Environ Biol Fish (2013) 96:273–286
DOI 10.1007/s10641-012-0001-x

Diel movements of out-migrating Chinook salmon *(Oncorhynchus tshawytscha)* and steelhead trout *(Oncorhynchus mykiss)* smolts in the Sacramento/San Joaquin watershed

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Received: 8 April 2011 / Accepted: 9 March 2012 / Published online: 29 March 2012

Abstract We used ultrasonic telemetry to describe the movement patterns of late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) smolts during their entire emigration down California's Sacramento River, through the San Francisco Bay Estuary and into the Pacific Ocean. Yearling hatchery smolts were tagged via intracoelomic surgical implantation with coded ultrasonic tags. They were then released at four upriver locations in the Sacramento River during the winters of 2007 through 2010. Late-fall run Chinook salmon smolts exhibited a nocturnal pattern of migration after release in the upper river. This is likely because individuals remain within a confined area during the day, while they become active at night and migrate downstream. The ratio between night and day detections of Chinook salmon smolts decreased with distance traveled downriver. There was a significant preference for nocturnal migration in every reach of the river except the Estuary. In contrast, steelhead smolts, which reside upriver longer following release, exhibited a less pronounced diel pattern during their entire migration. In the middle river, Delta, and Estuary, steelhead exhibited a significant preference for daytime travel. In the ocean Chinook salmon preferred to travel at night, yet steelhead were detected on the monitors equally during the night and day. These data show that closely related *Oncorhynchus* species, with the same ontogenetic pattern of out-migrating as yearlings, vary in migration tactic.

Keywords Diel · Chinook salmon · Steelhead trout · Smolt · Sacramento River · Migration

Introduction

Out-migration is a key process in the life history of anadromous salmonids. Juveniles which have spent

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from several months to years feeding and growing in upstream freshwater pools undergo smoltification and migrate downstream to the ocean, a process which requires physiological and behavioral adaptations (Moyle 2002). As they migrate downstream, the smolts will likely be exposed to a range of new habitats such as deltas and estuaries, with their associated biological and physical environments. It is reasonable to expect that the diel migration tactics of smolts will vary as a response.

Salmonid species display a wide range of diel migration tactics in different rivers (Ledgerwood et al. 1991). Bradford and Higgins (2001) found that within one river there may be variation among individuals of a stream-dwelling population depending on local habitat condition. Other studies described a change from diurnal activity in warmer months to a nocturnal activity in winter with resident fish (Metcalf et al. 1999; Burns et al. 1997; Valdimarsson et al. 1997).

Smolts may time the diel rhythm of their migration to optimize their chance of completing migration to the ocean. Predation risk may be lower at night when salmon rely heavily on chemical alarm cues at the expense of feeding opportunity during the day (Leduc et al. 2010). This rhythm may depend partly on water temperature. Ibbotson et al. (2006) found that at temperatures below 12°C, hourly rates of migration were significantly greater during the night, and no difference between diurnal and nocturnal hourly migration rates above 12°C. Diel rhythms may also be related to turbidity (Gregory and Levings 1998), predator avoidance (Rieman et al. 1991; Poe et al. Poe et al. 1991), or flow (Greenstreet 1992).

The objective of this paper is to examine the changing diel movements between 1+ hatchery late-fall run Chinook salmon smolts and 1+ hatchery steelhead smolts as they migrate down the Sacramento River through the Delta and San Francisco Bay Estuary (hereafter referred to as the “Estuary”) and into the Pacific Ocean. We also describe the difference in diel tactics that these two species exhibit during the emigration to sea.

Methods

Study area

The Sacramento River is the largest river in California and drains an area of about 70 000 km^2 (http://water.usgs.gov/GIS/huc_name.html). The river flows from the eastern slopes of the Klamath Mountains through the Central Valley, with the Sierra Nevada Mountains to the east and the Coast Range to the west. For this study we focused on the behavior of late-fall run Chinook salmon and steelhead smolts in the reach of the river below Keswick Dam in Redding, California commonly referred to as the Lower Sacramento, to ocean entry at the Golden Gate. We separated the study area into six reaches based on changes in habitat: 1) upper river from Redding to Hamilton City; 2) middle river from Hamilton City to Meridian; 3) lower river from Meridian to Freeport; 4) the Delta from Freeport to Antioch; 5) the Estuary from Antioch to the Golden Gate; and 6) the ocean (Fig. 1). The upper river is typical of a big tailwater with long shallow riffles, gravel bars, and deep pools. The middle river consists of deeper water with sandy banks and large woody debris strewn throughout the river. The lower river has been channelized with levees and is similar to a pipeline that channels water downriver with riprap banks. In this section water is pumped onto the adjacent fields for agricultural watering purposes. Overall, the river is wide in the upper portions and narrows as it extends downstream.

The river then flows into the Sacramento-San Joaquin Delta where it widens upon converging with the San Joaquin River creating the largest freshwater tidal Estuary on the United States Pacific Coast. The Delta has been modified for agriculture purposes and water exports to Southern California. This part of the watershed is more vegetated than other sections of river and contains many natural and man-made sloughs covering over one thousand square kilometers of land. At the west end of the Delta the Sacramento and San Joaquin Rivers flow into Suisun Bay. From Suisun the water flows through Carquinez Strait to San Pablo Bay, San Francisco Bay and then under the Golden Gate Bridge and into the Pacific Ocean.

Tagging and release

We tagged and released 1110 late-fall run Chinook salmon and 1100 steelhead smolts during December and January over four years, from January 2007 through January 2010, into the Sacramento River (Table 1). Yearling smolts were obtained from the Coleman National Fish Hatchery (CNFH) in Anderson, California and are offspring from a program that began in 1942. Late-fall run Chinook salmon smolts are comprised from nearly all hatchery stock with up to 25 %

