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Post-spawn migrations of hatchery-origin *Oncorhynchus mykiss* kelts in the Central Valley of California

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Abstract We used acoustic telemetry to study the post-spawn movement of *Oncorhynchus mykiss* kelts released in April 2005 and 2006 from the Coleman National Fish Hatchery, Anderson, CA. Following release, *O. mykiss* kelts demonstrated both anadromous and non-anadromous life histories, with some fish alternating life history strategies between years. Anadromy was most common, characterized by a short-term residence near the release site, followed by sustained downstream emigration once initiated. *O. mykiss* kelts demonstrating anadromy arrived at the Golden Gate Bridge from April to mid-July. Repeat spawning migrations of anadromous *O. mykiss* kelts began from late-September through October of the year of release. High fidelity back to Battle Creek was observed, occurring from late-September through November. While most *O. mykiss* kelts were anadromous, at least 10 % remained in freshwater, or residualized. *O. mykiss* kelts that residualized demonstrated two distinct patterns of movement: 1) residency near the release location, and 2) potamodromy. Overall survival was high with 36 % and 48 % of *O. mykiss* kelts released making a repeat spawning migration and demonstrating iteroparity in 2005 and 2006, respectively. Increase in body lengths of *O. mykiss* kelts that returned to the Coleman NFH were significantly greater for anadromous fish, compared to fish that residualized, but survival was higher for fish that residualized. Release of hatchery *O. mykiss* kelts could result in both positive and negative genetic and ecological effects to hatchery- and naturally-producing salmonids. We believe the benefits of releasing *O. mykiss* kelts at the Coleman NFH, including increased numbers and size of fish in the recreational fishery and genetic and demographic benefits to the hatchery brood stock outweigh the limited risk to natural populations that would result from predation and competition of the relatively small number of *O. mykiss* kelts that resided in fresh water.

Keywords Ultrasonic telemetry · Acoustic tagging · Steelhead · Migration · Life history · Residualism · Straying

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Introduction

Rainbow trout, *Oncorhynchus mykiss*, exhibit both anadromous (steelhead) and non-anadromous forms (Neave 1944; Shapovalov and Taft 1954). Recent studies have demonstrated gene flow between anadromous and non-anadromous *O. mykiss* (Zimmerman

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and Reeves 2000; Araki et al. 2007a, b; Heath et al. 2008; Zimmerman et al. 2009; Christie et al. 2011). Research also shows considerable variability and adaptability of life history strategies of *O. mykiss;* progeny can have dissimilar life history of the parents (Zimmerman and Reeves 2000; Araki et al. 2007a, b; Heath et al. 2008; Zimmerman et al. 2009; Christie et al. 2011). This diversity of life history strategies is believed to play an important role in population connectivity and resiliency.

O. mykiss are iteroparous, or capable of spawning more than once before death (Barnhart 1986; Busby et al. 1996). However, it is rare for steelhead to spawn more than twice; most that do so are females (Busby et al. 1996; Keefer et al. 2008). Decreased likelihood for iteroparity of males has been attributed to stressors associated with reproductive competition (e.g., Jonsson et al. 1991; Fleming and Gross 1994). Iteroparity is more common among southern steelhead populations than northern populations (Busby et al. 1996). Shapovalov and Taft (1954) reported that repeat spawners are relatively numerous (17.2 %) in California streams. In Battle Creek, a tributary to the upper Sacramento River, previous research indicated that the proportion of hatchery steelhead that spawn more than once was much lower than for naturally spawning fish (Hallock 1989).

The Coleman National Fish Hatchery (NFH) was established on Battle Creek, California in 1942 to partially mitigate for the loss of habitat resulting from the construction of Shasta Dam. The *O. mykiss* propagation program at Coleman NFH is focused on the anadromous life history form (steelhead). The principal objectives of this propagation program are to contribute to the Sacramento River sport fishery and maintain adequate adult escapement to Battle Creek to meet the hatchery's brood stock needs. Steelhead propagation at the Coleman NFH is intended to be operated as an "integrated" type program, where gene flow occurs into the hatchery brood stock from the naturally-spawning population in Battle Creek. The intent of an integrated hatchery program is for the natural environment to drive the adaptation and fitness of a composite population of fish that spawns both in a hatchery and in the wild (HSRG 2004) reducing domestication in the hatchery and genetic divergence of hatchery fish from the naturally-spawning population.

O. mykiss at Coleman NFH are currently spawned live using the process of air spawning. The practice of euthanizing *O. mykiss* adults prior to spawning to collect gametes was discontinued in 2001 following the Endangered Species Act (ESA) listing of the species (1997). The ESA listing includes *O. mykiss* propagated at the Coleman NFH. To initiate air spawning, a large diameter hypodermic needle, which is connected to a compressed air cylinder, is inserted into the body cavity of the female near the pelvic fin. Low pressure air (2 lb per square inch) gently fills the body cavity and displaces the eggs out the vent. Air spawning eliminates the need to cut open the body cavity to collect gametes and allows for live spawning of the female. After mild sedation, milt is expressed from reproductively mature males. Thus, since 2001, male and female *O. mykiss* have been reconditioned after they are spawned and then released, providing them the opportunity to demonstrate repeat spawning, or iteroparity.

