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Anadromous Salmonids in the Delta: New Science 2006–2016

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ABSTRACT

As juvenile salmon enter the Sacramento–San Joaquin River Delta (“the Delta”) they disperse among its complex channel network where they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. In the decades before 2006, tools available to quantify growth, dispersal, and survival of juvenile salmon in this complex channel network were limited. Fortunately, thanks to technological advances such as acoustic telemetry and chemical and structural otolith analysis, much has been learned over the past decade about the role of the Delta in the life cycle of juvenile salmon. Here, we review new science between 2006 and 2016 that sheds light on how different life stages

and runs of juvenile salmon grow, move, and survive in the complex channel network of the Delta. One of the most important advances during the past decade has been the widespread adoption of acoustic telemetry techniques. Use of telemetry has shed light on how survival varies among alternative migration routes and the proportion of fish that use each migration route. Chemical and structural analysis of otoliths has provided insights about when juveniles left their natal river, and provided evidence of extended rearing in the brackish or saltwater regions of the Delta. New advancements in genetics now allow individuals captured by trawls to be assigned to specific runs. Detailed information about movement and survival in the Delta has spurred development of agent-based models of juvenile salmon that are coupled to hydrodynamic models. Although much has been learned, knowledge gaps remain about how very small juvenile salmon (fry and parr) use the Delta. Understanding how all life stages of juvenile salmon grow, rear, and survive in the Delta is critical for devising management strategies that support a diversity of life history strategies.

KEY WORDS

Chinook Salmon, telemetry, Steelhead, otoliths, Delta Cross Channel, survival, migration

INTRODUCTION

All anadromous salmonid populations in the Central Valley must traverse the Delta twice during their life cycle: once as juveniles migrating toward the ocean and once as adults returning to their spawning grounds. However the functional role of the Sacramento–San Joaquin River Delta in the life cycle of anadromous salmonids depends on the extent to which different life stages use the Delta. For adult salmon, the Delta is a migration corridor through which they must pass on their homeward journey. For juvenile salmon, variation in origin (hatchery versus naturally produced), run, size, life stage, and life history strategy affects residence time in the Delta – actively migrating smolts (juvenile fish undergoing physiological transformation for entry into sea water) can travel through the Delta within days (Perry et al. 2010; Buchanan et al. 2013), whereas smaller rearing juveniles may reside in the Delta from weeks to months (Kjelson et al. 1982; del Rosario et al. 2013). These life stages have different rearing strategies and consequently make use of habitat in the Delta in very different ways.

Anadromous salmonids in the Central Valley display a wide range of alternative life history strategies (Healey 1991). Central Valley rivers harbor populations of Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead, the anadromous form of Rainbow Trout (*O. mykiss*). The Delta is unique among large estuaries on the West Coast of North America in that four distinct runs of Chinook Salmon traverse the Delta: the fall, late-fall, winter, and spring runs, named for the timing of the adult upstream migration. The winter and spring runs are listed as endangered and threatened, respectively, under the federal Endangered Species Act, which affects water management in the Delta; Central Valley Steelhead are also listed as threatened (SWRCB 1999; NMFS 2009).

Although the four runs of Chinook Salmon express a range of life history strategies, adult upstream migration timing is just one dimension of a much wider array of life history strategies that may also be characterized by variation in juvenile rearing tactics. Classic examples include stream-type versus ocean-type Chinook Salmon where juveniles of stream-type Chinook Salmon spend 1 to 2 years in fresh

water and juveniles of ocean-type Chinook Salmon spend just a few months in fresh water before they migrate to the ocean (Healey 1991). Most Chinook Salmon juveniles in the Central Valley express an ocean-type rearing life-history strategy, but vary in how much time they spend in the different habitats between runs and life-stages before ocean residence. Williams (2012) identified at least six alternative life history strategies used by juvenile Chinook Salmon from the four runs. For example, juvenile salmon may rear entirely within their natal tributary and then migrate quickly downstream as smolts through mainstem rivers, the Delta, and San Francisco Bay (Figure 1). Alternatively, some juveniles leave their natal tributaries as fry or parr and spend considerable time rearing in mainstem rivers or the Delta before they enter the ocean (Figure 1). Thus, a specific life history trajectory can be defined as a unique spatial pattern of habitat use over time (Figure 1; Moberand et al. 1997). However, life-history trajectories should be thought of as a continuous spatio-temporal distribution of habitat use, with dominant modes being classified as a particular trajectory.

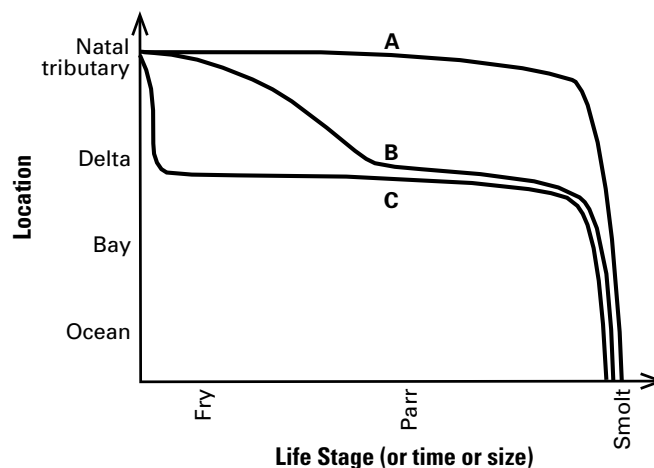


Figure 1 Conceptual model showing three alternative life history trajectories of juvenile Chinook Salmon illustrating different patterns of habitat use in the Sacramento–San Joaquin River Delta. Juvenile salmon may (A) reside in natal tributaries until migrating quickly to the ocean as smolts, (B) rear upstream of the Delta but also spend considerable time growing in the Delta before seaward migration, or (C) rear wholly in the Delta before emigrating. Many other life history trajectories are possible, each forming a unique pattern of habitat use over time or developmental stage. Adapted from Moberand et al. (1997) and Williams et al. (2012).

Diversity in life history trajectories within and among salmon populations buffers them against spatiotemporal variations in the environment. Termed the “portfolio effect” by analogy with stable returns from a diversified stock portfolio, a diversity of life history strategies has been shown to support more stable population trajectories over the long run (Schindler et al. 2010; Carlson and Satterthwaite 2011). In contrast, lack of diverse life history strategies results in populations that exhibit synchronous spatio-temporal patterns in habitat use, which can lead to boom-and-bust cycles when most individuals simultaneously experience favorable or unfavorable environmental conditions (Moore et al. 2010; Thorson et al. 2014). Lack of juvenile life-history diversity in Central Valley fall-run Chinook Salmon has been implicated as one of the primary causes of the collapse of this population in 2008 (Lindley et al. 2009).

Observed variation in life history strategies of salmonids in the Central Valley likely evolved from the diverse array of habitats historically present within the Central Valley—from seasonally inundated flood plains to the diurnally fluctuating tidal channels of the Delta to San Francisco Bay. Such diverse environments allowed a wide array of alternative strategies to be successful, i.e., for fish adopting a particular strategy to survive to eventually contribute to spawning. While the Delta historically played a critical role in supporting all life stages of juvenile salmon—fry, parr, and smolts—the contemporary Delta has been homogenized to such an extent that salmon populations must now contend with an alien environment, compete with alien species, and evade alien predators (Luoma et al. 2015). Thus, managing the Delta with the aim of recovering salmon populations rests on understanding how habitat and flow complexity affects the expression and maintenance of alternative life history strategies, and in turn, how each life history strategy contributes to the composition of Chinook Salmon populations in the Central Valley.

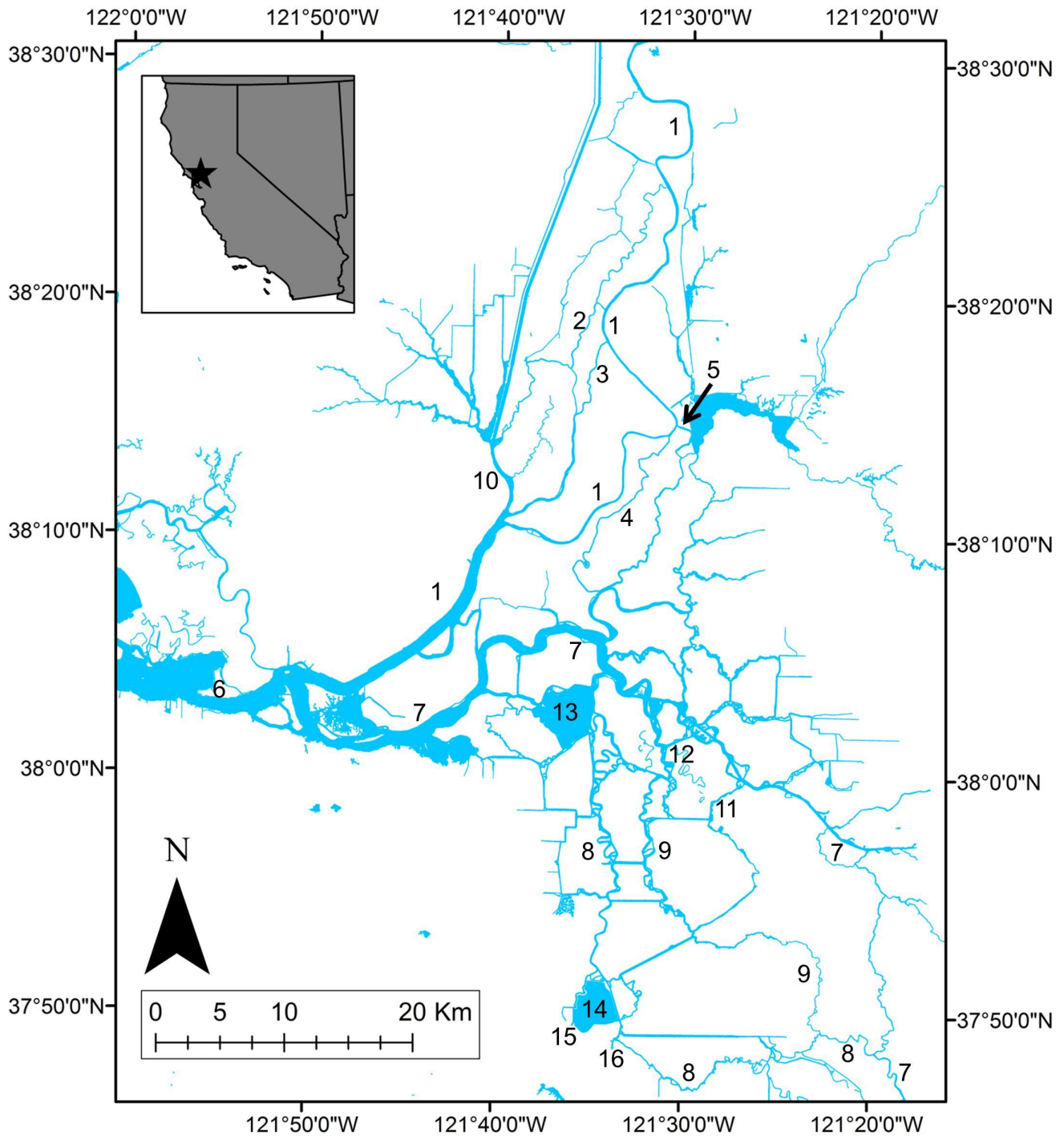
Understanding how different juvenile life stages of anadromous salmonids from the different runs use and survive in the Delta poses significant challenges. As juvenile salmon populations enter the Delta from upstream tributaries, populations disperse among the Delta’s complex channel network (Figure 2). This

dispersal process is driven by the relative quantities of discharge that enters each of the Delta’s channels, the horizontal distribution of fish (which likely varies by life stage) as they pass a channel junction, and tidal cycles that alter flow patterns at channel junctions (Perry et al. 2015; SJRGA 2013). Once fish enter a given channel, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation (Grossman 2016), feeding success, growth rates, and ultimately, survival. Water management actions alter the distribution and quantity of flow through the Delta’s channel network, and therefore influence the spatial distribution, habitat use, and route-specific survival of juvenile salmon on their seaward migration. Eventually, alternative migration routes converge at Chipps Island and the population once again comes together to migrate through San Francisco Bay.

