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Archival and acoustic tags reveal the post-spawning migrations, diving behavior, and thermal habitat of hatchery-origin Sacramento River steelhead kelts (*Oncorhynchus mykiss*)

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Abstract Acoustic and geolocating archival tags were deployed on steelhead kelts to study their post-spawning migrations, diving behavior and thermal habitat. Fourteen reconditioned steelhead kelts were surgically implanted with LAT2510 archival and V7-2 L acoustic tags, and released from Coleman National Fish Hatchery. An array of acoustic receivers in the Sacramento River and Delta, and the San Francisco Bay estuary detected the downstream movement of the steelhead. Two steelhead kelts (J and M) with archival tags were recovered at the hatchery after 219 and 285 days at liberty respectively. Based on changes in geolocations, vertical movements, and water temperatures, the migrations of steelhead J and M were divided into five and six phases respectively. Steelhead J moved into coastal California waters while steelhead M remained in freshwater for the majority of its time at liberty. Large increases in temperature and opacity were recorded before and after the ocean phases, likely as the steelhead moved through the Sacramento Delta. Both steelhead kelts remained relatively close to the surface throughout their migration but there were diurnal differences in the vertical movements. In freshwater, the steelhead tended to be deeper during the day (e.g., steelhead J: 3.08±1.50 vs 1.65±1.15 m, day vs night) but in the ocean, the steelhead were typically deeper during the night (1.32±1.61 vs 5.63±6.11 m). Both steelhead kelts appeared to be less oceanic than a previous study in Scott Creek, a small coastal stream approximately 100 km south of the mouth of San Francisco Bay. Although this study has a small sample size, the results suggest that steelhead kelts from a large river and estuary system, like the Sacramento River, may be relatively less oceanic than steelhead kelts from small coastal streams.

Keywords Salmonid · Electronic tag · Geolocation · Movement · Water temperature · Depth · Marine · Ocean · Freshwater

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Introduction

The ocean migrations of Pacific salmonids remain relatively poorly understood despite the scientific and commercial interest in these species (Pearcy 1992; Weitkamp and Neely 2002; Hayes et al. 2011). Over the past two decades, numerous studies have shown that variability in ocean survival strongly influences year-class strength of many salmonid species (e.g., Logerwell et al. 2003; Teo et al. 2009a). Understanding salmonid ocean migration and its influence on survival is therefore critical to the conservation and management of Pacific salmonid stocks. Hence, there is enormous interest in tracking Pacific salmonids during their ocean migrations and improving our understanding of their biology in the ocean.

The basic life history of steelhead, anadromous rainbow trout (*Oncorhynchus mykiss*), is generally understood (Quinn 2005). Steelhead juveniles often spend 1–3 years in freshwater before smolting and moving into the ocean (Busby et al. 1996). After residing in the ocean for 1–3 years, steelhead adults then return to freshwater to spawn. Some returning adults survive spawning and perform post-spawning migrations back to the ocean, and are known as kelts, which are potentially capable of returning to freshwater for subsequent spawning events. Thus, unlike many Pacific salmonids, the steelhead is iteroparous.

Our knowledge of steelhead ocean migrations is highly limited (Quinn and Myers 2004). Due to their relatively small population sizes and lower commercial value, steelhead populations are not as well-studied as more common Pacific salmon species (Quinn 2005). Traditionally, high seas catch and effort data coupled with coded wire tag deployments have improved our understanding of the large-scale ocean movements of many salmonid species (e.g., Burgner et al. 1992; Myers et al. 1996; Myers et al. 2005). However, these traditional methods are highly fisheries-dependent and coded wire tags only allow for the identification of release and recapture locations, which is an inherent drawback of non-electronic tags. Based on relatively few coded wire tag returns and catch-per-unit-effort data, North American steelhead kelts are thought to leave coastal waters early in summer and range across a broad swath of the North Pacific (Burgner et al. 1992; Myers et al. 2005).

In recent years, acoustic tags combined with networks of receivers have greatly improved our knowledge of the freshwater and coastal movements, and mortality of salmonids (e.g., Perry et al. 2010; Null et al. 2012; Sandstrom 2012). However, the elucidated scale of movements is dependent on the spatial scale of the receiver network and these networks remain largely in rivers and estuaries. In addition, these networks only extend out onto the edge of the continental shelf due to the difficulties and costs in installing and maintaining these receivers in the open ocean (see other studies in this issue).

In light of these difficulties, archival tags have recently been used to study the movements and thermal habitat of salmonids. Several previous studies have successfully used archival tags that record temperature and/or depth to determine the diving behavior and thermal habitat of several salmonid species (e.g., Walker et al. 2000; Ishida et al. 2001; Hinke et al. 2005; Nielsen et al. 2011; Hayes et al. 2011). Using these data, researchers were able to estimate the broad oceanic regions to which these fish migrated (Hayes et al. 2011). We can improve considerably upon the accuracy and precision of the estimated movements by using geolocating archival tags that record light as well as temperature and depth (Teo et al. 2004; Lam et al. 2008). These geolocating archival tags have been used for over a decade to estimate the daily positions of large pelagic fish, like tunas (e.g., Teo et al. 2007a), but these tags have generally been too large for use in salmonids (although see Wada and Ueno 1999 for an exception). The miniaturization and increasing capabilities of these tags are however beginning to open this window of opportunity for smaller fish.

