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Migration characteristics of hatchery and natural-origin *Oncorhynchus mykiss* from the lower Mokelumne River, California

S. Casey Del Real · Michelle Workman · Joseph Merz

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Abstract The lower Mokelumne River (LMR), located in the California Central Valley, supports a population of natural-origin *Oncorhynchus mykiss*. In addition, the Mokelumne River Fish Hatchery (Hatchery) contributes hatchery produced *O. mykiss* to the system annually. We conducted a 3 year acoustic tagging study to evaluate the migratory characteristics of LMR hatchery and natural-origin *O. mykiss* to the Pacific Ocean. Specifically, we analyzed downstream movement and migration rates, routes, and success of acoustically tagged *O. mykiss* of hatchery and natural origin under variable release locations in non-tidal and tidal habitats. Results from our study suggest there are significant differences in the proportion of hatchery and natural *O. mykiss* that demonstrate downstream movement. Fish origin, size, and release location all had a significant effect on whether an individual demonstrated downstream movement. Mokelumne origin *O. mykiss* that initiated downstream movement utilized numerous migration routes throughout the Delta during their migration towards the Pacific Ocean. We identified four primary migration pathways from the lower Mokelumne River through the Sacramento-San Joaquin Delta while the Delta Cross Channel was closed. However, several other pathways were utilized. Origin had a significant effect on *O. mykiss* success in reaching key points in the Delta and through the Estuary. Fish size had a significant effect on whether an individual reached the marine environment. Of the 467 *O. mykiss* tagged, 34 successfully reached the Pacific Ocean (Golden Gate Bridge), and of these, 33 were hatchery-origin and 1 was natural-origin. A higher proportion of hatchery-origin fish (10% of tagged) migrated to the ocean compared to natural-origin fish (<1%). Our study provides valuable information on the differences between hatchery and natural-origin *O. mykiss* migration characteristics as well as unique insight into the migratory behavior of little studied non-Sacramento River origin salmonids.

Keywords Mokelumne River · *Oncorhynchus mykiss* · Acoustic telemetry · Migratory behavior · Hatchery release strategies

Introduction

Steelhead rainbow trout (*Oncorhynchus mykiss*) exhibit one of the most complex life histories of the Pacific salmonids (*Oncorhynchus* spp.) including the ability to utilize a variety of diverse habitats and

S. C. Del Real (✉)
East Bay Municipal Utility District,
One Winemasters Way, STE K-2,
Lodi, CA 95240, USA
e-mail: sdelreal@ebmud.com

M. Workman
United States Fish and Wildlife Service,
4001 N. Wilson Way,
Stockton, CA 95205, USA

J. Merz
Cramer Fish Sciences,
13300 New Airport Road, Suite 102,
Auburn, CA 95602, USA

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flexible life history traits ranging from resident (rainbow trout) to anadromous (steelhead) forms (Behnke 2002; Good et al. 2005; Zimmerman et al. 2008). Populations of *O. mykiss* once extended throughout many of the tributaries and headwaters of California's Central Valley (CV) (Busby et al. 1996; McEwan 2001). Due to the popularity of *O. mykiss* propagation, they were widely stocked throughout the state dating back to the 1870s (Behnke 1992; Moyle 2002). Today, the majority of CV *O. mykiss* are restricted to nonhistorical or remnant spawning and rearing habitat below nonpassable dams and these populations are heavily subsidized by hatchery production to mitigate habitat loss and support a large sport fishery (Yoshiyama et al. 1996; Lindley et al. 2006). Even so, numerous stressors continue to impact CV *O. mykiss* including water diversions and withdrawals, dams and in-stream structures, conversion of riparian areas, species introductions, water pollution, and disruption of coarse sediment supplies (McEwan 2001).

The steelhead component of CV *O. mykiss* is difficult to monitor because they often migrate and spawn during periods of high, turbid waters and may survive spawning or die away from spawning grounds (McEwan 2001). Furthermore, *O. mykiss* juveniles often emigrate at larger sizes than CV Chinook salmon (*O. tshawytscha*) making them less susceptible to the most common migrant monitoring techniques used for CV salmonids (DuBois et al. 1991; McEwan 2001). In addition, data on the relationship, interaction, and contrasting dispersal patterns of steelhead and resident rainbow trout are limited (Busby et al. 1996; NMFS 2003). Recent advances in acoustic telemetry technology have allowed for the tracking of movement and migration of individual fish providing essential information in developing resource management objectives and recovery goals for CV *O. mykiss* (Welch et al. 2004; Hall et al. 2009).

In this study we employed acoustic telemetry technology to characterize migration patterns of hatchery and natural-origin *O. mykiss* in the lower Mokelumne River, California (LMR), a system with both hatchery and natural production. Specifically, we analyzed four parameters of migration: downstream movement, migration rates, migration routes, and migratory success to the Pacific Ocean (as defined by reaching the Golden Gate Bridge) against three variables: fish origin, size, and release location. Our objectives were to assess the differences in migration characteristics using the biological parameters identified above.

Study site

The Mokelumne River is a snow-fed system that drains approximately 1624 km^2 of the central Sierra Nevada. The river presently has 16 major water impoundments, including Salt Springs (0.175 km^3; completed 1931), Pardee (0.244 km^3; completed 1929) and Camanche (0.515 km^3; completed 1963) reservoirs. The LMR stretches 103 river kilometers (rkm) from Camanche Dam, the lowest nonpassable dam, to its confluence with the San Joaquin River within the central Sacramento-San Joaquin Delta (Delta) (Fig. 1). The river is considered part of the North Valley Floor Critical Habitat for CV *O. mykiss* (NMFS 2005). Between New Hope Landing and the San Joaquin River confluence, the Mokelumne River is connected to the Sacramento River via the Delta Cross Channel and Georgiana Slough and to the Central Delta via Little Potato and Little Connection sloughs (Fig. 2). The LMR currently supports two anadromous salmonids which are supported by hatchery production, fall-run Chinook salmon and *O. mykiss*. The Mokelumne River Fish Hatchery (Hatchery) produces *O. mykiss* to compensate for the decrease in natural fish production and habitat loss due to the construction of Camanche Dam. During years when the projected *O. mykiss* egg take did not meet the Hatchery's production goals, Mokelumne River stock was augmented with imported eggs and/or fry from the Nimbus Hatchery (American River), the Feather River Hatchery, and the Coleman National Fish Hatchery (Sacramento River) (Fig. 1). Anadromous, natural-origin *O. mykiss* in the LMR are listed as threatened under the Endangered Species Act (ESA) (NMFS 1998). However, the non-anadromous forms (rainbow trout) and hatchery-produced *O. mykiss* are not ESA listed. Both resident and anadromous forms of *O. mykiss* are present in the LMR (Satterthwaite et al. 2009).

