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Abstract:

Central Valley Chinook must pass through the San Francisco Estuary as juveniles and again as maturing adults. Much attention has been given to the effects on Chinook of management of the freshwater part of the estuary, and the Sacramento–San Joaquin Delta, and especially to the effects on Chinook of diversions of water from the Delta. Here, I review available information on juvenile Chinook in and around the estuary that seems most relevant to management of the estuary and of Chinook. Most naturally produced juvenile fall Chinook enter the estuary as small fish (<50 mm) that typically use tidal habitats, and anthropogenic changes in the Delta and around the bays have sharply reduced that habitat. Nevertheless, there is evidence that many surviving naturally produced fall Chinook leave fresh water at <55 mm length. Juvenile Chinook from other runs are older and larger when they enter the estuary, and probably pass through it more rapidly. Presumably, these have been less directly affected by loss of tidal habitat, but are also affected by degradation of the estuarine ecosystem. The effects of Delta diversions on Chinook vary strongly by run and river of origin; surprisingly few Sacramento River fall Chinook have been recovered at the diversions. Central Valley Chinook, especially fall Chinook, are strongly affected by hatchery culture that reduces juvenile life-history diversity, probably results in density-dependent mortality in the estuary, and presumably reduces fitness for natural reproduction. Hatchery culture diverts juvenile fall Chinook away from, and precludes for selection for, the life history trajectories followed by most naturally produced fish, to which more attention should be given.

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Juvenile Chinook Salmon *(Oncorhynchus tshawytscha)* in and Around the San Francisco Estuary

John G. Williams[1]

ABSTRACT

Central Valley Chinook must pass through the San Francisco Estuary as juveniles and again as maturing adults. Much attention has been given to the effects on Chinook of management of the freshwater part of the estuary, and the Sacramento–San Joaquin Delta, and especially to the effects on Chinook of diversions of water from the Delta. Here, I review available information on juvenile Chinook in and around the estuary that seems most relevant to management of the estuary and of Chinook. Most naturally produced juvenile fall Chinook enter the estuary as small fish (<50 mm) that typically use tidal habitats, and anthropogenic changes in the Delta and around the bays have sharply reduced that habitat. Nevertheless, there is evidence that many surviving naturally produced fall Chinook leave fresh water at <55 mm length. Juvenile Chinook from other runs are older and larger when they enter the estuary, and probably pass through it more rapidly. Presumably, these have been less directly affected by loss of tidal habitat, but are also affected by degradation of the estuarine ecosystem. The effects of Delta diversions on Chinook vary strongly by run and river of origin; surprisingly few Sacramento River fall Chinook have been recovered at the diversions. Central Valley Chinook, especially fall Chinook, are strongly affected by hatchery culture that reduces juvenile life-history diversity, probably results in density-dependent mortality in the estuary, and presumably reduces fitness for natural reproduction. Hatchery culture diverts juvenile fall Chinook away from, and precludes for selection for, the life history trajectories followed by most naturally produced fish, to which more attention should be given.

KEY WORDS

Chinook salmon, San Francisco Estuary, Sacramento–San Joaquin Delta, life history diversity.

INTRODUCTION

The San Francisco estuary provides seasonal habitat for several genetically distinct runs of Chinook (*O. tshawytscha*), of which two are already listed under the federal Endangered Species Act (ESA), and another is at high risk of extinction under existing criteria for hatchery influence described in Lindley and others (2007). The estuarine part of their juvenile life histories raise major social and economic problems, because large areas of what was once salmon habitat have been converted to human use, and because inflows and outflows of water to and from

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the estuary have been massively altered by water projects.

The San Francisco Estuary (Figure 1) is usually defined by tidal influence, and comprises the saline to brackish bays and the mainly freshwater but tidally influenced Sacramento–San Joaquin Delta; Chipps Island is the conventional boundary between the bays and the Delta. The Sacramento River flows into the Delta from the north, and the San Joaquin enters from the south; the Cosumnes, Mokelumne, and Calaveras rivers enter from the east (Figures 1, 2). Summer releases from reservoirs on the rivers maintain low salinity in the Delta. From the Delta, water flows to the bays, to diversions for local use, and also to the state and federal pumps that export water to the San Joaquin Valley and Southern California. Tidal influence extends to Sacramento and beyond Stockton.

This review deals with the biology, and especially the life history patterns, of juvenile Chinook in and near the San Francisco Estuary, but emphasizes naturally produced fish and matters relevant to management of the Delta or of Chinook. The review is a truncated, reorganized, and modified version of Williams (2009), prepared for the Delta Regional Ecosystem Restoration Implementation Plan. Some of the material presented here is taken from Williams (2006), but most is new. Other aspects of the biology and management of Central Valley Chinook and their habitats are covered in detail in Williams (2006), which also provides more background, context, and citations to the broader literature for most of the material discussed here.

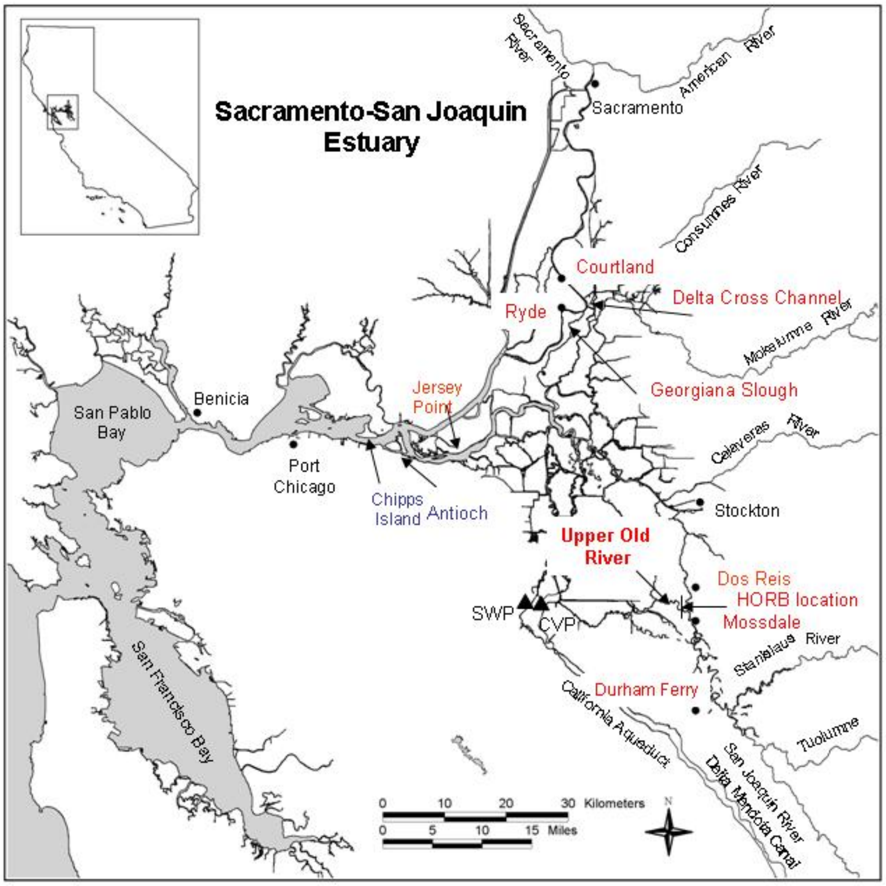

Figure 1 The San Francisco Estuary. Triangles on the south side of the Delta show the location of the state (State Water Project, SWP) and federal (Central Valley Project, CVP) pumps that divert water into the California Aqueduct and Delta Mendota Canal. Locations marked in red figure importantly in Interagency Ecological Program's coded-wire tag studies, intended to clarify the effects of the diversions on juvenile Chinook. Sherwood Harbor, mentioned in the text, is not shown but is close to Sacramento. Source: Newman (2008).

BIOLOGY AND ECOLOGY

Chinook in the Central Valley are commonly classified into four runs, named for the season in which adults enter fresh water: fall, late fall, winter, and spring. Fall Chinook, the most abundant, are the mainstay of the ocean fishery, but a tagging program begun in 2007 shows that the run is predominantly hatchery fish, as discussed below. Winter Chinook are listed as endangered under the federal ESA, and spring Chinook are listed as threatened. Genetic evidence (Hedgecock 2002) indicates that the spring Chinook in Butte Creek are a separate lineage from those in Mill and Deer creeks, and spring Chinook in the Feather River are closely related to fall Chinook. Thus, the four named runs correspond generally but not completely with genetic lineages. Like the named runs, management units of Chinook correspond generally but not exactly with the genetic lineages. For ESA purposes, fall and late fall Chinook are lumped together, as are all spring-run. Harvest is managed largely in terms of "Sacramento Fall Chinook," a category that ignores fall Chinook from the San Joaquin River and Delta tributaries. Dams block the upstream migration of adult Chinook on all major rivers (Figure 2).

Winter Chinook are now restricted to the upper Sacramento River, and wild spring Chinook (with little hatchery influence) are restricted to undammed Sacramento River tributaries, especially Mill, Deer, and Butte creeks (Lindley and others 2004). Late fall Chinook are mainly in the upper Sacramento River, but fall Chinook are widely distributed. A major restoration project intended largely to restore spring and fall Chinook to the San Joaquin River upstream from the Merced is now underway.

Anadromous salmonids reproduce in fresh water, but gain most of their growth in the ocean. Chinook reproduce naturally in gravel-bed streams. In the Central Valley, and in many other places, reproduction now also occurs in hatcheries, operated by the United States Fish and Wildlife Service (USFWS) or the California Department of Fish and Game (DFG). Upwards of 30 million Chinook, mostly fall-run, rear to fingerling or larger size in raceways at hatcheries on the Merced, Mokelumne, American, Feather and Sacramento rivers, and on Battle Creek, a tributary of the upper Sacramento. Some are released into the river near the hatchery, but others are trucked around the Delta and released into the bays (see Williams 2006 for an overview, and hatchery and genetic management plans such as Lee and Chilton 2007 or Cavallo and others 2009 for details).