In this study, we deploy both geolocating archival tags and acoustic tags on steelhead kelts from a Sacramento River hatchery to study their post-spawning movements and thermal habitat. This double-tagging approach combines the advantages of both tag types to enable us to track the fish through freshwater, estuarine, and marine environments. Steelhead kelts were chosen for this experiment due to their relatively large body size, which allows for double-tagging, and their high survival and return rates to the hatchery. Our primary objective is to provide initial observations on the post-spawning migrations, diving behavior and thermal habitat of steelhead kelts from the Sacramento River, especially during their ocean phase. Secondarily, this study will also help demonstrate the utility of archival tags in understanding the biology of salmonids in the ocean.

Materials and methods

Fourteen reconditioned steelhead kelts were surgically implanted with archival and acoustic tags, and released from the U.S. Fish and Wildlife Service's Coleman National Fish Hatchery (121.147°W, 40.398°N), located along Battle Creek, a tributary of the Sacramento River (Fig. 1). Adult steelhead returning to the hatchery are carefully handled and live spawned to collect eggs and milt. After spawning, the adult steelhead are placed into a holding pond for reconditioning and subsequent release. Nineteen reconditioned adult steelhead were arbitrarily selected from the holding pond and tagged with prototype LAT2510 archival tags (Lotek Wireless Inc.; 8 mm diameter x 35 mm, 4.25 g in air; beta-test version) and/or V7-2 L acoustic tags (Vemco Ltd.; 7 mm diameter x 20 mm, 1.6 g in air). Archival tags were programmed to record light level, pressure, and water temperature data every 240 s and acoustic tags were set to ping approximately every 60 s (actual transmission intervals varies randomly between 30 and 90 s). Twelve fish were implanted with both archival and acoustic tags, and seven fish were implanted with only an archival tag. Total weight of both tags was approximately 0.5% of the average body weight of the tagged fish.

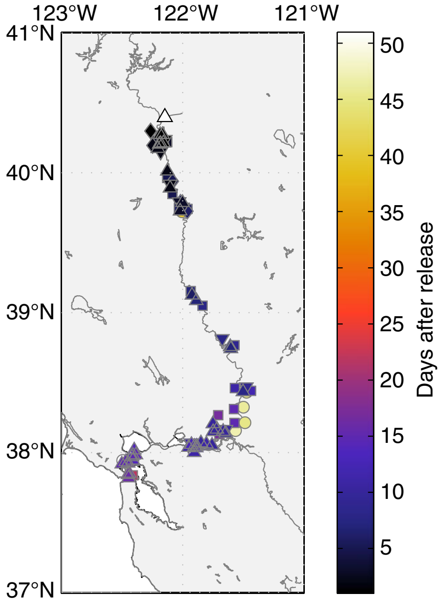

Fig. 1 Release location of steelhead kelts (white Δ) and approximate locations of acoustic tag detections. Five steelhead were detected after release and symbols indicate individual steelhead: A (◊), B (Δ), D (□), E (∇), and I (○). Locations of acoustic tag detections are jittered for clarity

To surgically implant the tags, each fish was first anesthetized with 90 mg L^{-1} tricaine methanesulfonate (MS-222) until they lost equilibrium. Each fish was then placed ventral side up onto a V-shaped foam cushion. A hose with recirculating freshwater containing 30 mg L^{-1} MS-222 was placed into the mouth of the fish for respiration and maintenance of anesthesia. A primary incision (~24–35 mm) was made into the peritoneal cavity and the tags were placed into the peritoneal cavity. A secondary incision (~2–3 mm) was made about 50 mm posterior of the primary incision and a 13 G aspirating trocar needle was pushed along under the skin, from the secondary incision towards the primary incision. After reaching the primary incision, the solid stylet of the trocar needle was removed and the light stalk of the archival tag was threaded through the outer cannula. After the cannula was removed, the primary incision was closed with 3–4 stitches and the secondary incision was closed with 1 stitch. The purpose of the secondary incision was to minimize any abrasion of the light stalk against the primary incision and thus promote healing. The fish were subsequently tagged with a conventional T-bar anchor tag (Floy Tag & Mfg. Inc.) and placed into a raceway to recover. After a 21-day recovery period, 14 tagged fish (eight with both archival and acoutic tags, and six with only an archival tag) were released into Battle Creek near the hatchery (Table 1). Five fish did not recover from the surgical procedure and were not released.

The California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu) deployed and maintains an array of more than 300 acoustic tag receivers in the Sacramento River and Delta, and the San Francisco Bay estuary. Data from these receivers are downloaded on a regular schedule by the Consortium and entered into an online database. The times and locations of detections from acoustic tags deployed in this study were extracted from this database.

Table 1 Tagging, release, and recovery information of steelhead kelts tagged with archival and acoustic tags. All deployments and recoveries occurred at Coleman National Fish Hatchery along Battle Creek (40.398°N, 122.147°W) (see Fig. 1)

Fish ID	Archival Tag ID	Acoustic Tag ID[a]	Sex	Length at Tagging (cm)	Date of Tagging	Date of Release	Date of Recovery[b]	Length at Recovery (cm)
A	A0143	16022	F	47.5	10 Apr 2008	01 May 2008		
B	A0148	16027	F	46.5	10 Apr 2008	01 May 2008		
C	A0149	16023	F	50.5	10 Apr 2008	01 May 2008		
D	A0162	16021	F	48.8	10 Apr 2008	01 May 2008		
E	A0159	16024	F	47.8	10 Apr 2008	01 May 2008		
F	A0150	16025	M	41.5	10 Apr 2008	01 May 2008		
G	A0156		F	45.0	10 Apr 2008	01 May 2008		
H	A0161		F	46.7	10 Apr 2008	01 May 2008		
I	A0155	16012	F	42.8	10 Apr 2008	01 May 2008		
J	A0171		F	44.7	10 Apr 2008	01 May 2008	14 Nov 2008	53.6
K	A0153		F	45.8	10 Apr 2008	01 May 2008		
L	A0158		F	46.0	10 Apr 2008	01 May 2008		
M	A0164	16020	M	45.5	18 Apr 2008	09 May 2008	27 Jan 2009	47.7
N	A0170		M	40.5	18 Apr 2008	09 May 2008		

