

DRERIP Delta Conceptual Model

Life History Conceptual Model for Chinook Salmon & Steelhead

Oncorhynchus tshawytscha & *Oncorhynchus mykiss*

Prepared by: John G. Williams, Consultant. jgwill@dcn.org

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For further inquiries on the DRERIP Delta Conceptual Models, please contact Hildie Spautz at hspautz@dfg.ca.gov or Mike Hoover at Michael_Hoover@fws.gov.

Graphic of *Oncorhynchus tshawytscha* shown on the cover is provided by the National Oceanic and Atmospheric Administration. Department of Commerce. NOAA's Historic Fisheries Collection # fish3007. 1906.

PREFACE

This Conceptual Model is part of a suite of conceptual models which collectively articulate the current scientific understanding of important aspects of the Sacramento-San Joaquin River Delta ecosystem. The conceptual models are designed to aid in the identification and evaluation of ecosystem restoration actions in the Delta and to structure scientific information such that it can be used to inform public policy decisions.

The DRERIP Delta Conceptual Models include both ecosystem element models (including process, habitat, and stressor models) and species life history models. The models were prepared by teams of experts using common guidance documents developed to promote consistency in the format and terminology of the models at http://www.dfg.ca.gov/ERP/conceptual_models.asp.

The DRERIP Delta Conceptual Models are qualitative models which describe current understanding of how the system works. They are designed and intended to be used by experts to identify and evaluate potential restoration actions. They are not quantitative, numeric computer models that can be “run” to determine the effects of actions. Rather they are designed to facilitate informed discussions regarding expected outcomes resulting from restoration actions and the scientific basis for those expectations. The structure of many of the DRERIP Delta Conceptual Models can serve as the basis for future development of quantitative models.

Each of the DRERIP Delta Conceptual Models has been subject to a rigorous scientific peer review process, as described on the DFG-DRERIP website and as chronicled on the title page of the model. The scientific peer review was overseen by Dr. Jim Anderson, at University of Washington for all species models and by Dr. Denise Reed, University of New Orleans, for all ecosystem models.

The DRERIP Delta Conceptual models will be updated and refined over time as new information is developed, and/or as the models are used and the need for further refinements or clarifications are identified.

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I. INTRODUCTION

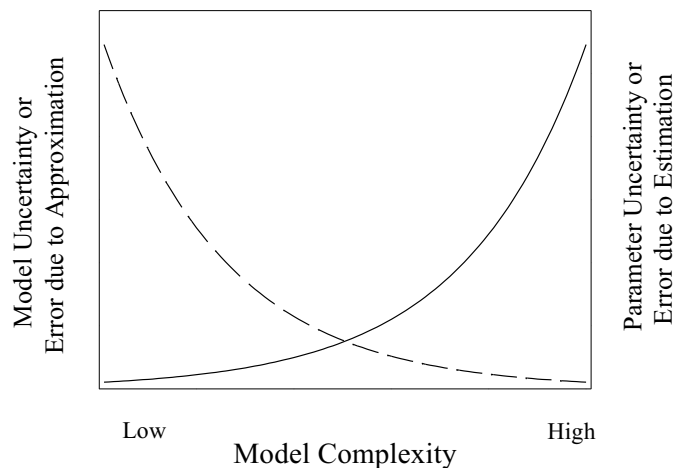
This report constitutes the conceptual model for Chinook and steelhead for the Delta Regional Ecosystem Restoration Implementation Plan (DRERIP). The report describes conceptual models, not numerical models, but several important considerations apply to both kinds, especially when they are used for management of living natural resources. First, the proper purpose of models is to help people think, not to think for them. Ignoring this can be disastrous, as exemplified by the current economic crisis. The world of credit default swaps was built on highly sophisticated models that persuaded many intelligent people that the associated risk was negligible, but they failed to recognize that a market based on houses that people could not pay for from their earnings is unsustainable.

In short, the most important “output” of a good conceptual or numerical model is clear thinking. To help people think, the model must be focused on selected features of the world that are thought to be important for the purpose at hand: in this case, management of the Delta. A model that tries to include everything will be too complex to be useful for this purpose.

Second, to be useful for management of natural living resources, numerical models must be unrealistic, because our knowledge of such resources is incomplete, and is based on data that includes measurement errors. According to Ludwig’s paradox, “Effective management models cannot be realistic” (Ludwig 1994:516), because two kinds of uncertainty must be balanced (Figure I-1; see Ch. 14 in Williams (2006) for elaboration of this point).

In our view, something similar applies to conceptual models of natural systems: to be useful, they must be simple. A schematic of the wiring in some electronic device is a conceptual model that may be useful as well as complex, but trying to develop a similar schematic of an ecosystem or part of an ecosystem is not useful, because our knowledge of such a system is much less complete than our knowledge of engineered devices, and we have only estimates of the relevant parameters.

Figure 1. Conceptual model of the trade-off between model uncertainty (dashed line) and parameter or estimation uncertainty (solid line). In a good predictive model these two types of uncertainty are balanced. Redrawn from Ludwig (1994). See Ch. 14 in Williams (2006) for more discussion of this matter.



Finally, reality is too complex to capture with a single model. Eric Lander, a noted geneticist who co-chairs President Obama’s Council of Advisors on Science and Technology,

recently remarked that “You can never capture something like an economy, a genome or an ecosystem with one model or one taxonomy – it all depends on the questions you want to ask” (NY Times, 11/11/08). Models are tools that we use to try to think, and multi-purpose tools generally do nothing well.

Therefore, although the complete life cycle of Chinook and steelhead is described here, the parts or aspects of the cycle that we think may be affected by management of the Delta are emphasized, and we try to keep it as simple as possible. More detail on most of the topics described here can be found in Quinn (2005), or in Williams (2006), from which this document draws very heavily.