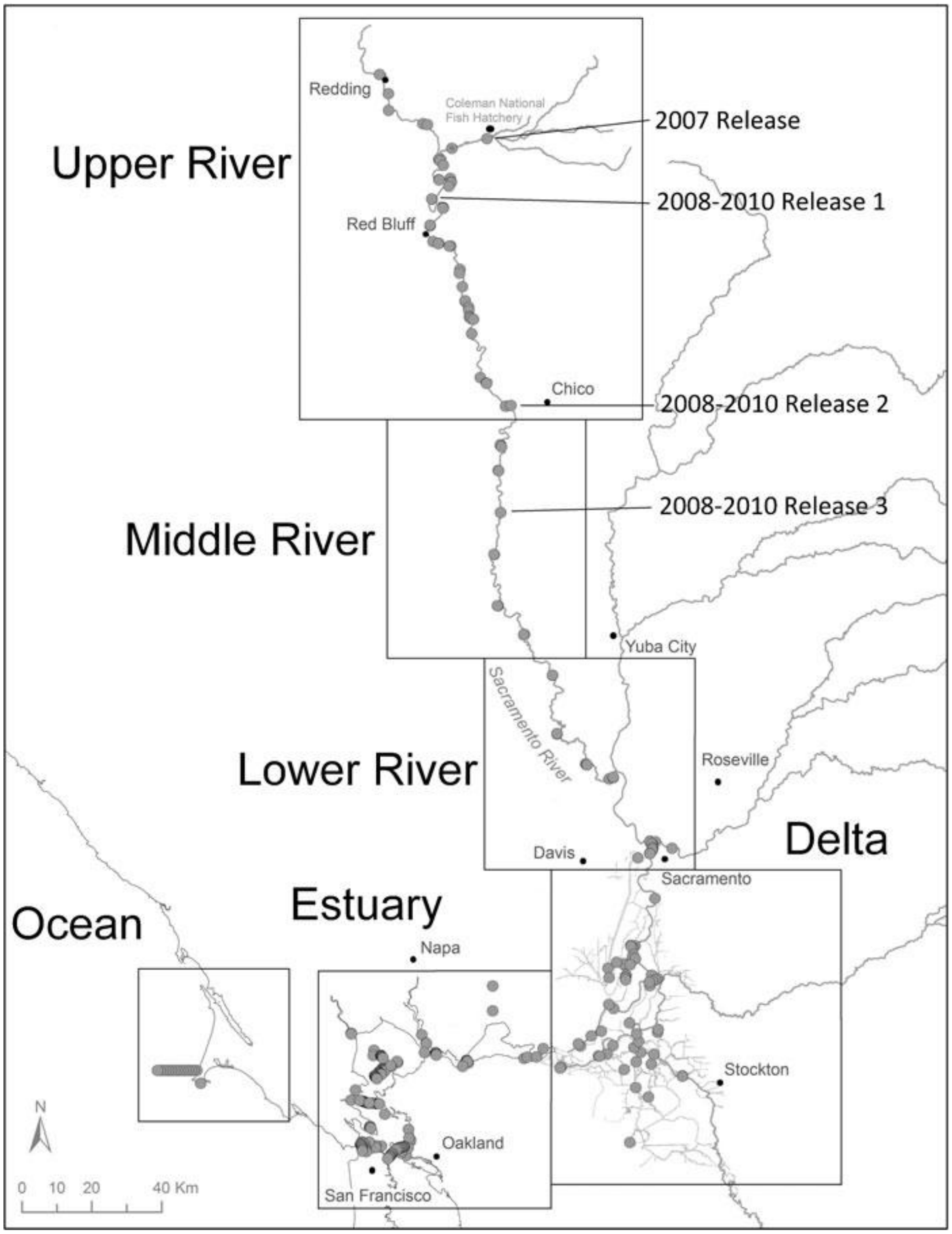

Fig. 1 Study area consisting of three reaches along the mainstem of the Sacramento River, the Delta, San Francisco Bay Estuary, and Pacific Ocean (reaches are delineated by rectangles). The locations of the tag detecting monitors are indicated by solid gray circles, release location for year 1 and release locations for following three years

crossed with hatchery adults. From 2001—2002 there was a maximum of 10 % incorporation of natural origin steelhead. Prior to 2008 returning hatchery steelhead were spawned with up to 10 % incorporation of natural origin. After 2008 there has been no incorporation of natural origin steelhead. These yearling salmonid smolts, from the CNFH, have been used for other studies (Perry et al. 2010; Ammann et al. 2012 (this issue); Michel et al. 2012 (this issue); Sandstrom et al. 2012 (this issue); Singer et al. 2012 (this issue), as well in studies of other life histories (Null et al. 2012 (this issue); Teo et al. 2012). Chinook salmon and steelhead smolts were implanted with Vemco 69 kHz V7 or V9 transmitters. The surgical procedures used to implant transmitters through an incision into the coelomic cavity of these fish are described in detail in Ammann et al. 2012 (this issue). Late-fall run Chinook salmon smolts and steelhead trout smolts were exposed to the same conditions prior to and during tagging/release. After surgeries, fish were held in tanks for observation prior to release. The smolts were transported in coolers with aerators to the release sites and held until release after dark. Temperatures were recorded in the coolers and river upon arrival, and tempered when necessary to avoid stress or mortality. During the first year fish were released into Battle Creek adjacent to the CNFH. In the

Table 1 Weight and length of Chinook salmon and steelhead

Species	Year	n	Average Weight (g)	SD	Average Length (mm)	SD	Release Sites (rkm)	Tag	Tag Ratio Ave	Tag Ratio SD
Chinook salmon	2007	200	46.6	9.75	165	11	534	V7-2L	3.5	0.7
Chinook salmon	2008	304	52.6	13.83	169	13	518, 414, 363	V7-2L	3.2	0.8
Chinook salmon	2009	300	38.9	7.88	152	8	518, 414, 363	V7-2L	4.1	0.8
Chinook salmon	2010	306	39.3	8.83	152	10	518, 414, 363	V7-2L	4.1	0.9
Steelhead trout	2007	200	111.6	29.16	217	18	527, 518	V7-1L	3.7	1.0
Steelhead trout	2008	300	116.8	21.13	224	13	518, 414, 363	V7-2L	4.2	0.7
Steelhead trout	2009	300	139.1	28.97	228	15	518, 414, 363	V7-1L	1.3	0.3
Steelhead trout	2010	300	91.1	27.2	196	19	518, 414, 363	V7-1L	2.1	0.7

next three years fish were released at three sites: 1) Jelly's Ferry; 2) Butte City; and 3) Hamilton City along the upper and middle portions of the Sacramento River. Fish were released at the same time at each site just after civil twilight.

Laboratory trials to evaluate effects of surgery and transmitters on a subsample of the fish used in this study were conducted in 2007 and 2008. For late-fall run Chinook smolts, transmitters had no significant effect on growth or survival out to 7-months (year 2007, n=75) or out to 5-months (year 2008, n=44), and there was no tag loss in either trial (Ammann et al. 2012 (this issue)). In two trials with steelhead smolts (2007, n=75; 2008, n=120), the fish with transmitters had reduced growth compared to the PIT-tag only treatment for the first 30 days, but no difference from then out to 6 and 5 months duration, respectively. There was no difference in survival for acoustic tagged, sham-surgery and PIT-tag only treatment and tag loss was 15 to 52 % over 2 to 4 months (Ammann in prep). The battery life of the tags are estimated to be 52 d for Chinook salmon and 140 d for steelhead but lasted longer in the tests. In the laboratory trial Chinook salmon tags were observed to last from 266–789 d (ave. 606 d) in 2007 and from 127–297 d (ave. 194 d) in 2010. No trials were conducted in 2008 or 2009 and only one trial was conducted on steelhead tags. The observed life of steelhead tags was from 214–1078 days (ave. 642 d) in 2007.