In this paper, we review new scientific insights about juvenile salmon in the Delta over the last decade. Our review focuses on new research that sheds light on (1) how juvenile salmon distribute and survive within the Delta’s channel network, and (2) how alternative life history strategies from the various runs use the Delta. The Delta must support a diversity of life history strategies if salmon populations are to persist in the face of climate change and other anthropogenic factors (Healey 1994; Healey and Prince 1995). Understanding how juvenile salmon that express alternative life history strategies distribute, rear, and survive in the Delta forms the knowledge base for understanding the effect of habitat and management actions aimed at protecting salmon populations.

GROWTH OF JUVENILE SALMONIDS IN THE DELTA

Growth rate is a critical metric for understanding how alternative life-history strategies perform because it integrates fish response to both biotic (e.g., competition, food quality and quantity) and abiotic (e.g., temperature) conditions over time, and because growth rate responds more quickly to changing conditions than metrics such as population size (Delta ISB 2015). However, growth of fish in their natural environment is difficult to measure without a large-scale mark-and-recapture study with individually



Legend

- | | |
|------------------------|------------------------------|
| 1. Sacramento River | 9. Middle River |
| 2. Sutter Slough | 10. Cache Slough |
| 3. Steamboat Slough | 11. Turner Cut |
| 4. Georgiana Slough | 12. Columbia Cut |
| 5. Delta Cross Channel | 13. Frank's Tract |
| 6. Chipps Island | 14. Clifton Court Forebay |
| 7. San Joaquin River | 15. State pumping facility |
| 8. Old River | 16. Federal pumping facility |

Figure 2 Map of the Sacramento–San Joaquin Delta showing important river channels and locations discussed in this review

tagged fish. Growth is often estimated as a change in mean size of sampled fish between location and sampling times or a change in mean size of batch-marked fish (e.g., coded-wire-tagged [CWT] fish) between release and recapture. Unfortunately, these measures of growth can be biased by size-selective sampling and mortality and mask variability in individual growth.

New findings based on structural and chemical otolith analysis (see [Box 1](#)) provides some insight about growth in the Delta and San Francisco Bay. For example, Miller et al. (2010) examined ratios of the concentrations of metals to calcium in the otoliths of harvested adult fall-run Chinook Salmon, which follow an ocean-type life history, and compared them to juvenile growth patterns determined from the otolith structure. They found that in 2003 and 2004 nearly 70% of returning adults had entered brackish waters as fry (typically ≤ 55 mm in fork length) or parr (56–75 mm) rather than as smolts (> 75 mm). Some adults that had exited freshwater as fry or parr passed into marine waters quickly, but approximately 25% displayed noticeable growth within brackish waters. Although previous research reported little

growth among juvenile Chinook Salmon during estuarine residence in San Francisco Bay (MacFarlane and Norton 2002), the findings of Miller et al. (2010) suggest that estuarine rearing was a life-history strategy that contributed to adult returns. Other river deltas and estuaries on the West Coast also serve as important rearing areas for fry or parr, including the Columbia, Skagit, and Fraser deltas, as well as those of river systems on Vancouver Island in British Columbia (Healey 1991; Greene et al. 2005; Bottom et al. 2005).

SUCCESSFUL JUVENILE LIFE-HISTORY STRATEGIES IN THE DELTA

A wide array of life-history strategies is observed within the Delta, and maintaining habitat to support all life-history strategies is important for population resilience. Understanding which strategies are actually successful—i.e., strategies in which juveniles ultimately survive to return as adults—can provide critical insights into the role of the Delta in salmonid population dynamics. In the past decade, chemical and structural otolith analyses have led to

BOX 1

Using Chemical and Structural Otolith Analysis to Reconstruct Juvenile Rearing Strategies

Otoliths are small bones found in the inner ear of vertebrates, including fish, and form part of the vestibular system. As the fish grows, the otolith accrues daily growth rings, similar to a tree laying down annual growth rings. The width of the otolith ring reflects the growth rate: wide rings indicate fast growth, and narrow rings indicate slow growth. Just as tree rings from a mature tree provide a history of the tree's growth through its life span, an otolith removed from an adult fish provides information on the juvenile growth of the fish, starting from emergence from the gravel.

Statistical models have been developed that relate otolith size to fish size (body length, commonly measured as fork length). Thus, via "structural analysis" of the otolith, it is possible to reconstruct the fish's juvenile growth patterns. Structural analysis has also been used to distinguish between naturally produced and hatchery reared adults (Barnett-Johnson et al. 2007).

Recent analytical methods have focused on chemical analysis of the otolith. The otolith is made of calcium carbonate taken from the water, but also stores trace elements reflective of environmental conditions in the rearing areas. In particular, strontium (Sr) and barium (Ba) isotopes are both found in otoliths. Both metals may vary in their environmental concentration along a headwater-to-ocean gradient, allowing researchers to make inferences about the rearing environment of juvenile fish from the concentrations of these elements, relative to calcium, in the otolith taken from the adult fish. The ratio of strontium to calcium (Sr:Ca) is found in higher concentrations in marine water, while the ratio of barium to calcium (Ba:Ca) is in higher concentrations in freshwater. By examining ratios of these metals to calcium in different parts of the otolith, it is possible to identify which part of the otolith was formed during the juvenile transition from freshwater to brackish or marine environments. Combining this result with the statistical relationship between otolith size and fish length, it is possible to estimate the size of the fish when it left freshwater (Miller et al. 2010).

A related approach tracks strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) in the otolith to reconstruct juvenile rearing and migration history. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio varies in the water of different freshwater streams in the Central Valley, and analysis of the isotope ratio from returning adults (i.e., harvest or spawners) can yield information on rearing type (natural vs. hatchery), natal stream, and size at exit from the natal stream (Sturrock et al. 2015).

important new insights about variation in the success of different juvenile life history strategies (Box 1). In their otolith analysis of adult Central Valley Chinook Salmon, Miller et al. (2010) found evidence of multiple juvenile life history strategies: among 99 adult fall-run Chinook Salmon from the Central Valley that were harvested in an ocean fishery and that had entered the ocean as juveniles in 2003 and 2004, 48% had left freshwater as parr, 32% as smolts, and 20% as fry. They were also able to detect evidence of prolonged rearing in brackish waters among approximately 25% of the parr migrants, 55% of fry migrants, and 3% of smolt migrants (total of 18 individuals), suggesting that estuary rearing (the Delta and San Francisco Bay) was more important to overall success than previously thought.

Sturrock et al. (2015) used otolith isotope analysis and structural analysis to reconstruct fish size and life stage at juvenile emigration for returning spawners that had emigrated from the lower Stanislaus River in 2000 and 2003. They compared the relative frequency of various juvenile life stages (fry, parr, and smolt-sized fish), that left the Stanislaus River as inferred from the otolith analysis to the relative frequencies observed from juvenile sampling at rotary screw traps during those years. This approach allowed them to estimate the long-term probability of surviving to adult spawning for different life stages at emigration from the Stanislaus River. Although fry and smolts collectively formed the majority of the juvenile emigrants from the Stanislaus River, a higher proportion of surviving adults had emigrated from the Stanislaus River as parr than as either fry or smolts in both years. Survival estimates from juvenile emigration to adult spawning were 0.0178 to 0.0274 for parr, compared to 0.0007 to 0.0019 for fry, and 0.0077 to 0.0120 for smolts, but 95% confidence intervals for parr and smolts overlapped (Sturrock et al. 2015). They further found that the fry outmigration strategy contributed little to adult returns in the dry year but up to 20% of the adult returns in the wet year.

Both Miller et al. (2010) and Sturrock et al. (2015) found that a high proportion of the adult catch was composed of parr emigrants and that the contribution of fry emigrants varied among years. These findings suggest that management that promotes a diversity of life-history strategies in the Delta is likely to be

more effective at improving population resiliency than that which focuses on one life-stage or one habitat type. Sturrock et al. (2015) also concluded that improvements in the estimates of the emigrating juvenile population size would facilitate efforts to understand the role of fry and parr in salmon population dynamics.

RUN TIMING, COMPOSITION, AND ABUNDANCE

Quantifying the contribution of different life history strategies to each race requires knowledge of when juveniles of specific life stages from specific runs occupy the Delta. Run timing is also particularly important for understanding when threatened and endangered runs are present in the Delta so protective water management actions can be implemented. Although juvenile salmon are present in the Delta in all months of the year (with peaks in winter and spring, Erkkila et al. 1950), understanding variation in juvenile migration timing and abundance among runs is complicated by overlapping size distributions among the runs during much of the year (Fisher 1994; Yoshiyama et al. 1998). In addition, identifying basin of origin is difficult because spatial distributions of juvenile salmon from the Sacramento and San Joaquin basins overlap in the much of the Delta.