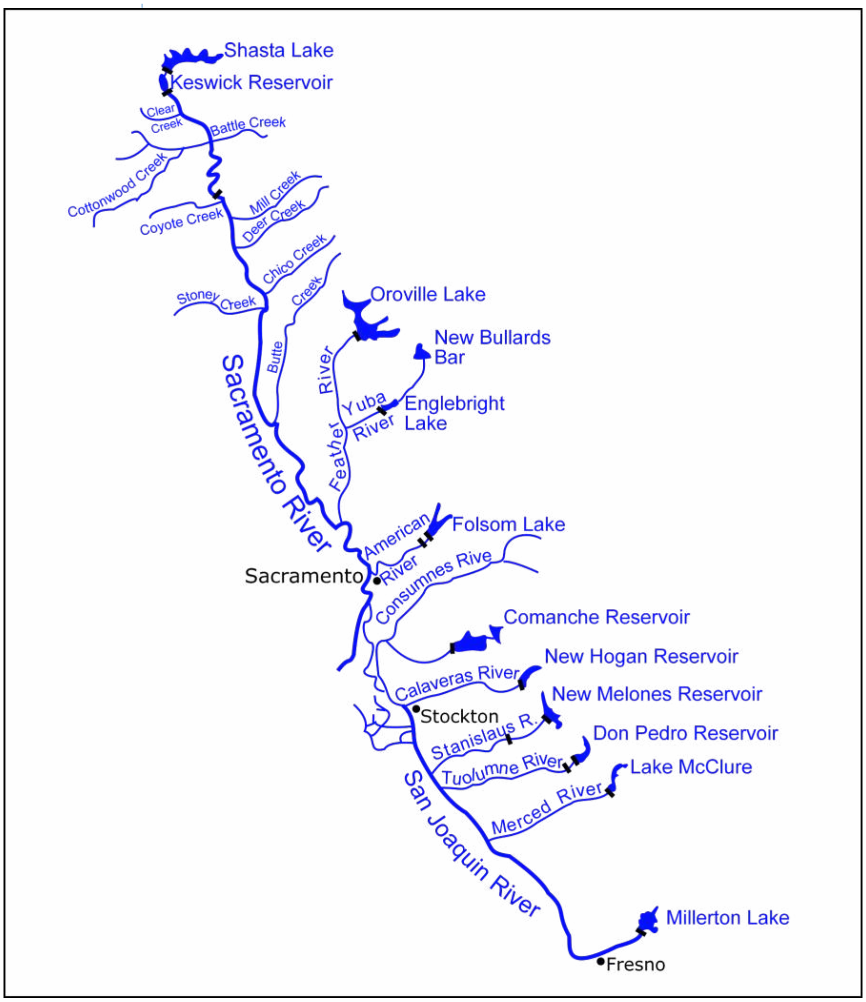

Figure 2 Major Central Valley Chinook streams. All major Central Valley rivers are blocked by large, impassable dams. Comanche Reservoir is on the Mokelumne River. Coleman National Fish Hatchery is on Battle Creek, tributary to the upper Sacramento River. The Red Bluff Diversion Dam on the Sacramento River is just upstream from Coyote Creek. Note that the rivers without dams are drawn ending at arbitrary points, not at the upstream limit for anadromous fish. Source: Williams (2006).

In Central Valley rivers with hatcheries, hatchery and naturally spawning salmon are best regarded as single, integrated populations that reproduce in one of two very different habitats. All fall Chinook may be part of one hatchery-dominated population, as discussed below. Hatchery influence on winter and late fall Chinook is still moderate (Williams 2006; unpublished data).

Hatchery culture modifies the natural life cycle in several important ways. Mates are selected by hatchery personnel rather than by the fish. Mortality during the egg and alevin stages is sharply reduced, so that selection for traits important for survival in natural redds is relaxed, and perhaps reversed for some traits (Williams 2006). The fish grow rapidly in the raceways, and are forced into approximations of what I describe below as the fingerling migrant or fingerling resident life history patterns. This affects the selective forces that act on them after their release, and thus differential survival. This is obvious for fish released into the bays that do not experience selection for traits related to the downstream migration, but applies to other traits a well (Goodman 2004).

That interbreeding with hatchery salmonids reduces the fitness of wild populations is generally accepted (Myers and others 2004; Araki and others 2008). Lindley and others (2007) developed criteria for assessing the risk of extinction within 100 years for populations of Central Valley Chinook and steelhead. For hatchery fish from the same diversity group (e.g., Central Valley fall Chinook), 20% hatchery fish among spawners over a single generation (four years) gives high risk, as does 10% over two or three generations or 5% over four or more.

Central Valley Chinook are subject to predation by humans, mainly in the ocean, but also in the rivers, as adults return to spawn, although harvest in the rivers is now targeted to specific runs. Harvest is a desired outcome of management, and the rate of harvest is an important management "knob" that is turned mainly in response to abundance. However, the harvest rate also affects how far hatchery fish influence the genetics of naturally reproducing fish (Goodman 2004, 2005).

Juvenile Life History Patterns

Various names are applied to juvenile salmonids at different stages of their development. Generally, "fry" have recently emerged from the gravel, and have no or few scales. "Parr" have developed scales, and dark vertical marks on their sides. As the fish go through physiological changes that prepare them for life in salt water, the parr marks fade, the sides and belly become more silvery, and the caudal or tail region lengthens; at this stage, the fish are called "smolts." The complex physiological changes involved are reviewed by Høgåsen (1998). Unfortunately, in the literature these stages are often distinguished simply by length, with different authors often using different criteria. Juveniles of appropriate size are also called "fingerlings."

The juvenile life histories of Central Valley Chinook are highly variable, and the young fish probably enter the ocean at lengths ranging roughly from 75 to 250 mm (Williams 2006; all lengths mentioned are fork lengths). The habitats where they gain most of this growth are also variable, from some that migrate rapidly through the Delta and grow mainly in the bays before they enter the ocean, to others that remain and rear in the gravel-bed parts of the streams where they incubated, and then migrate rapidly through the lower rivers, the Delta, and the bays.

Early in the 20th century, biologists recognized that some juvenile Chinook migrate to sea in the spring of their first year, while others remain in the stream through a winter and migrate the following spring. These were called "ocean-type" and "stream-type" (Gilbert 1913), but this dichotomy does not capture the actual range of juvenile life history patterns, since ocean-type fish migrate downstream at different times and rates (Healey 1991; Ewing and others 2001). In the Central Valley, late fall and winter Chinook migrate downstream and into the bays during the fall and winter, remaining near the spawning areas for a few days to several months, and spring Chinook are mostly ocean-type, although some behave like late fall or like stream-type Chinook. Larger juveniles can be found somewhere in the Central Valley in all months, and emerging fry can be found in most. Accordingly, juvenile Chinook of widely different sizes can be found in different Central Valley habitats at given times, and juvenile life histories are better regarded as broad patterns than as discrete trajectories. Nevertheless, it seems possible to distinguish six different life history patterns for juvenile Chinook in the Central Valley, ranked below in terms of increasing amounts of time spent in fresh water, and in terms of the habitats in which juveniles mainly rear (Figure 3). Similarly variable patterns have been described in other rivers (Burke 2004).

Fry Migrants to the Bays

Fry migrants to the bays (Figure 3, line A) travel directly to brackish water in the bays after emerg-

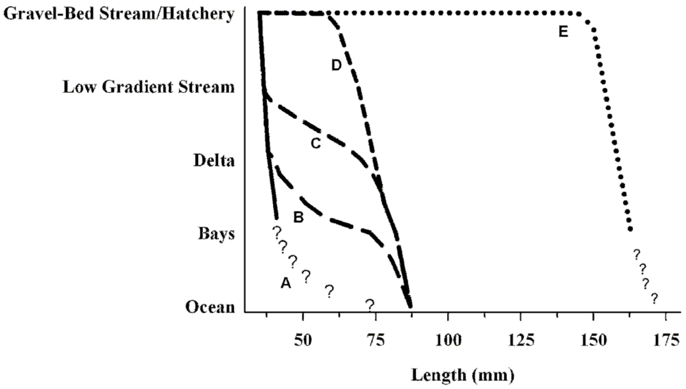

Figure 3 Conceptual “juvenile life-history space.” Lines show representative trajectories of growth and migration for naturally produced juvenile Chinook. **(A)** Fry emerge at ~35 mm, and may migrate directly to the bays; what they do when they get there is poorly understood. **(B)** Many fish migrate directly to the Delta and rear there (long dashed line); if they survive, they migrate through the bays to the ocean. **(C)** Some fry migrate to the lower rivers and rear there before migrating through the Delta and bays (medium dashed line). **(D)** Other fry emerge and remain in the gravel-bed reaches of the stream until they migrate, generally in spring, as fingerlings (short dashed line), **(E)** while others remain in the gravel-bed reaches through the summer and migrate as larger juveniles in the fall, winter, or spring. How long they remain in the bays is unknown. Except for fry, lengths are actually highly variable, so properly the figure should show broad smears rather than discrete lines.

ing from the gravel. Hatton and Clark (1942) captured significant numbers of ~40 mm juveniles at Martinez, just east of Benicia, in mid-March, 1939, when flows in the rivers were low enough that these fish must have moved voluntarily through Suisun Bay. Similarly-sized fish are captured in the Chipps Island trawl, especially in wet years (Brandes and McLain 2001), although the capture efficiency of the trawl is probably low for fish of this size (Williams 2006). Modest numbers of fry were captured in seines in Suisun, San Pablo and San Francisco bays in 1980, although fewer were taken in 1981 (Kjelson and others 1982). Only a few such fish are captured by the Interagency Ecological Program seine monitoring around the bays (SSJEFRO 2003), but this may reflect the large area over which such fish may be distributed. Miller and others (2010) reported that about 5% of 99 genetically identified Central Valley fall Chinook harvested off Oregon in 2006 left fresh water at less than 46 mm fork length, based on microchemical and microstructural analyses of otoliths.

