 2009 and 2010, reach specific success was very different between years. Intraspecies success to the ocean (fish detected at either the Golden Gate or the Pt. Reyes array) was similar across years, 19.2 % (n=96) of Chinook salmon smolts in 2009, and 23.6 % (n=118) in 2010; and 14.6 % (n=73) of steelhead in 2009 and 13.8 % (n=69) in 2010. Successful migration through the Delta declined for both species from 2009 to 2010. However, in contrast with 2009, in 2010 many of the surviving fish then proceeded to the Golden Gate, with very few losses throughout the bay. In 2010 the Freeport to Benicia reach (Delta) had the lowest migratory success rates for both species, whereas in 2009 the reach with the lowest migratory success rates for both species was Richmond to the Golden Gate. Between Carquinez and the Golden Gate (the bay) apparent mortality of late-fall run Chinook in 2009 exceeded that in 2010 and apparent mortality of steelhead in 2009 also exceeded that of the 2010 fish. The overall pattern observed in the data was an apparent flip-flop of regions of higher mortality, with the bay appearing to be more perilous to migratory juvenile salmonids in 2009 and the Delta more perilous in 2010.

Reach specific survival estimates and detection probabilities

Fifteen candidate models were developed and then ranked according to their AIC for Chinook salmon

Table 3 Success of Steelhead and Chinook for both 2009 and 2010, based on raw detections. Elkhorn Landing was the release site

	Success to Site 2009	From Release Site % 2009	Reach Specific % 2009	Success to Site 2010	From Release Site % 2010	Reach Specific % 2010
Steelhead						
Elkhorn landing	500			500		
I80/50	378	75.6	75.6	339	67.8	67.8
Freeport	357	71.4	94.4	310	62.0	91.4
Benicia	238	47.6	66.7	111	22.2	35.8
Carquinez	214	42.8	89.9	100	20.0	90.1
Richmond	160	32.0	74.8	92	18.4	92.0
Golden Gate	73	14.6	45.6	69	13.8	75.0
Chinook						
Elkhorn landing	500			500		
I80/50	488	97.6	97.6	482	96.4	96.4
Freeport	487	97.4	99.8	471	94.2	97.7
Benicia	307	61.4	63.0	205	41.0	43.5
Carquinez	266	53.2	86.6	194	38.8	94.6
Richmond	170	34	63.9	151	30.2	77.8
Golden Gate	96	19.2	56.5	118	23.6	78.1

(Table 4) and steelhead trout (Table 5). Steelhead survival estimates calculated in the top candidate model suggest that survival was higher through the Delta in 2009, than in 2010. Additionally, survival through the bay was lower in 2009 than it was in 2010 for Steelhead. This same pattern was seen for Chinook in the best model. Detection probabilities were consistently higher in 2010. This is likely due to the addition of monitors on the Carquinez and Richmond San Rafael Bridges. Complete survival estimates can be found for the top-ranked model for steelhead (Table 6) and for Chinook (Table 7).

While survival estimates varied depending on the year and release group the overall trend suggests that Chinook have a better chance of surviving the Freeport to Benicia route if they took the mainstem Sacramento route or West Delta route, as opposed to the East Delta. In 2009, steelhead taking the West and East Delta route had similar survival estimates, while the mainstem fish had better survival in this reach. However, steelhead in 2010 had much better survival in the West Delta and mainstem Sacramento than they did in the East Delta.

Discussion

We found that in both 2009 and 2010, migratory success from the release site at Elkhorn Landing, near Sacramento, to the Golden Gate (a distance of 207 km) was less than 25 % for both late-fall Chinook salmon and steelhead. However, migratory success varied considerably between reaches and between years. Success for both species in the Delta was above 60 % in 2009, yet dropped to below 45 % in 2010. Conversely, successful migration through San Francisco Bay was only around 50 % in 2009, yet increased to over 75 % in 2010. This apparent reversal in the relative success rates (which might be assumed to reflect mortality) may be counterintuitive, given that flows were higher in 2010, and increased flows are often associated with increased survival (Sims and Ossiander 1981). Survival of salmonid smolts in the Delta is positively correlated (r=0.95) with volume of flow and that the survival rate changed greatly as the flow changed. The survival was nearly 100 % when the flows were above 708 $m^3\ s^{-1}$ (25 000 cfs), but less than 20 % when the flows were near 283 $m^3\ s^{-1}$ (10 000 cfs) (Fischer et al. 1991). The paradox we observed may have resulted from indirect effects of climate and