A. On nomenclature:

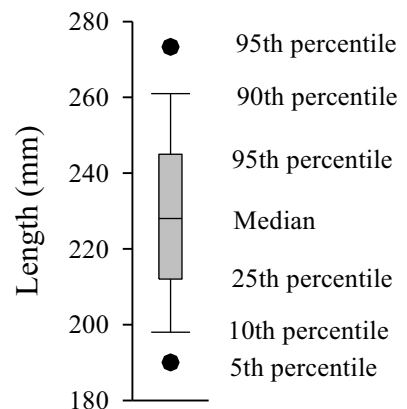
In the literature on Central Valley Chinook and steelhead, several terms are used with different meanings, which does not help an already difficult situation. For example, most people describe the area from the Golden Gate to the limit of tidal influence as the estuary, but MacFarlane and Norton (2002) apply that term only to the area influenced by the salinity of the ocean, essentially the area downstream from the Delta. This has caused many people to misunderstand their article. Similarly, the term ‘fry’ has been used to describe fish less than some length, such as 50 or 60 or 70 mm, with fish larger than that described as ‘smolts,’ although sometimes the distinction is between fry and ‘fingerlings,’ or fry and parr. Recently, CDFG has started describing fish in terms of physiological state rather than length; that is as fry, parr, silvery parr, or smolts, which is more appropriate for scientific purposes. Here, however, we often retreat to more traditional usage, and will refer to fry and fingerlings, with a division somewhere around 55 to 60 mm fork length. The term fingerling seems useful because it is a reminder that we are talking about small fish. By smolts we mean fish that are migrating rapidly and are well along in the physiological processes associated with smolting.

We use the term “salmon” to refer to both Chinook and steelhead, since both are members of the genus *Oncorhynchus*, the Pacific salmon, and steelhead were commonly called salmon in the 19th Century.

We distinguish ‘wild’ and ‘naturally produced’ fish by the extent of the hatchery influence in the population; the progeny of hatchery fish spawning in the wild are naturally produced.

All lengths given are fork lengths, unless otherwise noted.

Several of the figures in the report are “box plots,” which are conventional in science but may be unfamiliar to some readers. Box plots show distributions, as illustrated at right (with extra labeling) for the distribution of lengths of 346 unmarked juvenile steelhead captured at Chipps Island. If plots show more than two filled circles, they represent all outliers beyond the 10th and 90th percentiles.



Others of the figures show the factors influencing the probability of surviving the transition from one life stage to the next. These figures are numbered separately from the others, and follow the conventions for the DRERIP conceptual models.

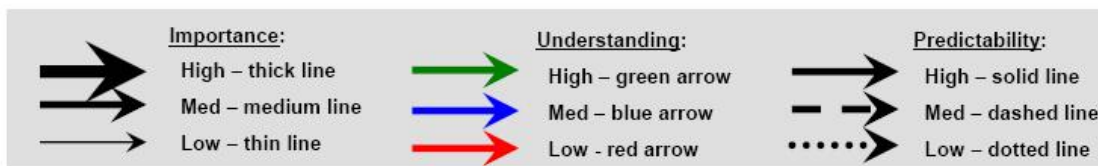
Linkages are depicted as arrows between cause (drivers) and effect (outcomes);

The **direction** of the effect is indicated by plus or minus signs;

The **importance** or magnitude of the effect is shown by line thickness;

Understanding about the relationship based on established literature knowledge is shown by line color;

The **predictability** of the effect is shown by line type.



These figures reflect the current understanding of Central Valley Chinook and steelhead, but they should be viewed with attention to the obvious limits to our understanding; for example, we did not anticipate the crash of the fall Chinook population in recent years, or do we understand why it increased before it crashed. Uncertainty does not justify inaction, but neither should it be ignored.

II. Biology

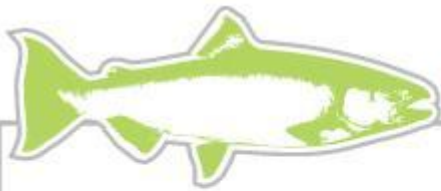
The Delta provides habitat for two species of Pacific salmon, Chinook (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). There are substantial differences between the species, but they are enough alike to treat them together for the conceptual models. Much less information is available on steelhead in the Central Valley than on Chinook, however. Lindley et al. (2007) commented that "... we are unable to assess the status of the Central Valley steelhead ESU with our framework because almost all of its roughly 80 populations are classified as data deficient." For the same reason, steelhead are given less attention here than they deserve.

Pacific salmon typically are anadromous. That is, they reproduce in fresh water, but migrate to the ocean to gain most of their growth. There are many exceptions, however, such as rainbow trout (non-anadromous *O. mykiss*), and there is a great deal of variation in life history patterns among the anadromous fish. A conceptual model that helps explain this diversity in life histories is described in the ecology chapter, but the emphasis here is on fish that migrate through or at least to the Delta, and so are directly influenced by management of the Delta.

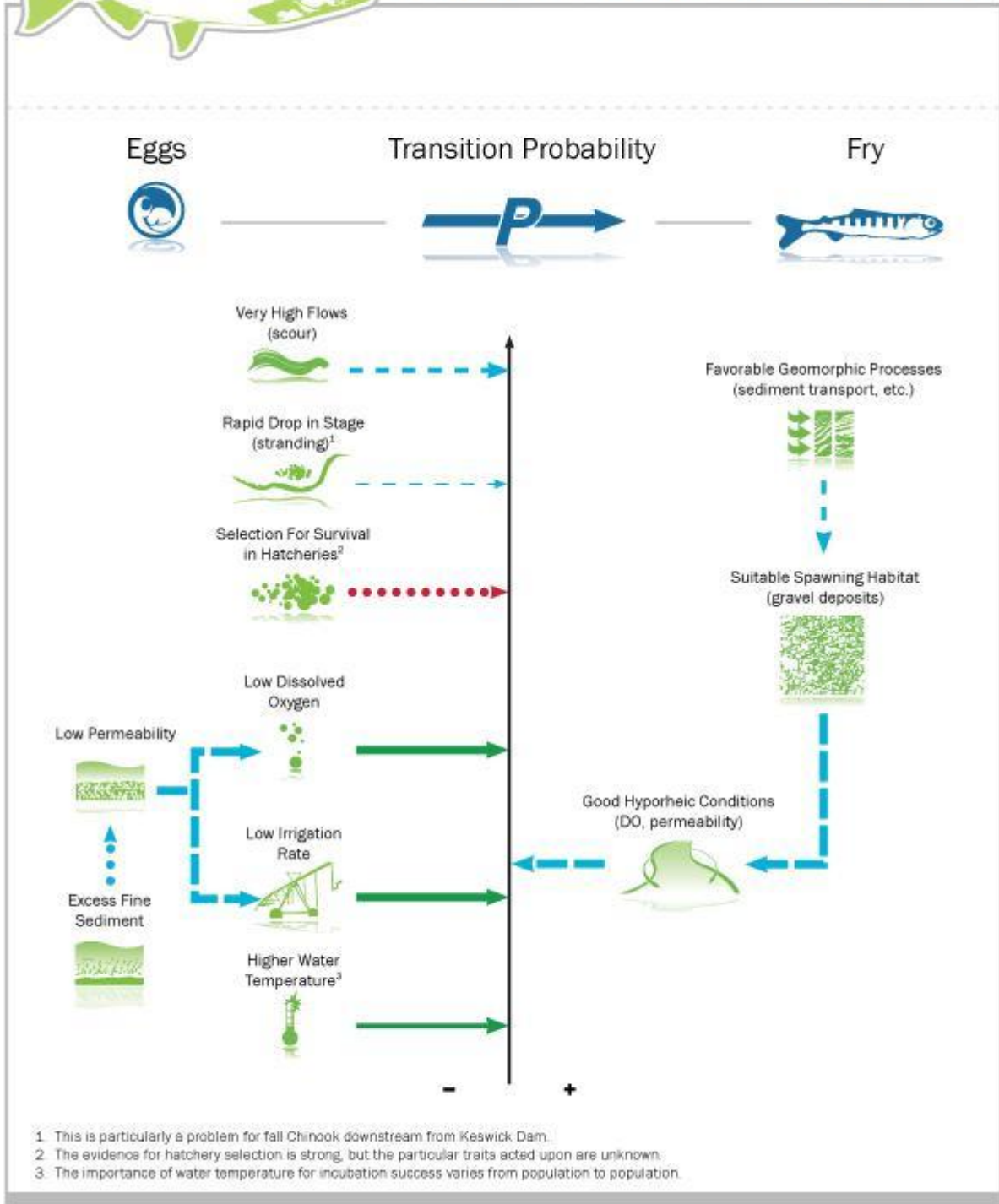
A. The life cycle of anadromous salmonids