Fry Migrants to the Delta

Fry migrants to the Delta (Figure 3, line B) also migrate downstream soon after emergence, but remain in the Delta and rear there for weeks to months before migrating into the bays. Presumably, Chinook that follow this life history historically reared in the then-abundant tidal habitat in the Delta (Williams 2006). Together with fry migrants to the bays, this is the most common life history pattern among juvenile fall Chinook, based on monitoring passage into the lower rivers (e.g., Figure 4), but the percentage that survive is not well known. About 15% of the Miller and others (2010) sample left the Delta between 46 and 55 mm fork length, and probably reared there for a short time.

Since very few hatchery fish are released at 55 mm or less in length, the 5% plus 15% of Miller and others’s (2010) sample that did so would have been naturally produced. How large a fraction they represented of the naturally produced fish in the sample is unclear, because Miller and others (2010) did not distinguish hatchery and naturally produced fish, which would have required an additional analysis. However, based on the finding by Barnett–Johnson and others (2007) that about 90% of a similarly sized sample from 2002 were hatchery fish, and the probable proportion of hatchery fish in returns in 2009 (see below), 75% hatchery fish seems a conservative guess. If this were the case, then the fry migrants to the Delta and the bays would be 80% of the naturally produced fall Chinook in the sample.

Fry Migrants to Low-Gradient Streams

Fry migrants to low-gradient streams (Figure 3, line C) move quickly downstream from the gravel–bed reaches where spawning occurs, and rear in low-gradient reaches in the valley floor before migrating rapidly through the Delta. Butte Creek spring-run exemplify this life history. Many wild Butte Creek spring-run fry are captured and tagged as they migrate out of the foothills and into the

Central Valley, and some are recaptured by USFWS sampling. The size of fish recaptured at Sherwood Harbor, near Sacramento, shows that they mainly rear upstream of the Delta, presumably in the Butte Sinks or the Sutter Bypass (Figure 5), until they are ~70 mm or more; then they move rapidly through the Delta (Figure 5B). The Yolo Bypass (Figure 6) offers similar habitat to Sacramento River populations when the river spills over the Fremont Weir, near Knight's Landing, and several studies indicate that fish do well there (Sommer and others 2001, 2005)

Fingerling Migrants

Fingerling migrants (Figure 3, line D) remain in gravel-bed reaches for a few months, and then migrate as larger (generally >60 mm) parr or silvery parr, in late spring if they are fall-run. The second, smaller mode in Figure 4B reflects this life history, which is followed by a larger proportion of the juveniles in the Mokelumne River and San Joaquin River tributaries than in the Sacramento River and tributaries, although there is considerable variation from year to year in the proportions (Williams 2006). The larger

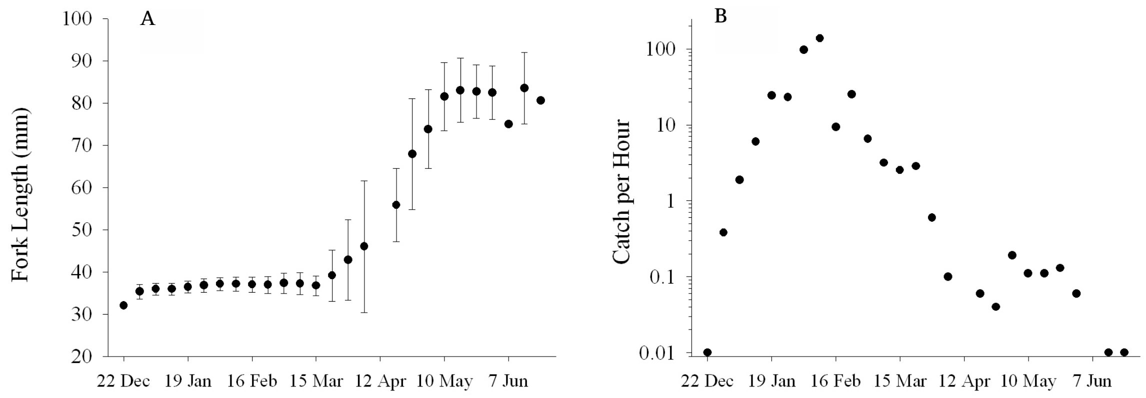

Figure 4 Mean length **(A)** and catch per hour **(B)** of juvenile fall Chinook salmon sampled in screw traps in 1999-2000 on the lower American River near the downstream limit of spawning habitat. Error bars show standard deviations. Note log scale in (B); the catch dropped sharply as size increased in March. Dates are approximately the middle of the sampling period. Data from Snider and Titus (2001); figure copied from Williams (2006).

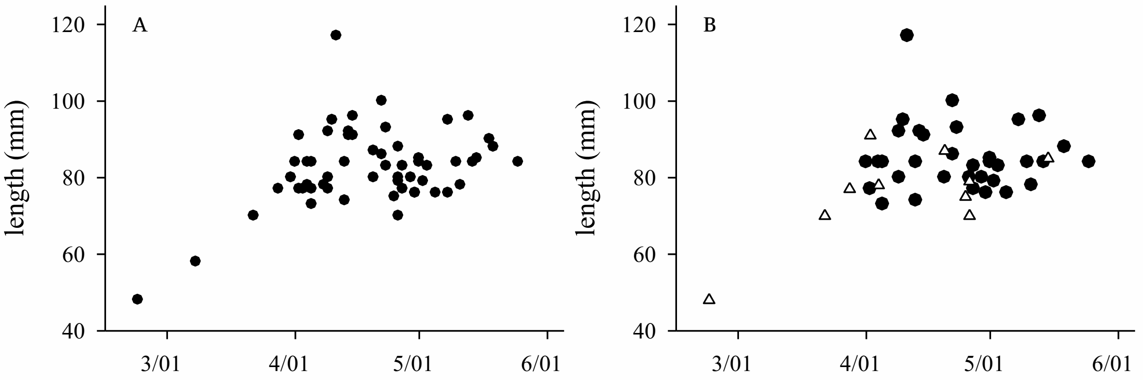

Figure 5 **(A)** Size at date of capture of wild, coded-wire tagged Butte Creek spring Chinook (n = 57), for all capture locations from Knights Landing to Chipps Island. **(B)** As above, for Chipps Island (circles, n = 34) and Sherwood Island (triangles, n = 10). Source: Data from the U.S. Fish and Wildlife Service, Stockton office.

migration rate and timing of the survivors are highly uncertain. Tissue samples from fish captured at Chipps Island are now being analyzed by NNFMS to assign fish to runs, so more information should soon be available about the size and time at which the different runs move into the bays.

Understanding Salmonid Life-History Diversity

There is great variability in the life history patterns of juvenile salmonids, even within single species such as Chinook, as discussed above. This variation is best understood for Atlantic salmon, as John Thorpe and colleagues have developed a conceptual model (Thorpe and others 1998). The conceptual model posits a set of condition-dependent “switches” that affect or control such aspects of behavior as feeding, migration, and maturation. Individual variation in the thresholds for the switches and variation in environmental conditions can then produce the observed variation in life-history patterns. The model embodies two important generalizations about salmonid life histories: that there are photoperiod-based “windows” of time in which life-history choices are made, and that these choices are based on the condition of the fish at some prior time, as well as on the condition of the fish shortly before the decision becomes manifest by, say, smolting or by sexual maturation (Thorpe 1989). Mangel (1994) developed this conceptual model into a numerical model, and it is currently extended and developed for steelhead, in a form that also allows assessment of evolution in response to altered environmental conditions (Mangel and Satterthwaite 2008; Satterthwaite and others 2009a, 2009b).

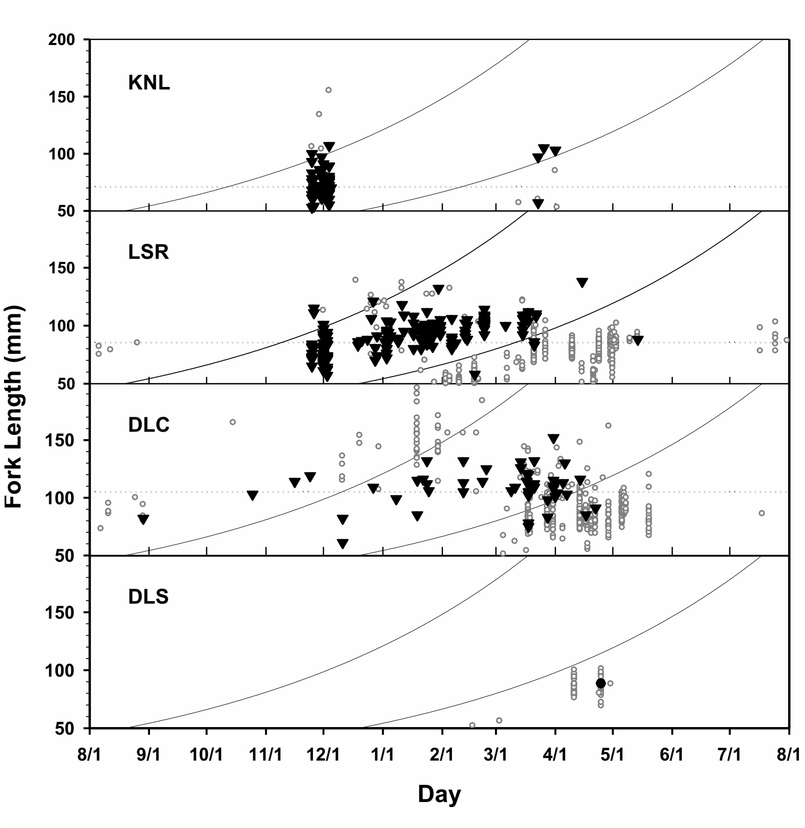

Figure 7 Fork length and day of capture for juvenile Chinook assigned to runs by Hedgecock (2002): Knights Landing (KNL, near Freemont Weir), the lower Sacramento River (LSR), the central Delta (DLC), and southern Delta (DLS). Winter Chinook are shown by black triangles, other Chinook by open circles; dotted lines show mean lengths for winter-run at the site. The curved lines show length at date criteria for winter-run. Copied from Hedgecock (2002).