Table 4 Candidate models and their ranks, according to AIC for late-fall Chinook

Results for Late-fall Chinook

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(t*Year*Route*Release) p(t*Year)}	4787.41	0	1	1	52	697.29
{Phi(t*Year*Route) p(t*Year)}	4843.41	56.00	0	0	34	790.73
{Phi(t*Year*Route*Release) p(t)}	4951.64	164.23	0	0	47	871.98
{Phi(t*Year*Release) p(t)}	4956.73	169.32	0	0	39	893.71
{Phi(t*Year*Route) p(t)}	4976.26	188.85	0	0	27	937.97
{Phi(t*region*year*route*release) p(t)}	4989.15	201.74	0	0	39	926.13
{Phi(t*Year) p(t)}	4995.82	208.41	0	0	23	965.72
{Phi(t*region*year*route) p(t)}	5019.03	231.62	0	0	23	988.93
{Phi(t*region*Year) p(t)}	5038.63	251.22	0	0	19	1016.69
{Phi(t*Release) p(t)}	5068.56	281.15	0	0	23	1038.46
{Phi(t*Route) p(t)}	5076.64	289.23	0	0	17	1058.77
Phi(t*Region*Route*Release) p(t)}	5087.96	300.55	0	0	23	1057.86
{Phi(t) p(t)}	5100.90	313.49	0	0	15	1087.08
{Phi(t*region*route) p(t)}	5118.21	330.80	0	0	15	1104.39
{Phi(t*region) p(t)}	5142.47	355.06	0	0	13	1132.70

flow– the 2010 releases occurred in March, 1 month later than in 2009. Additionally, during the 2010 outmigration period, the western coast of North America was experiencing El Niño conditions. A brief look at sea surface temperatures at the San Francisco Bar (http://www.ndbc.noaa.gov/station_history.php?station=46237) during the time in which the salmonids were migrating showed that the mean temperature was only slightly higher in 2010 (12.07±1.37°C SD in 2009, 12.43±0.84°C in 2010). This subtle difference

Table 5 Candidate models and their ranks, according to AIC steelhead trout

Results for Steelhead

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(t*Year*Route) p(t*Year)}	3399.09	0	0.78	1	35	693.21
{Phi(t*Year*Release*Route) p(t*Year)}	3401.67	2.57	0.22	0.28	53	657.53
{Phi(t*Year*Route) p(t)}	3486.36	87.27	0	0	27	797.18
{Phi(t*Year) p(t)}	3488.95	89.86	0	0	23	808.04
{Phi(t*Year*Release) p(t)}	3492.19	93.10	0	0	39	777.89
{Phi(t*Year*Release*Route) p(t)}	3492.94	93.85	0	0	47	761.66
{Phi(t*Region*Year) p(t)}	3501.35	102.26	0	0	19	828.68
{Phi(t*Region*Route*Year*Release) p(t)}	3520.67	121.58	0	0	40	804.26
{Phi(t*Region*Route*Year) p(t)}	3524.74	125.65	0	0	24	841.77
{Phi(t*Release) p(t)}	3534.71	135.62	0	0	23	853.81
{Phi(t*Route) p(t)}	3537.76	138.67	0	0	17	869.19
{Phi(t) p(t)}	3542.84	143.75	0	0	15	878.36
{Phi(t*Region*Route) p(t)}	3551.75	152.66	0	0	15	887.27
{Phi(t*Region) p(t)}	3558.87	159.78	0	0	14	896.44
{Phi(t*Region*Route*Release) p(t)}	3565.76	166.67	0	0	24	882.79

Table 6 Survival estimates and detection probabilities from the best fit model for Chinook. Estimates for the Pt. Reyes reach are confounded, as there are no downstream monitors