Iteroparity may confer several population-level advantages such as maintaining genetic diversity and reducing demographic risks by increasing the number of unique adult pairings across years (Crespi and Teo 2002; Niemela et al. 2006; Keefer et al. 2008). The iteroparous life history strategy also protects against cohort failure by allowing multiple spawning events by individual fish (Fleming and Reynolds 2004; Wilbur and Rudolf 2006). Additionally, steelhead exhibiting multiple spawning events may be more productive than semelparous conspecifics because of higher cumulative fecundity and lifetime fitness (Fleming and Reynolds 2004). Females demonstrate strong influence on nest site selection, spawn timing, and early juvenile survival; thus, iteroparity may be particularly important for females (Fleming 1996; Quinn 2005).

Iteroparity may specifically benefit the hatchery program by increasing the opportunity to mate unrelated fish from different brood years and because larger, older fish have increased fecundity and, perhaps, better gamete quality. Further, releasing hatchery-origin *O. mykiss* after spawning provides additional (and perhaps larger) fish for potential harvest in the sport fishery, which is the primary objective of the hatchery program.

Information is scarce on the migratory behavior of *O. mykiss* kelts in the Central Valley of California; migration timing, movement patterns, rate of residualism, and rate of iteroparity are not well understood. Our knowledge of the migratory behavior of *O. mykiss* kelts can be improved using ultrasonic transmitters combined with networks of receivers to track their movements. In this study, we tagged hatchery-origin *O. mykiss* kelts prior to their release from the Coleman NFH and tracked their movements to: 1) determine the migratory timing, movement patterns, rate of residualism, and rate of iteroparity, and 2) gain insight into both the potential benefits to the brood stock at the Coleman NFH and impacts to wild steelhead and Chinook salmon, *Oncorhynchus tshawytscha,* populations that could result from releasing *O. mykiss* kelts.

Methods

Study area

The Coleman NFH is located in the upper Sacramento River basin in the Central Valley of northern California, approximately 32 km southeast of the city of Redding, California. The hatchery is located on Battle Creek, approximately 9 river kilometers (rkm) upstream from the confluence with the Sacramento River.

Fish collection, holding and tagging

Adult *O. mykiss* were collected from Battle Creek at the Coleman NFH from early-October through late-February during 2005 and 2006. *O. mykiss* ascended a fish ladder into a concrete pond and were subsequently diverted into a building where they were anesthetized with carbon dioxide and maturity was assessed. Immature fish (i.e., firm muscle tone and lack of egg or milt expression during palpation) were returned to concrete ponds until mature. Once mature, fish were anesthetized with tricaine methanesulfonate (MS-222™) and spawned. After spawning, *O. mykiss* kelts were placed into a 9.1×15.2 m concrete and earthen holding pond where they were reared until early-March. Kelts were maintained on a diet of salmon eggs and commercial fish pellets (Bio Diet Brood®, Bio-Oregon, Inc.) until 48 h prior to surgery.

On 10 March 2005 *O. mykiss* kelts were seined from the holding pond, anesthetized in a 70 mg/L solution of tricaine methansulfate (MS-222™) and ultrasonic transmitters (VEMCO Ltd, Halifax, Nova Scotia Canada, model V16-4 H-R04K-69 kHz; 16×65 mm, weight in water 10 g, projected battery life 641 d) were surgically implanted into the peritoneal cavity. During surgery, a small submersible pump connected to rubber surgical tubing was used to circulate a solution of 35-mg/L MS-222 over the gills. The incision was closed using 4–6 simple interrupted sutures tied with surgeon's knots. Suture material was braided Polyglycolic Acid, a synthetic absorbable polymer, and was swaged-on to a 3/8″ circle reverse cutting needle (Vedco, Inc.). Transmitter weight was less than 2 % of the body weight of the steelhead tagged. Oxytetracycline was injected (0.5 cc per fish) through the incision into the peritoneal cavity immediately following suturing. A tissue adhesive (Vetbond™, Animal Care Products-3M Company) was applied to the incision area to ensure complete closure. *O. mykiss* kelts in very poor physical condition (e.g. exhibiting large colonies of *Flavobacterium columnare*) were not selected for surgery. *O. mykiss* kelts were photographed, fork length and weight were measured, and a conventional T-bar anchor tag (Floy Tag and Mfg. Inc.) with a unique identification number was inserted in the musculature near the dorsal fin. Following surgery, *O. mykiss* kelts were transferred to a 189-liter tank containing a PolyAqua® solution (approximately 1.3 ml/l; Kordon Division of Novalek, Inc.) until recovery from anesthesia. Once recovered, tagged fish were placed in concrete raceways (rather than being returned to the holding pond) and fed as previously described until release.