Array deployment

The California Fish Tracking Consortium (http://californiafishtrackingconsortium.ucdavis.edu) maintains an array of 420 monitors at over 186 locations in the Sacramento/San Joaquin Rivers, San Francisco Bay Estuary and coastal waters outside San Francisco Bay. This array is one of the largest in the world, spanning over 500 km from Redding, California to the Golden Gate Bridge in San Francisco, and includes a line of monitors off Point Reyes in the Pacific Ocean which are part of the Pacific Ocean Shelf Tracking Project (POST, http://www.postcoml.org/).

The V7 and V9 tags were detected by submersible, single channel monitors (VR2/VR2W and VR3, Vemco Ltd). To minimize signal collision by tags which are in the same place simultaneously, each tag had a random delay around a mean time interval (30 s for Chinook salmon, and 60 s for steelhead) between pulses. Range tests were conducted throughout the watershed to determine monitor deployment strategy. Detection ranges were from 50 m in the river to hundreds of meters in the brackish Delta. Monitoring stations were deployed either as single monitor sites where the monitor would detect tags across the entire river, dual monitor stations spaced 100 m apart on opposite sides of the river, or many monitor sites at bridges and open water sites. Detections were retrieved from the monitors at 3–4 month intervals for freshwater monitors, and semi-annually for the Golden Gate and ocean moorings.

Data analysis

More than 17 000 first detections on the monitors were used for analyses. Detections of fish during the first 24 h after release were eliminated to account for bias due to nighttime releases and to allow for acclimation to the river. False detection records were also discarded from the analyses. We considered a false detection to be a single detection on a monitor that did not coincide with a logical series of detections before and after it. False detections may also be a series of detections that do not appear to be that of a smolt (egg. persistent upstream movements of a fish that may have been in a predator). We plotted circular histograms with statistical software (Oriana version 3.21, Kovach Computing Services) using the first detection at each location with the assumption that the fish were migrating at that time. We then calculated the mean vector (Rayleigh's *r* coefficient) to determine whether or not detections were uniform throughout the day or clustered around a certain time. An 'r'-vector length of '1' indicates that all fish were detected at the same hour of the day and a length of '0' is evidence that fish were detected equally at every hour of the day.

We used the initial detection of tagged steelhead and Chinook salmon at each monitor and classified it as either day or night. Detections were classified as 'day' if the tagged smolt passed between sunrise and sunset for a particular reach and day. Likewise, detections were classified as 'night' if the detection occurred between sunset and sunrise. We determined the percentage of nighttime detections for each species, at each site, in each river reach for all years separately and combined. The time of sunrise and sunset was calculated for each detection using the algorithm developed by the National Oceanic & Atmospheric Administration (NOAA) (http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html) and implemented using R software (version 2.12.1, R Development Core Team 2010) the R package maptools (Lewin-Koh et al. 2010). A central latitude and longitude for each reach was used for all calculations.

We discarded monitors with less than 10 first detections and estimated the probabilities of tagged fish passing monitors at night based on logit-transformation. The predictions were then back-transformed to return to an estimate of probability. The number and patterns of fish detections for day and night monitoring, and river reaches, for both Chinook salmon and steelhead, were analyzed using a Poisson Generalized Linear Model as the detections are counts. The Poisson model included effects for day/night differences, river reach and species, along with all interactions among these effects. To keep the estimates in the allowable range we used a link function and to account for the difference between day and night at the time of year the fish were migrating (14 h of darkness) we used an offset function. Post hoc comparisons among the treatment levels were done based on the estimated least squares means. Following this factorial analysis, additional analyses involving stratified and paired comparisons were run that focused on the observed patterns for individual species or within particular river reaches.

To compare differences between species, the non-parametric Kruskal-Wallis One Way ANOVA on Ranks was used to determine whether or not there was a significant difference in percent nighttime travel in each reach. We used an ANOVA with Dunn's *post hoc* test to determine how similar the weight and length of fish of the same species were between years. We used the same test to compare weight and length between the two species.

We used a logistic Generalized Additive Model (GAM) to determine if there was a temperature trend for increasing daytime activity. We used the GAM to allow for the possible nonlinearity of the relationship between temperature and the logit of the probability of daytime activity. With this model we focused only on year-to-year and temperature effects and used spline functions to fit a nonlinear response. The GAM outputs t-stat and chi-square results. We used these same methods to analyze flow measurements. We used median turbidity values for each river reach because the information was non-finalized from the Department of Water Resources, California Data Exchange Center (http://cdec.water.ca.gov/).

Results

The V7 and V9 tags used in this study averaged 1.3 to 4.2 % tag weight to body weight ratio (Table 1). There was a significant difference ($P<0.05$) in the lengths and weights of Chinook salmon in all years except when comparing 2009 and 2010 weight, 2007 and 2008 lengths, and 2009 and 2010 lengths. Steelhead lengths and weights were also significantly different ($P<0.05$) in all years except for the comparison between 2007 and 2008 weights. The length and weight comparison between Chinook salmon and steelhead were significantly different ($P<0.05$).

There were approximately 14 h of darkness and 10 h of light during the winter months when these fish were migrating. The majority of detections occurred within three months (December through February) after release. In the upper river late-fall run Chinook salmon traveled almost exclusively at night with 90.6 % of detections recorded during these hours (Fig. 2). As Chinook salmon smolts moved downstream, the proportion of their diurnal movement progressively increased, although nocturnal movements remained significantly greater. In every reach of the study, except for the Estuary, there was a significant difference between night and day detections (Least Squares Means, $P_{upper}<0.001$; $P_{middle}<0.001$; $P_{lower}<0.001$; $P_{delta}<0.001$; $P_{estuary}=0.36$). In the upper river Chinook salmon smolts were uniformly detected throughout the night showing no preference for any one time period. The fish ceased migrating after sunrise and began migration again after sunset. In the middle and lower reaches salmon did not abruptly stop migrating at sunrise; rather there was a gradual decrease in detections. In the ocean there were 20 late-fall run Chinook salmon observations of which 13 occurred at night and 7 during the day (65.0 % and 35.0 %).

Steelhead smolts migrate more uniformly throughout the day in all regions of the river, Estuary and ocean compared with yearling Chinook salmon smolts (Fig. 3). As with Chinook salmon, nighttime detections of steelhead decreased as fish progress downstream, although the difference was less. In the upper river 63.0 % of detections occurred at night compared to 90.6 % of salmon smolts. Upon reaching the Estuary, the percent of nighttime detections decreased to 40.9 %, compared to 57.0 % of Chinook salmon. In the upper river there was a significant amount of nighttime travel. There was no difference between day/night detections in the lower river but significant preferences for daytime migration in the middle river, Delta, and Estuary (Least Squares Means, $P_{upper}<0.001$; $P_{middle}<0.001$; $P_{lower}=0.39$; $P_{delta}<0.001$; $P_{estuary}<0.001$). While there was a decrease in steelhead detections at night, there were no large shifts when the sun rose/set; detections were evident at all times during the day. There were six steelhead detections in the ocean of which three were during nighttime and three during the day. The Rayleigh's *r* coefficient decreased as Chinook salmon progressed downriver where the *r* for steelhead began to increase upon reaching the Delta and Estuary (Table 2).