Figure 1 depicts the natural life history of anadromous salmonids. Adult females dig nests called redds in gravel-bedded streams, the eggs are fertilized by males as the female deposits them in the redd, and the female covers the eggs with gravel. Embryos develop and hatch in the gravel, and the larval fish, called alevins, remain there and grow, nourished by egg yolk attached to their bellies. Around the time the remaining yolk is enveloped by the growing fish, the fish emerge from the gravel into the overlying stream as fry, ~ 25 mm long for steelhead, and 35 mm for Chinook. Factors affecting the transition from egg to fry are depicted in Life Stage Transition Figure 1.

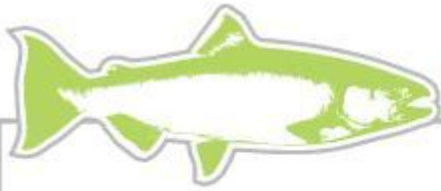
Although pink and chum salmon (*O. gorbuscha* and *O. keta*) migrate to sea directly after emerging, most salmon rear for months to years in fresh or brackish water before doing so. As the fish grow, they develop scales and dark vertical bands called parr marks on their sides that make the fish less visible in streams (Quinn 2005). Small parr are sometimes called fingerlings. Later, the fish go through various physiological changes that prepare them for living in salt water: externally, their shape changes, the parr marks fade, and the fish develop silvery sides and bellies that make them less visible from below. At this stage they are called smolts. Steelhead in Central Valley streams normally migrate at one or two years old. The age at which Chinook begin migrating is highly variable, however, as described in Chapter 4; the environmental factors affecting survival to the beginning of migration are depicted in Life Stage Transition Figure 2.



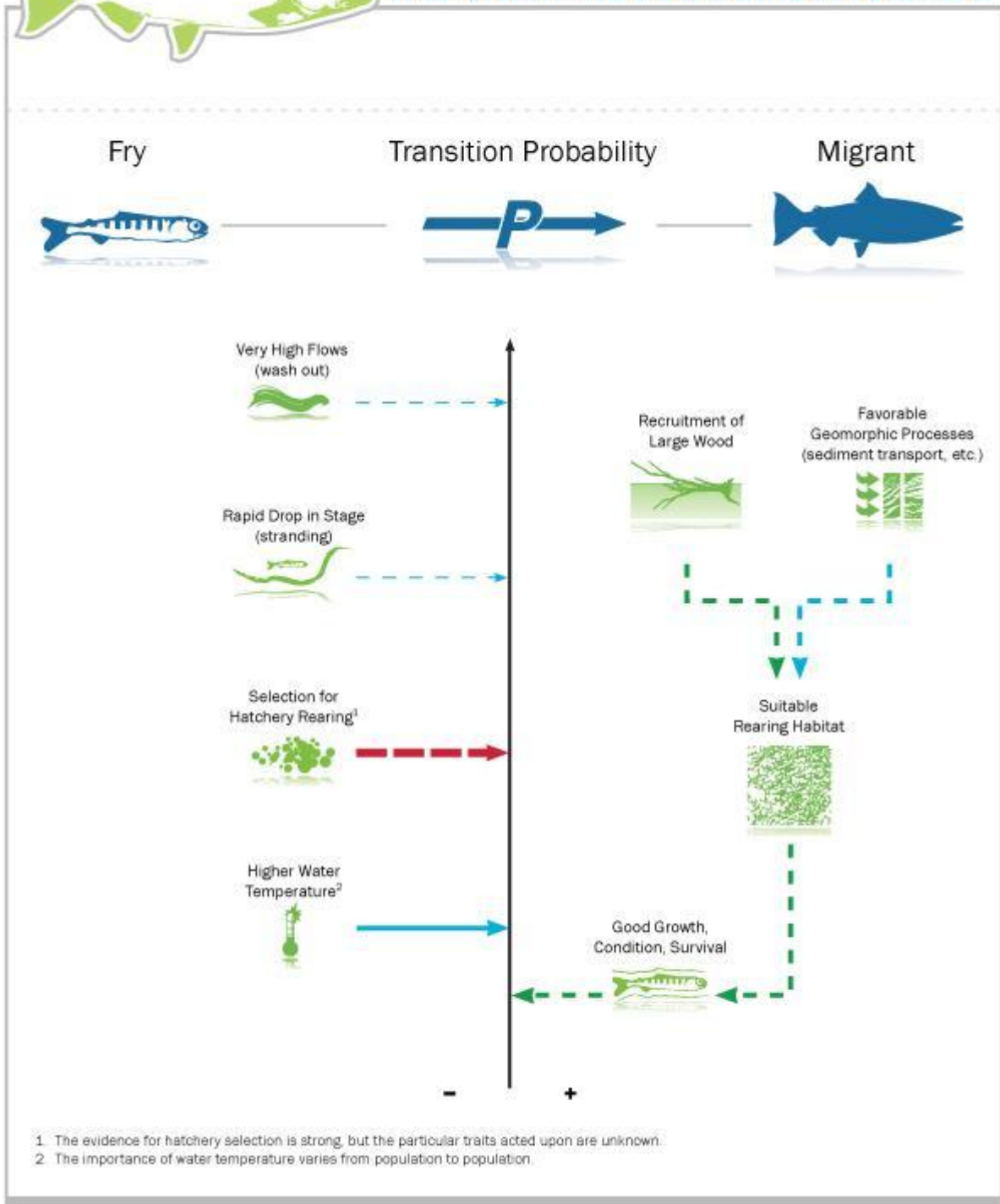
Transition Matrix: Chinook Salmon



Life Stage Transition 1.