Atlantic salmon and steelhead are stream-type fish, but most Chinook migrate downstream shortly after emergence, so it is clear that this model must be modified before it can be applied to them. Nevertheless, the fundamental insight remains that a fairly simple developmental program (the switches and thresholds), together with environmental variation and genetic variation in thresholds for the switches and in the timing of the developmental windows, can account for the observed variation in life-history patterns within and among species of Pacific salmon. As an example, Clarke and others (1992) showed experimentally that a photoperiod-sensitive switch controlled juvenile growth and age at smolting in stream-type Chinook from the Quesnel River in British Columbia. Fry exposed to longer days at emergence and early feeding grew slowly and did not develop traits associated with smolting in their first spring, whereas fry exposed experimentally to very short and then lengthening days grew rapidly in the spring and did develop such traits. This population spawns where winters are cold and embryos and alevins develop slowly (the incubation period is strongly temperature-dependent). Accordingly, fry emerge well after the winter solstice, and do not experience very short-day photoperiods, and so follow a stream-type life history. The same photoperiodic control of life-history patterns has been observed in other populations and species (Clarke and others 1989). This could explain why spring Chinook in the Central Valley are mostly ocean-type, since few spawn at high enough altitude to experience cold winters and long incubations. For example, in Butte Creek they are restricted to <350 m elevation, and fry emerge early enough to experience a short-day photoperiod. By the same reasoning, the stream-type life history may have been more common among Central Valley spring Chinook before dams blocked most high altitude spawning habitat.

The diversity of salmonid life-histories is not just a biological curiosity; rather, it helps to stabilize population numbers, through a "portfolio effect" (Figge 2004; Lindley and others 2009; Schindler and others 2010). It is intuitive that adults returning at different ages will tend to smooth out returns over years. Similarly, because of year-to-year variation in environmental conditions, the relative survival of different juvenile life histories presumably varies over years. In addition, juveniles that follow different life histories occupy different parts of the environment at any given time, so density-dependent effects will be fewer than if the same number of fish all pursued the same life history.

Juvenile Migration Rate

Juvenile migration is a complex matter, as suggested by the diversity of life history patterns described above, and despite many studies much about it remains unclear (Høgåsen 1998). If we take migration as a deliberate movement from one place to another, it is not even always clear whether juvenile salmon are migrating, or simply dispersing passively downstream. Sometimes fry are obviously being swept downstream by high flows (Williams 2006), but the downstream movement of large numbers of fry even during periods of low flows has seemed deliberate to most Central Valley salmon biologists, starting with Rutter (1904).

The migration rates and schedules of wild and naturally produced Chinook are highly variable, as implied by the diversity of life history patterns described above. Only a few Central Valley data are available, not enough to provide good estimates, except for Butte Creek spring Chinook (Figure 5). The migration rate of tagged hatchery fish can be estimated from the number of days between the release and recapture of fish collected in monitoring programs, but hatchery fish may have different migratory behavior, so these data are most useful for comparisons among hatchery populations. All hatchery winter and late-fall Chinook have been given coded-wire tags (CWTs) for some time, as have fall Chinook from the Merced River Hatchery, and about 8% of fall Chinook from Coleman Hatchery were tagged from 1995 to 2002. Twenty-five percent of fall Chinook have been marked since 2007, so more data are accumulating rapidly. The data presented here are from trawls operated by the U.S. Fish and Wildlife Service at Sherwood Harbor and Chipps Island, or from the fish salvage facilities at the state and federal pumps in the Delta.

Fall Chinook released near Coleman Hatchery on Battle Creek, a tributary to the upper Sacramento River, migrate rapidly, with median travels time of 8 days to Sherwood Harbor, near Sacramento, and 13 days to Chipps Island (Figure 8). This suggests that the migration rate slows as the fish approach the Delta, since it is about 355 km from the release site to Sherwood Harbor, and only about 80 km more to Chipps Island. The change from riverine flow to bi-directional tidal flow may account for the change in pace. By 2008, remarkably few of the fall Chinook released at Coleman had been recovered at the pumps (34 compared to 4,041 at Chipps Island), but, on average, the few that do tend to take much longer to get there than to Chipps Island. These fish were larger to begin with, or they grew well (~0.8 mm d^{-1}) along the way. Either the migratory behavior of Coleman fall Chinook keeps them away from the pumps, or those headed in that direction mostly perish.

Coleman late-fall Chinook do not migrate quite as rapidly to Sherwood Harbor as Coleman fall-run, despite their greater size (Figure 9). However, they appear to move more rapidly from Sacramento to

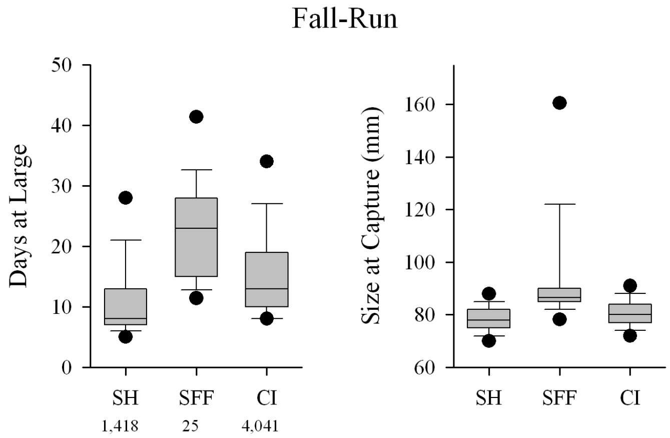

Figure 8 Days at large and size at capture of tagged fall Chinook released at Coleman Hatchery, and recaptured at Sherwood Harbor (SH, n = 1,418) the state fish facilities (SFF, n = 25), and Chipps Island (CI, n = 4,041). Seven fish collected at the federal fish facilities and two released in January as yearlings are not shown. Sample sizes are given below X-axis labels on the left panel. Distances from release sites are approximately: SH, 348 km; and CI, 435 km. Multiple paths lead to the fish facilities (Figure 1), but all will be somewhat longer than to Chipps Island. Source: USFWS data.

Chipps Island. More Coleman late-fall run have been recovered at the pumps than at Chipps Island (3,898 vs. 3,008), very different from the fall run. Much of this difference may be due to lower diversion rates and more intensive sampling at Chipps Island during the spring, but it seems that other factors such as migratory behavior must be involved as well.

Winter Chinook from Livingston Stone Hatchery on the Sacramento River near Keswick Dam migrate more slowly than other hatchery fish, with median travel times of 24 days to Sherwood Harbor and 45 days to Chipps Island (Figure 10), again suggesting that migration slows as it approaches the Delta. Travel time to the pumps is not as long as to Chipps Island, in contrast to the case with fall or late fall Chinook, although the hatchery winter-run collected at the pumps seem larger on average than those at Chipps Island, as with fall and late fall. Biological differences among the runs that we do not understand probably underlie these patterns.

Studying the migratory behavior of hatchery fish is tempting, because we have data with which to work, but we should remember that wild or naturally produced fish may behave differently; most obviously, hatchery fish cannot migrate until they are released. Hedgecock (2002) analyzed tissue samples from juvenile Chinook at the pumps, and reported the length and capture date of 711 fish identified as wild winter Chinook using microsatellite DNA; they were intermediate in size between the hatchery late-fall and winter Chinook, and arrived at the pumps slightly earlier in the year than hatchery winter-run (Figure 11), although they began migrating downstream sooner. Given that migration is associated with complex behaviors and physiological changes that may involve positive feedbacks (Høgåsen 1998; Ewing and others 2001), studying the migratory behavior of hatchery fish is particularly problematical when the first stage of migration is not volitional; that is, when fish are transported a substantial distance downstream before release. That fish trucked from Coleman Hatchery to Sacramento will have the same migratory behavior as fish that get there by swimming is a brave assumption.

Fortunately, it is now possible to obtain a good deal of information about the migratory history of wild and naturally produced Central Valley Chinook by microstructural and microchemical analyses of their otoliths (Barnett–Johnson and others 2005, 2008; Phillis and others 2008; Malamud-Roam and others 2008; Miller and others 2010). Such information is needed if we are to manage the Delta for the benefit of wild and naturally produced fish, rather than hatchery fish.