On 5 April, 2005, 25 *O. mykiss* kelts implanted with ultrasonic transmitters were released, along with the untagged fish that remained in the adult holding pond, into Battle Creek, CA at the site of the Coleman NFH. Tagged fish that were released included six males and nineteen females. Initially, 30 *O. mykiss* kelts were tagged. Four fish died within 24 h of surgery. Tags were removed from these *O. mykiss* kelts, disinfected, and surgically implanted into four additional *O. mykiss* kelts that were seined from the holding pond on the following day. The Food and Drug Administration requires a withdrawal time (at least 21 d) for depuration after the use of MS-222 before an animal can be released. This holding period allowed us to observe the progress of healing at the incision site and the mortality of tagged fish prior to release. During the depuration period, three tagged fish died. Two additional fish were eliminated from the study immediately prior to release, because the incision area appeared infected and had not completely closed.

The following year, six male and fifteen female *O. mykiss* kelts were released, along with the untagged fish that remained in the adult holding pond, into

Battle Creek, CA at the site of the Coleman NFH on 7 April 2006. Ultrasonic transmitters were surgically implanted into the abdominal cavity of 23 *O. mykiss* kelts on 14 and 15 March 2006, using the same methodology as in 2005. Tagged *O. mykiss* kelts were held as described previously. Two *O. mykiss* kelts died within 24 h of the surgeries. Ultrasonic transmitters from these fish were not re-implanted into any additional fish.

O. mykiss entering the hatchery in subsequent spawning years (October 2005–March 2006 and October 2006–March 2007) were inspected for presence of T-bar anchor tags and interrogated for the presence of an ultrasonic transmitter. *O. mykiss* kelts observed with a tag were anesthetized with carbon dioxide, photographed, and measured for fork length. The unique identification number of the T-bar anchor tag was recorded, which allowed for a comparison of the biological data collected prior to release. *O. mykiss* kelts were spawned and detained at the hatchery as previously described until April, when they were released into Battle Creek.

Ultrasonic receiver array

We monitored the movement of ultrasonically tagged *O. mykiss* kelts using an array of fixed-site ultrasonic receivers (VEMCO Ltd, Halifax, Nova Scotia Canada, model VR2) situated throughout the Sacramento River basin (Tables 1 and 2). Receiver locations are referred to by rkm, where the confluence of the Sacramento and San Joaquin Rivers was considered to be rkm 0. The location of the receivers extended from the upstream limit of anadromous fish migration at the Keswick Dam (rkm 484) downstream to the terminus of the San Francisco estuary at the Golden Gate Bridge (Table 1; Fig. 1). Receivers were also located in several large tributaries of the Sacramento River including the San Joaquin River, the American River, and the Feather River. Three receivers were placed in Battle Creek; one near it's confluence with the Sacramento River (rkm 436), one at the entrance to the Coleman NFH (rkm 9), and another between these locations near the Battle Creek Wildlife Area (rkm 5). Some receivers in this array were excluded from our results because they were located in close proximity to another receiver and provided redundant information or had low detection rates. In four cases, we merged the detections from multiple receivers that were located in close proximity, including: a receiver located near Bend, CA (rkm 415) and a receiver near Table Mountain (rkm 420); two receivers located near the Red Bluff Diversion Dam (rkm 391); three receivers located near Rio Vista, CA (rkm 12); and nine receivers located near the Golden Gate Bridge.

Five receivers were lost, stolen, or removed and two receivers were replaced during the two-year study period. A receiver located at the Battle Creek confluence (rkm 436) was stolen in approximately mid-May in 2005 and was replaced with a new receiver on 3 April 2006. Another receiver located in Battle Creek near the Battle Creek Wildlife Area (rkm 5) was lost during the winter of 2005 and was not replaced. A receiver at Scotty's Landing (rkm 317) was stolen approximately mid-June 2005 and replaced in mid-June 2006. A receiver in the Sacramento River at the confluence with Butte Creek (rkm 221) was lost or stolen around mid-June 2005 and was not replaced. A receiver at Brannon Island, located in the San Joaquin River, was relocated in the spring of 2005.

Results

Movement behavior

Migratory patterns of *O. mykiss* kelts implanted with ultrasonic transmitters were variable among individual fish released during both years. We observed fish that demonstrated both anadromous and non-anadromous (including resident and potamodromous behavior) life histories. However, most (90 %) *O. mykiss* kelts were anadromous and exhibited generally similar patterns of emigration and spawning migrations.

The predominant emigration pattern for anadromous *O. mykiss* kelts can be characterized by a short-term residence near the location of release followed by a sustained downstream movement to the Sacramento-San Joaquin River Delta (Delta) or Pacific Ocean (Fig. 2). Figure 2 depicts the emigration pattern for three fish; however, this pattern is generally representative of most fish in this study. The first detection of each individual at the confluence of Battle Creek with the Sacramento River occurred 1 to 80 d after release, with the median detection 18 d after release in 2005 and 23 d after release in 2006 (Table 1). After exiting Battle Creek, *O. mykiss* kelts generally exhibited persistent seaward migration with most fish entering the Delta,

Table 1 Median travel time, range of travel time, median travel rate, and number of detections at each receiver location for emigrating *O. mykiss* kelts