There were significant differences between species in each reach of the river. Year and river kilometer were both significant predictors of the percentage of night detections for late-fall run Chinook salmon ($P<0.001$). In all four years Chinook salmon preferred nocturnal movements when upstream, which gradually decreased as the fish moved downstream ($P<0.05$), but remained greater than 50 % nocturnal in every reach of the river (Fig. 4, Table 3). For steelhead, river kilometer was a significant predictor of nighttime detections ($P=0.01$), but year was not. Steelhead displayed a less pronounced but similar behavior pattern in 2007 ($P<0.01$) and 2010 ($P=0.037$), but showed no downstream change in diel activity in 2007 or 2009 (Fig. 4). We plotted a linear regression line (not shown) on the estimated probabilities vs. the river km and every line except for 2008 steelhead was significantly different from zero. The residuals about the linear regression fits showed increasing variation about the line with increasing distance downriver.

There were highly significant linear effects due to temperature for Chinook salmon (t-stat=11.49, $p<.0001$). There is an increase in activity with increasing temperature until the relationship plateaus (Fig. 5). Above 13°C the linear relationship between diel movements and temperature becomes nonlinear (chi-square 29.06, $p=0.0003$). There are fewer temperature measurements below 5°C and above 15°C which creates larger confidence bands outside those temperatures.

In the steelhead model (Fig. 6), the relationship is slightly decreasing or flat until 8°C creating a significant nonlinear relationship between daytime activity and temperature (chi-square 34.68, $p<0.001$). Above 8°C there is a significant linear increase in daytime activity with increasing temperature (t-stat=11.49, $p<0.001$). Above 18°C there are fewer temperature measurements creating larger confidence bands.

There were significant discharge effects for both species, but a little different in form. Chinook salmon were more likely to be detected during the day with increasing discharge regardless of flow direction (chi-square 365.3, $p<0.0001$). In the Estuary Chinook salmon were detected more during the day with reverse flows from the incoming flood tide. Between zero and approximately $-100\ m^3/s^{-1}$ there is an increase in daytime detection. As the downstream discharge increases from approximately $350\ m^3/s^{-1}$ Chinook salmon are also more likely to be detected during the day (Fig. 7).

For steelhead the effects are muted, and the increase in detection during flood tides is not as evident in the Estuary. In the rest of the system, steelhead are generally more likely to be detected during the day with

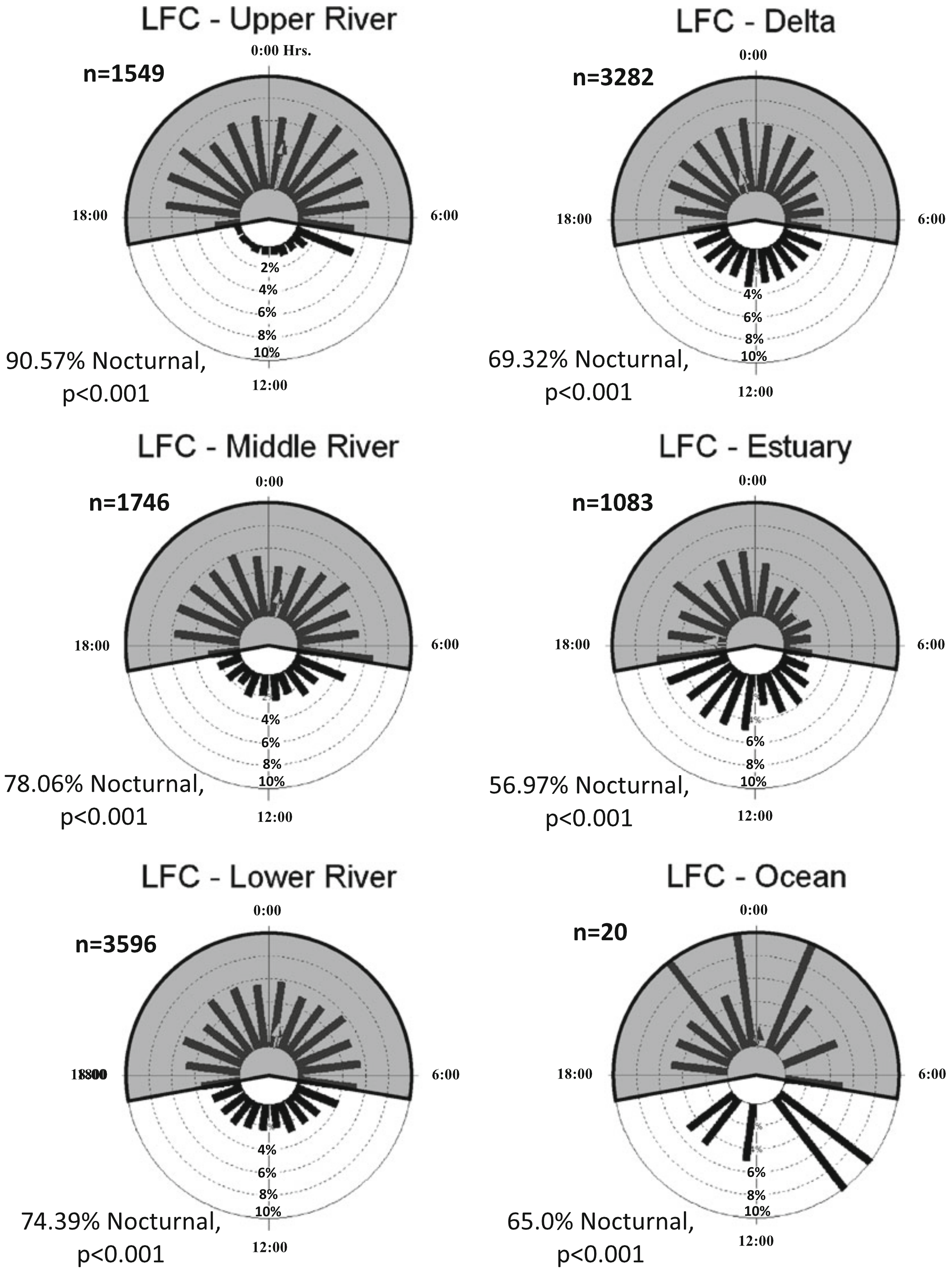

Fig. 2 Circular histograms with the percentages of late-fall run Chinook salmon smolts detected each hour during a 24 hday (all monitors combined in each reach). The top represents midnight and the bottom represents noon; the clear area depicts daytime and the shaded area depicts nighttime. The arrow (*r-vector*) denotes the mean time that all fish were detected. In all reaches, except for the Estuary, there is a significant preference for night migration. Note the shift from predominately nighttime detections in the upper river to less nighttime detections with each successive reach downriver. The percent nighttime detections increase again once the smolts enter the ocean. The statistics were based on 14 h of darkness and 10 h of daylight

