

Migration Patterns of Juvenile Winter-run-sized Chinook Salmon (*Oncorhynchus tshawytscha*) through the Sacramento–San Joaquin Delta

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ABSTRACT

The decline of Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*) remains one of the major water management issues in the Sacramento River. Few field studies have been published on winter-run, leaving gaps in our knowledge about their life history. This is especially true in the Sacramento–San Joaquin Delta, which provides essential rearing and migratory habitats for winter-run, and serves as the center of water operations for California. Using long-term monitoring data that identified winter-run-sized fish (“winter-run”) using length-at-date criteria, we examined patterns of juvenile migration in terms of geographic distribution, timing, numbers, and residence times. We analyzed the role of flow, turbidity, temperature, and adult escapement on the downstream movement (“migration”) of winter-run. Winter-run passed Knights Landing (rkm 144 or 51 rkm upstream of the Delta) between October and April, with substantial variation in peak time of entry that was strongly

associated with the first high flows of the migration season. Specifically, the first day of flows of at least $400 \text{ m}^3 \text{ s}^{-1}$ at Wilkins Slough (rkm 190) coincided with the first day that at least 5% of the annual total catch was observed at Knights Landing. While the period during which winter-run left the Delta spanned several months based on Chipps Island (rkm 29) catch data, the median catch typically occurred over a narrow window in March. Differences in timing of cumulative catch at Knights Landing and Chipps Island indicate that apparent residence time in the Delta ranges from 41 to 117 days, with longer apparent residence times for juveniles arriving earlier at Knights Landing. We discuss the potential importance of the Yolo Bypass floodplain as an alternative rearing and migratory corridor, contingent on the timing, duration, and magnitude of floodplain inundation. These results carry implications for habitat restoration and management of Sacramento River flows.

KEY WORDS

Winter-run Chinook salmon, emigration, juveniles, flow, Sacramento River, Sacramento–San Joaquin Delta.

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INTRODUCTION

California is unusual in having four different runs of Chinook salmon (*Oncorhynchus tshawytscha*): fall-run, late fall-run, spring-run, and winter-run (Fisher 1994; Yoshiyama and others 1998). Of the four types, the Sacramento River winter-run is unique in terms of migration timing. Winter-run is endemic to California's Central Valley, where only one population remains. Historically, winter-run spawned in the headwaters of the upper Sacramento River and its tributaries. Since the construction of Shasta Dam in 1945, winter-run spawning has been limited to a relatively small cold-water reach just downstream of Keswick Dam. The population's decline in the 1970 to 1980s, and restricted habitat range, are primary reasons for their endangered status under the federal Endangered Species Act (Federal Register 1994) and California Endangered Species Act (Title 14, Section 670.5). The migratory route between their upstream freshwater habitat and the ocean has been legally designated as critical habitat (Federal Register 1993), portions of which include rearing and migratory habitat through the lower Sacramento River and western Sacramento–San Joaquin Delta (Delta; [Figure 1](#)).

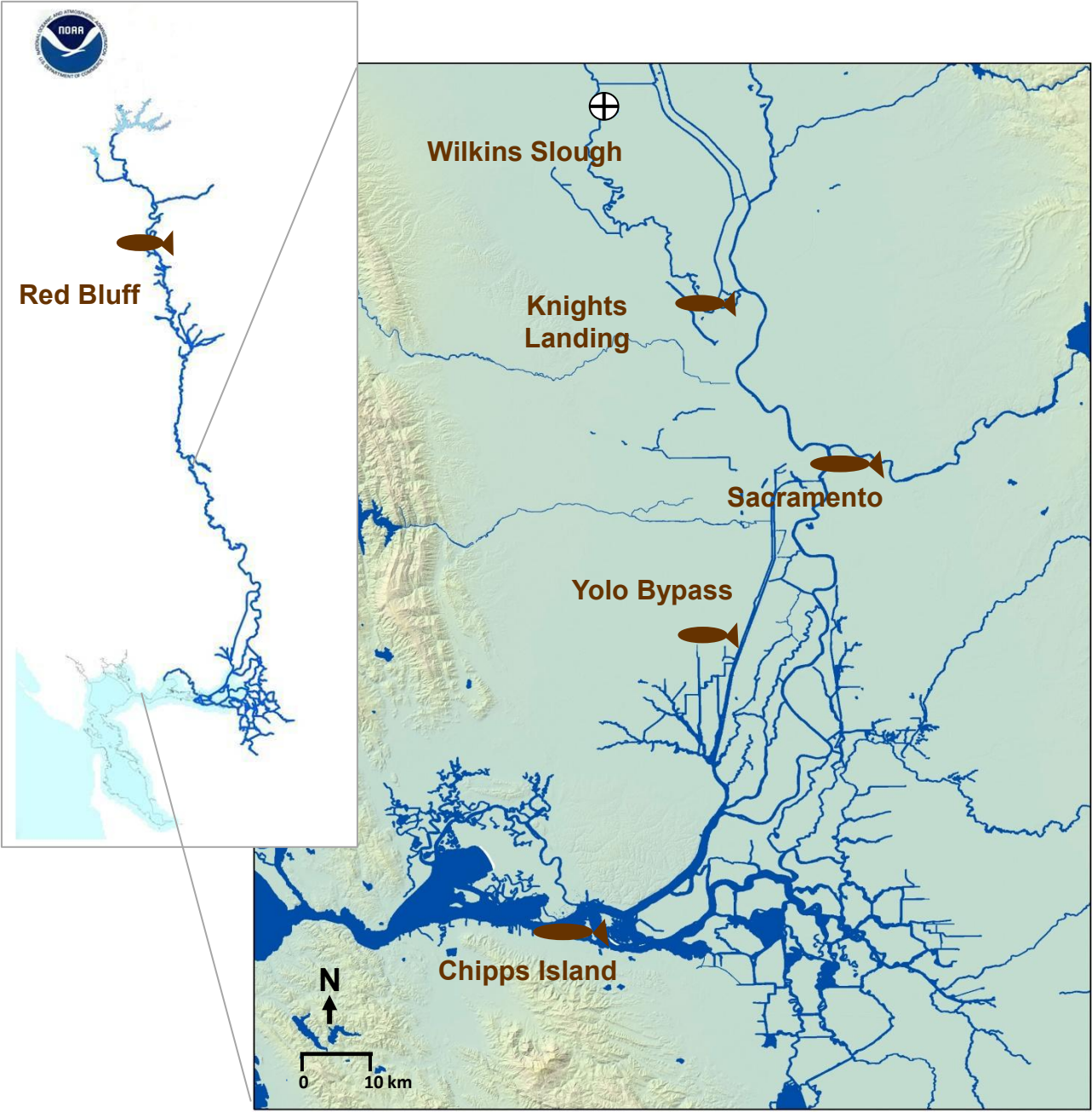
Because rearing habitat for winter-run Chinook salmon encompasses a broad geographic area, flow or water-temperature requirements to maintain their habitat can affect how water from Central Valley rivers is managed throughout the state. For example, during winter and spring, winter-run require protective actions associated with water diversions from the Central Valley Project and the State Water Project (NMFS 2009), which provide water for over 25 million people and a multi-billion dollar agricultural industry (Sommer and others 2007). The conflicts in managing Central Valley rivers for species protection and water-project operations are a management issue of national significance (Service 2007). At the very least, managing the Delta for winter-run protection requires knowledge of when this run is present in the Delta.

Despite the importance of winter-run salmon to the economy (i.e., balancing water for agriculture, urban, and fisheries use) and ecology (i.e., as an indicator species) of the region, there have been limited pub-

lished analyses of field data for this unique run of Chinook salmon, with the exception of studies such as Newman and Lindley (2006) and Newman and others (2006). There have been some basic descriptions of the life history of winter-run (Fisher 1992, 1994; Healey 1994; Moyle 2002; Williams 2006), assessments of sources of mortality such as predation, water diversion losses, and climate change (Lindley and Mohr 2003; Kimmerer 2008; Yates and others 2009), laboratory studies (Beckman and others 2007), evaluations of management options (Lindley and others 2007; Brown and others 2009), statistical and extinction modeling (Botsford and Brittnacher 1998; Newman and Lindley 2006; Newman and others 2006), and progress on genetics (Bartley and others 1992; Hedrick and others 1995, 2000; Kim and others 1999; Garrigan and Hedrick 2001). Relatively more has been published on various aspects of the life history and survival of other runs of Central Valley Chinook salmon (e.g., Brandes and McLain 2001; Sommer and others 2001; Williams 2006; Jeffres and others 2008; Newman and Brandes 2010; Perry and others 2010). We do not know how relevant this research is to winter-run. The primary reason for the lack of published information on juvenile winter-run in the Delta has been the difficulty in distinguishing among the different Chinook runs as they migrate downstream and into the Delta.