[a] Fish without an acoustic tag ID were not tagged with an acoustic tag

[b] Fish without a date of recovery were not recovered

Steelhead kelts returning to Coleman National Fish Hatchery were visually examined for tags. Tagged steelhead were euthanized and their peritoneal cavities were examined with a metal detector to retrieve the acoustic and archival tags. Preliminary examination of the archival tag data indicated that the pressure sensor of one recovered tag exhibited a drift of approximately 7 dbar between deployment and recovery. In order to correct for this drift, we performed zero offset correction on the pressure data prior to analysis, as described in Teo et al. (2004). Subsequently, tag-recorded pressure data were converted into depths by assuming 1 dbar was equivalent to 1 m of depth, which results in <2% of error and is negligible for the depths experienced by the fish (<100 m).

Light level, depth and water temperature data from the archival tags were analyzed in an effort to discern changes in relation to different habitats (e.g., freshwater, estuarine, and marine). We first plotted the archived data for the entire period at liberty and visually examined changes in diving behavior and water temperatures. Similar to a previous study with depth and temperature archival tags (Nielsen et al. 2011), changes in diving behavior and water temperature could be clearly delineated as migration into and from saltwater. We divided the data into several phases based on changes in water temperatures, vertical movements, and geolocations. For example, periods in freshwater typically have cyclical diurnal changes in water temperature and highly surface-oriented vertical movements (Nielsen et al. 2011). On the other hand, periods in the ocean are typified by deeper diving and the lack of cyclical changes in temperature (Nielsen et al. 2011) (also see Results for detailed description). In addition, the light-based longitude estimates (see below) for periods in the ocean are also expected to be west of the mouth of the San Francisco Bay estuary (122.479°W, 37.820°N). The daily distributions of temperatures and depths for each steelhead were calculated and examined for differences between phases.

The LAT2510 archival tag had onboard proprietary software that processed the light level and pressure data, corrected for light attenuation, and estimated the daily longitude and latitude using a 'template fit' algorithm (Ekstrom 2007). For steelhead that entered the ocean, we improved the daily latitude estimates by matching daily sea surface temperatures (SSTs) recorded by the tag with satellite-derived SSTs (global nighttime, 4 km resolution, 8 day averaged, MODIS thermal IR SSTs, ftp://podaac.jpl.nasa.gov). Tag-recorded SSTs were extracted from the water temperatures recorded within 4 m of the surface. Teo et al. (2004) provided a detailed explanation and analysis of the SST matching algorithm, and found that geolocation estimates from archival tags have root mean square errors of approximately 0.5–1.0°. However, the relatively shallow diving behavior of steelhead likely reduced geolocation errors in comparison to the large pelagic fish in that study. The archival tags also estimated and recorded the daily opacity of the water column, as part of its onboard geolocation algorithm. We used eq. 2 in Teo et al. (2009b) to transform tag-recorded opacity, which is in proprietary units (log units m^{-1}), into diffuse attenuation coefficients (m^{-1}).

Results

Based on results from acoustic tags, most of the steelhead moved rapidly downstream along the Sacramento River, after being released at Coleman National Fish Hatchery (Fig. 1). Out of eight steelhead released with acoustic tags (Table 1)—three fish were not detected after release; one (steelhead A) was last detected approximately 100 km downstream after 6 days at liberty; one (steelhead E) was last detected in Suisun Bay; and three fish (steelhead B, D, and I) reached the San Francisco Bay (Fig. 1). Steelhead B and D reached the San Francisco Bay after 2–3 weeks but steelhead I took 6–7 weeks.

Two steelhead kelts, J and M, were recovered at Coleman National Fish hatchery after 219 and 285 days at liberty respectively (Table 1). Even though steelhead M was at liberty for a longer period, steelhead J, which migrated to the ocean (see below), grew (8.9 cm) substantially more between release and recapture than steelhead M (2.2 cm), which did not enter the ocean (Table 1). Both archival tags were retrieved but acoustic tag 16020 could not be found, suggesting that steelhead M expelled its acoustic tag. Preliminary examination of the downloaded data revealed that the battery in steelhead M's archival tag had died prematurely after 188 days at liberty (12 November 2008), and the pressure and temperature sensors failed intermittently after 1 November 2008. Steelhead M's archival tag showed negligible drift of <1 dbar in the pressure sensor between deployment and recovery, and no correction was performed. In contrast, the battery of steelhead J's archival tag lasted until after recapture but its pressure sensor exhibited a drift of approximately 7 dbar between deployment and recovery, which was corrected.

Based on recorded water temperatures, diving behavior, and geolocations, we divided the post-spawning migrations of steelhead J and M into five (Fig. 2, Table 2) and six phases (Fig. 3, Table 3), respectively. During the initial post-release freshwater phase (Phase I), steelhead J experienced temperatures in the Sacramento River that fluctuated according to a daily cycle, warming during the day but cooling during the night (Fig. 4a). There was an average difference of 2.01±0.51°C (mean ± SD) between daily peak temperatures (13.60±0.32°C) in the afternoon and minimum temperatures (11.58±0.60°C) around dawn during Phase I. In addition, steelhead J tended to swim deeper during the day (Table 2). Subsequently, steelhead J experienced a spike in the daily average temperatures (Phase II), with water temperature reaching a maximum of 24.4°C (Fig. 2).