Two separate length-at-date models have been widely applied to quantify the race composition of fish sampled at different monitoring locations in the Delta based on their length on a specific date: Fisher (1992) ("river model") and Harvey et al. (2014) ("Delta model"). However, because fish of a given size from different runs may occupy the Delta at the same time, genetic analysis has revealed that these models are inaccurate, with the magnitude of bias depending on run, sampling location, and time of year (Hedgecock 2002; Pyper et al. 2013a; Harvey et al. 2014). Recent work from genetic analysis of tissue samples from fish collected in the Chipps Island trawl and at the pumping station fish facilities found that the river and Delta length-at-date models overestimated the proportion of winter and spring runs and underestimated the proportion of fall and late-fall runs (Figure 3). Bias in the estimates of race composition in fish sampling programs hampers our

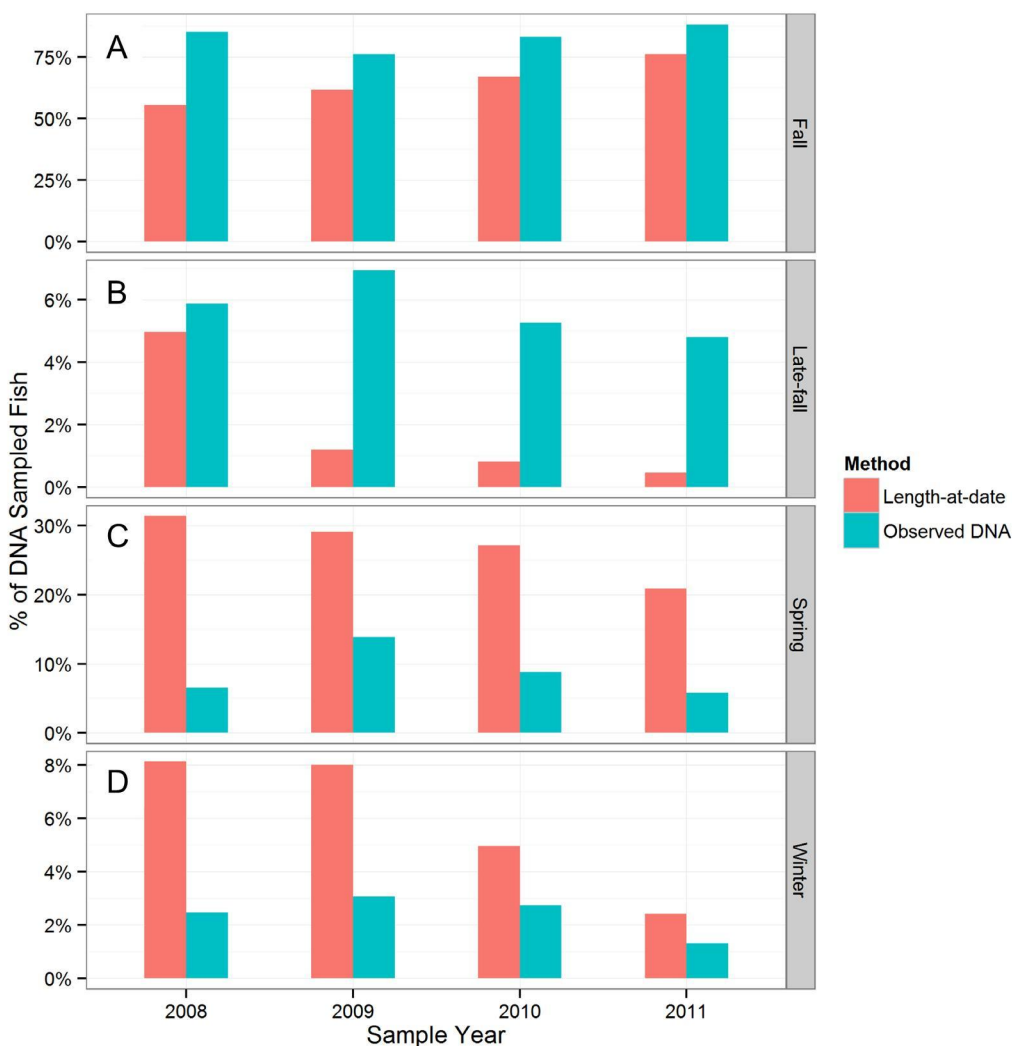


Figure 3 Comparison of run assignments based on length-at-date criteria versus DNA (observed and corrected) for juvenile Chinook Salmon caught in Chipps Island trawl and DNA assigned to run (Pyper et al. 2013a). For each sample year and assignment method, the percentage of total juveniles assigned to each run is shown. Sample year 2008 is defined as August 1, 2007 through July 31, 2008, and similarly for 2009, 2010 and 2011.

understanding of run-specific life-history attributes (such as size, timing, and relative abundance) in the Delta. In the future, implementation of a genetic sampling program at long-term fish monitoring stations (e.g., Chipps Island) would provide unbiased estimates of run composition and timing of juveniles from the different runs that migrate through the Delta (IEP-SAG 2013).

Despite their biases, the length-at-date models are used for to classify runs and understand the potential life-history strategies of specific runs. For example, del Rosario et al. (2013) analyzed migration patterns of winter-run-sized Chinook Salmon (using the river

length-at-date criteria) by examining differences in cumulative catch curves at two sampling locations: Knights Landing (51 km upstream of Sacramento), and Chipps Island (at the terminus of the Delta). Average residence time of winter-run-sized fish in the Delta was nearly 3 months. Median entry time into the Delta varied among years from mid-November to late January, and was strongly linked to the first major freshet of the winter. Yet among years, winter-run-sized fish exited the Delta over a narrow window in March. Consequently, between 1999 and 2007, median residence times ranged widely from 41 to 117 d. Although uncertainties remain regarding the length-at-date models, this research

sheds light on how migration strategies are linked to environmental cues that affect entry and residence times of winter-run-sized juvenile Chinook Salmon in the Delta.

Estimating absolute abundance of juvenile Chinook Salmon in the Delta has long been a goal of juvenile fish monitoring programs but has been difficult to achieve in practice (Dekar et al. 2013; IEP-SAG 2013). Juvenile abundance is an important parameter, particularly when viewed in a life-cycle context relative to the number of spawners or to abundance at some other point in time or space. “Abundance” may be estimated in two distinct ways: (1) by estimating the number of fish that pass a fixed sampling location over time (e.g., using trawls or screw traps), or (2) by estimating abundance over some spatial area at a particular point in time (e.g., using beach seines). However, in both estimation methods, the sampling gear captures only a fraction of the fish present. Consequently, estimating abundance requires expanding catch by an estimate of capture probability. Estimating capture probabilities for all gears, within and between years, for the size range of juvenile salmon caught has been difficult to achieve (Pyper et al 2013b). Catch is often used as an index of abundance (i.e., relative abundance) under the assumption of constant capture probability. Inferences about trends in abundance drawn from catch data may be seriously biased if capture probability varies over time or with environmental variables such as flow or temperature.

To estimate abundance of juvenile salmon, monitoring programs have recognized the need to explicitly estimate capture probability and factors that affect capture probability (Dekar et al. 2013; IEP-SAG 2013; Pyper et al 2013b). To estimate abundance of juvenile salmon passing Chipps Island, Kimmerer (2008) used the “fish flux method,” which assumed that capture probability was proportional to the fraction of the water volume sampled multiplied by the migration speed past the trawl. Subsequently, Pyper et al. (2013b) conducted an extensive analysis using three different data sets and analytical techniques to estimate capture probability from releases of CWT fish. Capture probability varied considerably from year to year, and this variation was not explained by covariates that would be expected to influence capture probability. Mean

capture probability estimates ranged from 0.006 to 0.012 compared to 0.04 from the fish flux method. Pyper et al. (2013b) cautioned against using the fish flux method because it considerably overestimated capture probability relative to empirical estimates obtained from CWT fish and could, therefore, seriously under-estimate true abundance.

To estimate the absolute abundance of juvenile salmon in the Delta from catch at monitoring sites, much work remains to develop sampling designs that account for capture probability. Ongoing efforts to develop such methods stand to considerably improve our understanding of abundance and its relationship to population dynamics and life history strategies employed by different runs of salmon in the Central Valley.

SURVIVAL OF JUVENILE SALMONIDS IN THE DELTA

Understanding how juvenile salmonids of different life stages and runs survive in the Delta is critical for devising restoration and management actions. Between the 1970s and 2006, mark-recapture studies using CWTs formed the basis of research to estimate survival of subyearling fry and smolts of Chinook Salmon in the Delta (Kjelson et al. 1982; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003). In general, this methodology involved marking tens of thousands of fish, releasing them at various locations in the Delta, and then recapturing them using a mid-water trawl at the outlet of the Delta at Chipps Island and in the commercial ocean fishery. Different release locations served as reference points to compare the relative probability of surviving through the Delta via different migration routes. Various statistical methods have been used to analyze the CWT studies, ranging from simple regression analysis of survival “indices” based on expansion of trawl counts (Kjelson et al. 1981; Kjelson and Brandes 1989; Brandes and McLain 2001) to sophisticated Bayesian hierarchical models that account for the multinomial structure of recapture data and for multiple sources of variation (Newman and Rice 2002; Newman 2003).

Recent analyses summarized the major CWT experiments occurring in the Delta through 2006, including both Sacramento River and San Joaquin

River studies (Newman 2008; Newman and Brandes 2010). These studies found modest evidence that closure of the Delta Cross Channel (DCC) gate improved survival of fish released at Sacramento. In addition, mean survival of fish released into Georgiana Slough, who then migrate through the interior Delta (the region to the south of the Sacramento River; [Figure 2](#)), was only 35% to 44% of the mean survival of fish that remained within the Sacramento River. Newman (2008) also found that for San Joaquin River fish, survival through the Delta was lower for fish that entered the Old River compared to those that continued to migrate down the San Joaquin. Newman (2008) also found weak (non-significant) evidence of a positive effect of export rate (the amount of water pumped out of the Delta) on survival of San Joaquin River fish, but noted that the tendency of high exports to occur with high inflow made it difficult to draw firm conclusions.

Although the CWT studies provided important information that helped us understand how water management actions affect the survival of juvenile salmon, major knowledge gaps remained. For example, until recently there remained a major lack of information about how juvenile salmon were distributed among the Delta's channel network once they entered the Delta. This understanding is critical, because even though survival may differ drastically among migration routes, the effect of each route on total survival in the Delta depends on the fraction of the population that uses each route. Because water management actions may differentially affect population components in different regions of the Delta, understanding both how survival varies among routes, and how fish distribute among routes, is critical for understanding how management actions at local scales affect total survival.

Starting in 2006, biotelemetry techniques began to replace CWT studies as a way to quantify migration behavior and survival of juvenile salmon in the Delta. Application of biotelemetry techniques entails deployment of telemetry monitoring stations at key locations throughout the Delta, implanting small transmitters into juvenile salmon, and then tracking their migration through the Delta ([Box 2](#)). In spatially complex settings such as the Delta, biotelemetry has a number of advantages over traditional mark-

recapture techniques that rely on the physical recapture of fish (e.g., CWTs). First, uniquely identifiable transmitters provide detailed information about the temporal and spatial movements of individuals migrating through a network of telemetry stations in the Delta. Second, the "capture" process is passive, so that an individual may be "captured" numerous times as it migrates unimpeded through the Delta. Third, the spatial arrangement of telemetry stations in the Delta can be tailored to the Delta's complex channel structure to quantify both movement among and survival within given migration routes. Last, because telemetry receivers are able to monitor for tagged fish continuously, detection probabilities are typically high (>0.75), and small sample sizes can yield high precision of parameter estimates.