Survival Estimates and Detection Probabilities for Chinook Salmon

Label	Estimate	SE	LCI	UCI
Phi Elkhorn to 180/50 Release 1 2009	1	4E-07	0.999999	1.00001
Phi 180/50 to Freeport Release 1 2009	1	3E-07	0.999999	1.00001
Phi Freeport to Benicia (MS) Release 1 2009	0.562987	0.048372	0.467032	0.654448
Phi Freeport to Benicia (WD) Release 1 2009	0.602543	0.068723	0.463472	0.726814
Phi Freeport to Benicia (ED) Release 1 2009	0.313323	0.073488	0.189372	0.47124
Phi Benicia to Carquinez Release 1 2009	0.895141	0.07521	0.639657	0.97622
Phi Carquinez to RSR bridge Release 1 2009	0.616018	0.084521	0.443327	0.763693
Phi RSR Bridge to GG East Release 1 2009	0.614797	0.095187	0.42061	0.778219
Phi GG East to GG West Release 1 2009	1	1.7E-06	0.999997	1.000003
Phi GG West to Pt. Reyes Release 1 2009	0.428481	0	0.428481	0.428481
Phi Elkhorn to 180/50 Release 2 2009	0.811651	0.035321	0.732612	0.871426
Phi 180/50 to Freeport Release 2 2009	1	2.3E-06	0.999995	1.000005
Phi Freeport to Benicia (MS) Release 2 2009	1	3E-07	1	1.000001
Phi Freeport to Benicia (WD) Release 2 2009	1	1.6E-06	0.999997	1.000003
Phi Freeport to Benicia (ED) Release 2 2009	0.699152	0.143073	0.37991	0.898116
Phi Benicia to Carquinez Release 2 2009	0.932502	0.063067	0.659682	0.989946
Phi Carquinez to RSR Bridge Release 2 2009	0.706509	0.079746	0.531134	0.836482
Phi RSR Bridge to GG East Release 2 2009	0.613944	0.086653	0.43717	0.765037
Phi GG East to GG West Release 2 2009	0.867951	0.124447	0.438998	0.98221
Phi GG West to Pt. Reyes Release 2 2009	0.980661	0	0.980661	0.980661
PhiElkhom to 180/50 Release 1 2010	0.687292	0.098508	0.472312	0.843677
Phi 180/50 to Freeport Release 1 2010	0.80474	0.118992	0.482992	0.947868
Phi Freeport to Benici (MS) Release 1 2010	0.849305	0.075682	0.638797	0.947258
Phi Freeport to Benici (WD) Release 1 2010	0.884648	0.063421	0.69404	0.962864
Phi Freeport to Benici (ED) Release 1 2010	0.477967	0.198467	0.161488	0.813182
Phi Benicia to Carquinez Release 1 2010	0.977109	0.041347	0.532603	0.999375
Phi Carquinez to RSR Bridge to GG West Release 1 2010	0.820426	0.056508	0.682974	0.906447
Phi RSR Bridge to GG East Release 1 2010	0.721483	0.055879	0.600318	0.817106
Phi GG East to GG West Release 1 2010	0.983648	10.21562	0	1
Phi GG West to Pt. Reyes Release 1 2010	0.959401	0	0.959401	0.959401
Phi Elkhorn to 180/50 Release 2 2010	1	1E-07	1	1
Phi 180/50 to Freeport Release 2 2010	1	0	1	1
Phi Freeport to Benicia (MS) Release 2 2010	0.513124	0.043704	0.427913	0.597579
Phi Freeport to Benicia (WD) Release 2 2010	0.365738	0.07088	0.240594	0.512081
Phi Freeport to Benicia (ED) Release 2 2010	0.300614	0.075987	0.174689	0.466054
Phi Benici to Carquinez Release 2 2010	1	2E07	1	1
Phi Carquinez to RSR Bridge Release 2 2010	0.729562	0.053734	0.612683	0.821449
Phi RSR Bridge to GG East Release 2 2010	0.6632125	0.063679	0.529599	0.774861
Phi GG East to GG West Release 2 2010	0.899202	9.338738	0	1
Phi GG West to Pt. Reyes Release 2 2010	0.999597	0	0.999597	0.999597
p 180/50 2009	0.017337	0.006499	0.008284	0.035923
p Freeport 2009	0.071824	0.012875	0.05033	0.101517

Table 6 (continued)