Transition Matrix: Chinook Salmon



Life Stage Transition 2

After months to years at sea, the maturing fish return to fresh water to spawn. Some species or populations are ready to spawn shortly after reaching fresh water, while others hold in the streams for several months while their gametes develop. Most adult Pacific salmon, including Chinook, invest all of their energy into reproduction, and die shortly afterwards. Most steelhead also die after spawning, but some, especially females, may survive. Although female steelhead put more energy into gametes than males, males typically look for other females after spawning, and so exhaust themselves (Quinn 2005; Williams 2006). For both species, females select spawning sites and males compete for access to them, but females exercise some choice by selecting the time when eggs are deposited.



Figure 1. Graphical depiction of the natural life cycle of anadromous salmonids, copied from NOAA. This conceptual model tries to show both morphological change and the habitats used.

The life cycle involves transitions from fresh water to salt water, and back again. Like other bony fishes, salmonids maintain their body fluids at about one-third the salt concentration of sea water. In fresh water, they take up water through their gills by osmosis and excrete water in dilute urine to maintain ionic balance. In the ocean the osmotic gradient is reversed, so the fish lose water through their gills that they replace by drinking sea water, and excrete the salts by active transport through specialized cells in their gills. The enzyme $\text{Na}^+ - \text{K}^+$ ATPase (hereafter simply ATPase) helps power the function of these chloride cells, and has been used as an assay for the readiness for release of juvenile salmon in hatcheries or as an index of progress in smolting (Clarke and Hirano 1995). Presumably, making the physiological transition to water

with a sharply different salt concentration is easier if it is done gradually, and temporary residence in an estuary allows this to occur.

For Chinook and steelhead in the Central Valley, the natural anadromous life history must be amended to include reproduction and juvenile rearing in hatcheries (Figure 2), which annually produce upwards of 30 million Chinook and 1.5 million steelhead (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. Harvest is included in Figure 3, a conceptual model from Goodman (2005). Harvest is a desired outcome of management, and the rate of harvest is an important management “knob” that affects the extent of the influence of hatchery fish on the genetics of naturally reproducing fish (Goodman 2004, 2005). As this suggests, it is misleading to think of the salmonid life cycle as frozen in time. To the contrary, populations and their life histories can evolve rapidly enough that management should take evolution into account (Wilson 1997; Stearns and Hendry 2004). This is discussed below in terms of local adaptation.

Figure 2. Conceptual model combining the natural and hatchery life cycles, copied from USFWS, Warm Springs Hatchery. Note that natural reproduction seems somewhat truncated in the image.

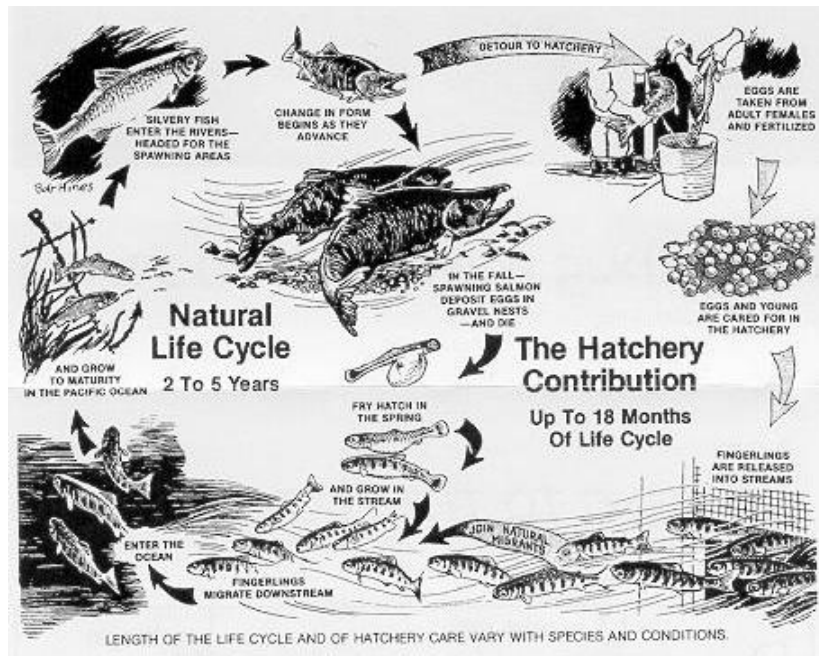
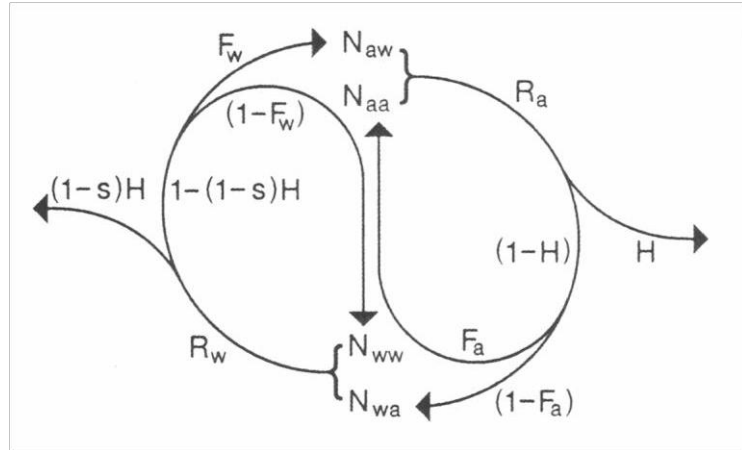


Figure 3, life cycle schematic, including hatchery production and harvest. N_{xy} is the number of spawner of origin y in habitat x , where w is natural and a is hatchery. R_y are the recruits, and F_y are the fractions of the natural and hatchery recruits taken into the hatchery. H is harvest, and s is the harvest selectivity for hatchery fish. Modified from Goodman (2004)



The juvenile life histories of Central Valley Chinook are highly variable, and the young fish enter the ocean at lengths ranging roughly from 75 to 250 mm (Williams 2006). The habitats where they gain most of this growth are also variable: at the extremes, some migrate rapidly through the Delta and grow mainly in the bays before entering the ocean, while others remain and rear in the gravel-bedded parts of the streams where they incubated and then migrate rapidly through the lower rivers, the Delta and the bays. This is discussed in more detail in the ecology chapter. Less is known about steelhead, but in the Central Valley they probably gain most of their growth in the gravel-bedded reaches. Most pass Chipps Island between ~ 215 and 245 mm in length (see the box plot in the Introduction).