Salmon and steelhead that emigrate out of the LMR must negotiate a maze of natural and man-made tributaries, sloughs, and river channels as they migrate through the interior Delta to reach the Pacific Ocean. As salmonids navigate the complex network of channels that have been significantly altered by water resource project operations, they are influenced by

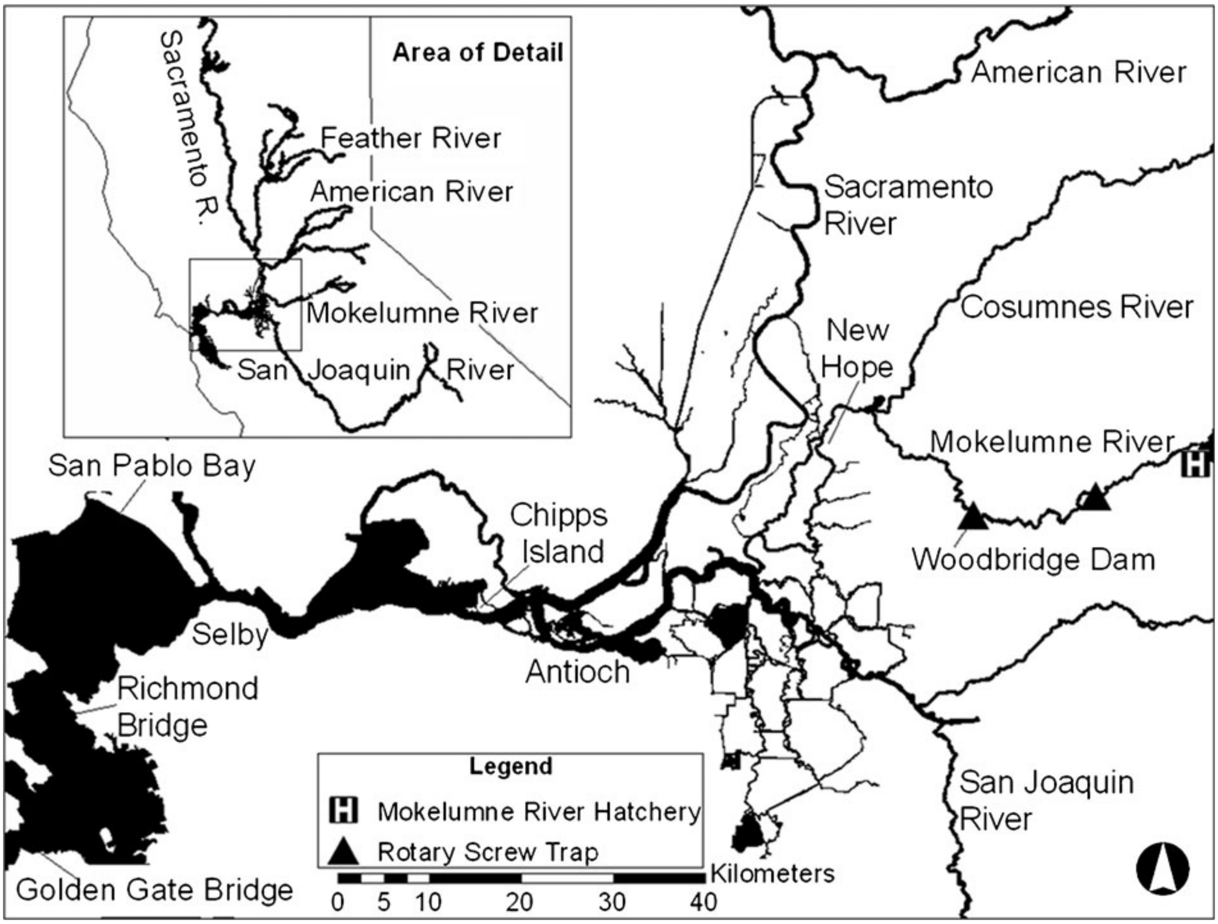

Fig. 1 Lower Mokelumne River in relationship to Sacramento, San Joaquin, Feather, and American rivers, Sacramento-San Joaquin Delta, and San Francisco Estuary

both anthropogenic impacts and environmental processes that affect migration rates, straying, predation, and survival (Perry et al. 2010). Migration through the highly modified Delta system may be significantly more risky than it historically was (Baker and Morhardt 2001; Brandes and McLain 2001) and the greatest management concern with respect to preserving anadromy in CV *O. mykiss* may be reduced survival of emigrating smolts (Satterthwaite et al. 2009).

Materials and methods

Fish collection

O. mykiss were collected from four sources within the LMR: (1) Hatchery-origin *O. mykiss* directly from the Hatchery, consisting of either Mokelumne River or Feather River broodstock (1 and 2 year-old fish); (2) Reconditioned kelts obtained from the Hatchery; (3) Natural-origin *O. mykiss* of various life stages collected using standard boat electrofishing techniques (Meador et al. 1993) at several locations throughout the non-tidal river (within 20 km of Camanche Dam); and (4) Actively outmigrating natural-origin *O. mykiss* captured at two rotary screw traps (RST) (downstream migrant traps used to sample emigrating anadromous salmonids) (Volkhardt et al. 2007) (Table 1). The downstream RST (Lower RST) is located near the Mokelumne River tidewater downstream of Woodbridge Irrigation District Dam (WIDD) below the Lower Sacramento Road Bridge, 61.8 rkm upstream of the confluence with the San Joaquin River. The upstream RST (Upper RST) is in the non-tidal portion of the LMR above the Elliott Road Bridge at rkm 87.4 (Fig. 1).