Perhaps as a consequence of differing migration rates, hatchery juveniles from different runs seem to differ in their propensity to end up at the state and federal pumps. Based on a simple tabulation of recoveries of tagged juvenile Chinook released at the hatcheries, the state and federal pumps entrain a much higher proportion of winter-run and late fall-run migrants from the Sacramento River—and fall-run migrants from the San Joaquin River—compared with trawl captures at Chipps Island from the United States Fish and Wildlife Service (USFWS) monitoring program. Few Butte Creek spring-run show up at the pumps, and even fewer fall Chinook released from Coleman Hatchery do so (Table 1). Geography probably explains the

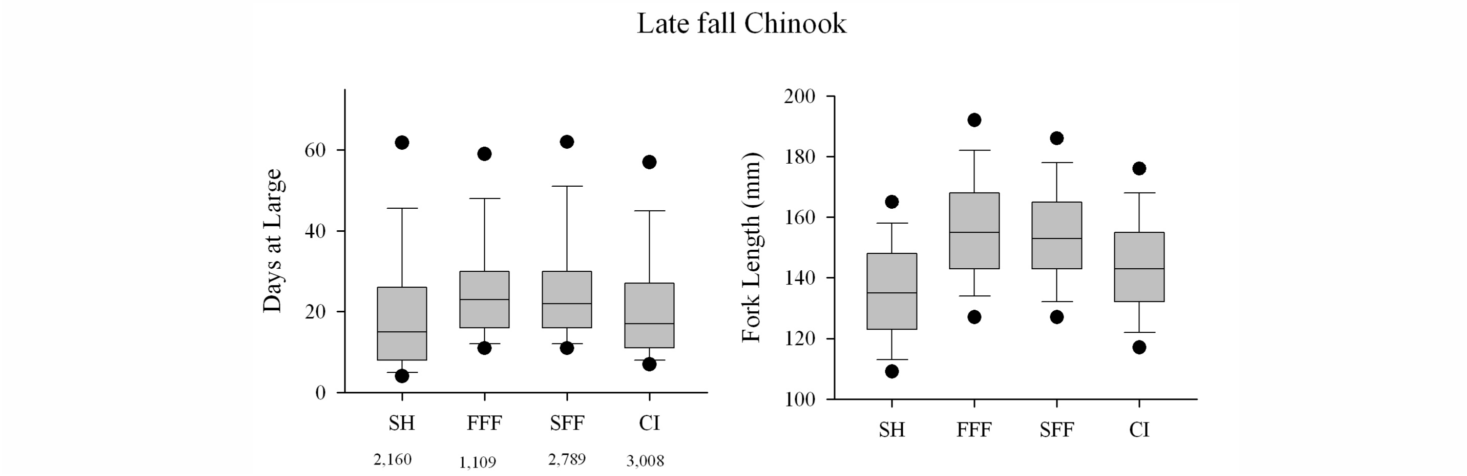

Figure 9 Days at large and size at capture of tagged late-fall Chinook released at Coleman Hatchery, and recaptured at Sherwood Harbor (SH), the federal fish facilities (FFF), the state fish facilities (SFF), and Chipps Island (CI). Sample sizes are given below the labels on the X- axis, left panel. Source: USFWS data.

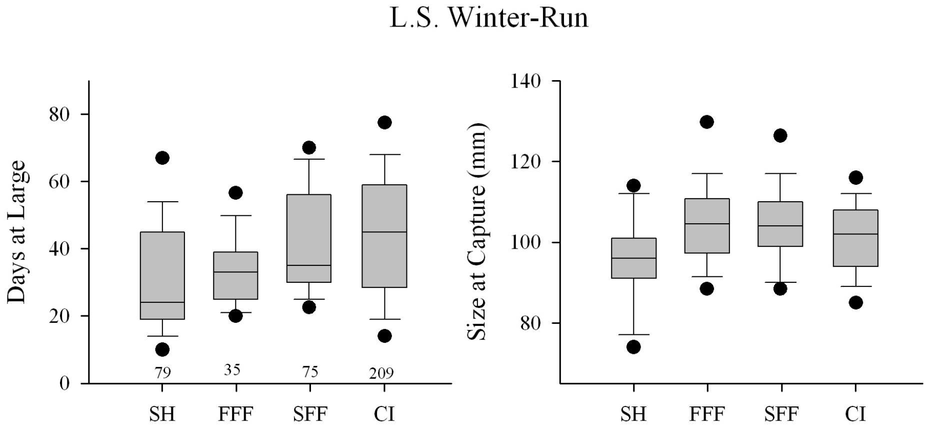

Figure 10 Days at large and size at capture of tagged winter Chinook released at Livingston Stone, and recaptured at Sherwood Harbor (SH), the federal fish facilities (FFF), the state fish facilities (SFF), and Chipps Island (CI). Sample sizes are given above the labels on the X- axis, left panel. Source: USFWS data.

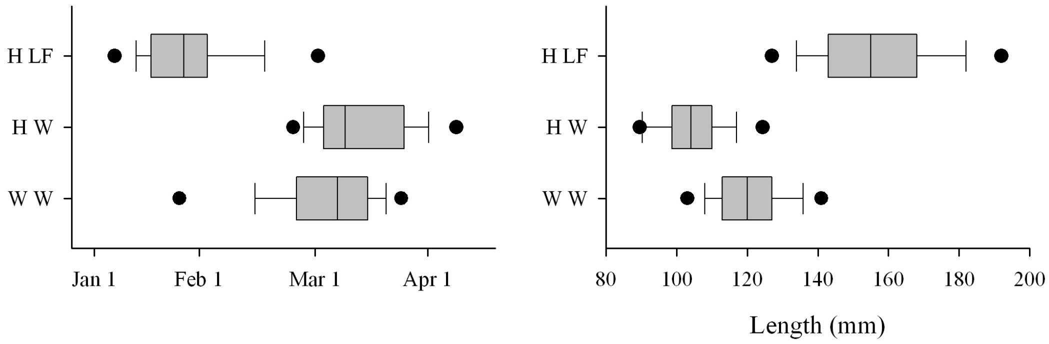

Figure 11 Distributions of dates of capture and length at capture for hatchery late-fall run (H 1LF), hatchery winter-run (H W), and wild winter run (W W) at the state and federal fish facilities. Source: USFWS data and Hedgecock (2002).

much greater propensity of Merced River fall Chinook to appear at the pumps, low pumping rates during spring help explain the low number of Coleman fall-run and Butte Creek spring-run, and more frequent sampling at Chipps Island in the spring affect the numbers taken there, so the differences reflected in the table are more apparent than real. Nevertheless, the differences in the ratios of the numbers taken at the pumps and at Chipps Island are so large that behavioral differences among the runs are likely to be involved. The data deserve more analysis.

Table 1 The number of marked or tagged fish recorded at the state and federal pumps and at Chipps Island: winter Chinook from Livingston Stone (LS) Hatchery, late fall Chinook from Coleman (C) Hatchery, wild Butte Creek (BC) spring Chinook, fall Chinook from Merced (M) River Hatchery, through spring 2008. Only fish released at or near the hatcheries are tallied. Data from USFWS.

	# at pumps	# at Chipps	Ratio
LS Winter	110	209	0.53
C Late Fall	3,898	3,008	1.30
BC Spring	3	34	0.09
C Fall	34	4,041	0.008
M Fall	2,570	250	10.28

Navigation by Juveniles

The sequential odor hypothesis (Harden Jones 1968) is the working model for homing in anadromous salmon in fresh water. That is, juveniles learn a series of odors during their seaward migration, and then follow these in reverse order on their return. Other genetic factors may also affect homing in fresh water (Quinn 2005), but these seem to be secondary. The sequential odor hypotheses implies that hatchery fish that are trucked to the bays should stray more often than fish released near hatcheries, and this is observed (SRFCRT 1994; unpublished CWT data). For example, 13 of the 17 tagged fall Chinook recovered in Clear Creek in 2009 were from the Feather River Hatchery, from which fish are trucked around the Delta; only three were from the nearby Coleman National Fish Hatchery, and one of these was released near the Delta.

The mechanisms by which juvenile salmonids find their way to the sea are less well known than the mechanisms by which they find their way back. In some situations, simply swimming (or drifting) downstream seems sufficient, but in other cases, such as the complex migration of juvenile sockeye though chains of lakes (Quinn 2005), it would be hopelessly inadequate. Besides using current, juveniles can orient themselves by the position of the sun and the plane of polarization of sunlight, and by the earth's magnetic field (Høgåsen 1998; Quinn 2005). In the Delta, tidal flows dwarf net seaward flows (Kimmerer 2004), and mechanisms besides sensing current seem necessary for navigation, and especially for rapid migration, through the Delta. Many simulation studies of juvenile migration through the Delta assume that the fish "go with the flow." Although tracking studies using newly released fish such as Perry and others (2010) do not contradict it, this assumption is questionable, especially for fish migrating naturally.

Juvenile Growth

The growth of juvenile salmon is strongly influenced by temperature and the amount of food available, known as "ration" in experimental studies. Based on studies of Central Valley fish reviewed in Williams (2006), the growth of fish fed to satiety in good laboratory conditions peaks at around 19°C for juvenile Chinook. In the Delta, and in the low-gradient streams, water is normally warmer than 20°C in the summer, and is often so in late spring (Figure 12). Thus, temperature and food supply are both "drivers" of juvenile growth, but other factors such as daylength and the individual fish's developmental program affect it as well. Size and life stage also affect growth, because growth (in length) in smaller fish is relatively more rapid, and growth (in weight) slows during smolting (Weatherby and Gill 1995).

Data on the size at age of naturally produced Chinook in the American River and the bays show considerable variability (Titus and others 2004; Figure 13), and a larger sample from the American River reported by Castleberry and others (1993) showed even more: the length of fish with ~125 otolith increments varied from about 40 to 80 mm.