B. Adult size, fecundity, and survival by life stage of Chinook and steelhead:

Chinook and steelhead have relatively few, large eggs, compared to most fishes of similar size, and average egg to fry survival is correspondingly high. However, although average egg to fry survival is high, it is also highly variable, and may be zero in many cases (Williams 2006).

Quinn (2005) compiled data from published studies on life-stage specific size and survival of wild or naturally reproducing Pacific salmon populations, and his results for Chinook and steelhead are presented in Table 1. Some studies reported survival from egg to fry or fry to smolt, and others estimated survival from egg to smolt. Quinn calculated separate estimates of adults per female using both sets of estimates, and the uncertainty in current knowledge is reflected in the different results from these two approaches. These data are from populations subject to fishing, which absorbs the surplus implied by adults per female being greater than two.

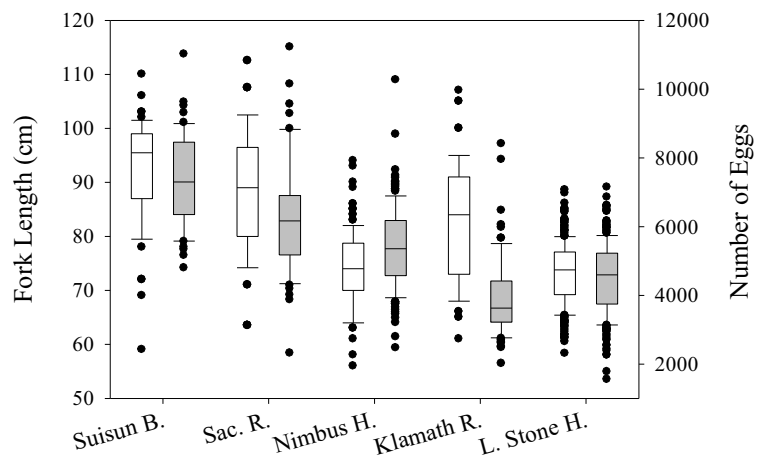
Table 1. Size, fecundity and survival estimates for Chinook and steelhead, copied from Quinn (2005).

Life History Stage	Chinook	Steelhead
Female Length (mm)	871	721
Fecundity	5401	4923
Egg size (mg)	300	150
Egg to fry survival	0.380	0.293
Fry size (mm)	35	28
Fry to smolt survival	0.101	0.135
Smolt size (mm)	60-120	200
Smolt to adult survival	0.031	0.130
Adults per female¹	6.4	25.5
Egg to smolt survival	0.104	0.014
Adults per female²	17.5	9.2

1. Calculated using egg to fry and fry to smolt survival estimates.
2. Calculated using egg to smolt survival estimates.

Historical data show that Central Valley Chinook used to be larger and more fecund than the averages given in Table 1 (Figure 4). On the other hand, Central Valley steelhead were smaller (Table 2). Current fecundity data for Central Valley Chinook are remarkably scarce, except for winter-run, but fall Chinook from a sample taken from the American River were small but fecund for their size (Figure 4). Note the lower fecundity of Klamath River Chinook for their size, which may reflect the steeper gradient and more arduous migration for fall Chinook in that river.

Figure 4. Distributions of size (open boxes) and fecundity (shaded boxes) for fall Chinook salmon collected in Suisun Bay ~ 1920, the Sacramento River ~ 1940, River Klamath River ~ 1920, and Nimbus Hatchery on the American River, 1997, and for winter Chinook from Livingston Stone Hatchery. Data from McGregor 1923b, Hanson et al. 1940, Kris Vyverberg, DFG, and John Rueth, USFWS. Copied from Williams (2006).



C. Age distribution of Chinook and steelhead.

One important aspect of life history variation among Chinook and steelhead can be summarized by tables showing the time spent in fresh and salt water. For most Chinook and steelhead, time can be specified in terms of winters in fresh water, as in Table 2, although some Chinook migrate past Chipps Island during the winter. Unfortunately, good information on the current age distributions of Chinook and steelhead in the Central Valley is only now becoming available. Table 2 gives qualitative “guesstimates” for Central Valley Chinook, based partly on data for one year in the Feather River given in Williams (2006). Table 3 gives quantitative data on four common life history patterns for Central Valley Steelhead in a somewhat different format, but the data are old and include only fish on their first spawning run, so older fish are not tabulated.

Table 2: Adult life history variation in Central Valley Chinook, based on various studies described in Williams (2006)

Winters in Fresh Water	Winters at Sea				
	1	2	3	4	5
0	Common	Common	Common	Scarce	~ nil
1	No data	Some	Some	Very scarce	~ nil

Table 3. Fork length in centimeters of Central Valley steelhead at various life stages, estimated from scale measurements of steelhead on their first spawning migration, for four life history patterns (age at return = years in freshwater/years in salt water). Data from Table 1 in Hallock et al. (1961).

Age at return	No. of fish	Length at salt water entry	Length at end of year 1	Length at end of year 2	Length at end of year 3	Length at capture
1/1	17	20.3	12.2			33.0
1/2	10	18.3	12.2	33.5		52.1
2/1	30	22.9	10.7	19.8		40.6
2/2	26	21.3	9.4	18.0	41.9	59.2