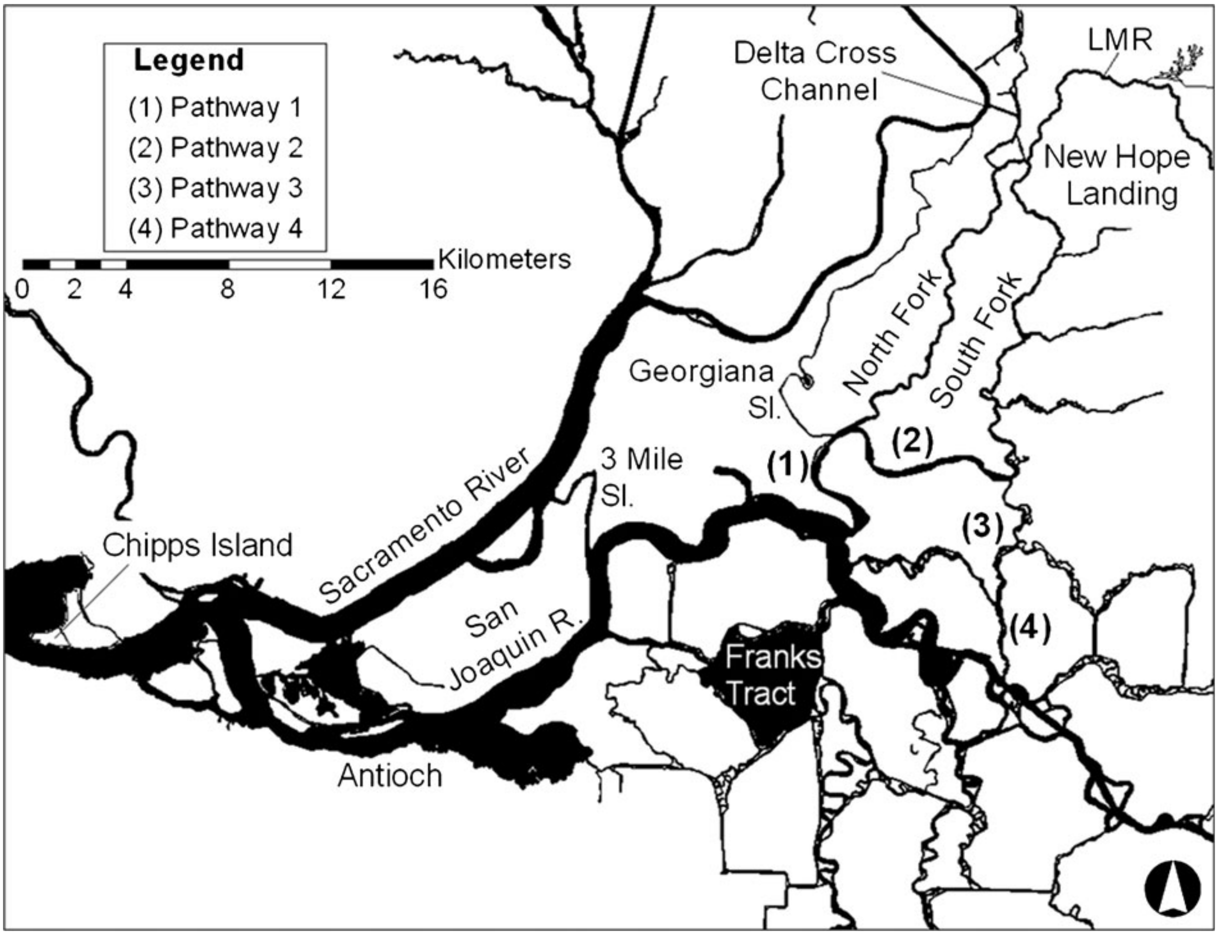

Fig. 2 Mokelumne River *O. mykiss* migration pathways through the Sacramento-San Joaquin Delta, California

Surgical implantation of tags

We surgically implanted acoustic transmitters and passive integrated transponder (PIT) tags in 467 hatchery and natural-origin *O. mykiss* between 2007 and 2009 (Table 1). The tag types included Vemco V9-2L-69 kHz R64K coded transmitters (implanted in 442 hatchery and natural-origin *O. mykiss* of various life stages) and Vemco V13-1L-69 kHz R64k coded transmitters (implanted in 25 reconditioned hatchery kelts). The V9-2L coded transmitters were 29 mm long, weighed 4.7 g in air, and had an estimated battery life of 292 days. The corresponding values for V13-1L coded transmitters were 36 mm long, weighted 11 g in air, and had an estimated battery life of 616 days. The PIT tags (manufactured by Destron Fearing) were 12.5 mm long and 2.0 mm wide and weighed 0.11 g in air. The minimum fork length (FL) of tagged fish was 180 mm to obtain an optimal transmitter-to-body-weight ratio that did not exceed 5% (Adams et al. 1998). Tag burden for all weighed fish was (mean±SE) 2.8±1.4%.