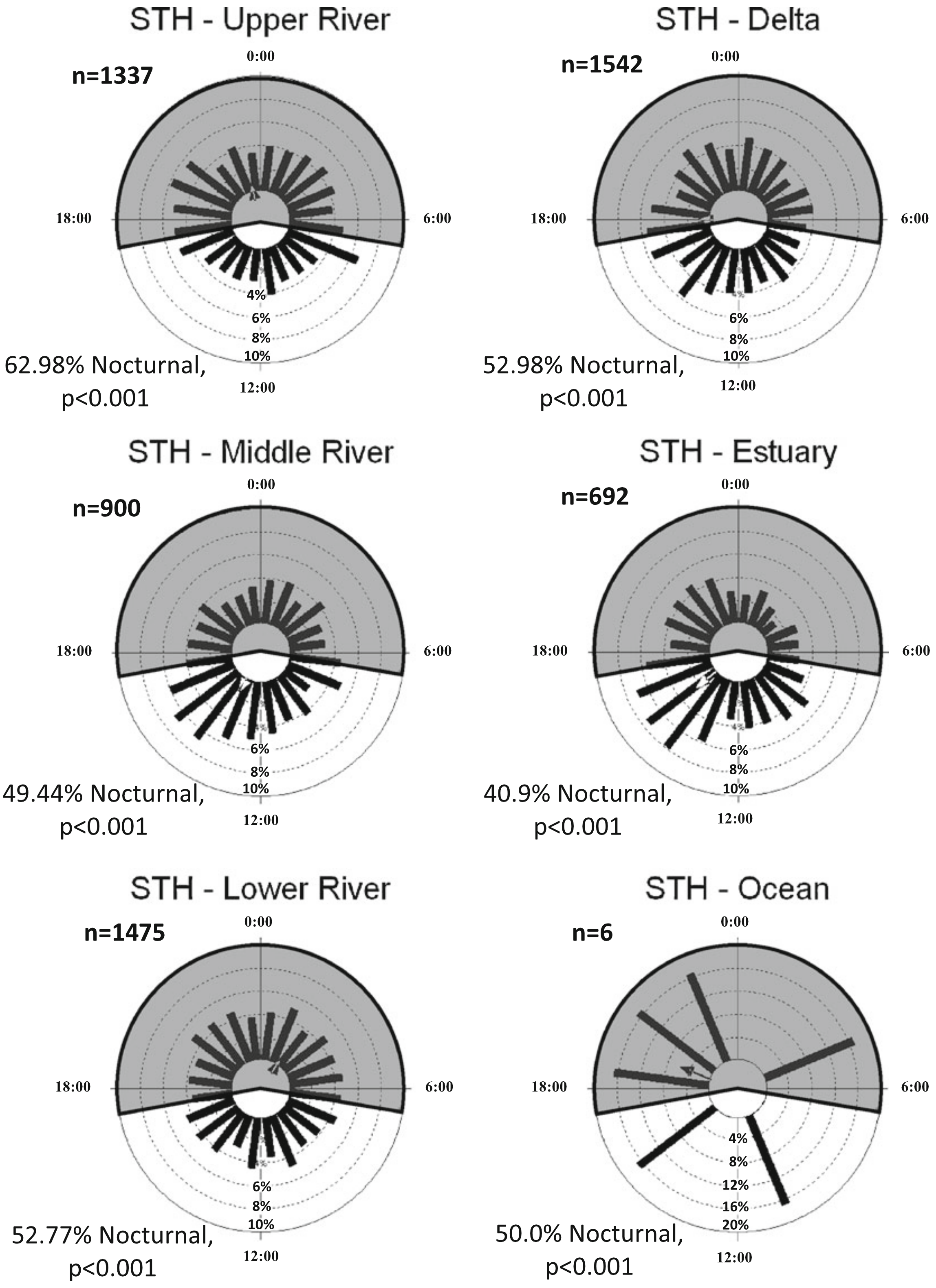

Fig. 3 Circular histograms with the percentages of steelhead smolts detected each hour during a 24 hday (all monitors combined in each reach). The top indicates midnight and the bottom indicates noon; the clear area signifies daytime and the shaded area signifies nighttime. The arrow (*r-vector*) denotes the mean time that all fish were detected. There was significance for nocturnal migration in the upper river; in the middle river, Delta, and Estuary there was significance for diurnal migration; in the lower river there was no preference for day or night migration. The statistics were based on 14 h of darkness and 10 h of daylight

Table 2 Detections of Chinook salmon and steelhead smolts in five regions of the Sacramento/San Joaquin watershed and in the ocean. (*Low power)

River Reach	Chinook salmon			Steelhead			Chinook salmon vs. Steelhead
	Night Detection	Mean Vector (Time)	Mean Vector Length (r)	Night Detection	Mean Vector (Time)	Mean Vector Length (r)	
Upper River	90.57 %	00:44	r=0.436	62.98 %	23:02	r=0.049	P<0.0001
Middle River	78.06 %	00:48	r=0.243	49.44 %	14:00	r=0.131	P<0.0001
Lower River	74.39 %	00:41	r=0.214	52.77 %	02:09	r=0.033	P<0.0001
Delta	69.32 %	22:48	r=0.198	52.98 %	18:01	r=0.085	P<0.0001
Estuary	56.97 %	18:23	r=0.195	40.9 %	15:23	r=0.221	P<0.001
Ocean	65.0 %	00:09	r=0.171	50.0 %	19:21	r=0.281	P=0.59*

increasing downstream discharge (chi-square 21.4, $p<0.006$). Once the downstream discharge reaches approximately 700 m^3/s^{-1}, steelhead are more likely to be detected during the day with increasing discharge and the oscillations that are seen at the lower readings disappear (Fig. 8).

Generally there was a decrease in nighttime detections with increasing turbidity. There was an overall increase in the median turbidity value with distance downriver, from 4.4 Nephelometric Turbidity Units (NTU) in the upper river to 31.9 NTU in the Estuary (Fig. 9). However, there was a decrease in turbidity from the lower river (16.2 NTU) to the Delta (9.0 NTU) but all values are higher than in the upper river where both species we found to be migrating at night.