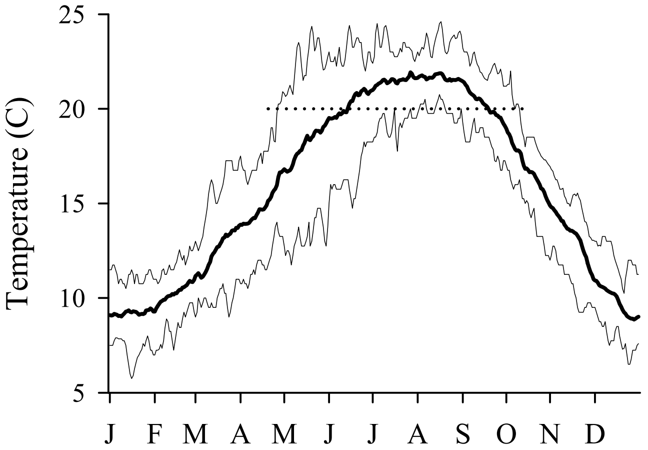

Figure 12 Daily minimum, maximum, and average ([min + max]/2) water temperature in the North Delta (Sacramento River at Freeport, near Sacramento) for 1994 through 2009. Dotted line shows 20°, ticks show the first of each month.

As another complication, fish of a given length vary in weight and in lipid content (Castleberry and others 1993), which can be viewed as energy stored for future growth as well as future activity. In at least some populations of stream-type Chinook, day-length at emergence strongly influences juvenile growth (Clarke and others 1992). In short, growth is not a simple response to current environmental conditions.

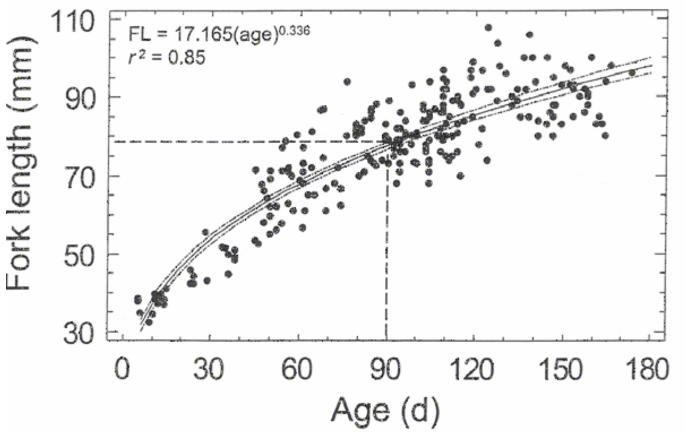

Figure 13 Size-at-age of juvenile Chinook salmon from the American River and San Francisco Estuary. Source: Titus and others (2004), courtesy of the American Fisheries Society.

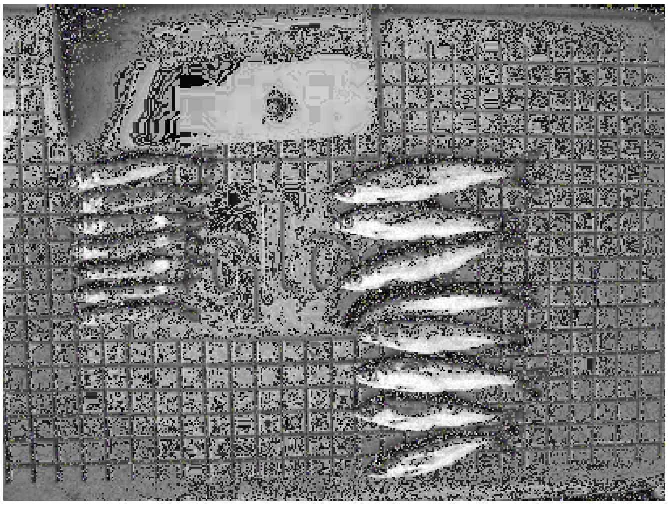

Figure 14 Comparison of juvenile Chinook from one enclosure on the Cosumnes River floodplain (right) and from another in the river downstream (left), which is tidal in this reach and so part of the Delta. Source: Jeffres and others 2008. Photo by Jeff Opperman.

Unpublished individual growth rates estimated from otolith microstructure, using the methods reported in Titus and others (2004), vary from 0.27 mm d^{-1} to 1.05 mm d^{-1}. Juvenile Chinook sampled in various Central Valley rivers grew at essentially the same rate on average as fish sampled in the Delta: 0.57 vs. 0.54 mm d^{-1} (Rob Titus, DFG, pers. comm. 2008). Kjelson and others (1982) reported that the growth of tagged fry released into the Delta averaged 0.86 mm d^{-1} in 1980 and 0.53 mm d^{-1} in 1981, and the mean size of juvenile sampled at the fish facilities varies from year to year (Williams 2006). This suggests that year-to-year variation in food availability in the Delta is significant, although the interaction with temperature complicates the question. Using hatchery fish in enclosures, Jeffres and others (2008) found that juvenile Chinook grew more rapidly on the vegetated Cosumnes River floodplain when it was inundated than in the river, either within or upstream from the tidally influenced area (Figure 14). Food was very abundant, and the fish grew well even though the water temperature averaged 21 °C for a week, with daily maxima up to 25 °C. This underscores the relationship between the availability of food and temperature tolerance.

An 11-year study by the National Marine Fisheries Service (NOAA Fisheries) found that on average, juvenile fall Chinook grow slowly in length (mean 0.33 mm d^{-1}) and hardly at all in weight during their migration through the bays, from Chipps Island to the Gulf of the Farallones, although they grow rapidly once they reach the gulf (Figure 15; MacFarlane and Norton 2002; MacFarlane and others 2005, B. MacFarlane, pers. comm. 2008). However, NOAA Fisheries sampling began in late April, after many fry migrants left the Delta. Moreover, the study used a trawl that probably was less effective for smaller juveniles, and sampled in open water where smaller juveniles are less likely to be. Accordingly, the results of the study are applicable mainly to what I have called fry migrants to low-gradient streams and fingerling migrants, or to hatchery fish. Nevertheless, given that survival in the ocean is size-dependent, this study raises the question of whether human modification of the bays, especially loss of tidal wetlands (Nichols and others 1986; Lotze and others 2006), has adversely affected Chinook. Poor growth in the bays also implies a strong potential for density-dependent mortality, which seems likely since millions of hatchery smolts are released into the bays. Potential density-dependent mortality should be regarded as a serious problem unless new evidence suggests otherwise.

USE OF HABITATS

Low-Gradient Streams

As juvenile Chinook migrate downstream into the Central Valley proper, they encounter low gradient reaches with fine-grained beds. Historically, during the winter and spring, the rivers were not contained by their channels and spread out over large areas, especially in the Sacramento Valley (Kelley 1989), so there was not a clear distinction between the Delta and flooded overbank habitat farther upstream (Williams 2006). The low-gradient rivers now flow mostly in confined channels with steep banks, but remnants of this formerly extensive habitat remain in the Butte Sinks and the Sutter and Yolo bypasses, and along unleveed reaches of the Cosumnes River.

When the Cosumnes River spreads out over its floodplain, juvenile fall Chinook do so as well (Moyle and others 2007). The fish grow rapidly

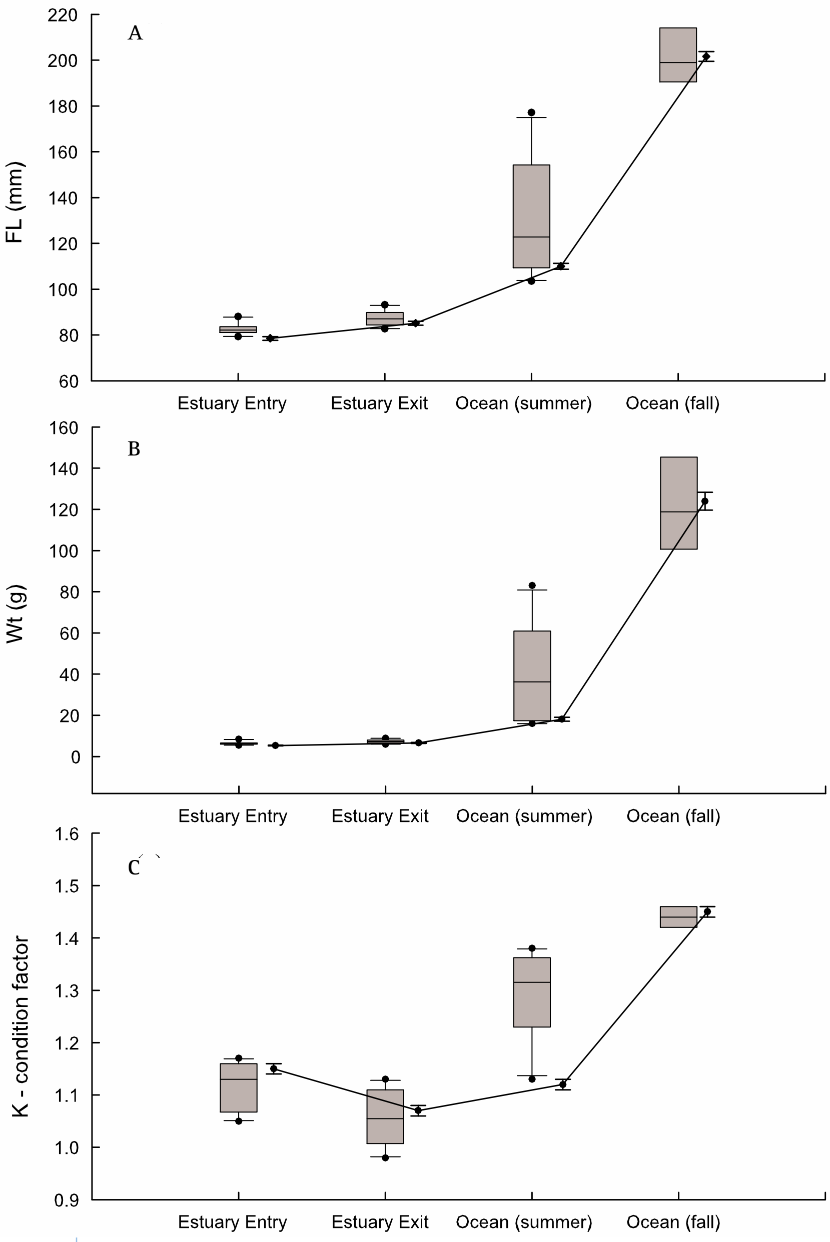

Figure 15 Size and condition of juvenile fall Chinook in the bays and ocean during 2005 (connected by lines) compared with data from 1998 through 2004 (box plots). Fish sampled in May and June at Chipps Island, and into the fall in the coastal ocean. "Estuary Entry" refers here to Chipps Island, at the downstream end of the Delta, and not to the upstream limit of tidal influence. Note also the size of the fish sampled at Chipps Island; most are >80 mm fork length. Source: Lindley and others (2009).