Location	River kilometer (rkm)	Median travel time (days)	Range of travel time (days)	Median travel rate (k/day)	Total number detected
2005					
Battle creek					
Battle creek wildlife area	5	7	<1–33	0.6	19
Sacramento river					
Battle creek confluence	436	18	1–38	0.5	21
Bend bridge	415	26	1–65	1.2	14
Red Bluff diversion dam	391	28	1–69	2.0	16
Thomes creek	365	28	2–70	2.9	16
Scotty's landing	317	30	3–69	4.3	11
Butte creek	221	40	29–70	5.6	12
Knight's landing	145	39	5–94	7.7	18
Rio Vista	19	43	31–96	10.0	14
San Joaquin river					
Brannon island	5	40	8–44	n/a	3
San Francisco estuary					
Golden gate bridge	–	46	35–98	9.7	13
2006					
Battle creek					
Battle creek wildlife area	5	Lost	–	–	–
Sacramento river					
Battle creek confluence	436	23	<1–80	0.2	20
Bend bridge	415–420	37	4–67	0.7	16
Red Bluff diversion dam	391	38	16–91	1.3	16
Thomes creek	365	40	16–94	1.9	16
Scotty's landing	317	Stolen	–	–	–
Butte creek	221	Stolen	–	–	–
Knight's landing	145	44	4–100	6.7	17
Rio Vista	19	73	7–102	5.8	7
San Joaquin river					
Brannon island	5	Removed	–	–	–
San Francisco estuary					
Golden gate bridge	–	47	10–84	9.4	15

as indicated by detections at Rio Vista (rkm 19) and Brannon Island (rkm 5; San Joaquin River), from April through June (Table 1; Fig. 2). Most (82 %) *O. mykiss* kelts observed in the Delta were detected at the Rio Vista receiver in the mainstem Sacramento River; however, some *O. mykiss* kelts were detected at the Brannon Island receiver in the lower San Joaquin River (Table 1; Fig. 1). *O. mykiss* kelts were detected at the Golden Gate Bridge receivers, and presumably entered the Pacific Ocean, from April through mid-July (Table 1). During their emigration, two fish also entered the Feather River for a short duration, prior to continuing to the Delta.

The spawning migration of most anadromous *O. mykiss* kelts showed a similar pattern. Upstream migration began in late-September through October during the year of release (Table 2; Fig. 2). *O. mykiss* kelts migrated rapidly upstream and entered Battle Creek in late-September through November. Entry into the Coleman NFH occurred as early as October, with most fish entering the Coleman NFH in December and January.

Table 2 Median travel time, range of travel time, median travel rate, and number of detections at each receiver location for returning *O. mykiss* kelts in 2005 and 2006

Location	River kilometer (rkm)	Median travel time (days)	Range of travel time (days)	Median travel rate (k/day)	Total number detected
2005					
Battle creek					
Coleman NFH	9	260	207–261	4.2	7
Battle creek wildlife area	5	189	185–192	12.8	2
Sacramento river					
Battle creek confluence	436	Stolen	–	–	–
Bend bridge	415	197	186–205	9.8	6
Red Bluff diversion dam	391	198	193–202	9.1	2
Thomes creek	365	191	176–203	10.0	7
Scotty's landing	317	Stolen	–	–	–
Butte creek	221	Stolen	–	–	–
Knight's landing	145	171	141–187	9.1	6
Rio Vista	19	170	137–182	1.2	5
San Joaquin river					
Brannon island	5	40	8–44	n/a	3
San Francisco estuary					
Golden gate bridge	–	155	153–156	–	2
2006					
Battle creek					
Coleman NFH[2]	9	265	246–305	4.3	5
Battle creek wildlife area[2]	5	Lost	–	–	–
Sacramento river					
Battle creek confluence	436	195	175–216	13.2	5
Bend bridge	415	197	172–221	12.0	6
Red Bluff diversion dam	391	194	170–219	12.4	6
Thomes creek	365	191	167–217	12.8	6
Scotty's landing	317	183	160–214	15.1	7
Butte creek	221	Lost	–	–	–
Knight's landing	145	175	100–198	11.1	7
Rio Vista	19	158	102–189	n/a	5
San Joaquin river					
Brannon island	5	Removed			
San Francisco estuary					
Golden gate bridge	–	162	137–166	–	7

Entry into Battle Creek often preceded entry into the hatchery by several weeks or more, as depicted by fish # 309 in Fig. 2.

Eight *O. mykiss* kelts showed patterns of movement that were atypical of the predominant movement behavior (Table 3); four of these were anadromous and four were non-anadromous. Atypical anadromous movement included two fish that returned to freshwater locations other than the hatchery during their spawning migration, one fish that moved upstream prior to emigrating, and one fish exhibited a delayed emigration. One of the fish that returned to a freshwater location other than the hatchery did not return to Battle Creek (i.e. "strayed").