The Delta provides habitats that are integral to the life cycle of winter-run Chinook salmon because each winter-run must pass through the Delta twice to complete its life history. Adults pass through the Delta enroute to upstream spawning areas in the Sacramento River in the winter (Kjelson and others 1981; Fisher 1994; Moyle 2002), and juvenile winter-run enter the Delta between late fall and winter before outmigrating to the Pacific Ocean between January and May (Fisher 1992). For the juvenile life stage of salmon, estuaries provide foraging and growth opportunities, a physiological transition zone from freshwater to saltwater, temporary refuge from predators in the ocean, and migration pathways to ocean feeding grounds (Bottom and others 2005). While little is known about the residence time specifically of winter-run juveniles in the Delta, recent acoustic studies based on yearling, hatchery-

 represents fish monitoring stations,  represents Sacramento River gaging station.



Sacramento-San Joaquin Delta and the Lower Sacramento River

Figure 1 The Sacramento River (left) and the Sacramento-San Joaquin Delta and lower Sacramento River (right)

raised, late-fall Chinook salmon suggest smolts that migrate during the winter, such as winter-run, generally tend to stay in the Delta only a few weeks (e.g., Perry and others 2010).

The quality and quantity of habitats available for Chinook salmon in the Delta depend largely on inflows from the Sacramento River (Brandes and McLain 2001; Sommer and others 2001). While increased stream flows are thought to provide the cues to trigger the onset of downstream migration of fry from their natal tributaries to the Delta (Kjelson and others 1981; Healey 1991), increased quantity of flows also provides additional rearing and migratory habitats. During high Sacramento River flow events, the Yolo Bypass floodplain, which is the only remaining floodplain in the lower Sacramento River basin, serves as an alternative rearing and migratory corridor for Chinook salmon (Sommer and others 2001; Williams 2006).

We use field data from several long-term monitoring programs to provide insight into the movements of juvenile winter-run as they emigrate downstream from the Upper Sacramento River to, and through, the Delta. For the purposes of this paper, we refer to these movements as “migration,” although we acknowledge that not all of the observed changes in distribution are necessarily directed or behavioral. It is possible, for example, that some of the movements into the Delta in response to flow simply represented passive displacement of fish downstream by high velocities. Nonetheless, we have chosen to use the term “migration” as it is commonly used to describe the downstream movements of young Chinook salmon (Healey 1991; Brandes and McLain 2001). Moreover, passive displacement is much less likely to be an issue in the lower reaches of the Delta, where strong tides mute the effects of inflow. We used catches at Knights Landing to represent migration into the Delta, although it is 51 rkm upstream of Sacramento, which is the entrance to the legally defined Delta.

Specifically, we examine juvenile migration patterns framed by four general questions:

1. Where and when are the winter-run-sized fish in the freshwater and estuarine systems of the Sacramento River and Delta?
2. How do environmental factors such as flow, turbidity, and water temperature affect the timing of winter-run-sized fish entry into the Delta?
3. How long do winter-run-sized fish rear in the Delta?
4. What factors affect the number of winter-run sized outmigrants each season?

A critical assumption of our analyses is that the length-at-date criteria used to identify juvenile winter-run are sufficient to represent downstream migration patterns of juvenile winter-run Chinook salmon. Hedgecock (2002) evaluated the accuracy of the length-at-date criteria assuming his genetic assignments were 100% accurate. He found that there was a 95.5% probability that the winter-run length-at-date criterion correctly identified a salmon as being winter-run, hence a 4.5% false negative probability. Here we use Hedgecock’s data with ours to further assess that estimate. As the accuracy of the length-at-date criteria is a subject of debate, the criteria remain relevant as they are currently the primary tool used to categorize Chinook salmon runs for winter-run management throughout the Central Valley (NOAA Fisheries 2009). For simplicity, hereafter we refer to winter-run-sized fish as winter-run.

METHODS

Chinook Salmon Data Sources

We obtained data on winter-run Chinook salmon from long-term field monitoring studies conducted by the California Department of Fish and Game (DFG) and U.S. Fish and Wildlife Service (USFWS). Winter-run were identified using the river model length-at-date criteria developed by Fisher (1992) and later modified to daily criteria (S. Greene, California Department of Water Resources, pers. comm., 1992; Appendix A). The length-at-date criteria are based on spawning periods of the four runs of Chinook salmon in the Central Valley, and an average growth rate of fall-run Chinook salmon raised in the Tehama-

Colusa Fish Facility near Red Bluff adjacent to the Sacramento River (Fisher 1992). These length-at-date criteria were applied to catches of juvenile salmon at Knights Landing, Sacramento, Yolo Bypass, and at Chipps Island to distinguish fish by run. The length-at-date criteria assume increasing fork length through the outmigration season, the same growth rate for juveniles within and between years, and no overlap in length-at-catch date between juveniles of the four runs of Chinook salmon in the Sacramento River.

Chinook salmon catch data were collected from 1998 to 2007 at the following locations (Figure 1): (1) Red Bluff, rotary screw trap, USFWS; (2) Knights Landing, rotary screw trap, DFG; (3) Yolo Bypass, rotary screw trap, DWR; (4) Sacramento at Sherwood Harbor, midwater and Kodiak trawl, USFWS; and 5) Chipps Island, midwater trawl, USFWS. The Sacramento trawl data were used as a supplemental data set to examine temporal and juvenile size distributions along the migration corridor. Winter-run spawner abundance data were from DFG (unpublished data).

Genetic data on Chinook salmon that are more recent (2004 to 2007) and more extensive (finer temporal resolution and more microsatellite DNA markers) than those used by Hedgecock (2002) were provided by B. Harvey, DWR (pers. comm., 2011), who analyzed fish salvaged at the fish facilities in the south Delta.

Sampling Methods

1. **Red Bluff.** Juvenile salmon emigrating downstream from the upper Sacramento River were sampled along a transect using four 2.4-m diameter rotary screw traps (E.G. Solutions® Corvallis, Oregon) attached via aircraft cables directly to Red Bluff Diversion Dam at rkm 391, as described in Poytress and Carrillo (2010). The rotary screw traps generally sampled in the east and west river-margins and mid-channel habitats simultaneously and continuously throughout 24-hour periods, and were serviced once daily. All fish captured were anesthetized, identified to species, and enumerated with fork lengths measured to the nearest millimeter. When capture of Chinook juveniles exceeded approximately 200 fish per trap, a random subsample was taken to include approximately 100 individuals, with all additional fish being enumerated and recorded. No data were collected for two emigration periods, 1999 to 2000 and 2000 to 2001, because funding lapsed in those 2 years.
2. **Knights Landing.** Juvenile salmon emigrating from the Sacramento River are sampled from October through June, 0.8 km downstream of the town of Knights Landing at rkm 144. Sampling was conducted using two 2.4-m diameter rotary screw traps (E.G. Solutions® Corvallis, Oregon) deployed approximately 15 m from the east bank, anchored in the river thalweg. The traps were fished 24 hours per day, 7 days a week, and serviced at least once daily during peak emigration periods. At each trap visit, up to 150 juvenile salmon of each run, based on the river model length-at-date size criteria, were measured (fork length) and weighed using a stratified random subsampling protocol.
3. **Yolo Bypass.** The Yolo Bypass is the primary floodplain of the Sacramento River, seasonally flooding in about two-thirds of years (Sommer and others 2001). Similar to the Knights Landing sampling, a rotary screw trap (EG Solutions® Corvallis, Oregon) was operated near the base of the Yolo Bypass during each study year (Sommer and others 2005). The trap was located in the Toe Drain, which is a perennial tidal channel that drains adjacent fields during low flow and the irrigation season, allowing sampling during both flood (inundation from Sacramento River) and non-flood periods. During much of the sampling period, the inundated width of the floodplain was 1 to 5 km. A 2.4-m diameter trap was used for all sampling. The traps were operated up to 7 days a week, with daily effort varying from 1 to 24 hours, depending on debris load and safety considerations. The number of salmon and their fork length were recorded in all years.
4. **Sacramento.** Juvenile salmon were sampled as they entered the Delta from the Sacramento River using two types of trawls at Sherwood Harbor,

located approximately 5 km downstream of Sacramento (rkm 88), as described in Brandes and McLain (2001). Sampling was generally conducted year-round 3 days per week. A Kodiak trawl was used to sample juvenile salmon from mid-October through March, which spans the great majority of the winter-run emigration period at Sacramento. A midwater trawl was used for the remainder of the year. Both trawls generally conducted ten, 20-minute tows each sampling day. The Kodiak trawl net was constructed of variable mesh sizes ranging from 5.1-cm stretch at the mouth to 0.6 cm just before a livebox, which contained 0.3-cm diameter perforations. The expanded mouth opening was 1.96 m x 7.6 m. The midwater trawl net was composed of six panes, each decreasing in mesh size, that ranged from 20.3-cm stretch at the mouth to 1-cm stretch just before the cod end, which was composed of 0.3-cm weave mesh. The extended mouth size was 4.15 m x 5 m. Both types of nets were fished 33 m behind the boat. Generally, up to 50 salmon per run were measured for length with the remaining counted.