Subsequent to the temperature spike, steelhead J moved into coastal California waters in Phase III of the post-spawning migration (Fig. 2, Table 2). Based on changes in diving behavior, estimated geolocations, and water temperature, steelhead J entered the ocean around 27 May 2008 and returned around 24 August 2008. In Phase III, diving behavior of steelhead J changed from being predominantly within the top 2 m of the water column to performing numerous dives >20 m (compare Fig. 4a with Fig. 5). Steelhead J also often exhibited crepuscular diving behavior during Phase III, typically diving to deeper depths at sunset before moving back to the surface at sunrise (Fig. 5), which led to generally deeper nighttime depths (Table 2). Changes in nighttime depths during the ocean phase appeared to be influenced by moon phase, with periods of shallower nighttime depths occurring during the full moon (Fig. 2). In addition, longitude estimates during Phase III were generally west of the mouth of San Francisco Bay (Fig. 6, Table 2) and water temperatures did not exhibit the typical freshwater diurnal cycle seen in Phase I (Fig. 5).

The return of steelhead J into freshwater was marked by a rapid increase in water temperature (Phase IV), followed by a relatively gradual decrease, coupled with cyclic variations, as the steelhead moved upriver towards the hatchery (Phase V) (Fig. 2). The return to the hatchery can be easily seen from the

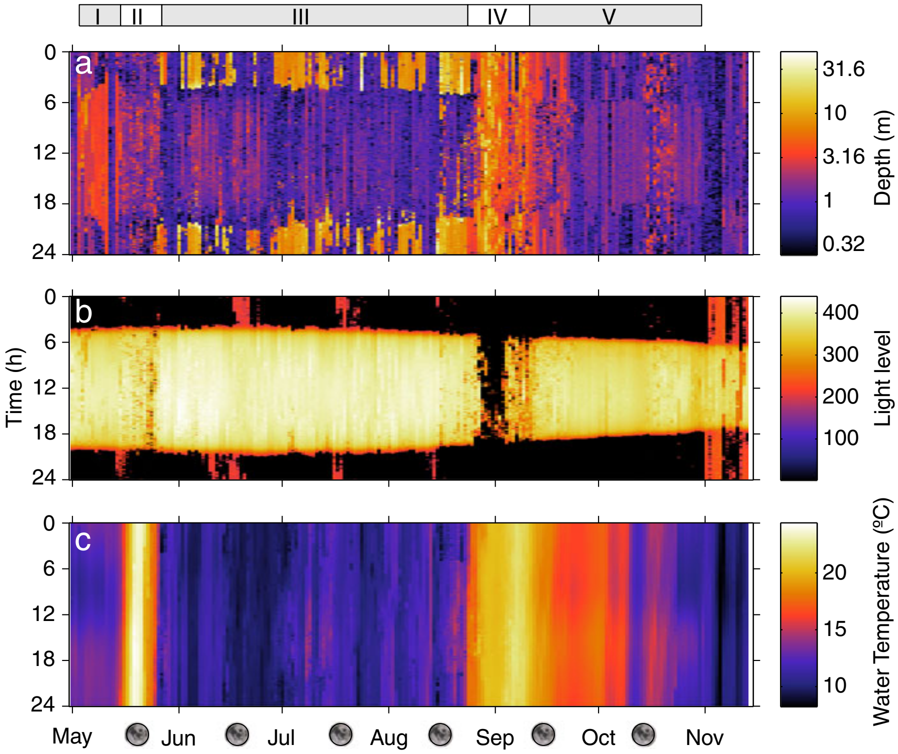

Fig. 2 Recorded **a** depths, **b** light levels, and **c** water temperatures from steelhead J every 240 s. Depths are plotted in log-scale. Light levels are recorded as relative log-scale units. *Bars* above panels indicate movement phases. Moons below panels indicate approximate full moon periods

relatively high light level during the night (Fig. 2). Interestingly, the archival tag from steelhead J also recorded a concomitant rise in opacity of the water column during both temperature spikes (Phases II and IV) (Fig. 7).

In a similar fashion, we divided the post-spawning migrations of steelhead M into six phases (Fig. 3, Table 3). The first two phases (Phase 1 and 2) were similar to those described for steelhead J. Phase 1 was marked by diurnal temperature cycles in freshwater (2.74±0.18°C difference between daily maximum and minimum temperatures) and very shallow diving behavior (Fig. 4b). In Phase 2, steelhead M also experienced a spike in temperatures (up to19.4°C). However, in contrast to steelhead J, steelhead M did not enter the coastal ocean after Phase 2. Instead, steelhead M likely stayed in the estuary for approximately 2 weeks after the temperature spike (Phase 3). During Phase 3, recorded temperatures did not exhibit cyclical fluctuations and the fish generally swam to

Table 2 Day and night water temperatures and depths (mean±SD) experienced by steelhead J during five phases of migration

Phase	Phase description	Start and end dates of phase	Day water temperature (°C)	Night water temperature (°C)	Day depths (m)	Night depths (m)	Average longitude (°W)
I	Initial Freshwater	03-May-08 14-May-08	12.43±0.81	13.12±0.55	3.08±1.50	1.65±1.15	122.42±0.37
II	First Hot Spike	15-May-08 26-May-08	19.38±3.37	19.22±3.36	1.86±1.16	1.62±1.81	121.71±0.68
III	Ocean and Estuarine	27-May-08 23-Aug-08	11.25±1.19	10.99±1.13	1.32±1.61	5.63±6.11	123.87±0.59
IV	Second Hot Spike	24-Aug-08 10-Sep-08	20.20±1.56	20.19±1.45	4.62±3.84	6.15±4.27	121.98±0.67
V	Return Freshwater	11-Sep-08 30-Oct-08	15.52±2.42	15.42±2.43	1.56±0.8	1.4±0.97	122.06±0.41