The four *O. mykiss* kelts that residualized, or became freshwater residents between spawning events

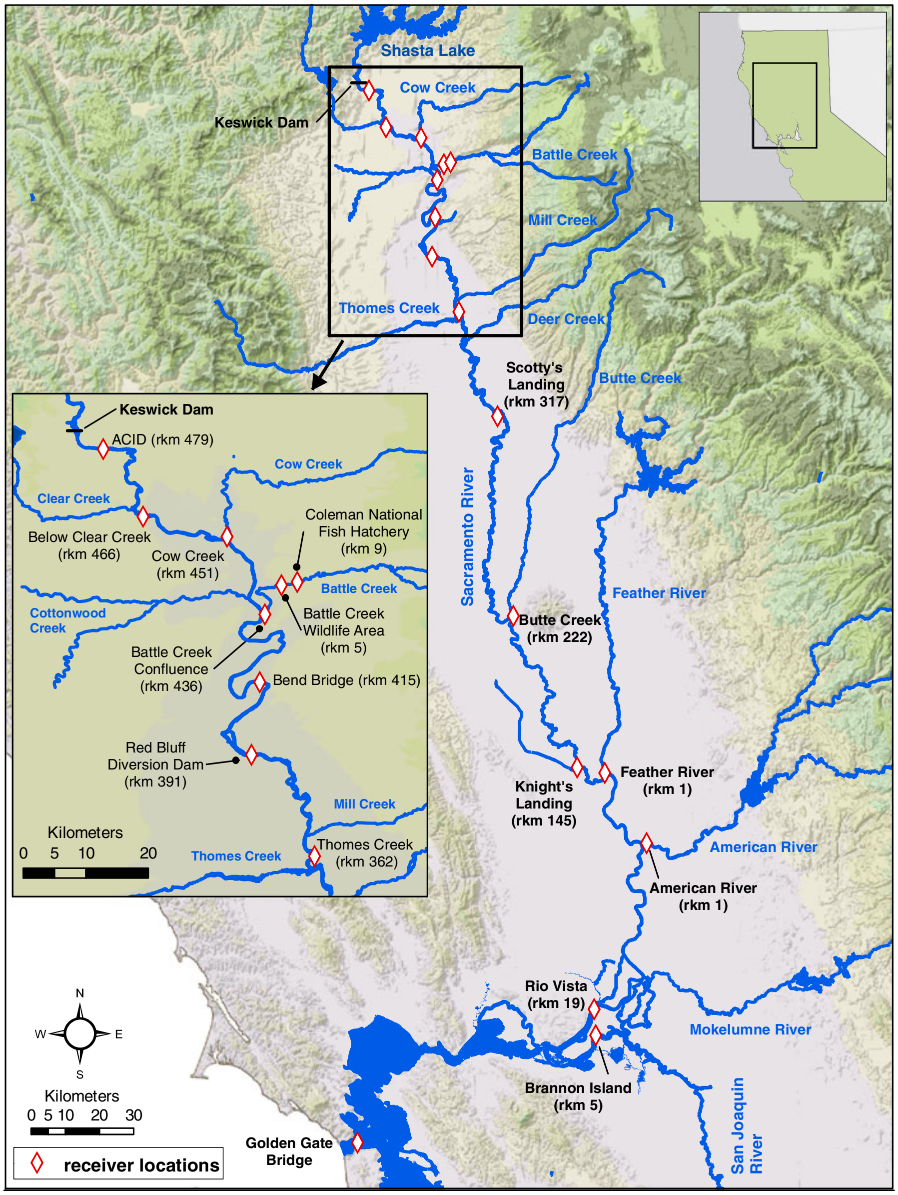

Fig. 1 Map of the Sacramento River and tributaries, Sacramento-San Joaquin River Delta, and San Francisco Estuary with locations of acoustic receivers displayed

(non-anadromous), displayed two general patterns of movement: 1.) residency near the release location, and 2.) potamodromy. At least one fish resided in Battle Creek for most of the year, whereas two fish appear to have residualized near Battle Creek in the Sacramento River. One small male demonstrated a potamodromous life history, migrating substantially within-river, traveling downstream to the vicinity of the Thomes Creek receiver at rkm 365 and was not detected again until it migrated upstream in mid-October. This *O. mykiss* kelt may have residualized in the Sacramento River or one of the tributaries which feed into the Sacramento River near that location, such as Thomes Creek, Mill Creek, and Deer Creek (Fig. 1).

Observed patterns of movement of some hatchery-origin *O. mykiss* kelts, changed between years, including individuals that demonstrated both anadromous and non-anadromous (i.e. potamodromous) behavior in separate years. One *O. mykiss* kelt, released in 2006, residualized in Battle Creek through the following winter, returned to the Coleman NFH where it was spawned and detained until April 2007 when it was released. After release, this *O.*

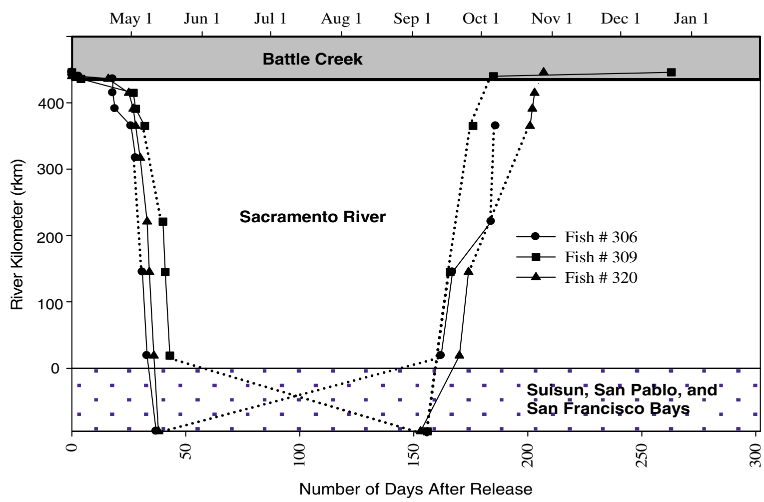

Fig. 2 Number of days after release until arrival at each receiver location in the Sacramento River and estuary for three ultrasonic transmitter tagged steelhead released in 2005. Dotted lines were interpolated to display estimated arrival time for steelhead that passed a location without being detected. Date is show at the top of the figure