Surgical tagging occurred in the field at various locations along the LMR and in the Hatchery. Standardized tagging procedures were used at each location. *O. mykiss* were anesthetized with tricaine methanesulfonate (natural-origin) or carbon dioxide (hatchery-origin) in aerated water until reactivity and responses to handling were minimal, but operculum movement was still present. Fish fork length and weight were measured and fish were placed ventral side up in a V-shaped wooden platform with a foam rubber saddle secured to a transportable open tank. Water within the tank was maintained at a level sufficient to keep the gills wetted and was changed every seven to ten surgeries. An acoustic transmitter and a PIT tag were inserted

Table 1 Mokelumne River *O. mykiss* acoustic telemetry release groups between 2007 and 2009

Year	Release Period	Origin	Life History	Release Group	Number	Ave. FL mm (SD)	Tag (number)
2007	February	hatchery	Yearling smolt	New Hope	57	210 (14)	V9 (57)
2007	February	hatchery	Kelts	On Site (Kelt)	6	525 (74)	V9 (2); V13 (4)
2007	Feb–May	natural	>1-year-old[a]	In River	60	309 (89)	V9(59); V13(1)
2008	January	hatchery	Yearling smolt	Antioch	35	221 (12)	V9 (35)
2008	February	hatchery	Yearling smolt	San Pablo	35	219 (17)	V9 (35)
2008	February	hatchery	Kelts	On Site (Kelt)	10	506 (46)	V13 (10)
2008	April	hatchery	Yearling smolt	On Site	30	252 (24)	V9 (30)
2008	Feb–April	natural	>1-year-old[a]	Upper RST	2	226 (33)	V9 (2)
2008	Feb–April	natural	>1-year-old[a]	Lower RST	9	238 (31)	V9 (9)
2008	Feb–May	natural	>1-year-old[a]	In River	54	266 (63)	V9 (54)
2008	September	hatchery	2-year-old	San Pablo (2-year-old)	30	394 (31)	V9 (30)
2009	January	hatchery	2-year-old	Moke River (2-year-old)	8	477 (54)	V9 (8)
2009	February	hatchery	Yearling smolt	New Hope	110	245 (22)	V9 (110)
2009	February	hatchery	Kelt	New Hope (Kelt)	9	497 (51)	V13 (9)
2009	Feb–May	natural	>1-year-old[a]	Lower RST	12	244 (62)	V9(11); V13(1)

[a] Length frequency data suggest these fish are 1–3 years of age (EBMUD unpublished)

RST Rotary Screw Trap; *Ave. FL* Average Fork Length

through a 2.54 cm incision into the peritoneal cavity of each fish just off the midline and anterior to the pelvic fins. The incision was made using a number 12 surgical scalpel blade and closed with 2–3 interrupted stitches. Tagged hatchery fish were held in raceways for 24 h following surgery to allow for recovery and assessed for abnormal behavior, tag shedding, or mortality before release. Fish tagged in the field were allowed to recover in aerated holding tanks prior to release the same day.

Fish release

In winter 2007, we initiated the first phase of the 3 year study by tagging and tracking three release groups consisting of hatchery yearling smolts, reconditioned hatchery kelts, and natural-origin *O. mykiss*. Between January and May of 2008, we implemented the second year of this study. In year two, we released eight tag groups, incorporated new release locations, and included hatchery-reared 2-year-old fish and actively-outmigrating natural-origin *O. mykiss* by focusing on RST captures. In 2009, year three of the study, hatchery, post-spawn kelts, and natural-origin *O. mykiss* of various life stages were tagged and released between January and May (Table 1).

O. mykiss releases at Antioch, Selby, New Hope Landing, and in the LMR at Elliott Road (Fig. 1) were pumped into a Freightliner transport truck, driven to their respective release location, and gravity fed into the receiving waters. On Site hatchery yearling smolt releases were pumped directly from the raceways via 15.24 cm diameter aluminum irrigation pipe into the LMR adjacent to the Hatchery. Kelts were placed in hauling tanks, transported to the river below the Hatchery, and released by using handheld dip nets. Tagged hatchery-origin fish were released either with other hatchery fish or independently. *O. mykiss* tagged during electrofishing surveys were released upstream of their collection site while fish tagged during RST operations were released downstream of the traps. All releases occurred during daylight hours.

Data collection

We used stationary Vemco monitoring receivers to detect our Vemco coded transmitters. We deployed 10 acoustic receivers (Vemco VR2W-69 kHz) in the LMR from the base of Camanche Dam to the confluence with the San Joaquin River. Each receiver recorded the identification number and time stamp from the coded acoustic transmitters as tagged fish traveled within the detection range, conservatively estimated to be 250 m (Espinoza et al. 2011). Data were downloaded quarterly in the field using a wireless personal computer interface. Members of the California Fish Tracking Consortium downloaded data from over 300 receivers deployed throughout the Sacramento-San Joaquin River System, Delta, and San Francisco Estuary. Data from downloaded receivers were submitted to the California Fish Tracking Consortium database which provided access to data from the full array of receivers. Following each release of tagged *O. mykiss*, the Consortium database was monitored for a minimum of 1 year to track fish movement.

Data analysis

Acoustic tag detection data were processed to eliminate false-positive detections following methods of Pincock (2008) and Skalski et al. (2002). False-positive detections typically occur when more than one tag is simultaneously present within the range of a given monitor, and simultaneous tag transmissions “collide” to produce a valid tag code that is not actually present at the monitor (Pincock 2008; Perry et al. 2010). We considered detections valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station and the detections were consistent with the spatio-temporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002).

Statistical analysis of movement, migrations rates, migration pathway selection, and migration success was based on fish detected by the array of receivers. Release groups that resulted in an expected frequency of less than five fish in more than 20% of the analyzed categories or an expected frequency of less than one in any category being analyzed were not included in statistical analyses (Zar 1984), but qualitative assessments were reported. All statistical tests were performed using JMP version 8.0.1.

Downstream movement

We compared movement by fish origin and release location across years using contingency table analysis (Chi square) (Table 1 for categories). We compared movement by size using ANOVA. Fish were classified into two main movement groups: downstream (towards the Golden Gate Bridge) or no downstream movement. The no downstream movement group is made up of those fish detected by the array of receivers that demonstrated no migration (no net directional movement) or upstream movement (movement away from the Golden Gate Bridge).