5. **Chipps Island.** Midwater trawl sampling was conducted within a 3-km section of river upstream of the western tip of Chipps Island (rkm 29), both upstream and downstream in the north, south and middle of the tidally influenced channel. Sampling was generally conducted year round at Chipps Island, between 3 and 7 days per week, with ten to twenty, 20-minute tows per day (Brandes and McLain 2001). The midwater trawl net used at Chipps Island had a mouth dimension of 7.6 x 9.7 m, and mesh size that ranged from 10.2-cm at the mouth to 2.5-cm stretch just before the cod end, which was composed of 0.8-cm knotless material. The net was fished 46 m behind the boat. Until January 1997, the mesh of the cod end of the net was 0.3 cm. After March 2001, the mesh of the cod end was 0.8 cm. Between 1997 and 2001, the mesh size of the net was either 0.3 cm or 0.8 cm. Because winter-run smolts are relatively large (i.e., range from 53 to 188 mm), we assumed the change in mesh size did not influence capture efficiency of winter-

run at Chipps Island. Generally up to 50 fish per run were measured for length with the remaining counted.

Environmental Data

Flow data for Sacramento River are from Department of Water Resources' California Data Exchange Center using the Wilkins Slough gauge station from 1998 to 2007 (Department of Water Resources, Dayflow: An Estimate of Daily Average Delta Outflow, <http://www.water.ca.gov/dayflow/>). Yolo Bypass flow data were obtained from the Dayflow database. Turbidity was measured in Nephelometric Turbidity Units (NTUs) using a LaMotte 2020 turbidity meter at Wilkins Slough near Knights Landing. Water temperature data was continuously measured using an electronic recording thermograph (HOBO data logger) attached to the rotary screw traps at Knights Landing. A hand-held thermometer was used to record temperature each time the traps were serviced. Flow, turbidity, and temperature data used in the analyses were from October 1 through April 30 of each year.

Data Analysis

To compare migration timing at various locations during outmigration, we constructed cumulative daily catch curves of winter-run on a per year basis using sample data from Red Bluff, Knights Landing, Yolo Bypass, and Chipps Island. The catch curves were scaled by total annual catches to control for differences in gear efficiency among sites, as well as abundances, given that population numbers diminished over time. Daily catches for Red Bluff and Knights Landing were imputed for days when the traps were not checked daily for fish but were still operating (e.g., if traps were checked 3 days after the last check and 15 fish were caught, then 5 fish were allocated per day). Daily catches at Chipps Island were linearly interpolated for non-sampled days (e.g., if the Chipps Island trawl fished on Monday and Wednesday and caught 10 and 14 fish, then the interpolated catch for Tuesday was 12 fish). The interpolation of data at Chipps Island was a simple missing data imputation approach to allow for comparisons with daily catches at the other locations. We assessed the effect

of misclassification of run types by the length-at-date criteria of catches at Knights Landing using month-specific estimates of false negative and false positive probabilities calculated from the genetics analysis of Chinook salmon salvaged at the South Delta fish facilities from 2004 to 2007 (B. Harvey, DWR, pers. comm., 2011). We based the correction of misclassification errors of the length-at-date assigned winter-run fish numbers on a method-of-moments estimator (Castleman and White 1995). The formula for estimating the number of genetic winter-run is $nwr = (ywr - n*FP)/(1 - [FP-FN])$, where nwr is the estimated number, ywr is the number labeled winter-run according to the length-at-date criteria, n is the total number of fish caught, FP is the false positive probability, and FN is the false negative probability.

To determine whether changes in environmental covariates such as flow, turbidity, and water temperature were associated with catches at Knights Landing, the time series of daily catches were superimposed on the time series for the covariates. The dates of the first relatively large catches, defined as the first day where the daily catch equaled or exceeded 5% of the total catch for the year (catch spike) were calculated and compared to the environmental time series. The date of the 50th percentile of the seasonal catch (median catch date) was similarly compared. In both cases, to identify sudden changes in the time series, environmental covariate time series were visually compared to the catch spike and median catch dates. The catch spike dates and median catch dates were both regressed on the flow, water temperature, and turbidity values on those same dates.

The relationship between the total seasonal catches at Knights Landing and the adult escapement that produced the juveniles was also examined graphically by scatterplots and scatterplot smoothers (i.e., locally weighted linear regression). We examined the relationship between total catch and seasonal average flows, turbidity, and water temperatures similarly. We also fit multiple regression of total catches on all four covariates.

Using data on the outmigration timing from the cumulative (scaled) daily catches from Knights Landing and Chipps Island, we estimated the appar-

ent residence time in the Delta by subtracting the date when the 50th percentile of the seasonal catch passed Knights Landing from the day when the 50th percentile of the catch passed Chipps Island. We emphasize that apparent residence time does not necessarily reflect the residence time of individuals through the Delta, but, instead, the analysis is intended to capture average trends in the population. To provide a measure of the uncertainty in apparent residence time, we also calculated two other estimates based on the dates that the 25th percentile and the 75th percentile of the catches had occurred, respectively.

Apparent residence time in the Delta can also be affected by daily survival probabilities. To assess the effect of survival on apparent residence time, we carried out a simulation analysis where arrival time was lognormally distributed with median arrival on day 20, and residence time was lognormally distributed with median residence being 87 days (thus departure time was the sum of arrival time and residence time). We assumed that the survival probability increased on a daily basis according to a logistic model; i.e., on day 1 $S\{d,1\} = 0.90$ and by day 219 $S\{d,219\} = 0.99$. We modeled arrival days, residence days, and survival on a given day as independent random variables. We calculated the apparent residence time by subtracting the median day of “departure” for all fish that survived at least to their departure day (arrival day plus residence day), from the median day for arrival of all fish that survived longer than arrival day. All the fish arriving at Knights Landing and all the fish reaching Chipps Island were used to make the calculation (i.e., catch sampling variation was eliminated). Note that we defined modeled residence time as the median residence time according to the lognormal distribution, namely 87 days, and that this was independent of whether or not a fish lived.

RESULTS

Comparison of Sampling Gear

One limitation of our study is that we relied on three different types of sampling gear that have different trap efficiencies: rotary screw traps (at Knights

Landing and Yolo Bypass), a Kodiak trawl and, secondarily, a midwater trawl for the month of April (at Sacramento), and a midwater trawl (at Chipps Island). Because correcting for trap efficiencies is not possible, given how the data were collected, we assumed similar trap efficiencies among and within years for each gear type, and relied on relative patterns of cumulative catch at each sampling location for comparisons. Of particular concern was whether the gear types may sample different size distributions of fish within the winter-run-size criterion, which could bias our interpretations of residence times of winter-run fish. To address this issue, we compared the fork

lengths of winter-run collected at Knights Landing, Sacramento, and Chipps Island and found the ranges in size distributions were similar for all sampling locations across gear types (Figure 2).

Patterns of Temporal and Spatial Distribution of Winter-run in the Sacramento River System

Winter-run appear to be present in the Sacramento River system or Delta nearly year round—they are first detected emigrating from their natal grounds at Red Bluff in July, and last detected leaving the Delta at Chipps Island as smolts as late as May (Figure 3).