Survival Estimates and Detection Probabilities for Chinook Salmon				
Label	Estimate	SE	LCI	UCI
p Benicia 2009	0.747211	0.029945	0.684184	0.801313
p Carquinez 2009	0.562963	0.042691	0.478291	0.644118
p RSR Bridge 2009	0.539326	0.052836	0.435565	0.639787
p GG East 2009	0.467008	0.057215	0.358314	0.578927
pGG West 2009	0.659505	0.071862	0.508465	0.783862
p Pt. Reyes 2009	0.328311	0	0.328311	0.328311
p 180/50 2010	0.101157	0.016714	0.072782	0.138938
p Freeport 2010	0.36211	0.02704	0.310954	0.416593
p Benicia 2010	0.902881	0.022344	0.84944	0.938722
p Carquinez 2010	0.645083	0.036705	0.570347	0.713352
p RSR Bridge 2010	0.805825	0.038976	0.718065	0.871169
p GG East 2010	0.806122	0.039935	0.715896	0.872787
p GG West 2010	0.994592	10.32927	0	1
p Pt. Reyes	0	0	0	0

may be one of several factors that influenced the location and abundance of salmon smolt predators, such as striped bass, which are more abundant in the ocean and estuaries during El Niño years (Moyle 2002). In the future, acoustic telemetry studies that pair the tagging of striped bass (and other predators of juvenile salmonids) and subsequent analysis of the relationship of movement patterns between species, would help to elucidate the extent of these predator/prey interactions.

In both 2009 and 2010 we observed a much higher initial loss for steelhead than for Chinook (Table 3). There may be several explanations for this. Some steelhead, unlike Chinook, will residualize and remain in freshwater for their entire lives (Moyle 2002). In addition, tag retention studies conducted on hatchery fish of both species indicate that there are differences in tag shedding. Sandstrom et al. (2012) concluded that after 60 days, steelhead tagged with dummy tags equivalent to a Vemco V7-2 L (which is 2.5 mm shorter in length then V7-4Ls used on the steelhead in this study) ultrasonic transmitters shed their tags 8 % of the time. In contrast, Ammann et al. (2011) concluded that after 120 days 100 % of Chinook tagged with V7-2Ls (the same tags used on the Chinook in this study) retained their tags, so that tag shedding is unlikely to be a source of error in our migratory success estimates for Chinook. Another possible bias is that steelhead may be more affected by the stress involved in transport, release, and acclimation to the new environment – over 100 steelhead each year were not detected anywhere downstream after release, compared with only several Chinook. While success within species was similar across years, successful migration to the ocean was higher in both years for Chinook salmon than steelhead, although this may not necessarily reflect different survival rates. In, addition to the potential for tag shedding, the random delay on the steelhead tags was nominally twice that of the Chinook, so fish being transported out of the Golden Gate at peak tidal flows are more likely to traverse the detection range of the array between pulses without being detected. Future comparative studies addressing transport stress across Pacific salmonid species could be useful to salmonid researchers. Additionally, residualized steelhead, malfunctioning tags, and fish that shed their tags may appear as a mortality when analyzing movement data. Developing a model used to adjust survival rates of acoustically tagged salmonids in a manner that adjusts for falsely assumed mortalities is another way that we intend to advance our analyses.

Previous studies of outmigrating salmon smolts in the Sacramento-San Joaquin drainage indicate that survival was affected by the route that the fish chose (Newman and Brandes 2010) and that the probability

Table 7 Survival estimates and detection probabilities from the best fit model for steelhead. Estimates for the Pt. Reyes reach are confounded, as there are no downstream monitors