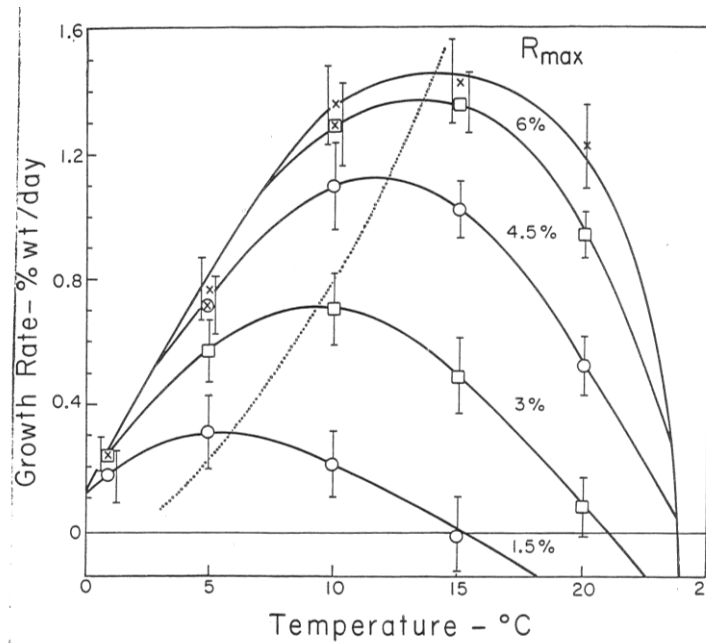
Variation in age at maturity buffers the population against environmental variation, since the consequences of reproductive failure or heavy mortality in early ocean life in any one year will be spread over several subsequent years, although the strength of this effect may be less than some suppose (Hill et al. 2003). Unfortunately, it appears that the age distribution of Central Valley Chinook has been reduced by about a year, probably by ocean harvest (Williams 2006).

Four sea-winter Chinook used to be common in the Central Valley, and there were a few five sea-winter fish, based on scale samples taken in 1919 and 1921 (Clark 1928). Only a few four sea-winter fish now occur. A rather different change has occurred with steelhead; it seems that many now forgo anadromy altogether, as discussed in the ecology chapter.

D. Juvenile Growth

The growth of juvenile salmon is strongly influenced by temperature and the amount of food available, known as “ration” in experimental studies. The best data are available for sockeye (*O. nerka*), shown in Figure 5, but the same general pattern applies to Chinook and steelhead, except that the temperature for maximum growth is higher. Based on studies of Central Valley fish, the growth of fish fed to satiety in good laboratory conditions peaks at around 19°C for Chinook and steelhead (Marine 2004, Myric and Cech 2000, 2001, 2002; 2004), although one study (Rich 1987) found maximum growth at a lower temperature; see Williams (2006) for more discussion of these studies.

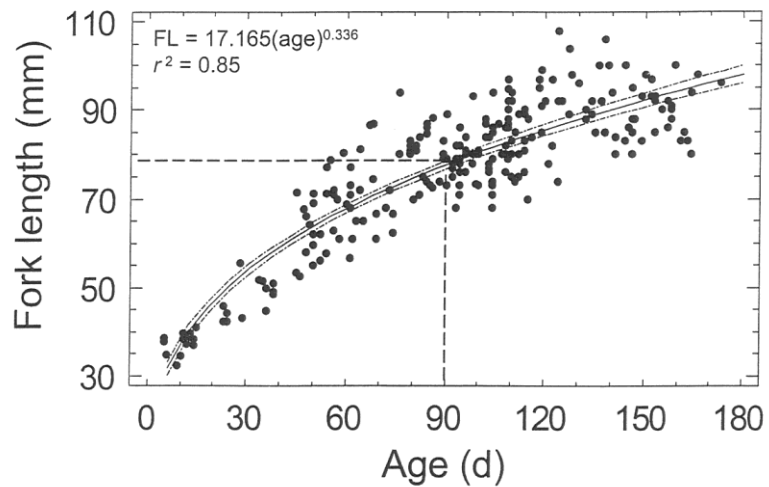
Figure 5. The relation between growth rate and temperature for different levels of ration for juvenile sockeye salmon. The dotted line connects temperature of maximum growth at each level of ration. Bars are two standard errors. Ration levels are given in percent body dry weight. Copied from Brett et al. 1969



Thus, temperature and ration are both “drivers” of juvenile growth, but other factors such as day length and the individual fish’s developmental program affect it as well, as discussed in the ecology chapter. Size and life-stage also affects growth, as growth in smaller fish is relatively more rapid, and growth (in weight) slows during smolting (Weatherby and Gill 1995). Growth also varies among individuals, even in laboratory conditions, as indicated by the error bars in Figure 9. Scofield (1920) noted regarding Klamath River Chinook that “Although from the same brood, hatchery practice and rearing pond, there was great variation in the size of the yearlings at the time of marking, the extremes in length being 1 3/16 to 5 inches ...” Data on the size at age of naturally produced Chinook in the American River and the bays show considerable variability (Titus et al. 2004; Figure 6), and a larger sample from the American River reported by

Castleberry et al. (1993) showed even more: the length of fish with ~125 otolith increments varied from about 40 to 80 mm. As another complication, fish of a given length vary in weight and in lipid content, 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 et al. 1992). In other words, growth is not a simple response to current environmental conditions, and fish in some sense “decide” how fast to grow. An obvious way that juvenile salmon can regulate their growth is behavioral. A fish may move up into the water column to feed, but risk being eaten itself, or it can burrow into the gravel and hide. Theory suggests that fish should adjust their behavior to minimize mortality per unit of growth, and observations support this idea (e.g., Bradford and Higgins 2001).

Figure 6. Size at age of juvenile Chinook salmon from the American River and from the San Francisco Estuary. Copied from Titus et al. (2004), courtesy of the American Fisheries Society.



Unpublished individual growth rates estimated from otolith microstructure, using the methods reported in Titus et al. (2004), vary from 0.27 mm d^{-1} to 1.05 mm d^{-1} . Interestingly, juvenile Chinook sampled in various Central Valley rivers grew faster on average than fish sampled in the Delta: 0.57 v. 0.54 mm d^{-1} (Rob Titus, DFG, pers. comm. 2008). Kjelson et al. (1982) reported that the growth of tagged fry released into the Delta mm averaged 0.86 mm d^{-1} in 1980 and 0.53 mm d^{-1} in 1981. This indicates that year to year variation in food availability in the Delta may be significant, and longer term variation may be important as well. Data on the size at date of fish collected at Chipps Island or the pumps should offer insight on this issue, as well as whether growth in the Delta is density-dependent.

Using hatchery fish in enclosures, Jeffres et al. (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 of the tidally influenced area. 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 implied in Figure 5.

An 11 year study by NMFS found that on average juvenile fall Chinook grow slowly in length (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 (MacFarlane and Norton 2002; MacFarlane et al. 2005, B. MacFarlane, pers. comm. 2008). Given that survival in the ocean is size-dependent, this raises the questions whether the human modification of the bays, especially loss of tidal wetlands (Nichols et al. 1986; Lotze et al. 2006), has adversely affected Chinook and steelhead, and whether naturally produced juveniles suffer from competition with hatchery fish in the bays. These questions deserve further study.