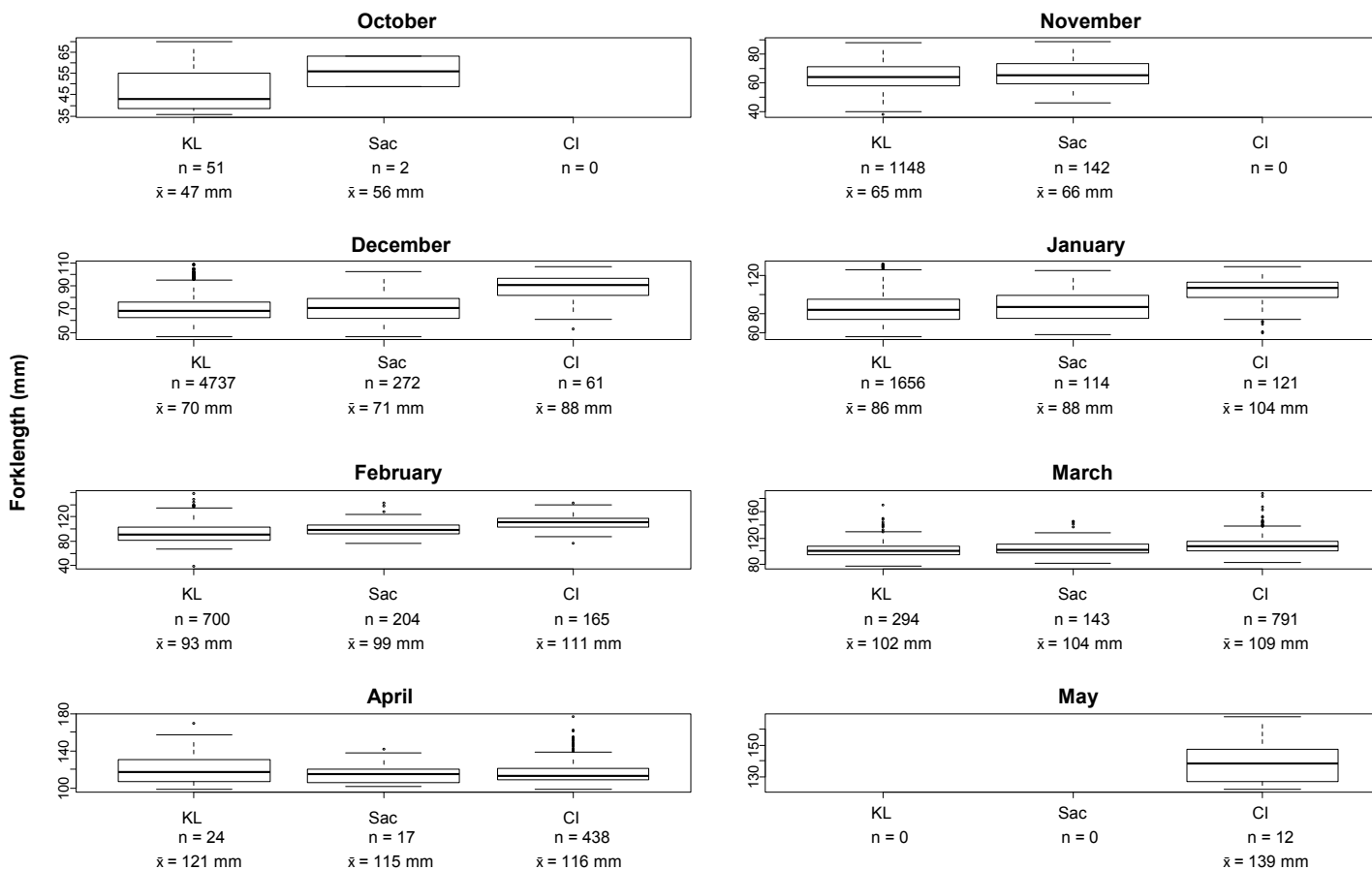


Figure 2 Comparisons of the size ranges of winter-run captured using rotary screw traps (at Knights Landing, KL), a Kodiak trawl (at Sacramento, Sac), and a midwater trawl (at Chipps Island, CI) by month from 1998 to 2007. The boxplot widths are proportional to the square root of the number of observations. Note: a midwater trawl was used to collect juveniles at Sacramento in the month of April. Sample size and mean monthly fork length are denoted by n and \bar{x} , respectively.

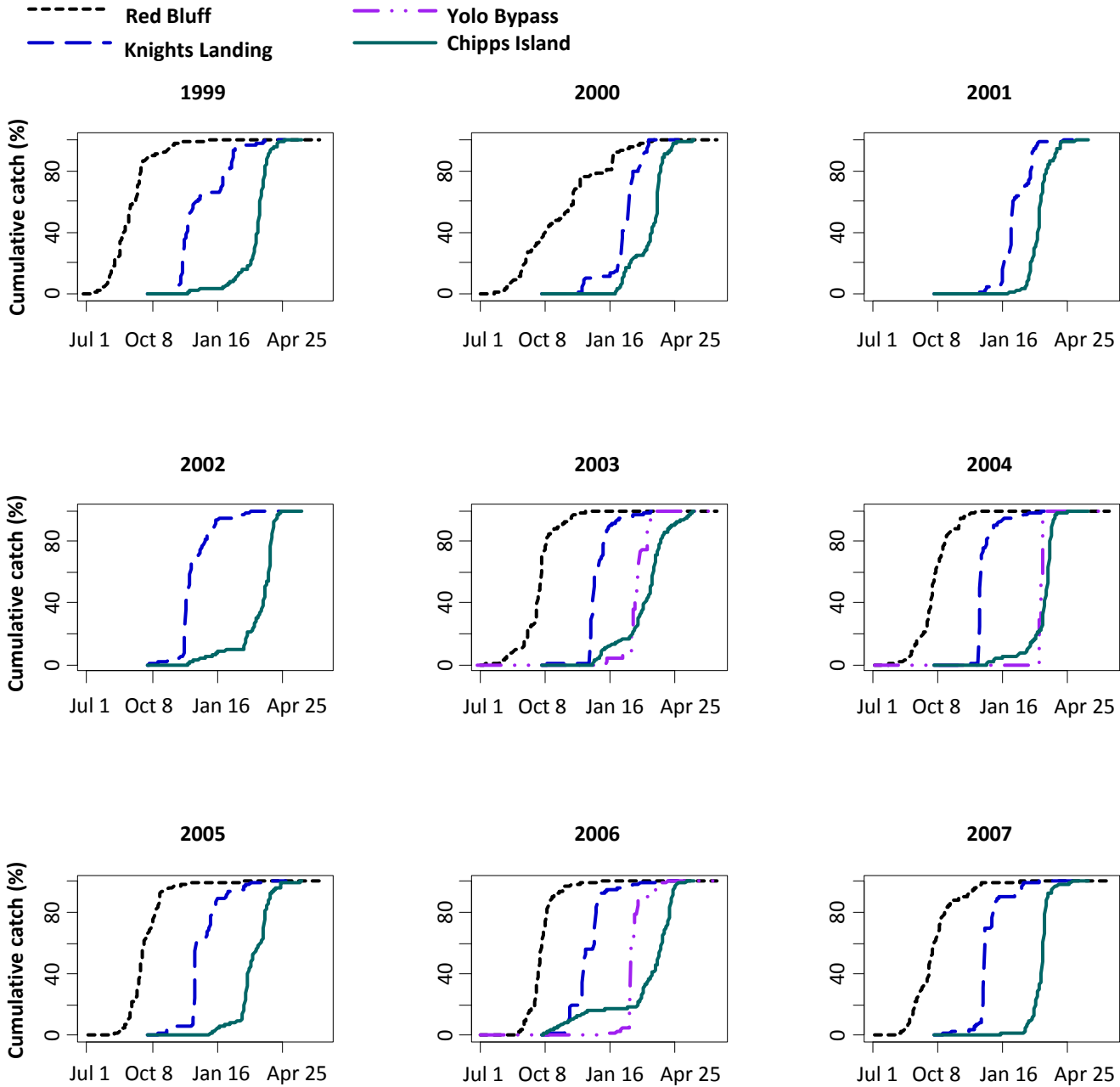


Figure 3 Cumulative daily catch of winter-run along the Sacramento River migratory corridor. Years refer to the spring emigration season.

Typically, the 50th percentile of the sampled population passes Red Bluff in early October, enters the Delta at Knights Landing 2 months later in December, and leaves the Delta at Chipps Island 3 months later in March.

The winter-run emigration season through the Delta occurs within 8 months (Figure 2). In general, the migration patterns followed the expected geographic trend, with catch increases starting in Knights Landing as early as October, followed by Sacramento, Yolo Bypass (when it floods), and Chipps Island (Figure 3). Winter-run juveniles are detected at Chipps Island as early as December and as late as May, representing a long window of departure for the population as a whole.

The false negative probabilities of winter-run identified using the length-at-date criteria, calculated on a monthly basis, were at most 1% to 2% throughout the year. The false positive probabilities were negligible in November and early December, gradually increased to roughly 25% or greater by January and February, and then declined in later months. In contrast, using data from Hedgecock (2002), we estimate that the probability that a non-genetic winter-run is wrongly identified as a winter-run fish (i.e., the false positive probability) is 11.6%. Given that the relative abundance of non-winter-run is so much greater than winter-run at certain times of the year, the fraction of false positives in a given sample can vary over the migration season. The effect of correcting for length-at-date misclassification errors of winter-run catches at Knights Landing was to truncate the later winter-run arrivals, so that the majority of winter-run had arrived at Knights Landing by early January, thus concentrating the distribution of arrivals in November and December.

Migration and Residence Time in the Delta

The hydrograph of the Sacramento River at Wilkins Slough varies each year, with the first rain events and subsequent increases in flow occurring at different times of the season (Figure 4). We observed substantial increases in cumulative catch of winter-run at Knights Landing which corresponded to a flow threshold of $400 \text{ m}^3 \text{ s}^{-1}$ at Wilkins Slough (Figure 5).

The first day that flows reached $400 \text{ m}^3 \text{ s}^{-1}$ was 1 day before the catch spike (or within 4 and 11 days before the catch spike in 1999 and 2000, respectively) and within 3 to 7 days before the median catch (or within 14 and 27 days before the median catch in 1999 and 2000, respectively). Correcting misclassification errors in the Knights Landing winter-run catches led to similar results. These results demonstrate that winter-run migrate past Knights Landing *en masse*, such that the catch spike and median spike are relatively simultaneous in most cases. The notable exception was in the 2000 spring emigration season when relatively few fish were captured at the monitoring stations throughout the season.