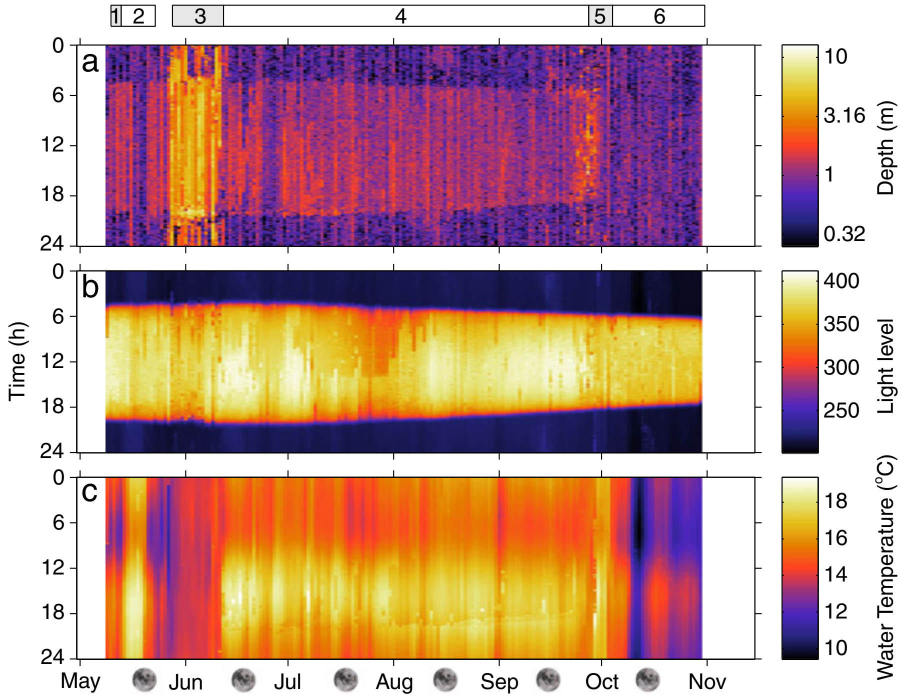

Fig. 3 Recorded **a** depths, **b** light levels, and **c** water temperatures from steelhead M every 240 s. Depths are plotted in log-scale. Light levels are recorded as relative log-scale units. *Bars* above panels indicate movement phases. Moons below panels indicate approximate full moon periods

deeper depths. However, the longitude estimates were consistently east of the mouth of San Francisco Bay, indicating that steelhead M likely remained in the river-estuarine system (Table 3). In addition, there was a period of 5 days between Phases 2 and 3, during which we did not explicitly describe as a phase because the water temperatures and diving behavior appeared similar to Phase 1.

After staying in the estuary for 2 weeks during Phase 3, steelhead M returned to freshwater and resided in freshwater for approximately 3.5 months (Phase 4). The water temperatures experienced by steelhead M during Phase 4 continued to have typical freshwater diurnal fluctuations (Fig. 3c), suggesting that the fish resided in freshwater during this period. In addition, steelhead M tended to swim to shallower depths during the night of Phase 4 (Table 3). Similar to steelhead J, steelhead M experienced a spike in average temperatures, albeit a smaller spike (Phase 5), followed by a general decrease in temperatures as it

Table 3 Day and night water temperatures and depths (mean ± SD) experienced by steelhead M during six phases of migration

Phase	Phase description	Start and end dates of phase	Day water temperature (°C)	Night water temperature (°C)	Day depths (m)	Night depths (m)	Average longitude (°W)
1	Initial Freshwater	10-May-08 12-May-08	14.20±1.13	14.49±0.69	1.23±0.33	0.72±0.35	122.17±0.25
2	First Hot Spike	13-May-08 22-May-08	15.93±1.81	16.15±1.58	1.10±0.40	0.79±0.37	121.94±0.54
3	Estuarine	28-May-08 11-Jun-08	13.85±0.48	13.98±0.44	3.59±1.27	2.57±1.70	121.76±0.68
4	Freshwater Residency	12-Jun-08 26-Sep-08	16.37±1.11	15.77±0.86	1.17±0.36	0.79±0.38	122.21±0.46
5	Second Hot Spike	27-Sep-08 03-Oct-08	16.19±0.97	16.20±0.82	1.42±0.91	0.94±0.48	121.89±0.43
6	Return Freshwater	04-Oct-08 30-Oct-08	13.12±1.42	12.88±1.23	0.81±0.31	0.77±0.32	122.00±0.26