Although mark-recapture statistical models have long been applied to telemetry data on migrating fish populations (Skalski et al. 1998, 2002), these statistical models had to be adapted to accommodate the spatial complexity of the Delta. Perry et al. (2010) developed a multistate mark-recapture model that was tailored to the hierarchical branching structure of the Delta ([Box 2](#)). This research represented a landmark advance in estimating the underlying components of survival of juvenile salmonids that migrate through the Delta.

For hatchery late-fall-run Chinook Salmon that emigrate from the Sacramento River, analysis of telemetry data has led to new insights about survival through the Delta and has supported findings of previous CWT analyses. Overall, survival through the Delta for hatchery-origin late-fall-run Chinook Salmon ranged from 0.17 to 0.54 for migration years 2006–2010 (Perry et al. 2010, 2013). This range of survival appears to be lower than observed in other large West Coast watersheds. For example, when survival rates of yearling Chinook Salmon in other systems are scaled to the same migration distance of the Delta (81 km via the Sacramento River), mean survival was 0.92 in the lower Columbia River (McMichael et al. 2010) and 0.67 in the Fraser River (Welch et al. 2008). Among migration routes, survival of juvenile salmon emigrating within the Sacramento River was always greater than twice that of fish entering the interior Delta via the DCC and Georgiana Slough, similar to findings of Newman (2008).

BOX 2

Translating Telemetry Data into Routing and Survival Estimates

One of the most important advances in juvenile salmon research over the past decade has been the use of telemetry techniques combined with multistate mark–recapture models to estimate survival and the proportion of fish using different migration routes. Here we take the opportunity to describe in a bit more detail how researchers design, implement, and estimate survival and movement parameters for these studies. For more detail, interested readers should consult Perry (2010), Perry et al. (2010), and Buchanan et al. (2013), and for a more general treatment of multistate mark–recapture models, see Nichols and Kendall (1995) and Lebreton and Pradel (2002).

A major challenge with quantifying survival of juvenile salmon in the Delta is the extreme complexity of the Delta's channel network. Historically, survival was estimated between a release and recapture point using coded-wire tags but there was little understanding of how fish used alternative migration routes between release and recapture points. Although telemetry techniques allow researchers to track migration pathways used by individual fish, translating these detections into robust survival and routing estimates requires design of a statistical mark–recapture model. Telemetry system design (i.e., the spatial arrangement of antennas or hydrophones in the Delta) dictates the structure of the mark–recapture model and, hence, the survival and movement parameters that can be estimated from telemetered fish (see [Figures B2.1A](#) and [B2.1B](#)) on page 11). Therefore, careful study design is critical to successfully applying mark–recapture models to a spatially complex system like the Delta. Study design involves (1) identifying parameters of interest, (2) designing the mark–recapture model to estimate these parameters, and (3) implementing the telemetry system required by the mark–recapture model. In our experience, many telemetry studies fail to follow these important steps, resulting in inability to estimate important survival and routing parameters.

Demographic parameters of interest are S_{hi} , the probability of surviving from telemetry station i to $i+1$ within route h , and ψ_{hl} , the probability of a fish entering route h at river junction l , conditional on fish surviving to junction l ([Figure B2.1B](#)). To estimate survival within a specific migration route, telemetry receivers must be deployed just downstream of the entrance to each migration route (channel) at a junction where the river divides into two or more channels. This arrangement of receivers also allows for estimation of routing probabilities, ψ_{hl} . For example, see sites A1 and B3 in [Figure B2.1A](#) at the junction of Sutter and Steamboat sloughs with the Sacramento River. Once

again, the structure of the statistical model and estimated parameters follow directly from the spatial arrangement of telemetry receivers in the Delta ([Figures B2.1A](#) and [B2.1B](#)).

The other important function of a mark–recapture model is to statistically distinguish between those individuals that have died in a given reach, and those that have survived but may not have been detected at downstream locations. Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h . Although high detection probabilities are one of the strengths of using telemetry techniques, seldom are telemetry systems able to perfectly detect every individual migrating past a site. Thus, jointly estimating survival and detection probabilities prevents negative bias in survival estimates.

These individual reach-specific survival and routing probabilities provide researchers a wealth of information about how juvenile salmon survive in specific reaches, and the proportion of fish entering a given migration route. However, these parameters may also be combined to estimate survival for an entire migration pathway through the Delta and the probability of fish using that pathway. The product of reach-specific survival probabilities that trace a specific pathway through the Delta estimates the total survival between beginning and ending points of the Delta (e.g., between Sacramento and Chipps Island) for fish that used that specific migration pathway (see bottom panel). These summaries provide a powerful way to compare alternative migration routes because they estimate survival between the same beginning and ending points of the Delta but for fish that used alternative migration pathways. Likewise, by multiplying the routing probabilities along a given migration pathway, we obtain the expected proportion of fish that used that migration route (see bottom panel). These provide the fundamental components that allow researchers to understand how survival within a migration route and the proportion of fish using that route influence total survival of fish migrating through the Delta.

(continued on page 11)

BOX 2 CONTINUED

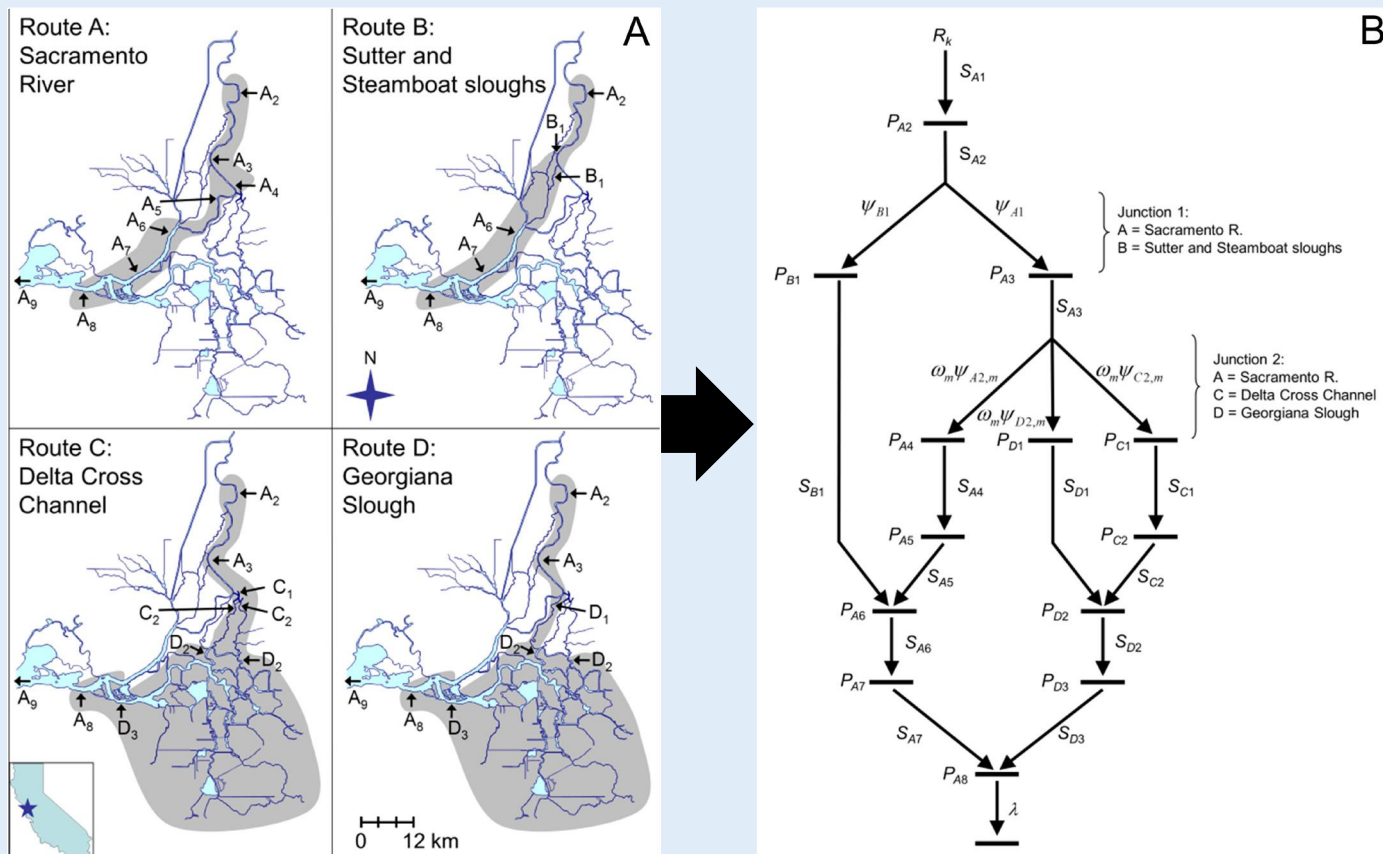


Figure B2.1 Approach for translating detections from a system of telemetry stations in the Delta into estimates of survival for each migration route. **(A)** shows the system of telemetry receivers that uniquely defines each migration route, **(B)** shows a schematic of the mark–recapture model and associated survival, detection, and routing parameters, and **(C)** shows how reach-specific survival parameters are summarized into survival for four different migration routes. Adapted from Perry et al. (2010).

Estimates of survival through the Delta for hatchery juvenile fall-run Chinook Salmon that emigrate from the San Joaquin River have been markedly lower than those from the Sacramento River. In addition, survival in the San Joaquin River has declined considerably since the 1990s and remained very low over the past decade (Figure 4). From 2003 to 2012, survival through the Delta has ranged from 0 to 0.11 among release groups, and has been ≤ 0.05 for 15 of 22 observations (Figure 4). Survival of San Joaquin River fall-run juveniles, estimated from telemetry tags, is considerably lower than survival of juvenile Chinook Salmon estimated from other large estuaries along the West Coast. When adjusted for different migration distances, juvenile Chinook Salmon survival has been estimated at more than 20 times greater in the Columbia River, and more than 15 times greater in the Fraser River, compared to San Joaquin River salmon (Buchanan et al. 2013).

Telemetry data provide more detailed spatial information on survival through the Delta than CWT data. In particular, unlike previous CWT studies,

telemetry data have provided little evidence for the hypothesis that survival of Chinook Salmon is consistently higher for fish that remain in the San Joaquin River compared to those that enter the Old River (SJGRA 2013; Buchanan et al. 2013, 2015). It is uncertain how much the relative survival in these two routes may depend on river conditions and the presence of either a physical rock barrier or a non-physical barrier (e.g., a Bio-Acoustic Fish Fence, Bowen et al. 2012; Bowen and Bark 2012) installed at the head of Old River to prevent fish from entering Old River. The goal of these barriers is to divert fish away from the Old River and into the San Joaquin River because the Old River leads fish towards the State Water Project (SWP) and federal Central Valley Project (CVP) where they may be entrained into water pumping stations. Unlike a physical barrier, the non-physical barrier does not divert flow away from the Old River into the San Joaquin River; it is possible that this additional flow is needed to boost survival of fish that remain in the San Joaquin River.