mykiss kelt emigrated to the Delta and was not observed again, demonstrating a transient life-history strategy including both anadromy and freshwater residency during consecutive years following spawning at the hatchery. Another fish was released in 2006, emigrated to the Pacific Ocean, returned to the Coleman NFH where it was spawned and detained until April 2007 when it was released. Subsequent to the second release, this *O.* mykiss kelt moved downstream to the Red Bluff Diversion Dam (rkm 391) where it remained until the following September when it began migrating upstream. This *O. mykiss* kelt demonstrated both anadromous and potamodromous migrations in separate years.

Survival, fate and performance

Most (90 %) *O. mykiss* kelts migrated to the Delta and 74 % were detected at the Golden Gate Bridge receivers and presumably entered the Pacific Ocean, demonstrating a movement pattern consistent with anadromy (Fig. 3). It is possible that additional *O. mykiss* kelts entered the Pacific Ocean but were not detected at the Golden Gate Bridge receivers. It is also possible that some *O. mykiss* kelts may have remained in the Delta or the San Francisco Estuary through the following winter.

Repeat spawning migration rates averaged 41 % in the 2 years of this study; 36 % in 2005 and 48 % in

Table 3 Tag number, tagging year, gender, migration behavior and description of migration for fish showing an atypical pattern in 2005 or 2006

Tag #	Year	Gender	Migration behavior	Returned to CNFH	Description
308	2005	Female	Residualized	Yes	Residualized in Battle Creek
310	2005	Female	Residualized	Yes	Residualized in Battle Creek or the Sacramento River
315	2005	Male	Residualized	Yes	Residualized in the Sacramento River or its tributaries near rkm 365.
322	2005	Male	Upstream Migration	No	Migrated upstream to rkm 452 after exiting Battle Creek, then emigrated to the Delta.
342	2006	Female	Delayed Emigration	No	Delayed emigration to the Delta, followed by multiple within-year migrations between the Delta and the Sacramento River at rkm 317.
354	2006	Female	Spawned Naturally (Stray)	No	Emigrated to Delta and made a spawning migration back to the Sacramento River to rkm 317.
356	2006	Female	Residualized	Yes	Residualized in Battle Creek
358	2006	Male	Spawned Naturally	No	Emigrated to the Delta and then made a spawning migration to Battle Creek.

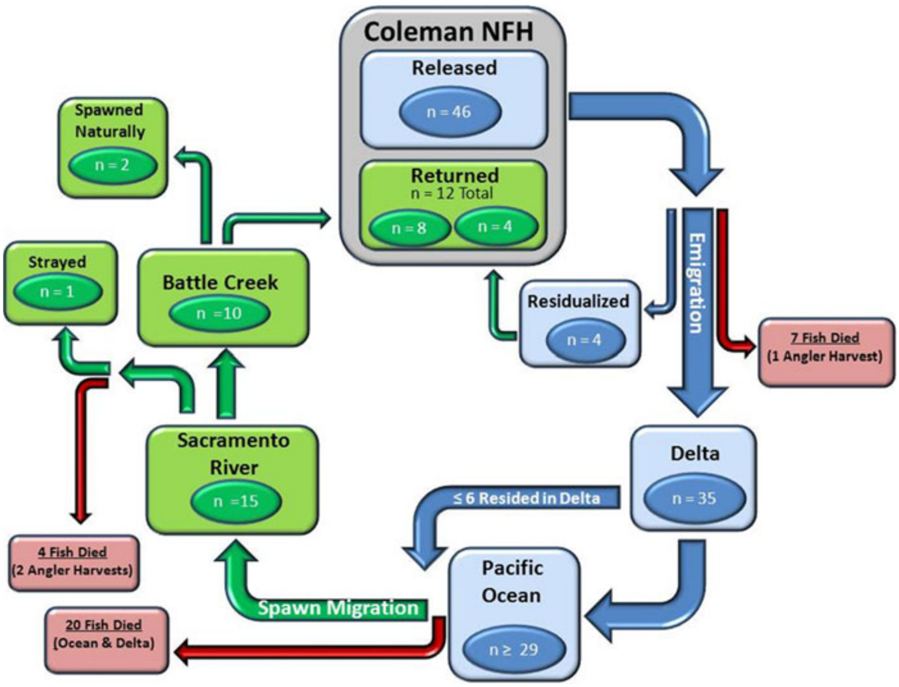

Fig. 3 Flow chart displaying the fate of 46 *O. mykiss* kelts released with ultrasonic transmitters in 2005 and 2006