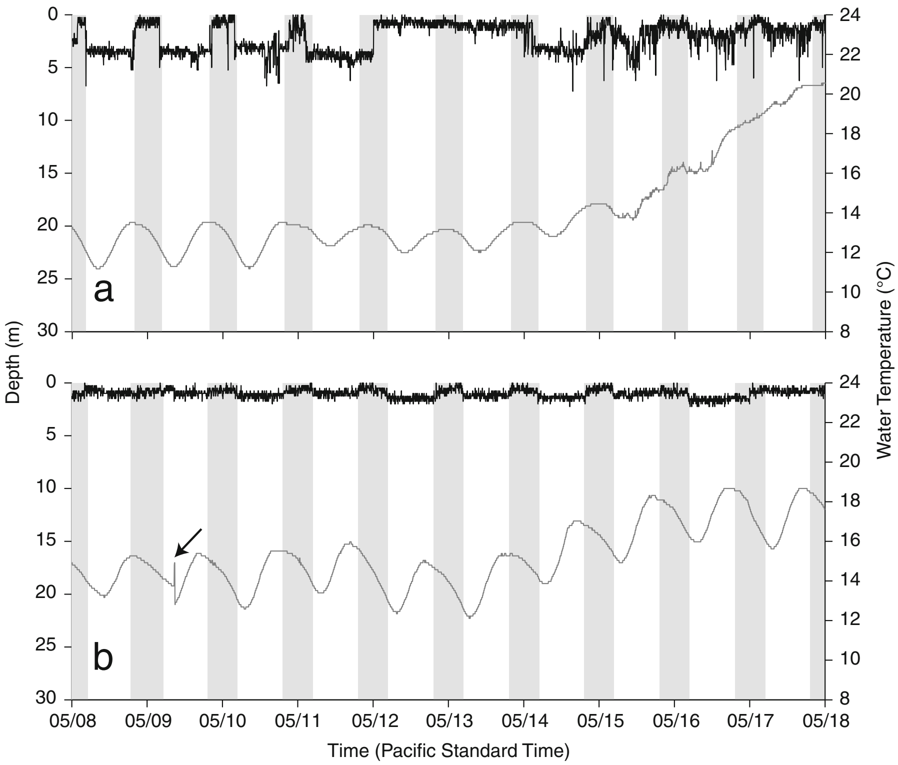

Fig. 4 Depths and water temperatures from steelhead **a** J and **b** M during 10-day periods in the Sacramento River. *Black* and *gray lines* indicate depths and water temperatures, respectively. *Gray* areas indicate night. *Arrow* indicates transfer of steelhead from holding tank and release into Battle Creek

moved upstream towards the hatchery (Phase 6) (Fig. 3c). Unlike steelhead J, both spikes in temperature were not associated with large increases in opacity for steelhead M and continued to have diurnal cycles (Fig. 7).

Over the entire periods at liberty, the maximum depths recorded by the archival tags were 51 and 12.5 m for steelhead J and M respectively. The recorded temperatures ranged from 8.2 to 24.4°C and from 9.4 to 19.4°C for steelhead J and M, respectively.

Discussion

This study documents one of the first uses of geolocating archival tags in salmonids, recording their

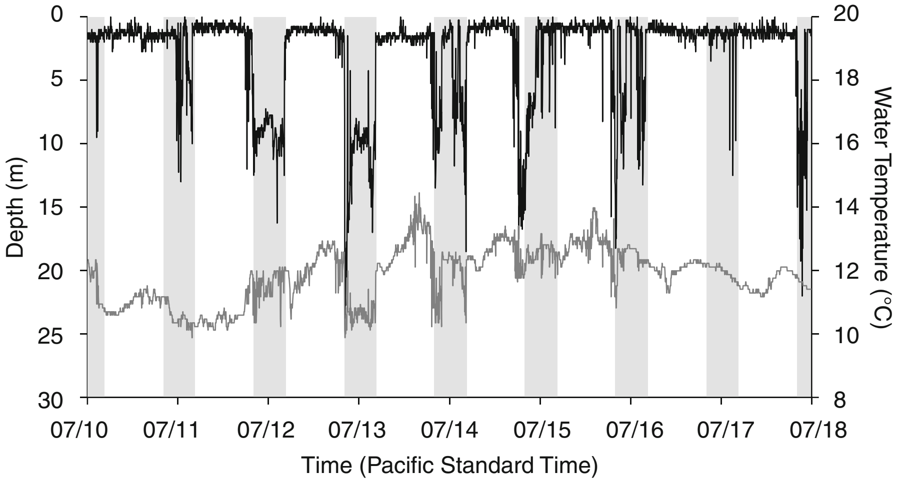

Fig. 5 Depths and water temperatures from steelhead J during a 8-day period in coastal California waters. *Black* and *gray lines* indicate depths and water temperatures, respectively. *Gray areas* indicate night

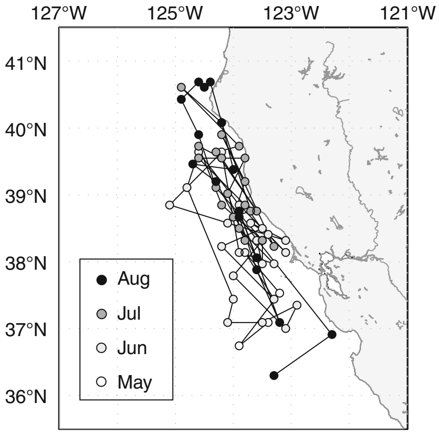

Fig. 6 Estimated marine movements of steelhead J by month from May to August 2008

emigration to the ocean and their return migration. These geolocating archival tags allow us to elucidate the horizontal movements of steelhead on their ocean migrations and fine-scale changes in vertical movements and thermal habitat. One of the limitations of this study is the relatively small number of tags deployed and recovered. This is unfortunately a common limitation of current salmonid archival tag studies due to high cost of tags and low rate of returns (e.g., Hinke et al. 2005; Walker and Myers 2009; Nielsen et al. 2011; Hayes et al. 2011). However, these results provide a detailed record of riverine, estuarine, and oceanic habitat utilization with detailed information on steelhead diurnal behaviors, ambient temperature preferences, and diving behaviors.