The dates that Wilkin Slough flows first reached 300, 400, or $500 \text{ m}^3 \text{ s}^{-1}$ during the migration season were typically close together. Flows of at least $400 \text{ m}^3 \text{ s}^{-1}$ were correlated with spikes in catch. The day of the $400 \text{ m}^3 \text{ s}^{-1}$ flow threshold was significantly correlated with the day of the catch spike ($R^2 = 0.98$, $p < 0.01$) and median catch ($R^2 = 0.92$, $p < 0.01$; Figure 6). We found the same significant correlation for a flow threshold of $500 \text{ m}^3 \text{ s}^{-1}$ and the day of the catch spike ($R^2 = 0.98$, $p < 0.01$) and median catch ($R^2 = 0.93$, $p < 0.01$); but not for a flow threshold of $300 \text{ m}^3 \text{ s}^{-1}$ (catch spike, $R^2 = 0.41$, $p = 0.07$; median catch, $R^2 = 0.36$, $p = 0.09$).

In contrast, there was no significant relationship between either measurement of catch and turbidity on the day of either the catch spike ($p = 0.74$) or the day of the median catch ($p = 0.95$; Figure 4). There was also no significant relationship between water temperature on the day of either catch spike ($p = 0.30$) or day of the median catch ($p = 0.52$; Figure 4).

Apparent residence time between arrival at Knights Landing and departure at Chipps Island was, on average, 87 days, or nearly 3 months (Figure 7). In some cases, average residence time was short, approximately 40 days (e.g., 2000, 2001), and in others it was long, over 110 days (e.g., 2002, 2006). The range of arrival time into the Delta was broad, as influenced by the timing of the first flow events that triggered migration; whereas the range of departure time was relatively narrow, suggesting winter-run juveniles tend to leave around the same time each

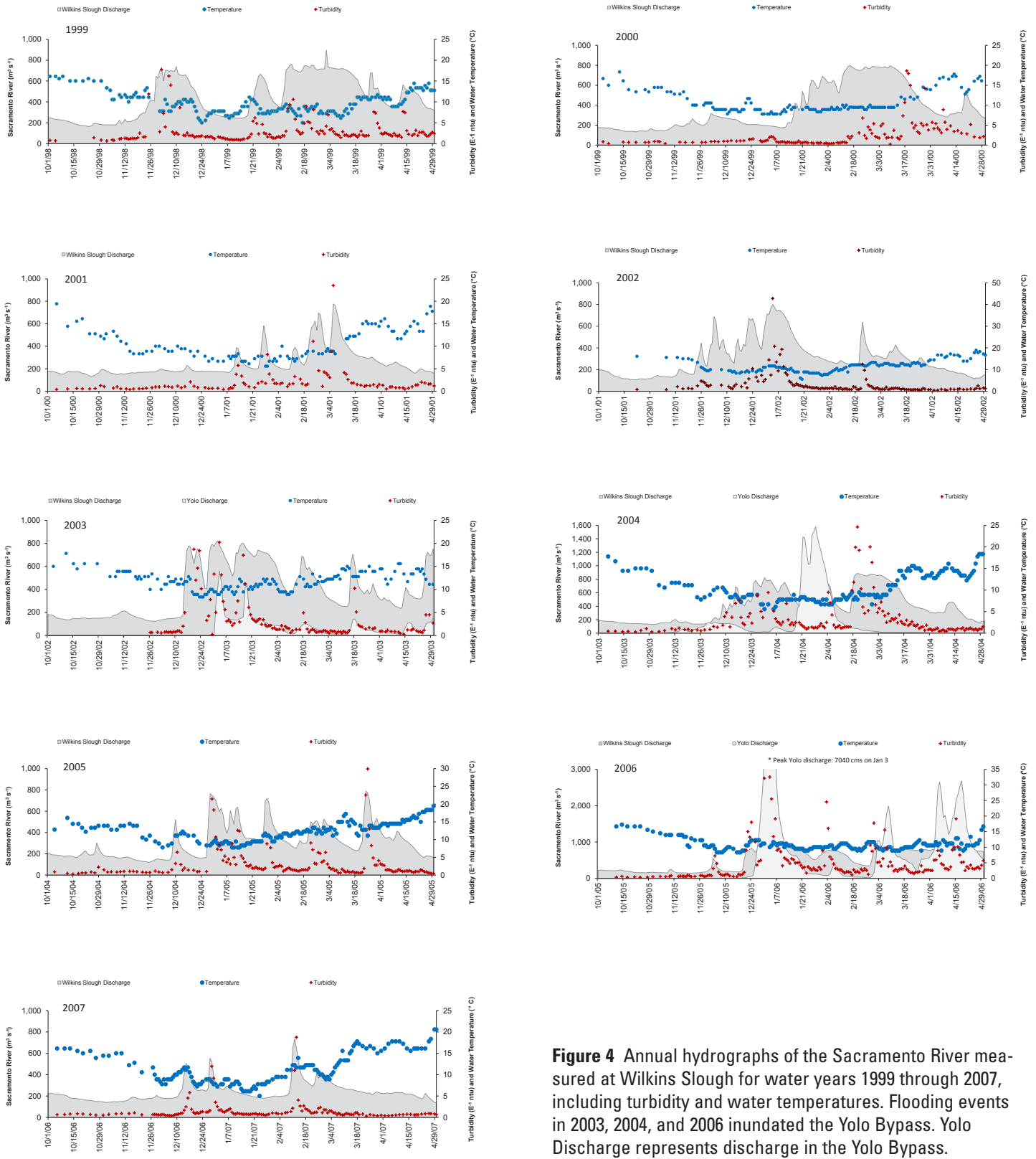


Figure 4 Annual hydrographs of the Sacramento River measured at Wilkins Slough for water years 1999 through 2007, including turbidity and water temperatures. Flooding events in 2003, 2004, and 2006 inundated the Yolo Bypass. Yolo Discharge represents discharge in the Yolo Bypass.