Migration rates

We estimated migration rates for fish that exhibited downstream movement as passage times of individual fish between receivers. The migration rate of a fish through each reach was calculated as the distance between receivers divided by the time. Time was defined as time of last detection at the previous receiver to time of first detection at next receiver. We analyzed migration rates (mean km/h) for each release group using ANOVA.

Migration routes

We compared migration pathways used by *O. mykiss* released in the Mokelumne River at New Hope or upstream that demonstrated downstream movement through the interior Delta to Chipps Island (Fig. 2). Four pathways were identified: 1) Pathway 1 down the North Fork of the Mokelumne River to the San Joaquin River; 2) Pathway 2 down the South Fork of the Mokelumne River to the North Fork and San Joaquin River; 3) Pathway 3 down the South Fork of the Mokelumne River into Little Potato Slough and through Potato Slough into the San Joaquin River; and 4) Pathway 4 down the South Fork of the Mokelumne River into Little Potato Slough, Little Connection Slough, and into the San Joaquin River. Other important pathways through the Delta included Franks Tract, Three Mile Slough, and Georgiana Slough. A fish was categorized as using a specific pathway if it was detected moving downstream through each primary section of a pathway (represented by detection stations) that led towards Chipps Island. Fish that used a combination of pathways or used sections of the interior Delta outside of these four pathways were described by the alternative migration corridor that was utilized. Statistical tests using contingency table analysis (Chi square) were performed on migration route selection of designated pathways through the interior Delta based on origin and release location. Route selection analysis based on size was performed using ANOVA.

Migration success

Key reference locations were established to assess migration success of each release group. These locations include WIDD, New Hope, Chipps Island, Richmond Bridge, and the Golden Gate Bridge (Fig. 1). The proportions of fish in each tagged release group detected at each reference location were based on release group totals. Each reference location site immediately downstream of release locations accounted for 100% of the upstream release group. Release groups located immediately upstream of a reference location were excluded from the analyses of migration success to the first downstream site. Migration success of all release groups were compared by origin using contingency table analysis (Chi square) and by size using ANOVA. Migration success of hatchery-origin yearling release groups were compared by release location using contingency table analysis (Chi square).

Results

In this study we tagged 330 hatchery-origin and 137 natural-origin *O. mykiss* of various life stages. Ninety-one percent (n=301) of all acoustically tagged hatchery releases and 37% (n=51) of natural-origin releases were detected by the array of receivers.

Downstream movement

Of the 404 acoustically tagged hatchery yearling smolts and natural-origin *O. mykiss* released, 169 demonstrated downstream movement, 124 demonstrated no downstream movement, and 111 were not detected by the array of receivers. Fish origin, size, and release location revealed differences between migration and residualization (no movement).

Fish origin had a significant effect on downstream movement of all *O. mykiss* release groups independent of release location between 2007 and 2009 (Chi square=25.26; P<0.001; Table 2). Comparing all hatchery yearling smolt and natural-origin *O. mykiss* release groups, a significantly higher proportion of hatchery-origin fish moved downstream (65%), than natural-origin fish (22%), independent of release location (Chi square=33.58; P<0.001). Of natural-origin fish that moved downstream, 64% were considered 'active migrants', based on the collection at RSTs. Of the natural-origin *O. mykiss* releases that showed no downstream movement, 95% (n=38) exhibited resident characteristics via non-directional movements detected by the receivers in the non-tidal LMR. Of the hatchery yearling releases that had no downstream movement, 95% (n=80) strayed upstream.

Fish size had a significant effect on downstream movement (F=11.29; df=1; P=0.001) across all release groups (Table 2). The average fork length of *O. mykiss* that demonstrated downstream movement was 262 mm with a standard deviation of 82 mm. The average fork length of *O. mykiss* that demonstrated no downstream movement was 295 mm with a standard deviation of 100 mm.

Movement of hatchery-origin *O. mykiss* yearling smolts differed significantly (Chi square=8.52; P= 0.036) based on release locations. Downstream movement was observed from all release locations. The Antioch release had the highest downstream movement with 83% towards the Pacific Ocean (Fig. 3). The On Site release in the non-tidal LMR had the second highest downstream migration (81%). The proportion of fish that exhibited no downstream movement from Antioch, San Pablo, and New Hope releases varied from 17% to 39%.

During the 2007 to 2009 study period, there was also a significant difference between the movement of natural-origin *O. mykiss* release groups (Chi square= 17.23; P<0.001). Of the fish that exhibited no downstream movement, 95% were part of the In River release groups collected during electrofishing surveys. Of the In River release group, 90% exhibited no downstream movement. In comparison, a higher proportion of the natural-origin fish tagged at the RST sites demonstrated downstream movement. Six out of eight tagged and released at the Lower RST and one of one at the Upper RST exhibited downstream movement (Fig. 3).

Due to the small sample size for release groups of kelts and 2-year-olds, they were not included in the statistical analysis of downstream movement by release location. However, detected movement of these life stages is noteworthy. Of the reconditioned kelt releases, 54% (n=13) demonstrated downstream

Table 2 The effect of *O. mykiss* origin, size, and release location on downstream movement, emigration pathway, and success to key landmarks within the lower Mokelumne River, Delta, and San Francisco Estuary. Values represent all release groups, except analyses of movement and migration success by release location which analyze hatchery yearling release groups. A *P*-value≤0.05 is considered significant (**Bold**)

			Migration Success by Location				
Qualifier	Movement	Pathway	WIDD	New Hope	Chipps Island	Richmond Bridge	Golden Gate Bridge
Origin	**<0.001**	ISS	ISS	**0.001**	**0.007**	**0.045**	**0.018**
Size	**0.001**	0.420	**0.027**	0.709	0.222	**0.005**	**0.001**
Release Location	**0.036**	0.618	ISS	ISS	0.105	ISS	ISS

WIDD Woodbridge Irrigation District Dam; *ISS* Insufficient sample size

movement. New Hope (Kelt) releases and On Site (Kelt) releases demonstrated 75% (*n*=6) and 44% (*n*=7) downstream movement, respectively. Of the 2-year-old releases, 17% (*n*=6) demonstrated downstream movement. Of the San Pablo (2-year-old) and Moke River (2-year-old) release groups, 14% (*n*=4) and 33% (*n*=2) demonstrated downstream movement, respectively.