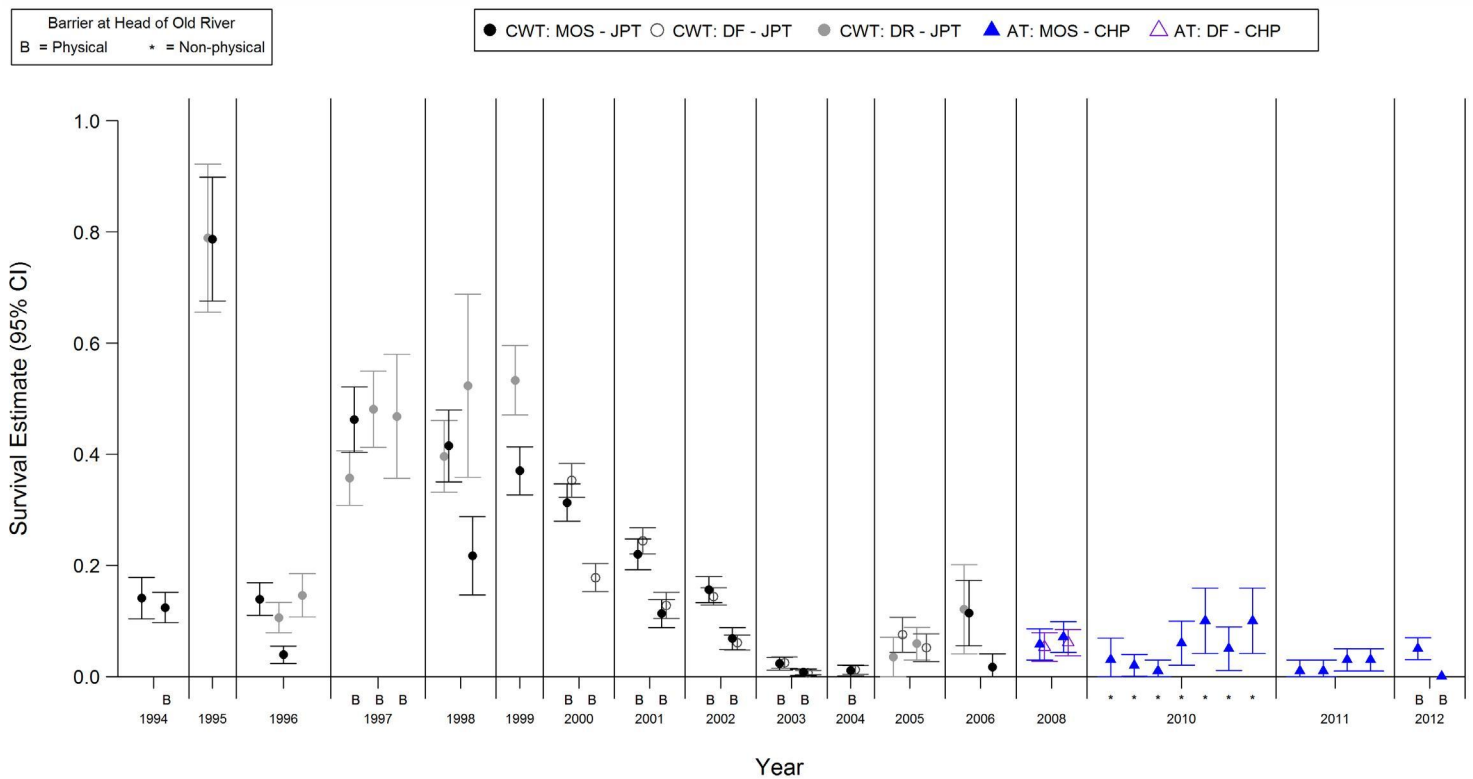


Figure 4 Estimated survival of fall-run Chinook Salmon from either Durham Ferry, Mossdale, or Dos Reis to either Jersey Point (coded-wire tags, CWT) or Chipps Island (acoustic telemetry tags, AT). Intervals are 95% confidence intervals (truncated to 0 if necessary). Data sources: Holbrook et al. (2009), SJRGA (2013), Buchanan et al. (2015).

Telemetry data from Delta survival studies have shown that survival tends to be higher in the upper reaches of the Delta compared to lower reaches. In the Sacramento River, survival rate per kilometer generally declined along a downstream gradient, with lowest survival rates occurring in the interior Delta and the region around Cache Slough (Perry 2010). In the San Joaquin system, survival estimates of juvenile fall-run Chinook Salmon from the region near the Mossdale Bridge to Turner Cut averaged 0.30 for 2008–2012, while survival in all possible routes downstream of the Turner Cut junction to Chipps Island averaged only 0.11 in 2008 and 2010–2012 (Holbrook et al. 2009; Buchanan et al. 2013, 2015; SJRGA 2013).

Low survival of both Chinook Salmon and Steelhead entrained into the SWP and CVP has been observed from numerous telemetry studies (Clark et al. 2009; SJRGA 2011, 2013). Nevertheless, in 2010 and 2011, when overall Delta survival was less than 0.10 for San Joaquin River fall-run Chinook Salmon, the majority (19 of 26 tagged fish) that reached Chipps Island were observed passing through the salvage facility at the CVP, where they were subsequently transported and released just upstream of the terminus of the Delta at Chipps Island (SJRGA 2011, 2013). Thus, this route may be an important contributor to over survival during periods when survival through in-river migration routes is very low.

Overall, the past decade has provided a great deal of information on survival in the two major migration routes defined at the head of Old River. Patterns of survival in these routes have not been consistent, however, and it is not yet understood which factors (e.g., river flow, barrier presence and type) determine survival in either route. Throughout the past decade, survival of fall-run Chinook Salmon smolts has been low in both routes.

A considerable amount of new information has been gained in the past decade on survival in the upper portions of the south Delta. Less is understood about survival in the lower reaches of the San Joaquin River and in regions such as Frank's Tract and the Old River and Middle River corridors. Studying survival in these regions is complicated by large river channels, strong reverse flows from tide, and attrition

of the tagged population from mortality and entry to other migration routes before they reach downstream regions.

MIGRATION ROUTING

Understanding entrainment rates at river junctions (the proportion of fish that enter each channel) at the upstream periphery of the Delta—Sutter Slough, Steamboat Slough, the DCC, and Georgiana Slough on the Sacramento River; and the Old River, Turner, and Columbia cuts on the San Joaquin River (Figure 2)—is critically important because entrainment rates control the proportion of the juvenile salmon population that take a particular migration route, and thereby affect how the population is distributed among channels that have spatially variable transit times and survival rates. The Delta Cross Channel and Georgiana Slough branch off the Sacramento River and divert fish into the interior Delta, where survival probabilities are lower (Perry et al. 2010; 2013) and fish have a higher probability of being drawn towards water pumping stations in the southern Delta (Newman and Brandes 2010) than fish that remain in the Sacramento River. Sutter and Steamboat sloughs branch off the Sacramento upstream of Georgiana Slough and the DCC; thus, fish taking these routes are not subject to entering the interior Delta. On the San Joaquin River, fish first encounter the junction of the San Joaquin River and Old River. Fish that remain in the San Joaquin River may subsequently enter Turner and Columbia cuts, which lead toward the Old and Middle rivers, where net flows may draw fish toward the pumping stations.

Before the telemetry studies that began in 2006, estimates of fish routing at river junctions were few (Schaffter 1980; Kjelson et al. 1989), and the hypothesis was that juvenile salmon distributed among river channels in direct proportionality to the fraction of mean river discharge that entered each channel. However, since 2006, the use of telemetry techniques has markedly improved our understanding of how river flow, tidal dynamics, and barrier installation or gate operation affect the migration routes of juvenile salmon (Box 3). Given new tools to understand migration routing at river junctions, research increasingly has been focused on critical river junctions that may determine the ultimate

fate of juvenile salmon. Initial studies first provided point estimates of the mean proportion of fish using different migration routes over an entire release group (Perry et al. 2010; Buchanan et al. 2013). These studies were followed by research to understand how tidally-varying river flows affect the probability of an individual entering different river channels (Perry 2010; Perry et al. 2015; SJRGA 2013). More recent research has focused on evaluating behavioral guidance structures (e.g., non-physical barriers) as management tools to divert fish away from low-survival migration routes and toward high-survival migration routes (Perry et al. 2014; Bowen et al. 2012; Bowen and Bark 2012).

In addition to survival, the mark-recapture models developed by Perry et al. (2010) and Buchanan et al. (2013) provided the first estimates of the proportion of fish that enter different channels at key river junctions, parameters critical for understanding the fraction of fish that were subject to the survival rates of a given migration route (Perry et al. 2013, see also [Box 2](#)). For example, Perry et al. (2010) found that 16% to 20% of the fish arriving at the DCC/Georgiana Slough junction entered Georgiana Slough and 38% of the fish entered the DCC.

These findings illustrate why accounting for routing at multiple river junctions is important for understanding how different fractions of the migrating population are subject to survival rates associated with different migration routes. Perry et al. (2013) further found that eliminating entrainment into the interior Delta (via Georgiana Slough and the DCC) could increase overall survival by 2% to 7%, given the route-specific survival probabilities estimated for six release groups between 2007 and 2010.

Research between 2007 and 2010 revealed that survival through the interior Delta was consistently lower than other migration routes for Sacramento River fish, which prompted managers to investigate use of non-physical barriers to alter migration routing at river junctions. On the San Joaquin River, there was also interest in keeping fish from entering the Old River, which directed fish toward the SWP and CVP. Therefore, a non-physical barrier known as a Bio-Acoustic Fish Fence (BAFF) was installed and tested at the entrance of Georgiana Slough on the

Sacramento River and at the entrance to Old River on the San Joaquin River. The BAFF consisted of a curtain of air bubbles, sound, and flashing lights intended to elicit a behavioral avoidance response that would keep fish from entering these migration routes. On the Sacramento River, the BAFF was shown to reduce the proportion of fish entering Georgiana Slough from 22.3% to 7.7% (Perry et al. 2014). However, the BAFF's effectiveness was shown to decrease with increasing discharge, likely because the fish were unable to avoid being swept into Georgiana Slough as water velocities increased. The physical barrier at the head of Old River was shown to better deter fish than the non-physical barrier at the head of Old River, although predation around both barriers was high (CDWR 2015).