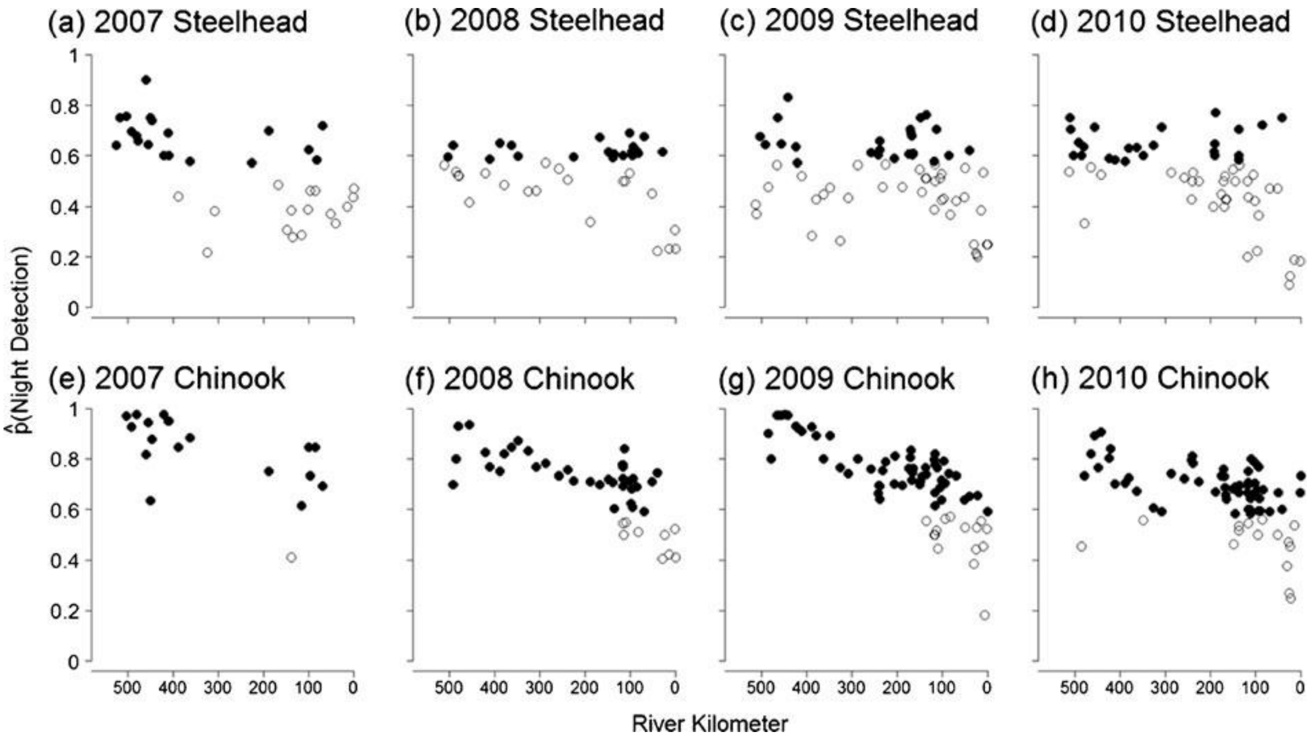

Fig. 4 Estimated probabilities of night detection versus river kilometer based on logit transformed proportions. Black points are night detections, white points are daytime detections based on 14 h of darkness and 10 h of daylight. Steelhead are the top four graphs for each year, Chinook salmon are the bottom four. 500 km is up river, 0 is ocean entry at the Golden Gate

Table 3 Summary of regressions in fig. 4. Percentage of nighttime detections and river kilometer in the Sacramento River

Species	Year	N = monitors	R^2	P	Slope and Intercept
Steelhead trout	2007	48	0.0151	0.0006	y=0.533+42.019
Steelhead trout	2008	58	0.014	0.3761	y=0.016+49.257
Steelhead trout	2009	88	0.0001	0.7658	y=−0.005+55.966
Steelhead trout	2010	94	0.0368	0.0368	y=0.032+46.351
Chinook salmon	2007	43	0.1336	0.016	y=0.041+71.788
Chinook salmon	2008	73	0.1461	0.0008	y=0.044+62.006
Chinook salmon	2009	84	0.3453	0.0001	y=0.092+55.225
Chinook salmon	2010	87	0.1371	0.0004	y=0.051+54.606

Discussion

Freshwater species commonly display plasticity in their diel phases (Reebs 2002) suggesting that fish may be nocturnal at some point in their life history and diurnal during another. To our knowledge this study is the first to show that these two species, with similar ontogenetic strategies, adopt different diel tactics during their seaward emigration from the same river. Additionally we show that both late-fall run Chinook salmon and steelhead trout exhibit plasticity in their diel tactic as they emigrate through a river, delta, estuary, and into the ocean.

As with our study, the frequency of capture in a rotary screw trap indicated that nocturnal movements of Chinook salmon are greater than diurnal movements in the upper Sacramento River (Gaines and Martin 2001). Juvenile Chinook salmon and steelhead displayed significantly more nocturnal movements while migrating past John Day Dam, 348 km from the mouth of the Columbia River (Brege et al. 1996). On the other hand both species were more active during the day in the upper estuary of the Columbia River (Ledgerwood et al. 1991). These studies were conducted many years apart and utilized different methods but offer evidence that diurnal activity is greater in lower portions of a river than farther up in the system.

Also on the Columbia River, juvenile steelhead exhibited an increase in migration rate with enhanced

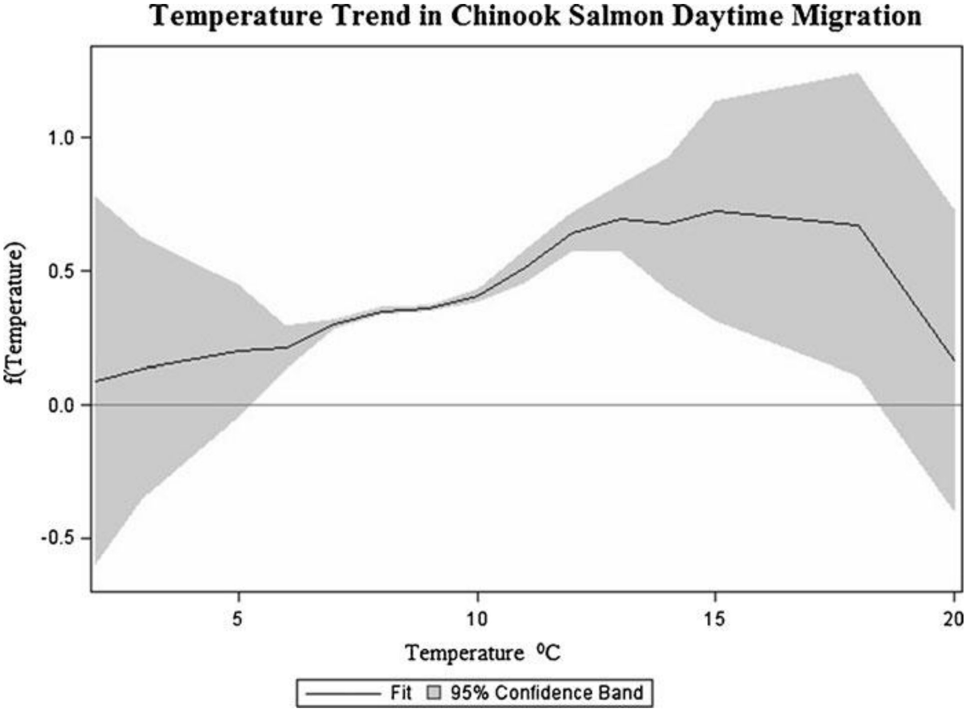

Fig. 5 Change in diel migration of Chinook salmon smolts in relation to temperature. The y axis depicts increasing diurnal detections