Migration rates

Between 2007 and 2009, there was no significant difference between the migration rates of *O. mykiss* from different release groups (F=1.80; df=9; *P*=0.072). The Antioch hatchery release of yearling smolts showed the greatest sustained migration rates with an average of 1.86 km/h. Kelt migration rates ranged from 1.58 km/h (On Site) to 1.64 km/h (New Hope) while 2-year-old *O. mykiss* migration rates ranged from 1.29 km/h (Moke River) to 1.61 km/h (San Pablo). The natural-origin In River release group had the lowest average migration rate of 0.72 km/h (Table 3).

We recovered ocean travel time data on five hatchery *O. mykiss* (two yearlings released at New Hope; one yearling released at San Pablo; one Moke River 2-year-old released at Elliott Rd.; and one kelt released at New Hope). Travel rates were calculated over approximate straight-line distances between the Golden Gate Bridge and the acoustic receiver array located off of Point Reyes (~54 km north of the Golden Gate). The New Hope kelt showed the greatest

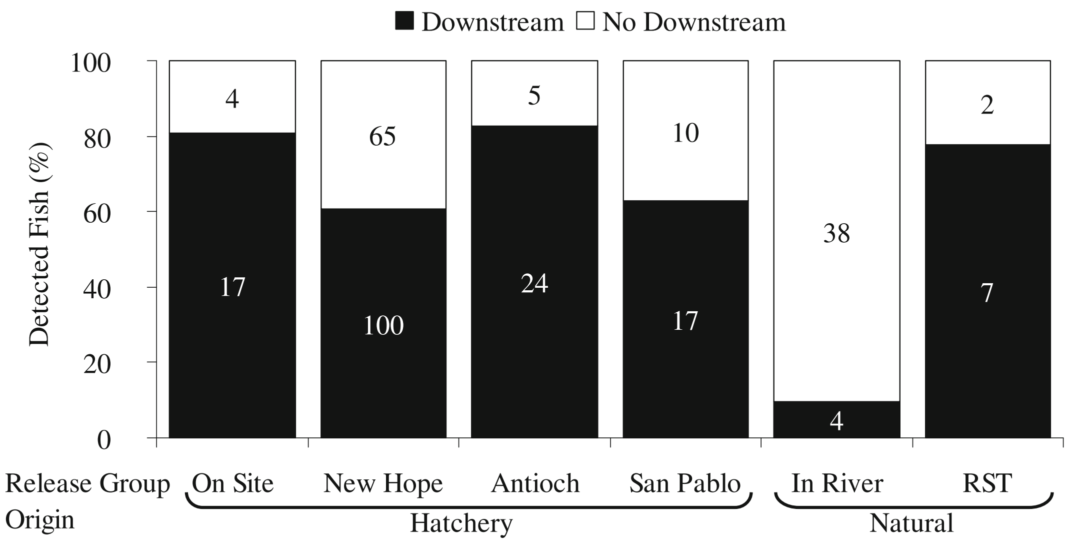

Fig. 3 The proportion of Mokelumne River *O. mykiss* demonstrating downstream movement by release location, 2007 through 2009. Values within the figure represent number of fish

sustained migration rate of 1.33 km/h and reached Point Reyes in 1.7 days. Hatchery yearling migration rates ranged from 0.02 km/h (San Pablo) to 0.17 km/h (New Hope) while the Moke River 2-year-old *O. mykiss* migration rate was 0.20 km/h. A New Hope yearling last detected at the Golden Gate Bridge 2 h before the New Hope kelt took 16 days to reach Point Reyes. A yearling released in San Pablo Bay spent just over 145 days traveling between the Golden Gate Bridge and Point Reyes.

Migration routes

Between 2007 and 2009, 67 acoustically tagged hatchery and natural-origin *O. mykiss* of various life stages released at or above New Hope Landing demonstrated downstream movement via the designated migration pathways. Migration route selection, based on all release groups, was not significantly related to fish size (F=0.88; df=2; P=0.420) or release above or within tidal influence (Chi square=0.96; P=0.618) (Table 2). Of the hatchery yearling smolts, 43% used Pathway 1, 23% used Pathway 2, 4% used Pathway 3, and 2% used Pathway 4. In addition, 28% used other pathways including Franks Tract (13%), Three Mile Slough (11%), and Georgiana Slough (4%). Fifty-seven percent of the reconditioned kelts migrated through Pathway 1 while 29% utilized Franks Tract and 14% migrated through Pathway 4. All of the fish from the Moke River (2-year-old) release group migrated through Pathway 1. Of the natural-origin *O. mykiss*, 60% used Pathway 1, 20% used Pathway 2, and 20% used Georgiana Slough.

Migration success

While migration proportions reflect low overall downstream success based on release totals, fish that reached the first reference location subsequently had relatively high migration success. On Site releases of hatchery yearling smolts had the highest overall success to the first downstream reference point with 57% detected. This was followed by 44% of On Site kelts reaching the first reference location downstream. Twenty-five percent of the Moke River release group successfully migrated to the first downstream reference point. In River releases of natural-origin *O. mykiss* had the lowest overall downstream detection at the first reference point (New Hope) with only 0.8% detected. There was a significant difference in the size of fish that successfully migrated to WIDD (F=5.32; df=1; P=0.027; Table 2). The average fork length of fish that reached WIDD was 332 mm while the average fork length of fish that did not was 433 mm. In addition, fish origin had a significant effect on migration success to New Hope (Chi square=11.39; P=0.001; Table 2).

Migration success between New Hope and Chipps Island ranged from 100% for Moke River 2-year-old fish to 50% of the natural-origin fish. Of the New Hope hatchery yearling and kelt releases, migration success to Chipps Island, the first downstream reference location, was 17% and 22%, respectively (Fig. 4). Fish origin (Chi square=7.29; P=0.007) had a significant effect on migration success to Chipps Island while size and release location did not significantly influence migration success through the Delta (Table 2).