On the San Joaquin River, the BAFF was tested in 2009 and 2010 to determine if it could be used to prevent fish from entering Old River. Both the BAFF configuration and placement in the river—as well as river flow and water velocity—were considered to be important factors in determining its effectiveness. However, during 2010 when the BAFF was present, survival was low in both the San Joaquin and Old River routes to Chipps Island, and there was no consistent survival benefit to remaining in the San Joaquin River. High flows prevented a third year of investigation into the BAFF in 2011, and a physical barrier was installed during the spring outmigration in 2012. From the telemetry studies in 2008–2011, the proportion of Chinook Salmon that entered the head of Old River ranged from 37% to 68%, and averaged 52% (Holbrook et al. 2009; SJRGA 2010, 2011, 2013). Tagged Chinook Salmon were less likely to enter Turner Cut, a tidally influenced junction that has no barrier, with estimates ranging from 0% to 32% (average = 14% in 2008–2012).

Many river junctions in the Delta are highly dynamic, with the direction and magnitude of flow that enters each channel varying on hourly time-scales with the tides. Consequently, the probability of a fish entering a given river channel will depend considerably on the time-specific hydraulic conditions it encounters upon arrival at a river junction. Furthermore, because fish behavior may determine both when fish arrive at a river junction and where fish are located in the channel's cross-sectional profile, physical and behavioral processes may interact such that the mean

BOX 3**Entrainment Zones and the Critical Streakline**

The conceptual model we use to study entrainment rates of juvenile salmon at junctions is based on the entrainment zone and critical streakline concepts. This conceptual model illustrates why we should not expect fish to distribute among channels in junctions in direct proportion to discharge. Just upstream of a river junction, passive particles within the parcel of water entering a side channel (the entrainment zone) have a high probability of entering the side channel and a low probability of remaining in the main channel (Figure B3.1A). The extent of each entrainment zone is determined by the location of the critical streakline (the red lines in Figure B3.1 on page 16), defined as the spatial divide between parcels of water that enter a side channel or remain in the main channel. The location of the critical streakline can be found by integrating velocity vectors over the channel cross-section until the accumulated discharge just equals the discharge entering the side channel. Recent research supports the entrainment zone concept by showing that fish located on either side of the critical streakline have a higher probability of entering their respective channels (Perry et al. 2014). Based on this conceptual model, the only condition under which fish enter river channels in direct proportion to flow is when their cross-sectional distribution is uniform and constant over time (Figure B3.1A). Yet migrating and rearing juvenile salmon are seldom, if ever, uniformly distributed within a river channel (Horn and Blake 2004; Perry et al. 2014), leading to entrainment rates that deviate from the proportion of flow entering each channel (Figure B3.1A; Cavallo et al. 2014; Perry et al. 2015). However, entrainment rates can be predicted by understanding how the combination of critical streakline position and cross-sectional

distribution of fish co-vary as a function of environmental variables such as tidal forcing, because the point at which the streakline bisects the fish's spatial distribution determines the entrainment probabilities. Critical streakline positions can be estimated on a 15-minute interval using existing long-term flow monitoring data.

The velocity distributions in junctions within the tidally forced regions of the Delta are complex in both space and time (Figure B3.2) because ocean tides propagating into the Delta influence water levels, discharges, and velocity structures well into the upland fringes of the Delta. For example, the tidal currents reverse in all of the river junctions in the Delta during low flow conditions. The critical streakline concept is therefore a way of collapsing the complexity of the tidally forced flow fields to their essence with regard to fish fates. For example, instead of having to map every single velocity in the entire flow field and compute Lagrangian trajectories within an entire junction we need only compute a single path — the critical streakline. To deduce those behaviors that lead to a change of fate, we need only determine whether a fish crosses the critical streakline. Behaviors that keep fish within each entrainment zone do not ultimately change the fish's fate. Therefore, the critical streakline concept has been used to good effect both in understanding why fish go where they go at junctions and in evaluating and optimizing the design of non-physical barriers. Thus, non-physical barriers that focus on moving fish from one side of the streakline to the other will effectively alter migration routing at a river junction.

(continued on pages 16–17)

fraction of fish that enter a river channel deviates from the mean proportion of discharge that enters a river channel (Box 3). For example, Perry et al. (2015) showed both that the probability of a fish remaining in the Sacramento River ranged from near zero during reverse-flow flood tides to near one during ebb tides, and that the probability of a fish remaining in the Sacramento River was higher than the proportion of discharge remaining in the Sacramento River. This finding was supported by Cavallo et al. (2015) who compiled empirical routing estimates from multiple telemetry studies. They found that the proportion of fish that entered distributaries (secondary channels that branch off a main channel) was consistently lower than the fraction of discharge that entered the distributaries.

FLOW, EXPORTS, AND OTHER FACTORS THAT AFFECT SURVIVAL

Nearly 30 years of CWT studies have formed the basis of understanding of how factors such as river discharge, gate operations, temperature, and turbidity affect the survival of juvenile salmon in the Delta. Analysis of CWT studies conducted in the Sacramento River demonstrated a positive effect of river flow on survival, a negative effect of water temperature, a negative effect of an open DCC gate, and a negative but sometimes non-significant effect of exports (Kjelson et al. 1981, 1989; Baker et al. 1995; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003, 2008; Newman and Brandes 2010). For San Joaquin River fish, Newman (2008) found evidence of

BOX 3 CONTINUED

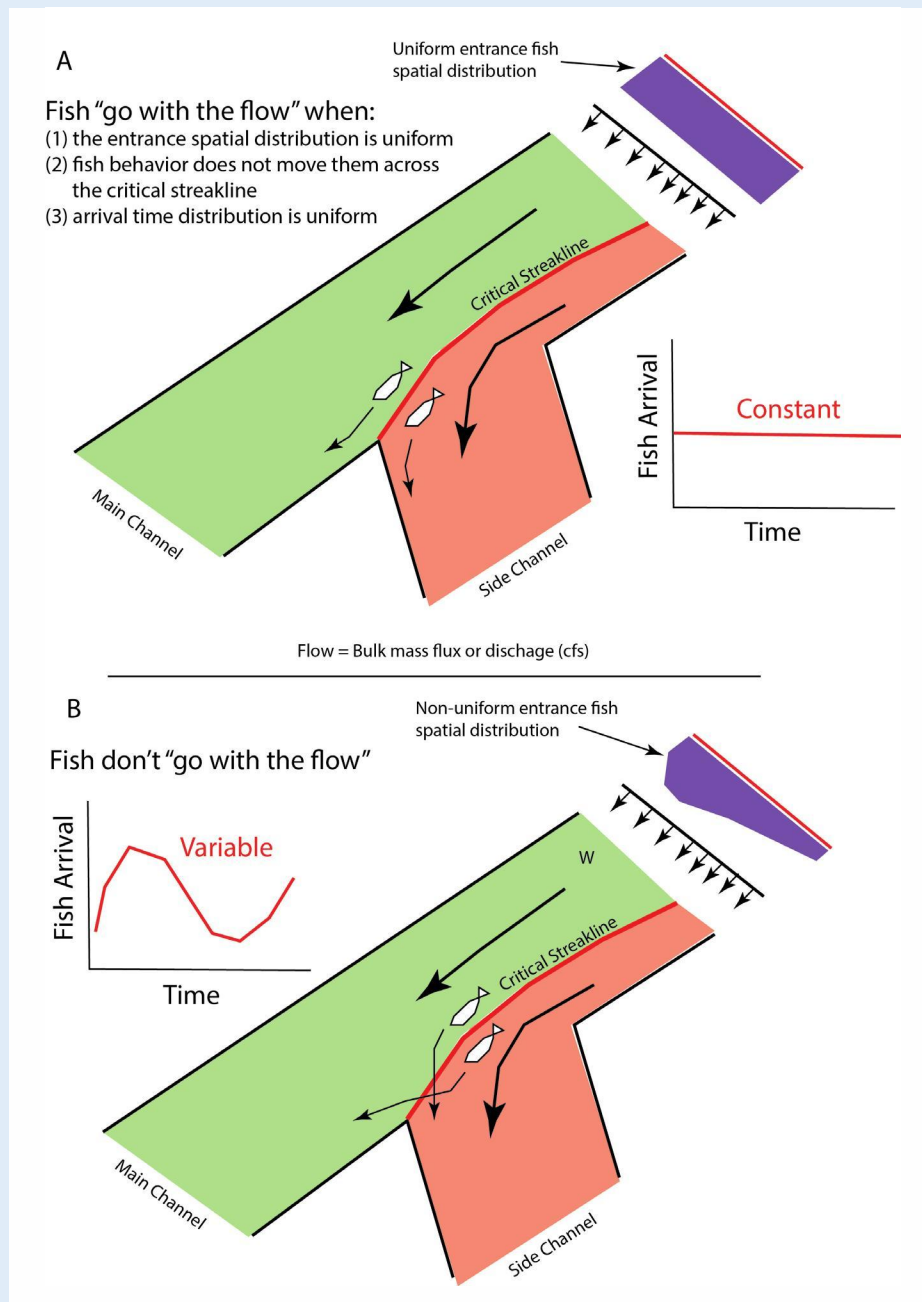


Figure B3.1 Red regions denote the entrainment zone for the side channel, whereas the green regions show the region where fish continue along the main channel. The red line between these regions is the critical streakline. **(A)** shows the required conditions for fish to "go with the flow"—in this case, the bulk as-measured discharge in each channel. These conditions include the spatially uniform fish-entrance distribution that is shown and behaviors that do not result in fish crossing the critical streakline. **(B)** shows the conditions that create situations where fish are not distributed in proportion to the flows in each channel. These conditions include a non-uniform fish-entrance distribution, variable entrance timing, and behaviors that cause fish to transit the critical streakline.