2006 (Fig. 3). Rate of return to the Coleman NFH averaged 26 % (Fig. 3) and overall iteroparity rate (survival to a second spawn), including fish that were presumed to have spawned naturally, was 33 %. The fate of most fish that didn't return to the hatchery cannot be known with certainty, but some mortality of these fish likely occurred prior to reaching spawning locations and at least three tagged *O. mykiss* kelts were harvested by anglers; one during emigration and two during the spawning migration. It is also possible that some *O. mykiss* kelts may have expelled the ultrasonic transmitters, as has been demonstrated in other studies (Welch et al. 2007; Nielsen et al. 2011; Teo et al. 2011). These fish would appear to be natural mortalities. However, we believe that the transmitter loss rate in our study was low, if it occurred at all, because all of the incisions had healed for the *O. mykiss* kelts that were released. Additionally, all fish returning to Coleman NFH that had a T-bar anchor tag also carried the expected ultrasonic transmitter. At least three additional *O. mykiss* kelts survived through the expected spawn timing of December through March, but did not enter the Coleman NFH. Two of these fish likely spawned in Battle Creek while another fish appeared to spawn in a non-natal area, or "stray." Generally, *O. mykiss* kelts showed high fidelity to Battle Creek with only one of fifteen (7 %) surviving fish straying to a non-natal spawning area. At least 9 % of the *O. mykiss* kelts in this study were non-anadromous.

Growth of anadromous fish was greater than for fish that did not emigrate. Eleven of the *O. mykiss* that returned to the Coleman NFH were measured for fork length (Table 4). One fish (# 315) was not measured because staff did not identify that it had an ultrasonic transmitter, but the transmitter was detected by the receiver at the Coleman NFH. It is possible that this fish may have shed the T-bar anchor tag that was attached prior to release. Additionally, an angler reported harvesting an *O. mykiss* (Fish # 306) in the Sacramento River downstream of the confluence of Battle Creek (rkm 436) and fork length was recorded and included in Table 4. However, we were uncertain of the accuracy of the measurement and have excluded the length from statistical calculations. A one-tailed student's *t*-test indicated that there was a significant effect for migration, $t(10)=3.31$, $p=0.008$, with emigrating (anadromous) fish showing more growth than non-anadromous fish. The mean increase of fork length of *O. mykiss* kelts returning to the Coleman NFH was 7.1 cm (range=4.0–11.0 cm; 13.4 % increase) for fish that emigrated and 1.6 cm; (range=0.0–2.8 cm; 3.1 % increase; Table 4) for fish that residualized.

Table 4 Return date, migration behavior, gender, fork length at the time of release (cm), fork length upon return, growth, and increase in length for tagged *O. mykiss* returning to the Coleman NFH in 2005 and 2006

Tag number	Migratory behavior	Year	Gender	Fork length (cm) at release	Fork length (cm) at return	Growth (cm)	% Increase in length
306	Emigrated	2005	Female	48.0	61.0	13.0	27.1
309	Emigrated	2005	Female	53.5	62.0	8.5	15.9
319	Emigrated	2005	Female	58.0	67.0	9.0	15.5
320	Emigrated	2005	Female	63.0	67.0	4.0	6.3
330	Emigrated	2005	Female	50.0	61.0	11.0	22.0
346	Emigrated	2006	Female	50.0	56.0	6.0	12.0
347	Emigrated	2006	Male	53.0	60.0	7.0	13.2
352	Emigrated	2006	Female	49.0	56.0	7.0	14.3
364	Emigrated	2006	Female	50.0	54.0	4.0	8.0
Mean						7.1	13.4
308	Residual	2005	Female	48.2	51.0	2.8	5.8
310	Residual	2005	Female	57.0	59.0	2.0	3.5
315	Residual	2005	Male	45.0	Unknown	–	–
356	Residual	2006	Female	45.0	45.0	0.0	0.0
Mean						1.6	3.1

[a]Fork length was estimated by the angler that harvested Fish # 206

Discussion

Residualism (including both resident and potamodromous behavior) and anadromy are expressions of the natural phenotypic diversity of *O. mykiss*. This diversity of life history strategies is believed to result in benefits to the population in terms of population resiliency and connectivity. Results of this study suggest a trade-off between resident and anadromous life history strategies. Hatchery-origin *O. mykiss* that emigrated grew significantly more in length than fish that residualized, suggesting estuarine and marine environments were more productive. The increased growth exhibited by anadromous *O. mykiss* likely confers fitness advantages over nonanadromous *O. mykiss*. Quinn et al. (2011) demonstrated that length was positively correlated with egg size and fecundity in *O. mykiss*. Fleming (1996) suggested that larger egg size in salmonids may result in fitness benefits such as larger juveniles (Fowler 1972; Glebe et al. 1979; Thorpe et al 1984; Beacham et al. 1988), which may have faster growth (Brown 1946; Bagenal 1969), higher social status (Wankowski and Thorpe 1979), and reduced susceptibility to starvation (Bagenal 1969; Hutchings 1991), predation (Parker 1971; Patten 1977; Taylor and McPhail 1985), and parasites (Boyce 1974). However, these advantages that may result from increased growth come at the expense of higher rates of mortality for fish that emigrated. The overall iteroparity rate of *O. mykiss* kelts that emigrated was lower than for fish that residualized, suggesting a higher rate of mortality is associated with this life history strategy.