Between Chipps and Richmond Bridge, migration success between reference locations ranged from 100% of On Site kelts, Moke River 2-year-old fish, and New Hope kelts to 36% of New Hope yearlings. Seventeen percent of the Antioch yearling release were detected at the first downstream reference location. Fish origin (Chi square=4.02; P=0.045) and size (F=8.09; df=1; P=0.005) significantly influenced success to Richmond Bridge (Table 2).

Migration success from Richmond Bridge to Golden Gate Bridge was relatively high in comparison to total release group success. Larger fish had a better chance of reaching both the Richmond and Golden Gate bridges (locations with higher salinity). Fish origin (Chi square=5.55; P=0.018) and size (F=11.18; df=1; P=0.001) had a significant effect on migration success to the Golden Gate Bridge (Table 2). Of the hatchery yearling smolt releases, 20% of On Site, 14% of San Pablo, and 9% of Antioch releases reached the Golden Gate Bridge. The New Hope release group had the lowest percentages of success to the Golden Gate Bridge with 4% in 2007 and 5% in 2009. On Site releases of reconditioned kelts had the highest proportion reach the Golden Gate Bridge with 33% in 2007. However, in 2008, only 10% of On Site kelts reached the Golden Gate Bridge. Twenty-two percent of the New Hope reconditioned kelts and 25% of the 2-year-old hatchery Moke River release group reached the Golden Gate Bridge. One natural-origin fish was

Table 3 Migration rates of acoustically tagged *O. mykiss* with downstream final detections

Release Group	Mean Rates (km/h)	Standard Error of the Mean	Minimum	Maximum
On Site	1.52	0.24	0.25	4.11
New Hope	1.06	0.10	0.01	4.06
Antioch	1.86	0.23	0.31	3.78
San Pablo	1.52	0.24	0.01	2.87
In River	0.72	0.49	0.40	1.57
RST	1.51	0.37	0.15	2.76
On Site (Kelt)	1.58	0.37	0.39	3.99
New Hope (Kelt)	1.64	2.44	0.14	2.58
Moke River (2-year-old)	1.29	0.70	1.22	1.35
San Pablo (2-year-old)	1.61	0.57	1.24	1.81

recorded successfully migrating to the Golden Gate (Fig. 4).

Discussion

Acoustic technology has provided a method to better compare hatchery-origin and natural-origin *O. mykiss*. In a state-dependent life history model, Satterthwaite et al. (2009) predicted a mixture of anadromous and resident *O. mykiss* in the Mokelumne River, but with anadromous fish dominating given baseline survival assumptions. Our results demonstrate the Mokelumne River *O. mykiss* population is a mixture of resident and anadromous fish and that origin (hatchery vs. natural) has a significant effect on whether an individual fish demonstrates migration tendencies. We showed that hatchery fish had a significantly higher propensity to migrate, while the natural population demonstrates very little anadromy.

Downstream movement

In an effort to increase survival and promote returns, the Hatchery has utilized numerous release locations for hatchery-reared *O. mykiss*. However, returns have remained low. We found that release location can significantly influence downstream migration trends in hatchery yearling smolt *O. mykiss* even though all hatchery release groups demonstrated relatively high downstream movement (59%).

The natural-origin *O. mykiss* population in the LMR exhibits both anadromous and non-anadromous life histories. Of the acoustically tagged natural-origin fish detected by the array of stationary receivers, 78% demonstrated no downstream movement. Conversely, once a natural-origin fish began downstream migration (for instance *O. mykiss* captured at a RST) they continued in a downstream direction at a relatively high proportion.

Migration rates

While results did not show significant differences in overall migration rates, they did provide information on *O. mykiss* ocean travel rates when currently little such data is available. Limited information on coded-wire tag recoveries suggest that hatchery steelhead may travel together in the ocean environment as tagged juvenile fish released at similar locations and times were recovered together at sea up to 3 years later (McKinnell et al. 1997). Burgner et al. (1992) reported ocean travel rates across approximate straight-line distances for steelhead tagged offshore and recovered within 50 days. The mean migration rate from release to recovery locations was 50 km/day while the fastest fish averaged 85 km/day for 17 days. The average ocean travel rate for Mokelumne River hatchery-origin *O. mykiss* was 9 km/day and the fastest fish averaged 32 km/day (kelt released at New Hope). These data demonstrate *O. mykiss* exhibit a wide range of variability in ocean movement and migration rates.