there (Figure 14), and most move back into the river as the water level declines and the floodplain drains. Similarly, juvenile salmon move into the bypasses, and also grow well there (Sommer and others 2001, 2005). Other fishes also use this habitat, and although many are stranded when water levels recede, these are mostly the introduced species; stranding losses of Chinook and other native species are usually modest (Sommer and others 2005; Jeffres and others 2008).

The Estuary

The distribution of juvenile Chinook in the modern Delta in spring has been studied and described by Erkkila and others (1950) and by the Interagency Ecological Program (IEP; Kjelson and others 1982; Brandes and McClain 2001). The IEP monitors the current distribution of juvenile Chinook in the Delta by seine surveys (Low 2005; Pipel 2005). Generally, density is highest along and near the Sacramento River, but juveniles occur throughout the Delta. The strong tidal flows in the Delta probably provide a sufficient explanation for the dispersal of juveniles, which was documented before the federal pumps were put in service (Erkkila and others 1950), but exports, active dispersal, and other factors probably affect it as well.

Historically, the Delta was a vast tidal wetland (Atwater and others 1979; TBI 1998), but most Delta channels are now confined by levees and have steep banks, like most low-gradient river reaches upstream. Although there are few data on the use of tidal wetlands by juvenile Chinook in the Delta, this is well documented elsewhere (Lott 2004 and citations therein), and probably was particularly important for fish that arrived in the Delta as fry.

The diversity of juvenile Chinook in the Delta is reflected in the size at date of fish captured at the state and federal pumps on the south side of the Delta (Figure 16). The pattern in Figure 16 shows graphically that life history types described above are not really discrete, but rather parts of a continuum. Larger juveniles, ~100+ mm, begin to appear at the pumps in August. The number of larger juveniles increases into March, then drops quickly in early April; these are the fingerling resident and classic stream-type fish. Fry migrants to the Delta, ~40 mm, begin to appear in January, and continue through most of March. Larger fry migrants, fry residents, and some fry migrants to low-gradient streams, begin to appear in March, followed by fingerling migrants, and continue until mid-summer, when the Delta becomes too warm for juvenile salmon.

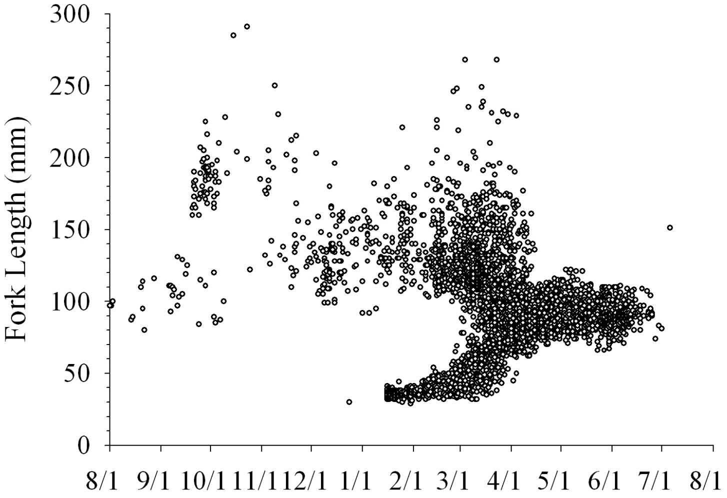

Figure 16 Juvenile Chinook at the Delta diversions; size at date of 6,752 juvenile Chinook sampled at the CVP and SWP diversion facilities in the Delta from August 1995 through July 2001. Note that many data points are obscured by others in the figure. Source: Redrawn from Hedgecock (2002).

The distribution of juveniles in the bays is not well known. A few small juveniles are collected around the margins of the bays in the IEP seine surveys (SSJEFRO 2003) and in Suisun Marsh (e.g., Matern and others 2002), and there is good evidence that they contribute significantly to returns of fall Chinook (Miller and others 2010). Fry use moderately saline (15 to 20 ppm) habitats in other estuaries (Healey 1991), so the salinity of much of the bays should not be an obstacle for them, even in dry years. More small juveniles are captured in or entering the bays in wet years (Kjelson and others 1982, Brandes and McLain 2001), but they have also been found there in dry years (Hatton and Clark 1942). The slow growth of larger juveniles in the bay (Figure 15) may reflect anthropogenic changes in the bays, since early descriptions (e.g., Scofield 1913) suggest abundant food for Chinook. If so, such degradation of the bays is probably a significant problem for fall and spring Chinook, since survival in the ocean presumably increases with fish size and condition.

Based on studies of other estuaries, Chinook that migrate to the estuary as fry tend to rear there for some time, while Chinook that rear to fingerling size (~60+ mm) or larger somewhere upstream tend to pass through the estuary more rapidly (Healey 1991; Burke 2004). Small Chinook occupy mainly shallow water around the margins of the estuary, often moving up into tidal marsh channels on the flood tide, and retreating back to subtidal areas late on the ebb tide (Levy and Northcote 1982; Lott 2004). The juveniles tend to move into deeper water and down the estuary as they grow (Healey 1980; 1991). Juvenile Chinook are opportunistic feeders, although they may be selective in particular habitats, and although reports on diet vary from study to study, broad patterns are evident. Smaller juveniles occupying marsh channels often feed heavily on larval and pupal chironomids (e.g., Shreffler and others 1992; Lott 2004). This has been observed in a remnant tidal marsh in the Delta (Simenstad and others 2000), as well as in overbank habitats close to the Delta (Sommer and others 2001, 2005; Jeffres and others 2008).

As the fish grow, larger prey become more important, and as they move farther offshore and into deeper water, their diet shifts toward prey that are available there. Most habitat in the Delta is now subtidal, because most channels are leveed with steep banks, and the prey available for fry reflect this. The best data are from Kjelson and others (1982), who summarized their own and earlier studies as follow:

> Crustacea and insects dominated fry stomach contents, with an increase in crustacea ingestion downstream. Cladocera and Diptera were consumed frequently in the Delta, while in brackish San Pablo and San Francisco bays, consumption of copepods, amphipods, and fish larvae increased. Similar food habits were described for older fry and smolts in Delta studies by Rutter (1904), Ganssle (1962), and Sasaki (1966).

Although many of the fish in Kjelson and others's (1982) samples were small (<50 mm), there were larger ones as well. Larger juveniles sampled at Chipps Island by MacFarlane and Norton (2002) fed mainly on amphipods (Corophium), but also post-larval crabs, flies, shrimp, and (non-fly) insects.

Environmental Constraints on Life-History Patterns and Use of Habitats

There are several serious constraints on salmon life history patterns in the Central Valley. Loss of habitat above the dams is the most obvious. Loss of overbank and tidal habitat to levees has been described above, and capture and storage of snowmelt runoff behind dams sharply reduces access to overbank habitat. Diversions in the south Delta that supply large amounts of water to the San Joaquin Valley and Southern California make that habitat perilous, especially for San Joaquin fall Chinook (Table 1). Much effort has gone into studies of the effect of these diversions on the survival of hatchery juvenile fall and late-fall Chinook (e.g., Newman and Rice 2002; Newman 2003, 2008; earlier studies reviewed in Brandes and McLain 2001). Generally, these show that diversions do reduce survival, but survival also varies with other factors such as flow, temperature, and salinity, and none of the effects clearly predominates.

High summer water temperature is another serious constraint, as mentioned above. Juvenile Chinook in the Central Valley do not migrate to the Delta during summer, although juvenile Chinook do migrate into estuaries in other rivers during that season (Ewing and others 2001;Quinn 2005). The precise nature of the constraint is uncertain. The temperature tolerance of juvenile Chinook depends on aspects of their environments such as food supply, discussed above, and predation risk. Some juvenile Chinook inhabit warm (~20 °C) Central Valley streams through the summer and appear to survive well, although presumably they suffer temperature stress (Werner and others 2005). However, they do not have to contend with predatory fishes there. This is not the case in the Delta, or the larger rivers. Since the metabolic and digestive rates of predatory fishes also increase with temperature, so does the risk of predation for small salmon. Coded-wire tag studies have shown that survival in the Delta begins to decrease at temperatures that juveniles survive easily in the tributaries (Baker and others 1995; Newman and Rice 2002; Newman 2003; Newman 2008), and probably this is because of increased predation. Whatever the cause, the lower rivers and Delta are too warm for juvenile Chinook in the summer.