BOX 3 CONTINUED

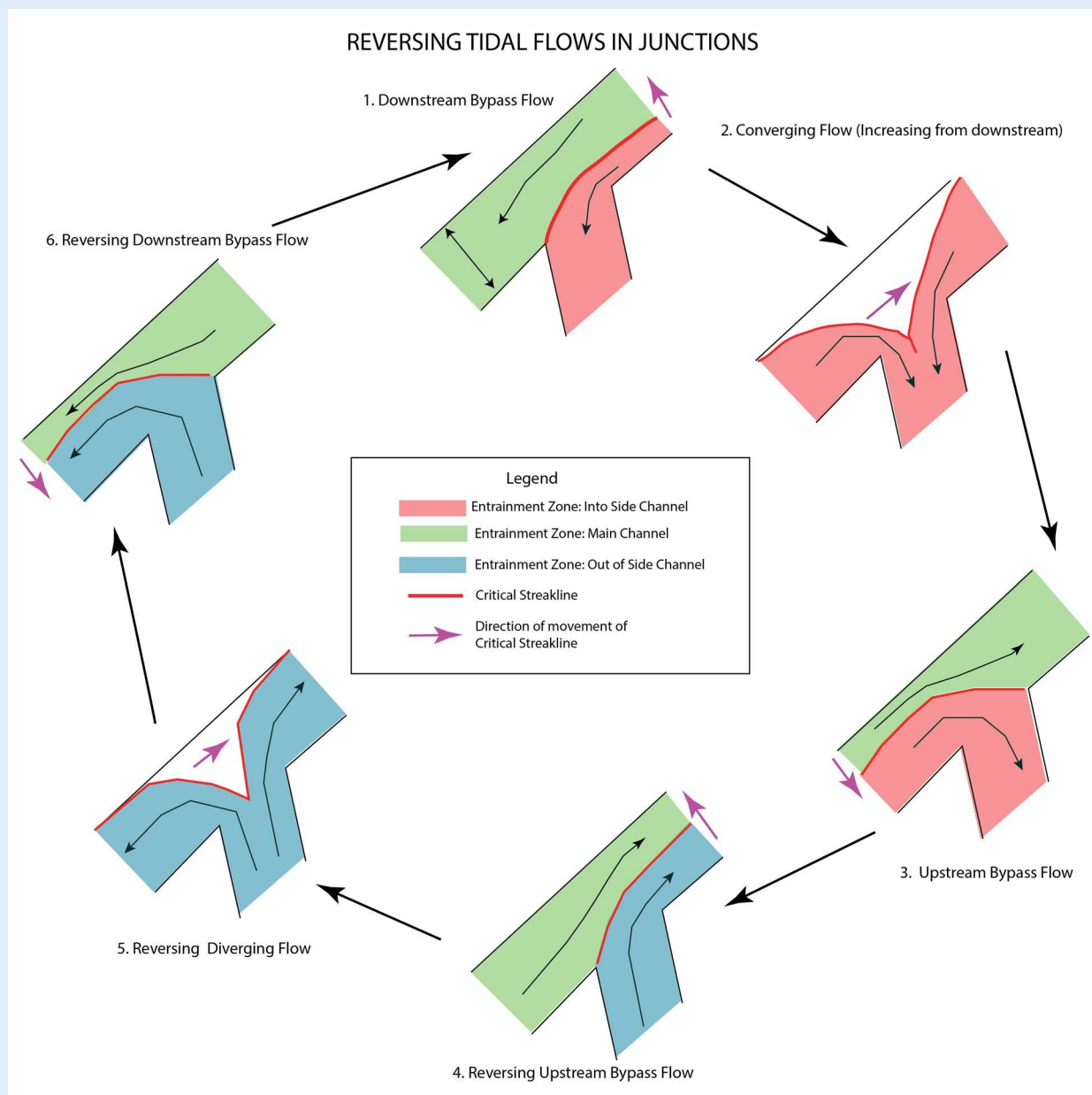


Figure B3.2 Critical streakline dynamics at a typical river junction in the Delta as the tide changes from flood to ebb twice a day. Almost all channel junctions in the Delta exhibit this sequence of changing flow patterns during periods of low river inflow. The exceptions are junctions at the Delta Cross Channel and Georgiana Slough: in these junctions, reversing flows rarely occur and when they do it is weak and short-lived. Finally, this sequence, including the direction of movement of the streakline, can be reversed depending on the phase relation between the main and side channels. The white (unshaded) regions represent “slack water” or negligible velocity regions.

a positive effect of inflow on survival; he also found weak (non-significant) evidence of a positive effect of export rate on survival, but noted that the tendency of high exports to occur with high San Joaquin River inflow made it difficult to draw firm conclusions.

Although telemetry studies have been relatively small-scale to date, with only a few years of replication, analyses are now beginning to paint a fuller picture of how survival in the Delta varies with environmental variables. For example, Perry et al. (2010) found that survival of juvenile late-fall-run Chinook Salmon was positively related to discharge and fish size in the Sacramento River and in Sutter and Steamboat sloughs. Perry's flow-survival relationship was very similar to that found by Newman (2003) when compared for a common reach and fish size, despite the different time periods, methods (coded-wire tag vs. acoustic tag), and fish sizes used in the studies (Figure 5).

One of the primary benefits of using acoustic telemetry rather than CWTs is the ability to estimate survival on smaller reaches throughout the Delta. Now that multiple years of telemetry data are becoming available, more work is needed to relate survival to environmental variables at finer spatial scales within the Delta to understand how these factors affect survival in different regions. For example, survival may be related to river flows upstream, but not in lower reaches of the Delta where the magnitude of tidal flows swamps net flows. Such hypotheses are difficult to test with CWT studies, but are feasible with telemetry. Moreover, river discharge, in and of itself, does not influence survival but rather is the master variable in the Delta (*sensu* Mount et al. 2012) that affects the underlying mechanisms that influence survival. For example, discharge affects turbidity and fish migration rates, both of which affect predator encounter rates and, ultimately, survival. Survival models such as the XT model—a predator-prey model that expresses survival as a function of travel time, travel distance, and predator densities (Anderson et al. 2005)—hold promise for helping us to better understand the mechanisms that underlie correlative relationships such as those in Newman (2003) and Perry (2010).

Inference about the direct effect of water exports on survival of juvenile salmonids in the south Delta

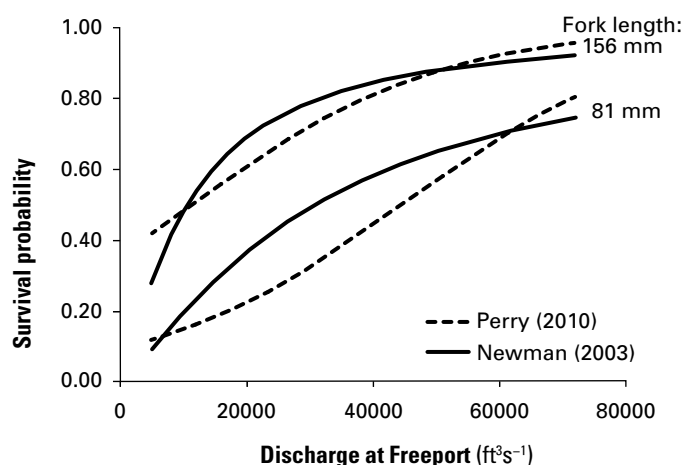


Figure 5 Comparison of flow-survival relationships obtained by Newman (2003) and Perry (2010). Survival relationships are compared for a common reach (Sacramento River from Ryde to Chipps Island) at a common fish size from each study (mean = 156 mm in Perry [2010] and 81 mm in Newman [2003]). For Newman (2003), results are from the hierarchical model with year-specific capture probabilities and all covariates set to their mean values, except for discharge and fish size. For Perry (2010), results are shown at the median of release group-specific intercepts with the Delta Cross Channel gate set to closed. Note that the flow-survival relation extends beyond the range of observed fish size and discharge in each study; the purpose here is to compare the shape of these relations between studies.

has been based on salvage rates at the water export facilities, and the connection between salvage and entrainment loss. Salmonids that enter the water export facilities (i.e., either pass the trash racks at the CVP or enter the Clifton Court Forebay outside the SWP) are said to be “entrained.” Entrained fish may either enter the water conveyance canals, be diverted via louvers or screens away from the canals to a holding tank (“salvaged”) and transported by truck around the rest of the Delta, be preyed upon before reaching the fish guidance structures to the holding tanks (“pre-screen mortality” or “pre-screen loss”), or die during the salvage and transport process.

Salvage of CWT fish provides indirect evidence of mortality from exports under the assumption that a constant fraction of fish that enter the facilities is salvaged. Recent analysis of historical coded wire tag data from fall Chinook Salmon released in the San Joaquin River has found higher rates of salvage

during periods of higher exports (Zeug and Cavallo 2014). Nevertheless, the overall proportion of tagged release groups recovered from salvage has been low (average < 1% for both Sacramento River and San Joaquin River release groups from 1993 through 2007; Zeug and Cavallo 2014); however, the proportion salvaged does not account for the fish that die from being diverted off their migration routes before they arrive at the fish facilities, or how well salvage counts may reflect total entrainment in the facilities. Kimmerer (2008) estimated that at 10% pre-salvage survival (i.e., 90% combined loss from initial entrainment from both pre-screen loss and imperfect fish guidance efficiency at louvers or screens), the proportion of winter-run Chinook Salmon released in the Sacramento River that die in the fish facilities (“proportional loss”) could be as high as 30% at combined exports of $300 \text{ m}^3\text{s}^{-1}$. When Zeug and Cavallo (2014) estimated the combined direct loss at the CVP and SWP relative to total migration mortality, the relative loss from entrainment from exports was as high as 17.5% for San Joaquin River releases.

Analyses of CWT data have compared recovery rates of fall-run Chinook Salmon released at either Durham Ferry or Mossdale on the San Joaquin River to those released at Jersey Point, using tags recovered from the trawls at Chippis Island and Antioch, and tags captured in the ocean fishery. Comparing recovery rates from upstream and downstream groups of fish in this way is an attempt to isolate survival through the Delta to Jersey Point from survival in the ocean. These analyses show positive relationships between survival to Jersey Point and flow when the barrier is installed at the head of Old River (SJRG 2007, 2013). Another way of looking for an effect of flow is by comparing counts of adults that return to hatcheries and spawning grounds or migrate upstream past dams (“adult escapement”) with conditions during the juvenile outmigration 2.5 years earlier. Such comparisons have been made using both San Joaquin River flow at Vernalis and the ratio of Vernalis flow to export rates. Statistically significant associations were found between adult escapement and both Vernalis flow and the ratio of flow to exports: adult returns tended to be higher when Vernalis flows were higher, and also when the ratio of flow to exports was higher and the barrier had not been installed at the head of Old River (SJRG 2007).

The effect of exports on survival in the immediate vicinity of the water export facilities is understood better than effects farther away. At the CVP, a fish insertion experiment found higher efficiency of the fish guidance structures (“louver efficiency”) for juvenile Chinook Salmon when water velocities in the intake canals were higher (Sutphin and Bridges 2008). Because export rate determines water velocity in the CVP, higher CVP export rates translates into potentially higher survival to salvage, at least for fish in the immediate vicinity of the CVP. Furthermore, an acoustic telemetry study at the CVP found a higher probability of juvenile Chinook Salmon entering the facility at higher water pumping rates, although Steelhead behavior was more variable (Karp et al. 2014, unreferenced, see “Notes”). At the SWP, the water pumping plant and fish collection facility are accessed through the Clifton Court Forebay (CCF), which is isolated from the Delta by radial gates that are opened several hours each day to allow freshwater to enter the reservoir; fish may also enter the CCF when the gates are open. Tagging studies using passive integrated transponder tags and acoustic telemetry tags in the CCF have estimated high pre-screen loss for Steelhead (0.78 to 0.82; Clark et al. 2009), which is similar to estimates for Chinook Salmon reported by Gingras (1997). Gingras (1997) also reported that pre-screen loss in the CCF declined as exports increased for Chinook Salmon. The Steelhead tagging studies in the CCF did not examine a relationship between pre-screen loss and export rate, but compared movement rate (i.e., time to salvage) within the CCF to export rate, and found no statistically significant relationship (Clark et al. 2009).