Survival Estimates and Detection Probabilities for Steelhead Trout

Label	Estimate	SE	LCI	UCI
Phi Elkhom to 180/50 2009	0.828629	0.037245	0.743048	0.889929
Phi 180/50 to Freeport 2009	1	1E-07	1	1
Phi Freeport to Benicia (MS) 2009	0.898	0.045987	0.766946	0.959271
Phi Freeport to Benicia (WD) 2009	0.738349	0.093568	0.522014	0.879393
Phi Freeport to Benicia (ED) 2009	0.791391	0.092839	0.557527	0.919497
Phi Benicia to Carquinez 2009	0.882348	0.063369	0.693898	0.961258
Phi Carquinez to RSR Bridge 2009	0.856703	0.101689	0.541064	0.968069
Phi RSR bridge to GG East 2009	0.531836	0.091866	0.355341	0.700709
Phi GG East to GG West 2009	1	5.98E-05	0.999883	1.000117
Phi GG West to Pt. Reyes 2009	0.261186	21.37851	0	1
Phi Elkhorn to 180/50 2010	0.725212	0.054341	0.607304	0.818309
Phi 180/50 to Freeport 2010	0.91465	0.090799	0.523001	0.990543
Phi Freeport to Benicia (MS) 2010	0.7403	0.083363	0.549256	0.869596
Phi Freeport to Benicia (WD) 2010	0.66825	0.098578	0.457291	0.828042
Phi Freeport to Benicia (ED) 2010	0.40753	0.102376	0.230545	0.612271
Phi Benicia to Carquinez 2010	0.966342	0.029029	0.833125	0.99398
Phi Carquinez to RSR Bridge 2010	0.932232	0.037539	0.811051	0.97782
Phi RSR Bridge to GG East 2010	0.716216	0.056568	0.593938	0.813251
Phi GG East to GG West 2010	0.843623	0	0.843623	0.843623
Phi GG West to Pt. Reyes 2010	2.13E-05	0	2.13E-05	2.13E-05
p 180/50 2009	0.154719	0.023203	0.114479	0.205818
p Freeport 2009	0.379063	0.033249	0.316394	0.446046
p Benicia 2009	0.699348	0.037071	0.622137	0.766698
p Carquinez	0.486956	0.04661	0.39703	0.577734
p RSR Bridge 2009	0.507939	0.062986	0.386469	0.628478
p GG East 2009	0.329725	0.064366	0.217506	0.465406
p GG West 2009	0.545752	0.085351	0.379592	0.70231
p Pt. Reyes 2009	0.261186	21.3785	0	1
p 180/50 2010	0.384504	0.046149	0.298872	0.477945
p Freeport	0.384143	0.050636	0.290799	0.48688
p Benicia 2010	0.941177	0.025521	0.866351	0.975304
p Carquinez 2010	0.687499	0.051822	0.578272	0.779236
p RSR Bridge 2010	0.946429	0.030089	0.846641	0.98262
p GG East 2010	0.755102	0.061432	0.61654	0.855342
p GG West 2010	0.996784	0	0.996784	0.996784
p Pt. Reyes 2010	2.13E-05	0	2.13E-05	2.13E-05

of selecting a particular migratory route is positively correlated with the fraction of total river discharge that flows through that route (Perry et al. 2010). Entrainment in the interior delta (East Delta) is negatively correlated with survival (Newman and Brandes 2010; Perry et al. 2010) Perry et al. (2010) found that 8.8 % of fish were entrained into the interior delta when the DCC was closed, whereas 35.2 % were entrained when it was open. In our study, which took place while the DCC was closed, we found that the proportion of fish migrating through the interior delta was consistently higher for both species, 14.3–15 % for Chinook and 17.0–18.8 % for steelhead. It has been suggested that fish entrained in the East Delta have lower survival rates than other routes (Perry et al. 2010), although it is important to note that Perry defined "survival" as migration to Chipps Island. This was consistent with our results - throughout the duration of our study, fish migrating through the East Delta had lower overall survival than fish choosing either the West Delta or the mainstem Sacramento River, with the exception of West Delta steelhead in 2009 (Fig. 6). Several factors may have interacted to produce conditions that were unfavorable for steelhead, including water temperatures, increased suspended sediment loads in the water, and spatio-temporal distribution of steelhead smolt predators.

Survival is negatively related to total distance traveled during migration to the ocean (Muir et al. 2001; Smith et al. 2002). Because of the convoluted configuration of the East Delta smolts choosing this migratory pathway undoubtedly have a longer route to the ocean, and encounter obstacles not seen by fish choosing other routes (e.g. Central Valley Project and State Water Project pumping facilities). The pumping facilities have taken many precautionary measures to reduce fish loss; however the predator assemblages in the forebays, the physical stress of going through the salvage process, and the subsequent transport and re-release into the river may be too much for the smolts to overcome. Previous studies of juvenile fall run Chinook suggest survival is negatively associated with water exports (Kjelson et al. 1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003). Additionally, the Operations Criteria and Plan (OCAP) Biological Assessment (BA) (USBR 2008) contains regressions of monthly steelhead salvage at the Central Valley Project and State Water Project pumping facilities, which shows a significant relationship between number of steelhead salvaged and the amount of water exported during the months of January through May, the same time that our tagged fish where in the Sacramento River Watershed. Our study suggests that entrainment in the east delta was negatively correlated with success to the ocean.