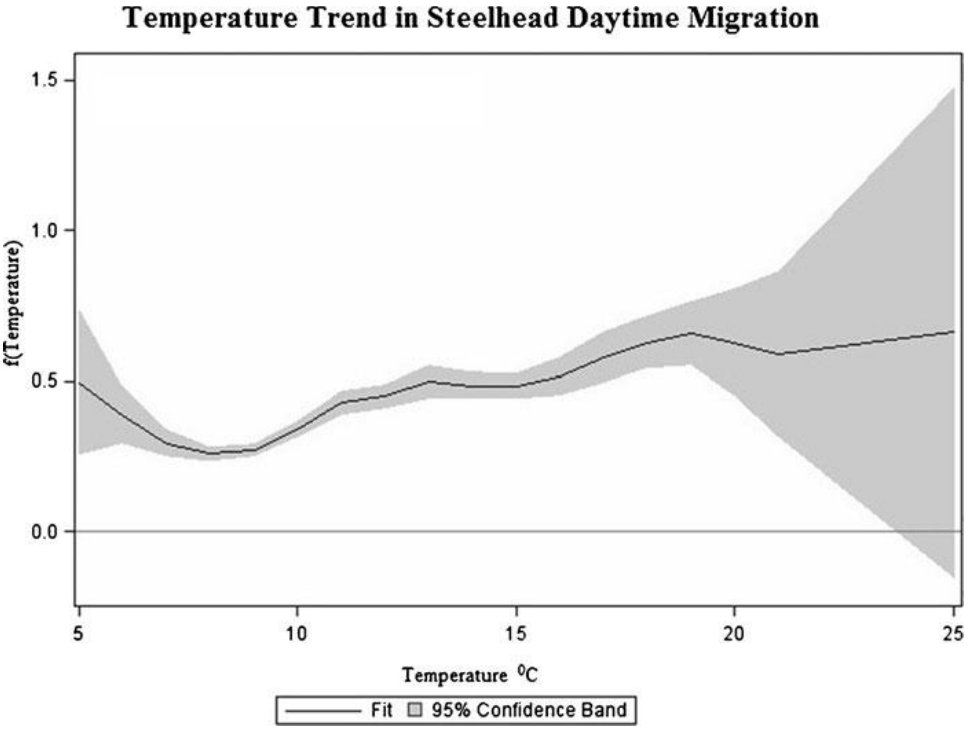

Fig. 6 Change in diel migration of steelhead smolts in relation to temperature. The y axis depicts increasing diurnal detections

flow (Giorgi et al. 1997). On the Sacramento River, migration rates of Chinook salmon smolts were positively related to flow (Michel et al. 2012 (this issue)). We found that discharge influenced the diel tactics of both species but to a greater extent with Chinook salmon. Once smolts reach the Sacramento-San Joaquin Delta there are many channels/sloughs through which they may move. Flows vary with the tides on hourly time scales (Perry et al. 2010). Upon reaching the Carquinez Strait these movements are heavily influenced by the tides. Many smolts make repeated upstream and downstream movements until eventually migrating successfully to the ocean (Chapman et al. 2009). Although the water is very turbid in the Estuary the diel pattern of

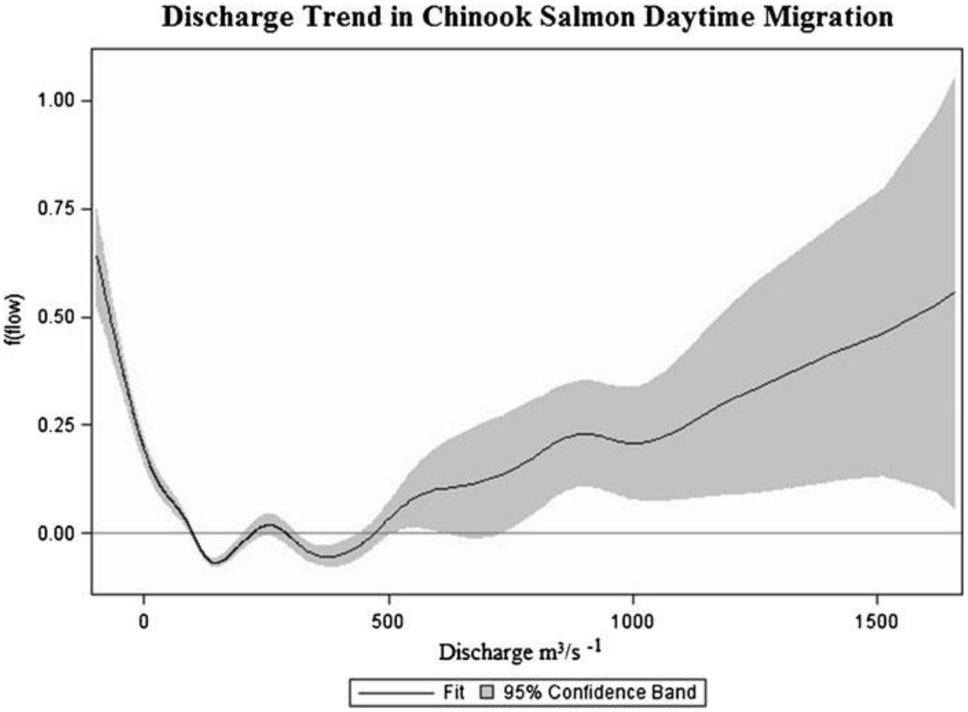

Fig. 7 Change in diel migration of Chinook salmon smolts in relation to discharge. The y axis depicts increasing diurnal detections