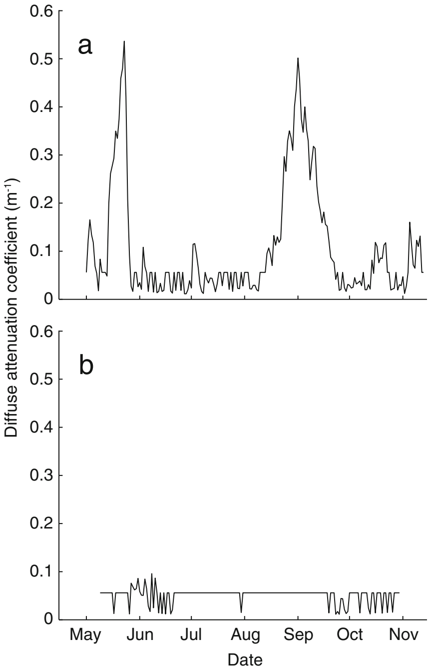

Fig. 7 Estimated diffuse attenuation of the water column along the migratory path of steelhead **a** J and **b** M

Horizontal movements

In this study, both steelhead kelts recovered from a hatchery in the Sacramento River ecosystem appear to be less oceanic than a previous study in Scott Creek, a small coastal stream approximately 100 km south of the mouth of San Francisco Bay (Hayes et al. 2011). One steelhead remained in the river-estuarine system while the other stayed in coastal California waters. In contrast, Hayes et al. (2011) found that both recaptured steelhead kelts from Scott Creek likely migrated to the Gulf of Alaska, based on temperatures recorded by temperature-only archival tags. This suggests that steelhead kelts from a large river and estuary system, like the Sacramento River, may tend to be less oceanic than steelhead kelts from small coastal streams. The relationship between migratory pattern and river size has been postulated by Savvaitova (1975) in Kamchatka steelhead. Savvaitova (1975) observed that anadromous steelhead migrating far offshore in the North Pacific tend to predominate in small rivers (<100 km) while coastal and river/estuarine types tend to dominate larger rivers (250–300 km) (reviewed in Quinn and Myers 2004).

Size and growth of the steelhead also appear to vary with migratory history. Steelhead J, which migrated into the coastal ocean, grew substantially more than steelhead M, which remained in the river-estuarine system. Although sex-differentiated growth and/or behavior may have played a role in the growth differences between the two fish (see Table 1), observations in the California Central Valley and Kamchatka suggest that steelhead juveniles and adults that migrate into the ocean tend to grow faster and larger (Pavlov et al. 2008; Null et al. 2012). This relationship between river size, migratory pattern, and fish growth may be related to the availability of freshwater/estuarine feeding grounds and their productivity (Pavlov et al. 2008). Small rivers tend to be less productive and food resources maybe relatively poor. On the other hand, food resources in larger rivers and estuaries may be adequate for survival and maturation of resident steelhead (Pavlov et al. 2008). The migratory history of an individual fish may also change from riverine to oceanic and vice versa (Zimmerman et al. 2003). There is evidence of a tradeoff between higher survival in steelhead that remain in the river versus higher growth in steelhead that emigrate into the ocean (Null et al. 2012). Both genetic and environmental factors likely interact and influence the migratory pattern of steelhead but relatively little research has been done to understand the anadromy patterns in steelhead (Quinn and Myers 2004). Our study does not have a large enough sample size to estimate proportions of migratory types. However, our results do suggest that future research be performed on larger numbers of steelhead from both large rivers and small coastal streams in order to validate these observations and elucidate the processes that influence anadromy in this species. With a larger sample size, future studies may discover an even greater diversity of migration patterns and life history strategies in steelhead populations.

Besides improving our understanding of the processes that affect anadromy patterns, increased knowledge of which areas of the ocean are used by different steelhead stocks may improve our management and conservation of these stocks. For example, if the steelhead stocks from small coastal streams tend to be more oceanic than stocks from large river-estuary systems, we hypothesize that ocean conditions will have a stronger influence on the survival of stocks from small coastal streams like Scott Creek.

Vertical movements and thermal habitat

Similar to previous studies, steelhead kelts in this study remained relatively close to the surface throughout the entire post-spawning migration and exhibited dives below 20 m in the ocean (Walker and Myers 2009; Nielsen et al. 2011). However, there appeared to be subtle diurnal differences in the vertical movements at different phases of the migration. During the initial post-release freshwater phase, the steelhead were deeper during the day but the opposite pattern was observed during the ocean phase, with the steelhead being deeper during the night. Steelhead in this study also often exhibited diving behavior during dawn and dusk crepuscular periods, similar to large pelagic fishes (Block et al. 2001; Teo et al. 2007a). In contrast to previous studies in Alaskan waters on steelhead (Walker et al. 2000; Nielsen et al. 2011), the steelhead in this study tended to dive deeper during the night in the ocean. Steelhead adults in Alaskan waters appear to be at deeper depths during the day for the majority of their time in the ocean. For example, Nielsen et al. (2011) found that most dives (>20 m) by steelhead kelts from Alaska, occurred during the day but the deepest dives (> 32 m) occurred at night. On the other hand, studies on other salmonids in various locations and seasons have shown a variety of depth preferences, depending on location and season (Walker et al. 2000; Hinke et al. 2005; Walker and Myers 2009). The diving behavior of steelhead in the ocean also appeared to be influenced by moon phase, with the full moon tending to result in shallower nighttime depths. This is different from the pattern exhibited by large pelagic fish like bigeye tuna and swordfish, which tend to dive deeper on nights of the full moon (Schaefer and Fuller 2002; Dewar et al. 2011). The abovementioned differences in diel depth preferences may be due to a variety of factors (e.g., prey availability, presence of predators, and water temperature) but this study was not designed to determine the relative importance of these factors. A larger study with individuals tagged in a variety of locations and seasons, coupled with stomach contents analysis, may be necessary to elucidate the factors that influence diving behavior.