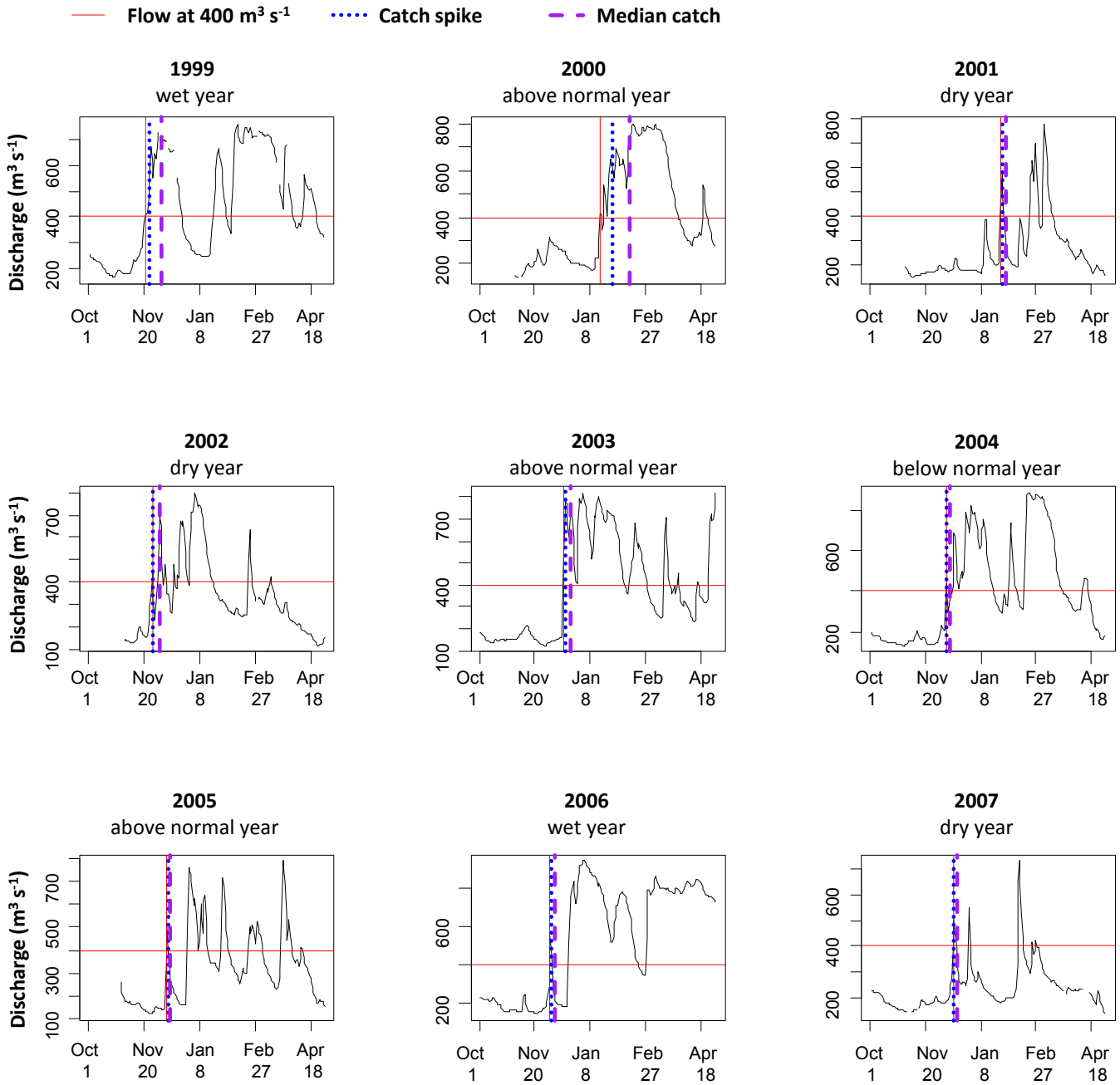


Figure 5 Flow threshold of $400 \text{ m}^3 \text{ s}^{-1}$ triggers abrupt and substantial winter-run migration into the Delta at Knights Landing. The first day that flows reached $400 \text{ m}^3 \text{ s}^{-1}$ (solid vertical line) is nearly coincident with the day of catch spike (increase of 5% of cumulative catch; dotted line) and the day of median catch (50th percentile of cumulative catch; dashed line). Years refer to spring emigration season.

year (Figure 7). The effect of daily mortality rates on apparent residence time reduced the median residence time from 87 days to 79 days (Figure 8). The effect of length-at-date misclassification errors on apparent residence time can only be imperfectly assessed, because corrections were only done at Knights Landing. Assuming a truncation of the later departure dates (at Chipps Island) similar to that resulting from the corrections made to catches at Knights Landing would not sizably affect apparent residence time.

The scatterplots and multiple regressions did not suggest any relationships, linear or otherwise, between total seasonal catch of winter-run at Knights Landing (number of fish/day/season) and mean flow during the emigration season ($p = 0.93$), mean turbidity ($p = 0.40$), mean water temperature ($p = 0.27$), and adult escapement ($p = 0.31$).

Use of Alternative Migratory Corridors

The use of the Yolo Bypass floodplain as an alternative rearing and migratory corridor likely depends on the timing, duration, and magnitude of the Sacramento River spills that inundate the floodplain. During the 9-year period from 1999 to 2007, the Yolo Bypass was inundated from the Sacramento River in 6 of those years. Although winter-run were detected in the floodplain during all 6 years, abundance was fairly limited, except in 2003, 2004, and 2006 (Figure 3). Since sampling was not conducted to determine how many fish entered the Yolo Bypass when it flooded, the only method to determine population numbers is through those fish caught leaving the floodplain. In the 3 years where winter-run were relatively abundant in the Yolo Bypass, the majority of fish exited the floodplain as it drained after high flow events (Figure 9).

The residence time in the floodplain for winter-run is primarily driven by the timing of the weir spill, and subsequent drainage of the floodplain. For some years, it was difficult to determine residence time because of multiple flood events that allowed entrance into the floodplain over longer time-periods. Based on the timing of weir spills, there is evidence that some winter-run reared for at least 68 days during 2003, while a few exited within days of entrance

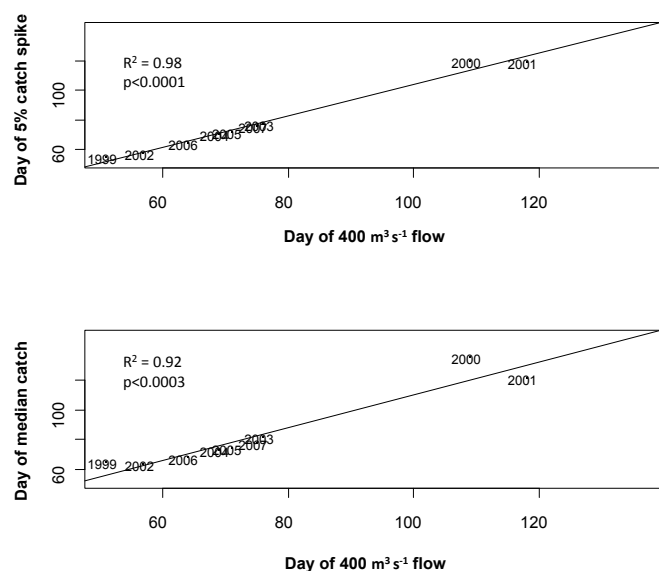


Figure 6 The day of $400 \text{ m}^3 \text{ s}^{-1}$ flows at Wilkins Slough in the Sacramento River is significantly correlated with the day of the 5% catch spike (top) and the day the 50th percentile of fish was captured at Knights Landing (bottom).

(Figure 9). Although some fish were captured shortly after inundation, the majority of winter-run left the Yolo Bypass during drainage events (2003, 2004, 2006; Figure 9). During the 3 years we studied, 80% to 100% of the winter-run exited the floodplain as the floodplain drained into the Toe Drain.

DISCUSSION

Because winter-run Chinook salmon are an important species influencing regional water management (USFWS 2007; NOAA Fisheries 2009), a critical first step in management is to describe the timing of juvenile winter-run as they migrate through the Delta. Despite the challenges surrounding winter-run identification using the length-at-date criteria (e.g., Williams 2006), our results provide a quantitative assessment of the distribution trends in winter-run distribution because their presence and abundance are used to manage water through the Delta. Though the correction of misclassification errors from length-at-date classification of winter-run fish at Knights Landing tended to concentrate the arrival time distribution by truncating later arrivals (according to

length-at-date assignments), our overall conclusions were largely unaffected.

Migration Timing

The flow in the Sacramento River measured at Wilkins Slough appears to have a strong effect on immigration past Knights Landing. The patterns are apparent for a wide range of water year types. For example, early rain events in 2006, a wet water year, brought winter-run to Knights Landing starting in mid-November. In contrast, the late-arriving rain events of 2001, a dry water year, showed winter-run at Knights Landing arriving in late January. The 2003

above normal water year brought rain events and winter-run to Knights Landing in mid-December.

Our results are consistent with previous studies that winter-run juveniles are present in the Sacramento River and Delta over an especially broad period. These juveniles were first detected as fry emigrating from their natal grounds at Red Bluff in July, and last detected leaving the Delta at Chipps Island as smolts as late as May. This result is consistent with Williams (2006), who reported a lengthy time-period for winter-run fish. Similarly, our analyses confirm the suggestion of Williams (2006) that there is substantial variation in timing of entry into the Delta.