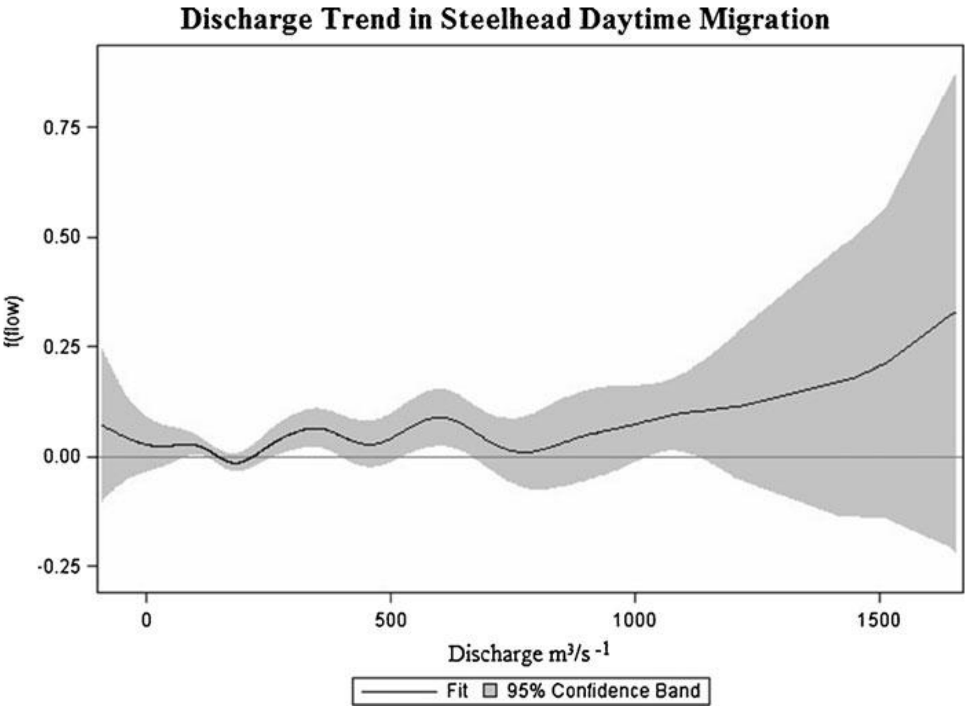

Fig. 8 Change in diel migration of steelhead smolts in relation to discharge. The y axis depicts increasing diurnal detections

Chinook salmon is heavily influenced by flow. Chinook salmon were more likely to be detected during the day with increase in discharge, especially during flood tides. Although steelhead were more likely to be detected during the day, we did not find that the tides affected their diel tactics as much as with Chinook salmon.

Turbidity increases rapidly with discharge (Saraceno et al. 2009) which may reduce predator success but it may also make feeding more difficult (Confer et al. 1978). In a laboratory study, Gregory and Levings (1996) found that turbidity reduced the encounter rate with predators and that turbidity significantly reduced the effectiveness of cover (vegetation) for juvenile Chinook salmon. When they field tested the hypothesis that predation by piscivorous fish is reduced in turbid compared with clear water they found that turbidity reduced predator success (Gregory and Levings 1998). They suggested that predators are generally active throughout the day in turbid water but exhibit a stronger diel activity pattern in clear water. As turbidity increased to 35 NTU the foraging activity of juvenile resident Atlantic salmon declined (Robertson et al. 2007). This may have been the case in this study once these smolts reached the Estuary where turbidity commonly exceeded that level. Juvenile salmonids are also vulnerable to avian predation (Ryan et al. 2003), but turbidity

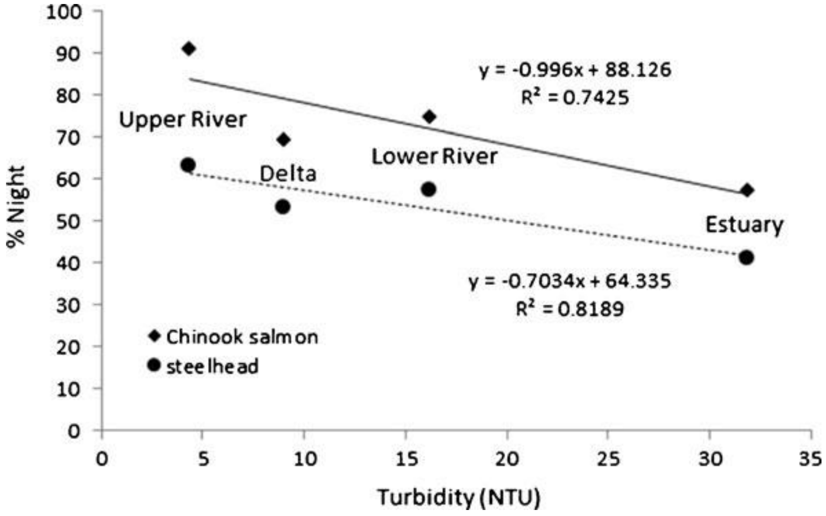

Fig. 9 Percent night detection of Chinook salmon and steelhead smolts, in four reaches of the Sacramento River, versus median turbidity (all four years combined)

may reduce avian predation on juvenile salmonids. Seaward migrating Atlantic salmon were preyed upon less successfully by piscivorous birds after turbidity levels increased due to rains (White 1936).

Rain events may also influence water temperature (Saraceno et al. 2009) which has been shown to affect the diel behavior of salmonids. Atlantic salmon migrate during nighttime when temperatures are below 7°C and during daytime at temperatures above 14°C (Thorpe et al. 1994). In a laboratory study, the switch was attributed to a lower metabolic demand and reduced escape abilities in cold water (Metcalf et al. 1999). Metcalf et al. discussed the minimize *u/f* rule stating that fish should minimize risk of predation (*u*) and maximize food intake (*f*). This is most likely true for the smolts in our study except smolts must maximize migration as well as food intake while minimizing risk of predation. As temperature increases metabolic rates and food intake increase so the behavior of these fish should reflect changes in their environment and physiology. In our study the increase in daytime activity with rising temperatures occurred across all reaches as temperature fluctuated daily within each reach.

While we offer temperature, flow, and turbidity as possible causes for the change in diel patterns of emigrating juvenile salmonids, these fish also encounter different predators and changing habitats. The migration of hatchery Atlantic salmon smolts was influenced by a hierarchy of environmental cues of spate, light intensity, and water temperature (Greenstreet 1992). Juvenile Atlantic salmon, residing in a river, exhibited different activity patterns depending on body size (Hiscock et al. 2002). In our study steelhead were significantly larger than Chinook salmon smolts. This may have made them less susceptible to predation or less affected by increased flow. The differences we found between years may also be attributed to body size within each species. These results may not be similar to those of other runs of Chinook salmon in the Sacramento River or to wild fish. Many studies have found physiological and behavioral differences between hatchery and wild fish (Gale et al. 2004; Fritts et al. 2007; Serrano et al. 2009; Powell et al. 2010) therefore, caution must be exercised when extrapolating these results from hatchery smolts to wild populations.

In summary, we have found that hatchery Chinook salmon and steelhead smolts change their diel tactic as they migrate seaward in the Sacramento River watershed, and that each does so in a different manner. These changes could not be attributed to any one variable. It is likely a complex interaction between intrinsic and extrinsic factors that influences these diel tactics.

Acknowledgments Funding for the project was provided by a CALFED Bay Delta program grant; project U-05-SC-047 (A. Peter Klimley and R. Bruce MacFarlane Principal Investigators). We would like to thank Kevin Niemala, Kurt Brown, and Scott Hamelburg of the U.S. Fish and Wildlife Service (Coleman National Fish Hatchery) for providing late-fall run Chinook salmon and steelhead smolts and for their support during tagging. We would like to thank Ethan Mora for GIS support and Niel Willits for statistical support. Special thanks to Chuck Morton and Charlotte Cashin from Caltrans for their help with the deployment and download of monitors on bridges in the Bay area. We would also like to thank Bob Null for assisting with downloads in the Upper River.

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