O. mykiss kelts in this study showed variable and transient life history strategies in the Central Valley of California, suggesting that factors other than genetics, such as environmental conditions or physiological state, may play a role in determining whether individual *O. mykiss* emigrate or residualize. Pavlov et al. (2008) suggested that the key characteristic determining residency versus anadromy in the Kamchatka trout *Parasalmo mykiss* is food availability in proximity to spawning grounds. However, we are not aware of any previous study which has demonstrated that individual adult *O. mykiss* will alternate between an anadromous and a resident life history subsequent to maturation. In some populations, anadromous *O. mykiss* kelts have been shown to have variable time between spawning migrations with fish spawning both on consecutive and alternating years (Burgner et al. 1992; Lohr and Bryant 1999; Nielsen et al. 2011). All *O. mykiss* kelts in this study demonstrated consecutive spawning migrations.

It is important to note that iteroparity rates presented in this study do not account for *O. mykiss* that did not survive the spawning and handling process at the Coleman NFH and, therefore, should not be projected to the entire spawning population. Hallock (1989) estimated that 1.1 % of the entire *O. mykiss* population returning to the Coleman NFH, had entered the hatchery the previous year. Similar monitoring of *O. mykiss* returning to the Coleman NFH from 2005 to 2009 indicated that iteroparity rates averaged 3.9 % (range: 1.7–7.7 %) of the total number of spawning fish.

Allowing hatchery-origin *O. mykiss* to spawn multiple times results in several benefits to the integrated hatchery propagation program. A primary tenet associated with operating an integrated hatchery propagation program is to maintain similar traits of the wild population in the hatchery brood stock. Tendency to repeat spawn is likely controlled at least partly by genetics, and fish demonstrating iteroparity are thought to contribute substantially to the genetic structure of some salmonid populations (Fleming and Reynolds 2004; Keefer et al. 2008). Therefore, it may be important to include iteroparous individuals in the hatchery brood stock at the Coleman NFH. Allowing for repeat spawning of hatchery fish also results in overlapping of cohorts, which protects against year-class divergence, inbreeding, and loss of genetic diversity.

Maintaining a genetically diverse hatchery *O. mykiss* population with traits similar to the naturally-spawning population is essential to reduce impacts to the naturally-spawning population. Reducing divergence of fish produced in the hatchery reduces impacts to the natural population when hatchery *O. mykiss* inadvertently spawn naturally. We observed several hatchery-origin *O. mykiss* kelts in this study that did not return to the hatchery and likely spawned naturally. Likewise, some natural spawning undoubtedly occurs as a result of releasing *O. mykiss* juveniles produced at the Coleman NFH.

Another benefit of releasing *O. mykiss* kelts is the increase in numbers of fish available for the recreational fishery. *O. mykiss* kelts that return to spawn multiple times are also generally larger and more desirable to fisherman. Additionally, during years of low abundance, *O. mykiss* kelts can contribute substantially to the brood stock at the Coleman NFH, which helps to ensure that juvenile release targets are achieved. Numbers of adult *O. mykiss* brood stock collected at the Coleman NFH are variable and 24.3 % of the brood stock spawned in 2010 consisted of *O. mykiss* kelts as a result of poor survival of a cohort of juveniles released from the production program.

Release of hatchery *O. mykiss* kelts could result in negative ecological effects to naturally-producing salmonids. The potential for negative effects is increased if hatchery fish remain in freshwater, or "residualize" (McMichael et al. 1997; Araki et al. 2007a, b; Kostow 2009). The general effects of hatchery-produced fish on natural fish, as described by Steward and Bjornn (1990), may be exacerbated if a substantial portion of the hatchery-produced salmonids residualize. Hatchery-origin *O. mykiss* kelts that residualize in the Central Valley of California will compete with and potentially consume native con-specifics and other species, including ESA-listed threatened spring and endangered winter Chinook salmon.

In an attempt to mitigate impacts that could result from releasing hatchery-origin *O. mykiss* kelts from the Coleman NFH, the fish are held after spawning until late-March or early-April, after naturally reproducing steelhead have completed spawning. Hatchery-origin *O. mykiss* are released with the anticipation that they will migrate to the ocean; however, as demonstrated in this study, few (10 %) *O. mykiss* kelts residualized. The rapid emigration that was observed for most *O. mykiss* kelts in this study indicates that negative interactions resulting from competition with or predation on ESA-listed salmonids such as endangered winter Chinook salmon and threatened spring Chinook salmon in the riverine environment are limited to a short duration (generally less than 2 months). Given the short duration of freshwater residence and the relatively small number of kelts that residualized, and considered within the context of the vast numbers of other predatory species in the Central Valley, impacts to ESA-listed salmonids resulting from competitive interactions between and predation by O. mykiss kelts is likely negligible. We believe the benefits of releasing *O. mykiss* kelts at the Coleman NFH, including increased numbers and size of fish in the recreational fishery and genetic and demographic benefits to the hatchery brood stock outweigh the limited risk to natural populations that would result from predation and competition of the relatively small number of *O. mykiss* kelts that resided in fresh water.

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