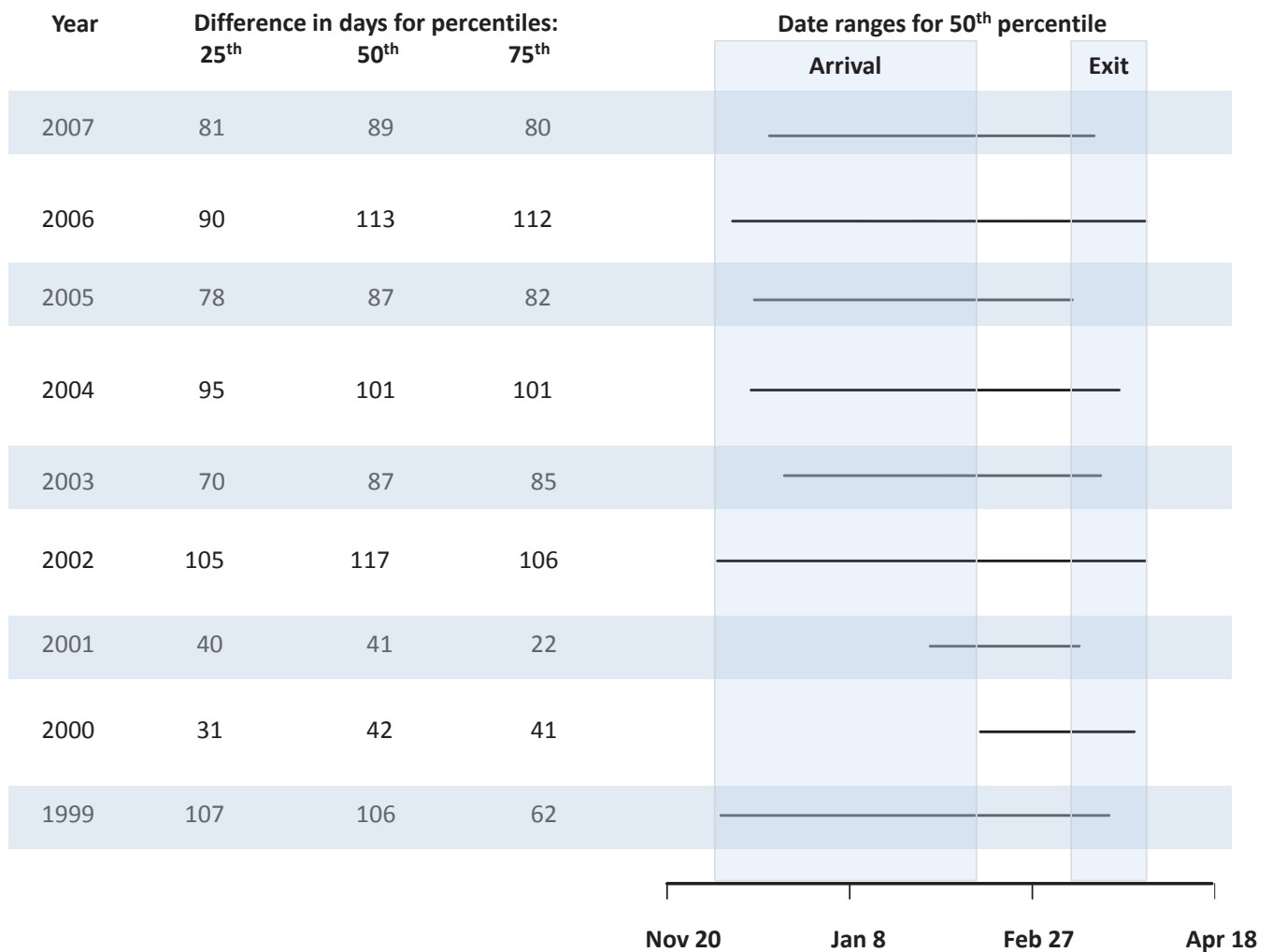


Figure 7 Residence time of winter-run in the Delta of the 25th, 50th, and 75th percentiles of cumulative catch, based on the difference in arrival date at Knights Landing and departure date at Chipps Island. Horizontal lines represent the residence time of the 50th percentile for the year.

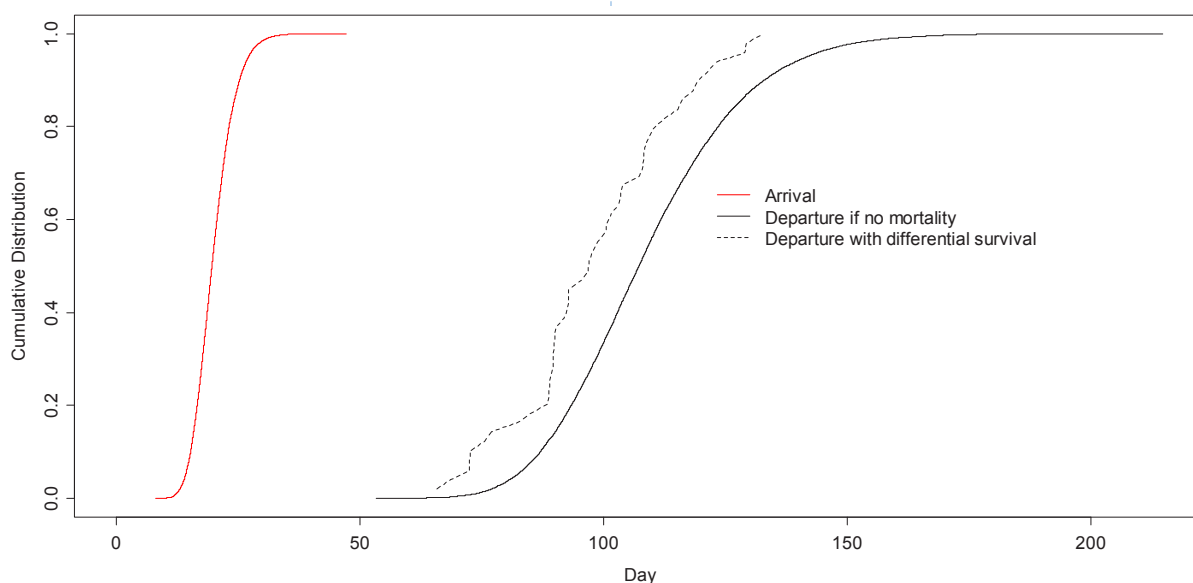


Figure 8 Simulated cumulative distributions of days of arrival and departure with and without mortality. Median residence time without mortality = 87 days and with mortality = 79 days. Survival increases from 0.9 at day 1 to 0.99 by day 219.

Our results strongly suggest that migration past Knights Landing occurs fairly quickly and follows the first major flow events of the year, the timing of which varies each year. Although departure from the Delta spans several months, our results also suggest that the median population of winter-run tend to leave around the same time each year, regardless of when winter-run entered the Delta. What factors trigger their regular departure from the Delta is a subject for subsequent study.

Migration Cues

The migration patterns of winter-run in the Delta are tied to hydrologic patterns of flow in the Sacramento River. We observed a consistent pattern where the first flows of at least $400 \text{ m}^3 \text{ s}^{-1}$ in the season triggered migration to Knights Landing. This flow threshold, in response to the first large rain event of the season, was correlated with the timing of migration, regardless of when the first large rain event occurred in the season. This finding underscores the important role flows have on migration cues of winter-run juveniles. The winter-run migration patterns described support other studies that show Chinook salmon migrate in response to flow increases (Healey

1991; Connor and others 2003; Sommer and others 2005). Others have also found that increased stream flows resulting from storm runoff triggered increased catches of Chinook salmon fry from their natal tributaries to the Delta (Kjelson and others 1981; Healey 1991).

Although we found that flow was a consistent precursor to the onset of migration, the specific cues responsible for downstream movement of winter-run remain unclear. As noted previously, the observed movements were not necessarily active migration, since we cannot rule out the hypothesis that at least part of the patterns was caused by passive downstream displacement of young fish at high flows (e.g., Brandes and McLain 2001). Even if the movements represent active migration, the cues are difficult to identify because several factors change simultaneously with flow, including turbidity, olfactory cues, velocity, and food supply (Høgåsen 1998).

There also may be regional variability, because other studies have found temperature to influence juvenile migration patterns (e.g., Sykes and others 2009). In our analyses, temperature did not appear to be a major factor, despite wide temperature variation during the migration period. Although the relationships

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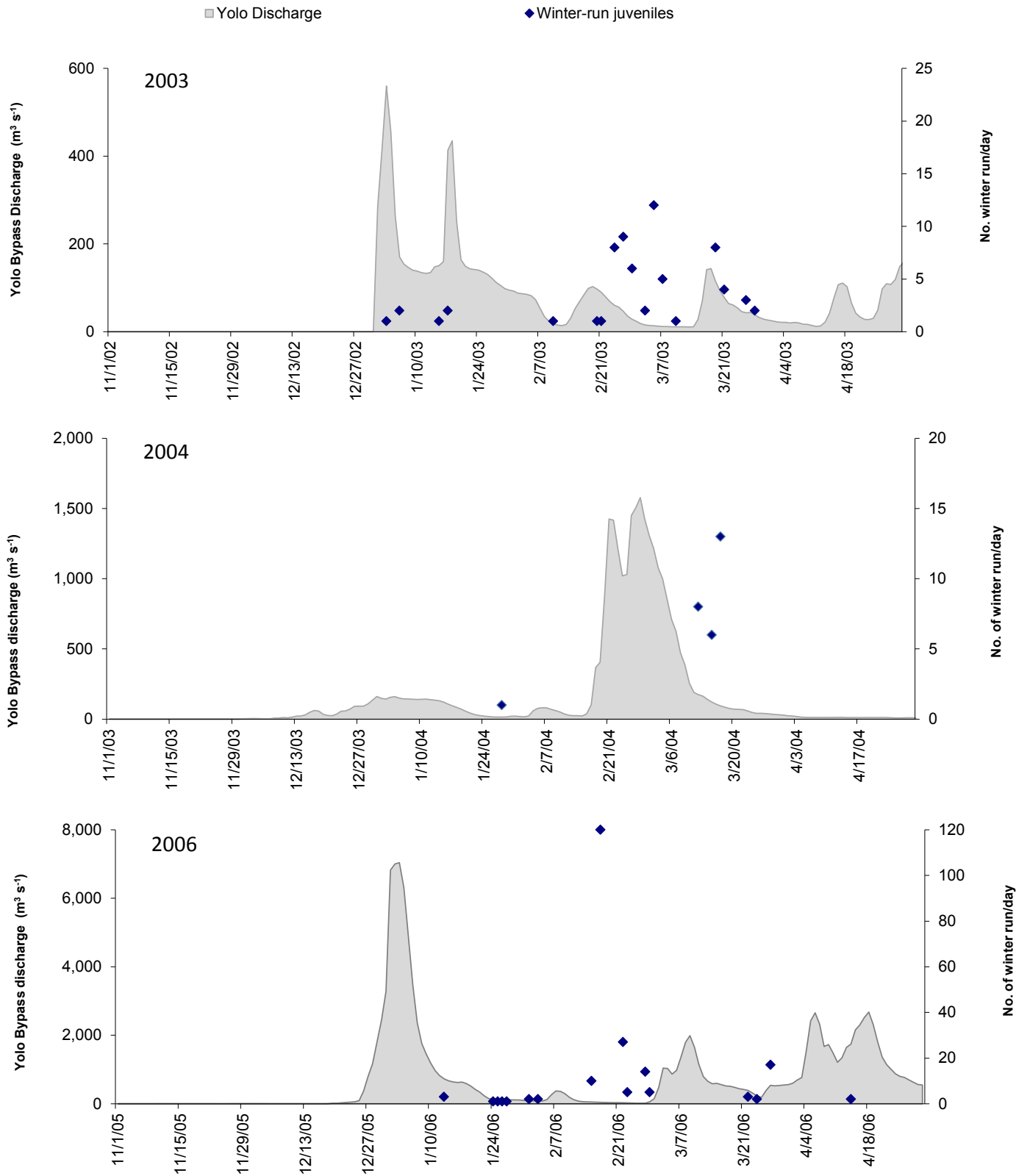