E. Temperature tolerance:

Salmon are ectotherms (cold-blooded), so their body temperatures are close to that of the water around them. Salmon do not tolerate warm water, and the Delta and lower rivers are unsuitable habitat for them in summer. However, salmon's response to temperature is affected by factors such as the availability of food, as discussed above, so, like growth, the temperature tolerance of salmon is affected by other factors in the environment.

Large embryos probably are the life stage least tolerant of warm water, because their metabolic rate increases with temperature, but they obtain oxygen and dispose of metabolic wastes only by diffusion through the egg wall. In laboratory studies with constant temperature through incubation (egg and alevin life-stages), mortality starts to increase at about 12 or 13°C, and increases sharply around 14 or 15°C (Williams 2006). In consequence, Central Valley streams are not suitable spawning habitat in summer except at high elevations, or where special circumstances such as inflows from large springs or releases from deep reservoirs keep the water cool. However, early-stage embryos seem somewhat more tolerant of warm water (Geist et al. 2006), so that Chinook spawning at 15 or 16°C in the fall may avoid harm if normal seasonal cooling occurs.

Juveniles tolerate temperatures of 20°C or even higher, provided food is abundant and the habitat is otherwise good, as in the Cosumnes River floodplain study described above. Juvenile steelhead probably are even more tolerant, as evidenced by the more southerly limit of their natural range. However, such warm temperatures do induce stress. At daily mean temperatures above 18-19°C, juvenile steelhead in the Navarro River develop elevated levels of a heat-shock protein, hsp 72 (Werner et al. 2005). At the least, this imposes a metabolic cost.

Adult Chinook can also tolerate about 20°C (Williams 2006). In Butte Creek in 2002 and 2003, adult spring Chinook suffered heavy mortality from columnaris, a bacterium, following more than a few days with mean temperatures > 21°C. There is also evidence of prespawning damage to gametes in 2002 (Williams 2006), so conditions in Butte Creek (Figure 7) probably represent the thermal limit for populations of spring Chinook, and global warming makes the prospect for the Butte Creek population dim.

Although juvenile steelhead and some juvenile Chinook stay in Butte Creek through the summer, 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 et al. 1995), probably because of increased predation. Whatever the cause, the lower rivers and Delta are too warm for juvenile Chinook and steelhead in the summer

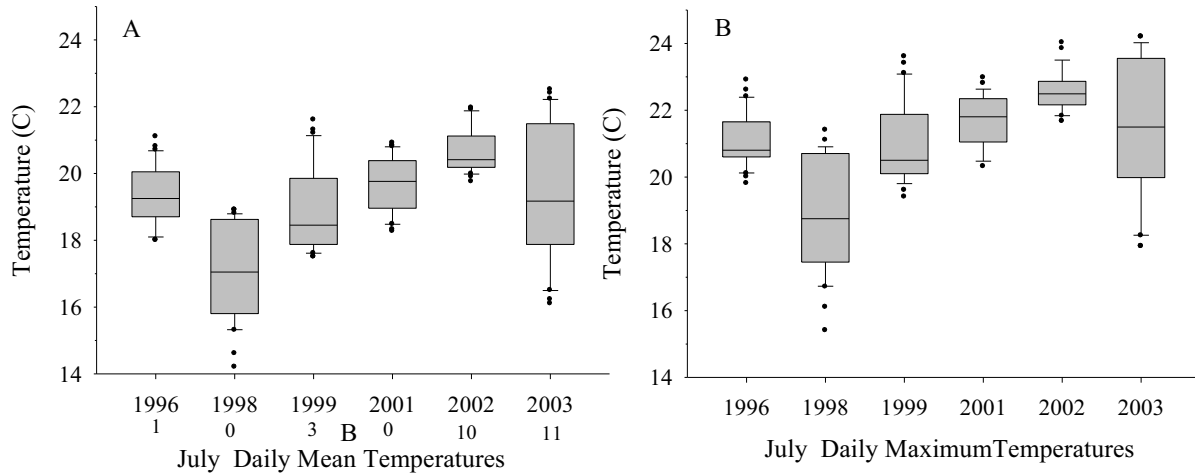


Figure 7. Daily mean (A) and daily maximum (B) water temperatures at the Pool 4 monitoring site in the reach of holding habitat on Butte Creek: The number of days with mean > 21°C in each year is shown below the date in A. July 2002 was consistently warm; July 2003 was cool early but warm later. Copied from Williams (2006); data from CDWR and CDFG.

F. Dissolved oxygen

The oxygen in water molecules is tightly bound to a carbon atom, but fish can take up dissolved oxygen through their gills. Generally, there is enough dissolved oxygen for Chinook and steelhead in flowing streams, but eggs and alevins are often under some level of oxygen stress (Williams 2006). This is particularly true for Central Valley fish, since the metabolic demands of the organism increase with temperature, the amount of dissolved oxygen that water can hold varies inversely with temperature, and fish in Central Valley streams generally incubate at relatively high temperatures. In the surface streams, dissolved oxygen is mainly an issue on the San Joaquin River near Stockton, where low flow and high biological demand in late summer and fall causes a “DO sag” (Lee and Jones-Lee 2003; Jassby and Van Nieuwenhuyse 2005). The low DO may delay migration up the San Joaquin River by adult fall Chinook, as discussed in the stressors chapter.

III. Distributions:

A. Historical distributions:

Chinook and steelhead were once widely distributed in Central Valley rivers, going just about anywhere they could swim. The past distribution of Chinook has been estimated from

historical accounts by Yoshiyama et al. (1996; 2001). Lindley et al. (2004, 2006) estimated that there were about 18 independent populations of spring Chinook, 4 independent populations of winter Chinook, and 81 independent populations of steelhead, based largely on the historical data compiled by Yoshiyama et al. (1996), and on factors such as stream gradient, basin size, and temperature. Winter Chinook inhabited streams in volcanic terrain in the upper Sacramento drainage where large springs provided substantial inflows of cool groundwater year-round: the McCloud, Little Sacramento, and Pit rivers, and Battle Creek. Spring-run probably were the most widely distributed Chinook; they ascended rivers to high enough elevations that summer temperatures remained tolerable, and because they migrated during spring snowmelt runoff, they could pass over barriers that were impassable during lower flows. Fall Chinook spawned at lower elevations than other runs, but also used accessible higher elevation habitat such as the McCloud River. However, they remained separate from other runs by spawning later in the fall than spring Chinook (Williams 2006), but earlier than late fall-run. There is little information on the natural range of late-fall Chinook (Williams 2006), but evidently they spawned at high enough elevation that the streams remained habitable for the juveniles through the summer, and spawned later than fall-run. Steelhead presumably went higher into watersheds and into smaller tributaries than Chinook, but good information on their natural range is also lacking (McEwan 2001).