These results highlight the need to improve our understanding of the dynamics of smolt outmigration through the Sacramento River watershed, and the factors that affect their migratory behaviors. Future studies pairing the tagging of piscivorous fish and juvenile

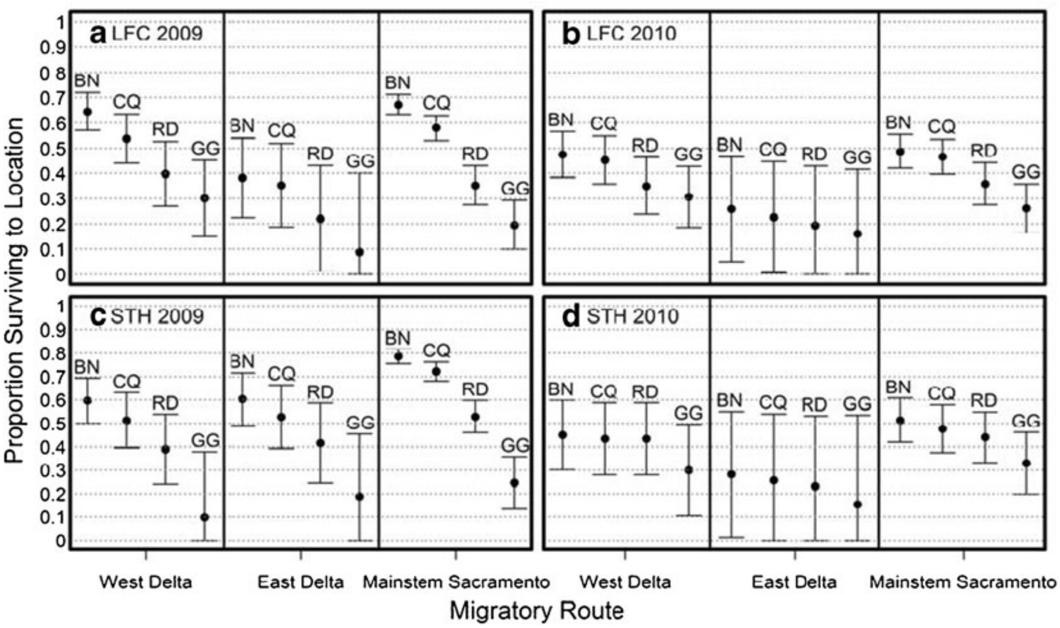

Fig. 6 Proportion of fish from each group successfully migrating to different reaches in the San Francisco Bay based on route selection through the Delta. Figure is divided by species, year, and route. The bars on the graph indicated 95 % confidence intervals in regards to our estimates of successful migration. The following abbreviations were used for location code: Benicia Bridge (BN), Carquinez Bridge (CQ), Richmond Bridge (RD), and the Golden Gate (GG). The following abbreviations were used to identify the species of reference: Late-fall Chinook salmon (LFC) and steelhead trout (STH)

salmonids in order to elucidate the intricacies of the spatio-temporal movements of predators in relation to prey availability are needed. Comprehensive studies designed to highlight the interactions of flow, temperature, turbidity, climate change, diel movements, pumping operations in the Delta, and predator abundance and interactions would fill in gaps in our knowledge of juvenile salmonid migration.

Acknowledgments Funding for this project was provided by the San Francisco Bay Long Term Management Study through the San Francisco District of the United States Army Corps of Engineers. This project could not have been completed without the help and support of the following people: Ethan Mora, Mike Thomas, Phil Sandstrom, Cyril Michel, Arnold Ammann, Kurtis Brown, Scott Hamelburg, David Woodbury and members of the California Fish Tracking Consortium.

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