Figure 9 Emigration pattern of winter-run captured at the toe drain of the Yolo Bypass in water years 2003, 2004, and 2006.

between turbidity and flows are often linked, there was no detectable threshold of turbidity that was correlated with the catch of the winter-run population.

Residence Time

Earlier work suggested that fall-run Chinook salmon fry can rear in the Delta for up to 2 months at a time before migrating to the ocean (Kjelson and others 1982). Perry and others (2010) found that most tagged, hatchery-reared, late fall-run yearlings migrated through the Delta in just a few weeks, although some migrated over several months. The most surprising finding from our study was that apparent residence times between Knights Landing and Chipps Island for the winter-run were, perhaps, up to 3 months. Because we relied on comparisons of cumulative catch curves that may be biased by annual variation in mortality between the different sampling points and, also, may contain winter-run misclassification errors (K. Newman, USFWS, unpublished data), these findings have inherent uncertainties. However, even when we assumed differential survival probabilities, apparent residence time was only reduced by ~11%, still indicating juveniles stayed in the Delta for a couple of months. It seems a reasonable hypothesis that winter-run residence time may be much longer than previously assumed. Recent microchemistry analyses of adult winter-run otoliths indicate that some individual juvenile winter-run rear in the Delta for up to 4 weeks (P. Weber, University of California, Berkeley, unpublished data), somewhat shorter than what we have concluded.

Life-history variation spreads risks of mortality in uncertain environments (Healey 1991). These life-history diversities can be expressed in terms of variations in size and age at migration, duration of freshwater and estuarine residency, and time of ocean entry, among others (Lindley and others 2009). Although length-at-date misclassifications may truncate the distribution of dates of departure from the Delta (as measured by catches at Chipps Island), the duration of departure may extend to several months. Although early and late portions of the emigrating population may make up a relatively small percentage of the population, these individuals are important

for maintaining the biological diversity within the population because they leave the freshwater habitat under a range of conditions, and likewise enter the ocean habitats under variable marine conditions.

High flow years create opportunities for additional migration pathways. Specifically, high Sacramento River flows increase the diversity of available rearing habitats for winter-run during their residence. These additional habitats include the Yolo Bypass floodplain, and narrow terraces on the leveed channels throughout the north Delta. As has been observed for fall-run Chinook salmon (Sommer and others 2001, 2005), winter-run likely benefit from this seasonal floodplain because of increases in both food and habitat area, as long as they leave the floodplain before they are stranded by receding floodwaters. However, even with potentially varying survival in the floodplain, providing alternative migratory corridors is a key component to habitat diversity contributing to winter-run life history diversity (McElhany and others 2000).

Magnitude of Migration

Our results showed no clear relationship between mean flow at Wilkins Slough during the migration period and total catch of winter-run at Knights Landing. In contrast, Brandes and McLain (2001) found that juvenile Chinook salmon abundance (catch per cubic meter) in the north Delta (between January and March) and leaving the Delta as smolts at Chipps Island (between April and June) increased during higher flows (Brandes and McLain 2001). They also found that the abundance of smolts migrating into the Delta at Sacramento between April and June was inversely related to flows in February, and concluded that high February flows brought a higher proportion of the Chinook salmon population into the Delta as fry between January and March, leaving a smaller proportion of the population to immigrate into the Delta as smolts during April through June. Most of the juvenile salmon in the Brandes and McLain (2001) analyses were, presumably, fall-run.

Other studies suggest a strong positive relationship between adult winter-run escapement and total catch of winter-run juveniles in the upper Sacramento

River (Martin and others 2001). However, approximately 250 rkm further downstream, our results indicate the relationship between adult winter-run escapement and total catch of their winter-run juveniles at Knights Landing was not significant. This may have been because of one or more factors including: (1) the length-at-date criteria we used were not sensitive enough to capture juvenile, genetic winter-run abundance trends; (2) trap efficiency varied among years so total catch estimates were not very accurate; and (3) there is enough variability in juvenile survival from Red Bluff to Knights Landing to mute effects of adult escapement.

Management Implications

Research and management. As noted earlier, the results of this study depend on data for winter-run as identified by length-at-date criteria. Because there are uncertainties in the identifications, a major management recommendation is to carry out genetic analyses of salmon catches entering the Delta, within the Delta, and exiting the Delta to assess the accuracy of arrival and residence time distributions. Based on substantial recent progress in genetic tools (e.g., Hedrick and others 2000; Garrigan and Hedrick 2001), such analyses are highly feasible. In addition, recent studies suggest that analyses of otolith microchemistry may provide another key tool to assess the timing and duration of Delta rearing.

Winter-run presence in the Delta. In our identification of the flow threshold that triggers significant migration of winter-run juveniles in the Delta, managers can use the timing of the first flow events of the season that are at least $400 \text{ m}^3 \text{ s}^{-1}$, measured at Wilkins Slough, to indicate when this endangered species is likely in the Delta system. These high flow events could signal the need for protective measures until winter-run juveniles leave the Delta. The regularity in their departure time from the Delta could help identify the time-span when protection for winter-run should be in effect. The residence times we have approximated could also be used to estimate the duration for which high quality, quantity, and diversity of habitats should be made available to winter-run as they rear in the Delta for several months.

Ensuring habitat diversity. Restoring and maintaining rearing and migratory habitats in the Delta and Yolo Bypass will promote population diversity. Our preliminary finding that winter-run migration through the Delta is substantially longer than previously assumed suggests that improving habitat conditions through this corridor should be a high priority for species management. Providing for alternative rearing and migratory habitats in Yolo Bypass may spread risk in case of catastrophic events, if conditions result in equal or greater survival than in other parts of the Delta. The availability of this alternative floodplain migratory route, however, currently depends on Sacramento River flow conditions that allow for Yolo Bypass floodplain inundation. This has increased interest in modifying Fremont Weir at the top of Yolo Bypass to allow flows to inundate the floodplain at lower Sacramento River flows (e.g., NMFS 2009) and provide winter-run more frequent access to the floodplain. But survival under these conditions is unknown, and research is needed to confirm the expected benefits. The reduction in flows in the mainstem Sacramento River to provide for additional flooding in Yolo Bypass may negatively affect survival for fish that use the mainstem Sacramento River as a migration corridor (Perry 2010), and is another consideration. For species benefits, the floodplain access ideally should coincide with timing of winter-run migration.

Habitat diversity allows for expression of different life-history strategies in salmon rearing and migration (Bottom and others 2005; Miller and others 2010). Maintaining viable Chinook salmon populations depends on natural processes that drive spatially and temporally diverse habitats (McElhany and others 2000). For example, without life history diversity, populations are more susceptible to poor environmental conditions (Lindley and others 2009). For species such as winter-run that rely on flows for migratory cues, it is critical to restore and preserve hydrologic variability. Because the quantity and timing of flows are key to providing habitats available for winter-run to rear in the Delta, any proposal to reduce Sacramento flows coming into the Delta, or to further modify the flow patterns from the natural hydrograph, will likely affect the migratory success

of winter-run and the viability of this endangered species.

ACKNOWLEDGEMENTS

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of NOAA's National Marine Fisheries Service, the U.S. Fish and Wildlife Service, the California Department of Water Resources, or the California Department of Fish and Game. We thank B. Poytress for providing data from the U.S. Fish and Wildlife Red Bluff Juvenile Salmonid Monitoring Program. We thank J. Israel, L. Grimaldo, L. Conrad, B. Leach, B. Oppenheim, J. Roberts, D. Lawson, J. Milbury, and two anonymous reviewers for comments that improved the manuscript. We would also like to acknowledge the many biologists and field technicians that have spent countless hours collecting the field data.

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