Over the entire migration, the steelhead kelts experienced a wide range of temperatures. In freshwater, water temperatures varied according to a diurnal cycle by about 2–3°C, due to solar warming followed by subsequent cooling in the evening. The steelhead also experienced a large increase in temperature just before reaching the estuary and ocean. This temperature spike coincided with an increase in the opacity of the water, suggesting that the water during this period was warm and murky. The steelhead were likely moving through the Sacramento Delta, which has relatively warm and murky water (Pers. Obs.) (also see the California Data Exchange Center operated by the California Department of Water Resources, http://cdec.water.ca.gov). During the ocean phase, steelhead J did not experience highly variable temperatures because the fish remained in coastal California waters and did not dive much below the surface mixed layer. Since steelhead J dived deeper during the night, the steelhead experienced slightly cooler temperatures during the night. However, these slight diurnal differences in temperature are not likely to be biologically significant.

The pattern of ocean temperatures recorded by the tags is consistent with the migratory patterns observed in the steelhead kelts. In a previous study, water temperatures showed a consistent decrease from approximately 12 to 8°C as steelhead kelts moved from coastal California waters to the Gulf of Alaska, before warming again as the fish returned to coastal California (Hayes et al. 2011). However, steelhead J from this study did not experience any consistent change in water temperature as it remained in coastal California waters. Nielsen et al. (2011) found a similar lack of consistent change in the ocean temperatures experienced by steelhead kelts from Ninilchik River, Alaska, which was likely due to the steelhead in that study remaining in coastal waters. Ninilchik River enters the ocean via Cook Inlet, a large estuary opening into the Gulf of Alaska. The observation of steelhead kelts from a large river and estuary system remaining in coastal waters is consistent with the pattern observed in this and previous studies (Pavlov et al. 2008).

Use of archival tags in salmonids

This study demonstrates some of the benefits and limitations of using archival tags on salmonids. These archival tags excel at providing detailed information on the movements and in situ thermal habitat of salmonids on their ocean migrations. We can observe changes in their vertical and horizontal movements in different habitats and environments. With enough geolocation data, we can use coincident remotely-sensed environmental data to determine how changing environmental conditions affect their movements (e.g., Teo et al. 2007b). In addition, adding other sensors onto these tags (e.g., conductivity sensors and 3-D accelerometers) will increase the capability of these tags, albeit at the expense of increasing tag cost.

However, depending on marine survival rates, tag return rates may be low (especially for studies on smolts). Therefore, studies with large number of deployed tags will be necessary to obtain enough recovered tags for statistical analysis and modeling (e.g., Kurota et al. 2009). The current high cost of tags is prohibitive and has limited the scale of recent salmonid studies with these types of tags (e.g., this study; Nielsen et al. 2011; Hayes et al. 2011). On the other hand, tag manufacturers recognize the importance of tag cost in these studies and relatively low-cost tags designed specifically for salmonids may not be far off in the future (P. O'Flaherty, Lotek Inc., pers. comm.).

Current geolocation algorithms, based primarily on changes in light level and water temperature, are not able to track the fine-scale horizontal movements of fish in river systems. Therefore, we deployed acoustic tags concurrently on a subset of released fish in this study. Unfortunately, out of the two fish that returned, one was not implanted with an acoustic tag and the other expelled its acoustic tag. However, we believe that, if a network of acoustic receivers is already in place, the concurrent use of archival and acoustic tags will allow researchers to leverage the best characteristics of each type of tag in different environments. Acoustic tags allow us to track fish movements and mortality at different stages of a track, wherever a network of acoustic receivers is available (see other studies in this issue). For example, Null et al. (2012) estimated the median travel speeds of steelhead kelts on their outgoing (0.2–10.0 km d^{-1}) and return (1.2–15.1 km d^{-1}) migrations at different reaches of the Sacramento River. On the other hand, archival tags provide detailed information on vertical movements and thermal habitat, as well as horizontal movements in the open ocean, where deployment of acoustic receivers is difficult and costly.

Expulsion of tags by salmonids, especially steelhead, is a recurrent problem of acoustic and archival tagging studies (Welch et al. 2007; Nielsen et al. 2011). In this study, we know of one acoustic tag that was expelled by steelhead M but more tags may have been expelled. Steelhead smolts appear to expel tags from the peritoneal cavity at a higher rate as compared to other salmonids (Sandstrom 2012). Therefore, in future studies, it may be better to attach tags through the dorsal pterygiophores via pins (Walker et al. 2000; Hayes et al. 2011) or some other attachment method. Another advantage of attaching the tags to the exterior of the fish is the ability to use tags that measure conductivity in addition to depth and temperature. Conductivity measurements allow us to clearly determine the time an animal leaves or returns to estuarine and freshwater habitats (Walker and Myers 2009). It will be important that a series of experiments are performed in the near future to determine the optimal method for tag attachment on salmonids at different life stages. In addition, it may be useful perform experiments to evaluate the effect of different tag materials and coatings on expulsion rates (Cooke et al. 2011).

Overall, the ability to collect detailed information on salmonid movements and thermal habitat is very important to understanding the processes that affect their survival at various stages. There will therefore likely be a growing number of studies using a combination of archival and acoustic tags to track these fish in the near future, especially if the cost of tags becomes less prohibitive.

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