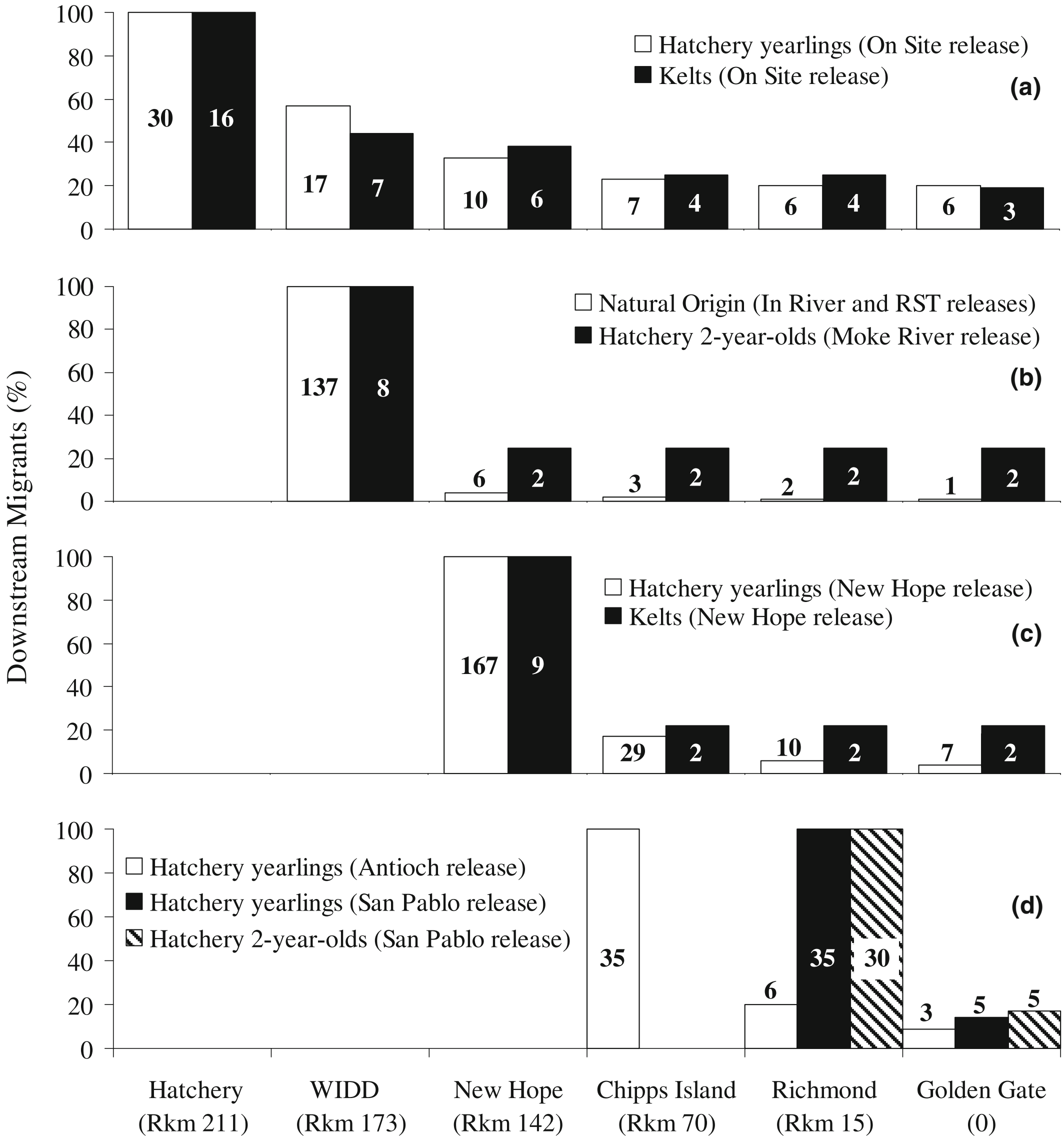

Fig. 4 Proportion of release groups observed at key reference points. Release groups are organized by release location (a–d). Values within the figure represent release group totals followed by fish detection totals at each downstream reference location

Migration routes

Steelhead emigrating from the Mokelumne River have numerous migration pathway options when traversing the complex network of natural and man-made channels of the interior Delta. Each migration route poses different benefits and risks associated with migration rates, energy costs, predation, and entrainment that ultimately affect migration success. Due to the small number of fish migrating through the Delta and the utilization of diverse migration routes, current and future management actions in the Delta may disproportionately affect Mokelumne River *O. mykiss*.

Migration success

In seawater challenges, Beakes et al. (2010) found that CV *O. mykiss* survival off the California central coast varied significantly with fish size (with larger fish being more likely to survive than smaller fish). Similarly, we observed that success to key reference locations within the saline environment of the San

Francisco Estuary was significantly related to fish size.

If we gauge 'successful' migration as migration to the Golden Gate Bridge, a majority of our successes have been of hatchery-origin. Reconditioned kelts released On Site in 2007 had the highest proportion reach the Golden Gate Bridge, thus active reconditioning of hatchery spawned kelts may be a viable option for increasing anadromy. On Site releases of both hatchery yearling and reconditioned kelts performed well during the study period, but continued releases adjacent to the hatchery will need to be weighed against potential negative impacts to natural-origin salmonids rearing in the LMR.

Management implications

The diversity of *O. mykiss* life history forms demonstrates the relative phenotypic plasticity of the species (McEwan 2001). The year round presence of Age 1+ *O. mykiss* of various life stage categories sampled during fish community surveys on the LMR (Merz 2002) reflects the flexible life history patterns of *O. mykiss* within the Mokelumne River. Zimmerman et al. (2008) revealed that the Central Valley *O. mykiss* population is skewed towards the non-anadromous resident form as 77% of the analyzed *O. mykiss* in his study were progeny of resident rainbow trout. Similarly, results from our study suggest a large proportion of natural-origin *O. mykiss* in LMR demonstrates a resident life history.

Due to the precipitous declines of *O. mykiss* in the Central Valley and an apparent shift towards the non-anadromous life history forms, the connection between anadromous and non-anadromous *O. mykiss* and their management as a single or separate population has profound implications for conservation and recovery (Busby et al. 1996; Zimmerman and Reeves 2000; McEwan 2001). Since anadromous and non-anadromous trout may form an interbreeding population (Seamons et al. 2004; Araki et al. 2007) with females producing progeny with opposite life history traits (Viola and Schuck 1995; Riva-Rossi et al. 2007; Zimmerman et al. 2008), steelhead management may need to include protection of non-anadromous forms and the connectivity between the resident and anadromous fish (McEwan 2001).

The largest population declines of natural-origin *O. mykiss* in California were a consequence of the dam building era prior to the 1960s as spawning and rearing habitats became isolated (McEwan 2001). However, continued declines of *O. mykiss* numbers imply additional threats and stressors still need to be addressed. For anadromous species migrating out of the Mokelumne River, Delta management remains a critical issue influencing migration success. While the Delta Cross Channel remained closed throughout the study period, its management is presumed to substantially influence Mokelumne River salmonids. Further investigation is needed to assess its effects on salmonid migration, straying, and survival. In addition to Delta management, suppression of anadromous life history traits, loss of genetic diversity, and introgression of hatchery rainbow trout into natural-origin populations continue to be serious concerns for steelhead conservation and management.

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