Conditions in the ocean and probably in the bays are another constraint on juvenile life history patterns. The biological productivity of the coastal ocean and the Gulf of Farallones rises sharply in the spring when changes in the coastal winds shift currents to a predominantly southward flow, which induces upwelling of nutrient-rich water from the coastal shelf and slope (Ainley 1990; Lindley and others 2009). The timing of this spring transition varies from year to year, and can strongly affect factors such as the nesting success of seabirds. Presumably, the survival rate of juvenile Chinook increases with increasing biological productivity in the gulf. Roth and others (2007) reported a relationship between seabird nesting success, which also depends on the productivity of the gulf, and the subsequent abundance of fall Chinook. The importance of ocean conditions has been emphasized by the recent crash in the abundance of fall Chinook, for which poor ocean conditions seem the most likely proximate cause (Lindley and others 2009). Juveniles that enter the ocean in late fall or winter do so at much larger size.

LOCAL ADAPTATION AND DOMESTICATION

Even streams in the same geographical area may provide different environmental challenges for salmon populations, and the strong tendency of salmon to return to their natal stream allows local adaptation to develop. Transplantation experiments in New Zealand, where Chinook were introduced about a century ago, show that such adaptation can develop fairly quickly (Unwin and others 2003). Although cases where local adaptation has been rigorously demonstrated are relatively few (Quinn 2005), there are many situations in which it seems highly likely, such as Atlantic salmon from an upper tributary of a river in Scotland that start their downstream migration sooner than salmon from a lower tributary (Stewart and others 2006). As a local example, CWT studies suggest that juvenile Chinook from a San Joaquin River tributary, the Merced River, survive better when released into the San Joaquin River than juveniles from the Feather River, tributary to the Sacramento (Newman 2008). Traits related to juvenile migration seem a logical target for selection that leads to local adaptation.

Hatcheries are now a prominent habitat for Central Valley Chinook, and Barnett-Johnson and others (2007) showed by otolith analyses that that only 10 ± 6% of 158 Chinook taken in the ocean party boat fishery off Central California in 2002 were naturally produced. Subsequent genetic analysis showed that these were fall Chinook (R. Barnett-Johnson, USBR, pers. comm., 2009). There is good evidence that hatchery populations evolve to become more fit for a hatchery-based life cycle, and less fit for a natural life cycle (Araki and others 2008). Older evidence is summarized in Williams (2006), but recent evidence from a study of steelhead in the Hood River, Oregon, is even stronger. By comparing the reproductive success of naturally spawning steelhead with one or two hatchery parents, Araki and others (2007) demonstrated a rapid loss of fitness for natural reproduction. For such reasons, Lindley and others (2007) developed criteria for hatchery influence to assess the viability of Central Valley Chinook and steelhead.

The “adaptive landscape” is a conceptual model that helps explain why hatchery culture results in lower fitness for natural reproduction. For an organism in a given environment, a level of fitness is associated with each combination of genes, or more specifically, of alleles (think of fitness as the propensity to have descendents). This can be visualized for one or two genetic dimensions, and for two dimensions looks like a topographic map, but with contours of equal fitness rather than elevation. The conceptual model can be applied to populations, except that each dimension then shows the frequency of an allele in a population. Natural selection will tend to move the population “uphill,” toward higher fitness, although when genes interact, or multiple alleles affect the trait, there may be multiple fitness peaks, some higher than others (Figure 17).

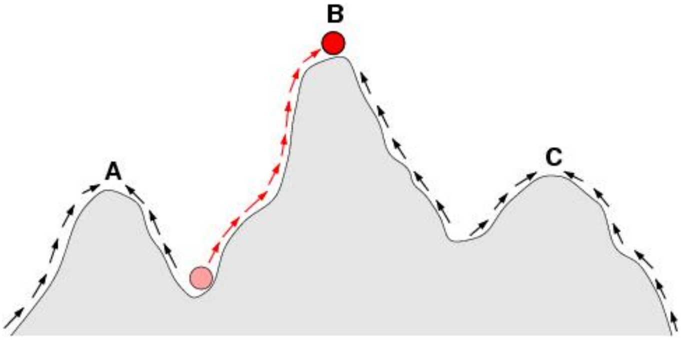

Figure 17 Cartoon of an adaptive landscape, in one genetic dimension. The vertical distance shows fitness, and the horizontal axis shows combinations of gene frequencies. Arrows show the direction of selection, and the red ball shows a population evolving from lower to higher fitness. Source: Wikipedia, attributed to C. O. Wilke.

From this point of view, consider the situation of a population that lives in two different environments, each with its own adaptive landscape, such as a salmon population that reproduces both in a river and in a hatchery. There are two possible outcomes. Either the population will shift toward the fitness peak in one habitat or the other, or it will be caught somewhere in the middle, with intermediate fitness in both habitats. Neither natural nor artificial selection can maximize the fitness of a population for both environments.

This can be modeled (e.g., Goodman 2005), and the modeling indicates that a shift toward one peak or the other can happen rapidly. Data on fall Chinook in the upper Sacramento River and a tributary suggests that such a shift may have occurred in that population, perhaps in the generations from the late 1970s to the early 1990s. Returns to Battle Creek, including Coleman Hatchery, have gone from a small percentage of the run to most of it (Figure 18). Assuming that these represent the naturally reproducing and hatchery components of the run, the run is now dominated by hatchery fish. Moreover, the total numbers of fish in the years around 1960 are about the same as in the years around 2000, so hatchery fish may not have supplemented naturally produced fish in the upper Sacramento River, but rather, replaced them.

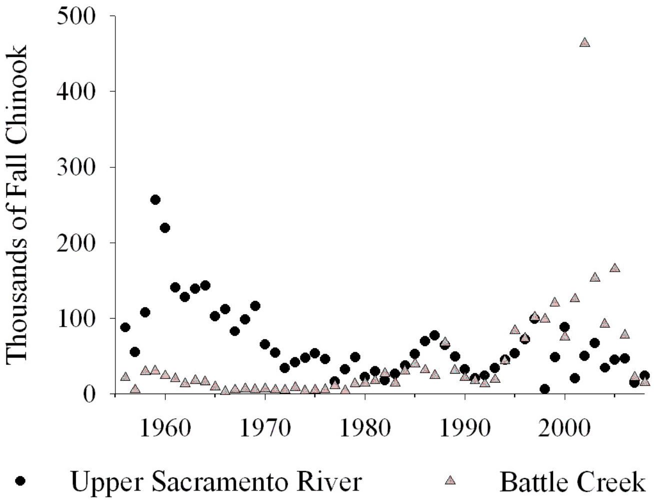

Figure 18 Number of adult fall Chinook returning to the upper Sacramento River (above Red Bluff) and to a tributary, Battle Creek, including Coleman Hatchery. Updated from Williams (2006).

Similar data do not exist for other Central Valley rivers where hatcheries are on the main stem, but other data also suggest large percentages of hatchery fall Chinook. Analyses of otoliths showed that 97% of 200 fall Chinook collected in 2004 in the Mokelumne River were hatchery fish, as were 55% of 154 three-year-old fish collected in 2002 or 2005 in the Stanislaus River (Barnett-Johnson 2010; R. Barnett-Johnson, USBR, pers. comm., 2009]). Since 2007, 25% of hatchery fall run have been tagged and marked by clipping the adipose fin. Almost all Central Valley Chinook return as 2-, 3-, or 4-year-olds, so in 2010, essentially all returning hatchery fall Chinook are 25% marked. Preliminary reports on the number of marked fish indicate that hatchery fish generally dominate the run, except for Clear and Butte creeks. Results in 2009 were similar, although more uncertain because the proportion of 4-year-olds has not yet been reported from scale samples.

Millions of naturally produced juvenile fall Chinook migrate into the estuary every year, but it seems that few of them survive to return as adults. We have remarkably little understanding why this should be, but it is clear that a hatchery-based life cycle does not involve selection for the fry migrant estuarine life history patterns that most naturally produced juveniles follow.

SUMMARY

Naturally produced Central Valley Chinook must migrate downstream from the gravel-bed reaches where they incubate and hatch, through low-gradient reaches and the estuary to reach the ocean, where they gain most of their growth. Four runs are commonly distinguished by the season in which adults enter fresh water: fall, late fall, winter, and spring, and these correspond generally but not completely with genetic lineages and management units. All four runs are produced in hatcheries, especially fall and spring.

The size at which juvenile Chinook migrate to and through the estuary varies widely, as does the rate and timing with which they do so, but all spend enough time there that conditions in the estuary must be important for them. Six different life history types can be distinguished, although these are really parts of a broad continuum extending from fish that migrate rapidly through the freshwater part of the estuary into the bays as fry, to fish that rear for a full year in the gravel-bed reaches before migrating through the estuary to the ocean.

The importance of the estuary for the various life history types varies inversely with their size; presumably fry migrants to the bays or the Delta must gain considerable size there before entering the ocean if they are to survive. Larger migrants pass through the estuary more rapidly, and larger juvenile fall Chinook apparently grow little in the bays. Late fall, spring and winter Chinook enter the estuary mainly as larger juveniles, although winter Chinook tend to be somewhat smaller.

The vast majority of the fry migrants to the estuary are fall Chinook, and most there is evidence that a substantial percentage of surviving naturally produced fall Chinook enter the estuary as fry, and move into brackish parts of it by the time they reach 55 mm fork length. This suggests that management should pay more attention to fry migrants, and less to larger migrants. Although large number of naturally produced fall Chinook enter the estuary, and relatively few of them are recovered at the pumps, the majority of adult fall Chinook are hatchery fish. Under the criteria developed by Lindley and others (2007), Central Valley fall Chinook should be listed as endangered. Effective management of Central Valley Chinook will require more information than is now available on the life histories of naturally produced Chinook that survive to spawn.

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