UNCERTAINTIES FROM TELEMETRY DATA

Although use of telemetry techniques has vastly improved our level of understanding about migration and survival dynamics of juvenile salmon in the Delta, these studies have important limitations. For example, most published studies to date have used large, actively migrating salmon smolts (e.g., late-fall-run Chinook Salmon of hatchery origin) because transmitter size restricts the minimum size of fish that may be tagged. Thus, fish used in telemetry studies may be larger than their naturally produced counterparts, larger (on average) than the hatchery population from which they are sampled,

and larger than most of the juvenile salmon that migrate through the Delta. Ongoing technological advancements continue to miniaturize transmitters. Thus, recent studies using the latest transmitter technology are able to tag fish as small as 90 mm, which allows for studying a wider array of sizes and run types of salmonids. On the Sacramento River, ongoing telemetry studies are now investigating migration and survival of winter-run and spring-run Chinook Salmon, runs of specific management interest because of their status as listed under the federal Endangered Species Act. In the future, we expect that these studies will provide important insights into run-specific survival in the Delta. Even with these new technologies that allow smaller fish to be tagged, understanding survival and rearing tactics of fry and parr will remain a significant knowledge gap, at least for the foreseeable future.

Most studies, even those now tagging smaller fish, still rely on hatchery-origin fish as their study subject. This situation will likely not change in the near future because it is difficult to catch enough naturally produced fish to tag at most monitoring locations in the Delta and because the origin of captured fish is often unknown. Because behavior and survival of hatchery-origin fish may differ from that of wild fish (Reisenbichler and McIntyre 1977; Kostow 2004), care must be taken when inferences are drawn from hatchery fish about survival of wild fish. For example, inferences from hatchery fish about absolute survival of wild fish may not hold, but factors that influence relative differences in survival among migration routes (e.g., interior Delta relative to Sacramento River) may act similarly on both wild and hatchery populations that migrate through the Delta during the same time period.

An additional complication with interpreting telemetry data is distinguishing between detections of surviving study fish and detections of predatory fish that have eaten the study fish and still have the telemetry tag in their gut. Depending on the spatio-temporal patterns of detection of salmon and predators of tagged salmon, detections from predators may bias survival estimates. This is particularly problematic for survival and behavioral studies on smaller spatial scales and near the water export facilities, where large populations of predators congregate and complex hydrodynamics

may influence salmonid behavior in unknown ways. Telemetry studies in the Delta have made efforts to identify and remove detections suspected of coming from predators (SJRG 2010, 2011 and 2013; Buchanan et al. 2013; Romine et al. 2014). New statistical techniques to distinguish movement patterns of smolts from those of predators have recently been developed for spatially explicit two-dimensional (2-D) telemetry data (Romine et al. 2014) and for presence-absence detection data (Gibson et al. 2015). New telemetry tags that alert researchers to predation events are undergoing testing and may reduce uncertainty in interpreting telemetry data.

SPATIALLY EXPLICIT MODELS OF SALMON IN THE DELTA

Management actions that influence the quantity and distribution of water in the Delta affect how juvenile salmon populations distribute among and survive within those channels. Consequently, spatially explicit models are needed to understand how management actions at specific locations affect juvenile salmon survival within the Delta's complex channel network (Rose et al. 2011; Delta ISB 2015). These models explicitly represent the Delta as a hierarchical channel network to simulate how fish move among and survive within different channels. Over the past decade, salmon simulation models have begun to explicitly represent the Delta's channel structure to varying degrees of resolution and complexity.

Spurred by recommendations from a workshop on Central Valley salmonid life cycle models (Rose et al. 2011), NOAA is currently developing a stage-structured life cycle model that explicitly includes the Delta (Hendrix et al. 2014). This model has two key features critical to understanding the Delta's role in the salmon life cycle. First, alternative life-history strategies of fry and smolts in the Delta are explicitly represented in this model. Entry timing and residence time of fry in the Delta is driven by a density-dependent response to habitat capacity in upstream habitats that vary as a function of discharge. Second, an agent-based model for the Delta is being developed based on DSM2-PTM, a particle tracking module to the widely used DSM2 hydrographic simulation model (Kimmerer and Nobriga 2008). Dubbed the ePTM (enhanced Particle

Tracking Model), this model adds salmon-like behaviors to the particles such as active swimming, nocturnal or diurnal migration, and selective tidal stream transport.

Another life cycle modeling effort that explicitly represents the channel structure of the Delta is the IOS model (Zeug et al. 2012), which uses the Delta Passage Model (Cavallo et al. 2011) to represent the Delta's channel structure. The Delta Passage Model represents the Delta as a coarse network of reaches and channel junctions. This model simulates the travel times of fish through each reach; routing at critical channel junctions (e.g., the DCC and Georgiana Slough), which may depend on discharge when fish arrive at a junction, and survival within each reach, which may also be driven by discharge when fish enter the reach.

The current efforts to develop spatially explicit models for the Delta were made possible by the availability of spatially explicit data from acoustic telemetry studies. Because the acoustic telemetry data provide information about migration rates, survival, and routing of juvenile salmon in different regions of the Delta, this data is proving critical to setting parameters for spatially explicit models. For example, parameters were set for migration routing and survival relationships in the Delta Passage Model based on findings of telemetry survival studies. In addition, behavioral parameters in the ePTM are being estimated by calibrating the ePTM to acoustic telemetry data.

Spatially explicit models of juvenile salmon in the Delta are in their infancy and have followed on the heels of acoustic telemetry studies that provide the data to inform these models. An agent-based model of juvenile salmon coupled to a 3-D hydrodynamic model of the Delta does not yet exist, but has been recognized as a critical need to understand key drivers, identify information gaps, and support management of water and fishery resources (Delta ISB 2015). Over the next decade, we expect these modeling approaches to mature as hydrodynamic models to drive salmon models, analytical techniques for fitting models to data, and computing resources to support model runs are developed.

DROUGHT-RELATED EFFECTS

Significantly less precipitation and warmer temperatures since the spring of 2012 have led to statewide drought conditions. These conditions resulted in record low flows and high water temperatures and likely caused substantial negative population-level effects on salmon populations. For instance, during 2014, estimated egg-to-fry mortality of naturally spawned winter-run juveniles was 95% because of water temperature during egg incubation. The full ramifications of the recent drought on salmon populations have yet to be realized until adults return to spawn. How juvenile salmonids in the Delta have been affected by drought is unknown.

Recent drought conditions led to many emergency water management strategies that are typically governed by the federal Endangered Species Act (NMFS 2009) and state water quality control plans. Emergency actions included changes in winter and spring reservoir release schedules, DCC gate and CVP/SWP export facility actions, and temperature control device operations at Shasta Dam. The drought and subsequent emergency actions have spurred a number of interagency teams to evaluate the likely effects of drought on salmon populations and to design monitoring frameworks that are better able to quantify population responses to drought at key "checkpoints" in the freshwater environment, including the Delta.

An interagency team developed a conceptual model to evaluate how reduced flows, increased DCC gate openings and exports, and additional constraints on flexibility of operating temperature control devices affected a number of physical and biological metrics (USBR 2015). Observations from fish and ecosystem monitoring for the 2013 cohort of winter-run Chinook Salmon were compared to outcomes from a recent comparative period (2007–2012). Based on this information, the drought affected multiple stages of winter-run Chinook Salmon through an extended period of the cohort's freshwater residence during 2014 (Table 1), and will likely have consequences as this cohort returns to the river as adult spawners.

A larger analysis of environmental conditions and consequences for salmon during 2015 and 2016 is being pursued as part of the Interagency Ecological Program's Management, Analysis and Synthesis

Table 1 Effects of drought conditions and water operations in 2014 on the 2013 brood year of winter run Chinook Salmon. Adapted from USBR (2015).

Metric	Brood years 2007–2012	Brood year 2013	Interpretation
Estimated egg to fry survival above Red Bluff Diversion Dam	17.5% – 48.6%	15.1%	Lowest survival in natal rearing areas during drought conditions
Residence time above Knights Landing	65 – 164 d	133 d	Resided in river for similar period compared to recent years
Residence time in Delta Cross Channel	21– 116 d	3 d	Resided in Delta for shorter period compared to recent years
Duration of salvage period	109 – 216 d	42 d	Resided in South Delta and present in Delta for shorter period compared to recent period
Duration of connectivity with Yolo Bypass		0	

(MAST) project known as SAIL (Salmon Assessment of Indicators by Life stage). An important finding thus far is that finer temporal and spatial monitoring of each population cohort is necessary to understand spatial and population level responses to drought and other environmental factors. In addition, early life stage transitions may be affected more by management, physical, and biological mechanisms (e.g., rearing habitat and disease) than we can currently quantify with available monitoring data. This synthesis work is essential to understanding mechanisms and consequences of drought, and may yield insight into how to better cope with climate change.

CONCLUSIONS

Because of the complexity of the Delta's channel network and its complicated sampling environment, answering questions about how juvenile salmon use, grow, and survive in and through the Delta has been a major challenge. Fortunately, during the past decade, technological advancements that have miniaturized acoustic transmitters and novel application of otolith microchemistry and genetic methodologies have resulted in the ability to obtain more detailed information about individual fish. These new technologies have advanced our knowledge of how different life stages and runs of juvenile salmon move, rear, and survive in the Delta.

Knowledge gaps remain about the dynamics of naturally produced juveniles and of fry and parr life stages in the Delta. These life stages are expected to rear for some time in the Delta rather than migrating quickly to the ocean. Given additional

focus on estimating capture efficiency and absolute abundance of juveniles in the Delta, researchers can begin to quantify how abundance varies with habitat characteristics to better understand the habitat needs of the juvenile salmonids that rear in the Delta for a considerable length of time. Improvements in juvenile fish sampling methods and juvenile population monitoring, combined with expanded chemical otolith analysis and genetic sampling, hold the potential to shed further light on these questions. By coupling fine-scale hydrodynamic models of the Delta with agent-based models of juvenile salmon, researchers are beginning to use models to understand how water management actions and climate change might influence movement and survival of juvenile salmon in the Delta.

Much has been learned about salmon in the Delta over the past decade, yet much remains to be learned. With continued drought and ongoing climate change, maintaining viable salmon populations will become even more challenging. Better understanding of how different life stages use the Delta will help inform management actions to ensure that the Delta is capable of supporting the diversity of life-history strategies expressed by Central Valley Chinook Salmon and Steelhead populations.

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NOTES

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