Since salmon are anadromous, the distribution of any population includes habitats between the spawning grounds in gravel-bed streams and the oceans, including the Delta. Juveniles can and do swim upstream, so Chinook habitat in the Central Valley extends into small tributaries, such as Rock Creek near Chico, that are dry in the summer and do not support spawning (Maslin et al. 1999). These are relatively warm and biologically productive, and the young salmon grow rapidly there. As many as a million juveniles may still use these habitats.

Salmon habitat also extended widely across the valley floor. 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), to provide extensive floodplain habitat for juvenile salmon (Williams 2006). The overbank habitat along the lower rivers graded into the extensive tidal marsh habitat of the Delta and the bays. Although data are lacking, it seems likely that juvenile salmon historically used tidal and subtidal habitats all across the Delta. In a report on studies of Chinook in 1897 and 1898, Scofield (1899) described a few fish collected in the bays and the Delta, and observed that:

If this small number of salmon taken in salt water represents, as it unquestionably does, the first big movement of young salmon out of the river, it at first appears that more of them should have been found, but when we consider the vast expanse of territory the lower Sacramento covers with its many channels and bayous, to say nothing of San Pablo and Suisun bays, it is not so strange that so few were found—in fact, the strange part of it is that so many were found—and we can realize the vast number that must have distributed themselves in these waters.

B. Current geographical distributions:

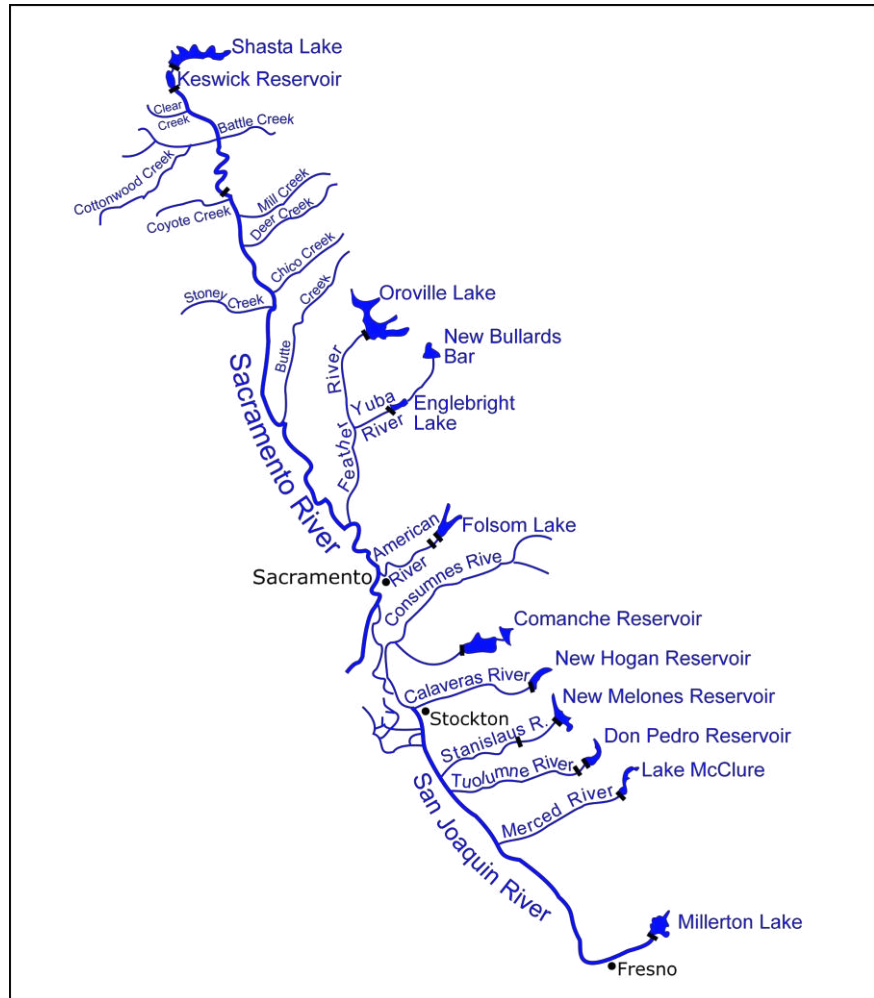
Current distributions of Chinook and steelhead are sharply constrained by impassible dams (Figure 8), or, on the San Joaquin River, by diversions. Fall Chinook, which still have access to the part of their natural range below the dams, are now most widely distributed, and are the only Chinook in the San Joaquin River and Delta tributaries. Winter Chinook persist only in the Sacramento River below Keswick Dam. Independent populations of spring Chinook remain in Mill, Deer, and Butte creeks, where migrations are not blocked by dams. Chinook enter the Feather and Yuba rivers in spring and hold over through the summer, but genetically the Feather River fish are very similar to fall-run, and the population is heavily influenced by hatchery fish; the same is probably true of the Yuba River population. Small populations of spring Chinook occur in several other Sacramento River tributaries such as Clear and Chico creeks, and a few nominal spring Chinook are reported in the mainstem. Late fall Chinook persist in the Sacramento River and apparently occur in various tributaries, but whether the tributary populations are viable is uncertain. *O. mykiss* remain widely distributed, but the number of naturally reproducing anadromous fish seems to be small, perhaps a few thousand, and there are few good data on them (Lindley et al. 2004, 2007; Williams 2006).

Along the streams and in the Delta, levees constrain the current distribution of juvenile salmon to the channels, except for the Butte Sink, the Sutter and Yolo bypasses (Figure 9), unleveed reaches of the Consumes River, and remnant tidal marshes in the Delta. Levees also block most of the tidal wetlands around the bay (Atwater et al. 1979). The loss of overbank and tidal habitat for juvenile rearing may rival the importance of the loss of upstream habitat for spawning. For example, habitat in the Butte Sinks and the Sutter Bypass probably accounts for the recent success of Butte Creek spring Chinook. The Yolo Bypass and the overbank habitat along the Consumes River provide good habitat when juvenile Chinook have access to them (Sommer et al. 2001, 2005; Jeffres et al. 2008).

Formerly an extensive tidal marsh, the Delta is now a web of constrained channels (Figure 10). The distribution of juvenile Chinook in the Delta in spring has been studied and described Erkkila et al. (1950) and by the Interagency Ecological Program (Kjelson et al. 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 preceded export pumping (Erkkila et al. 1950), but exports, active dispersal, and other factors probably affect it.

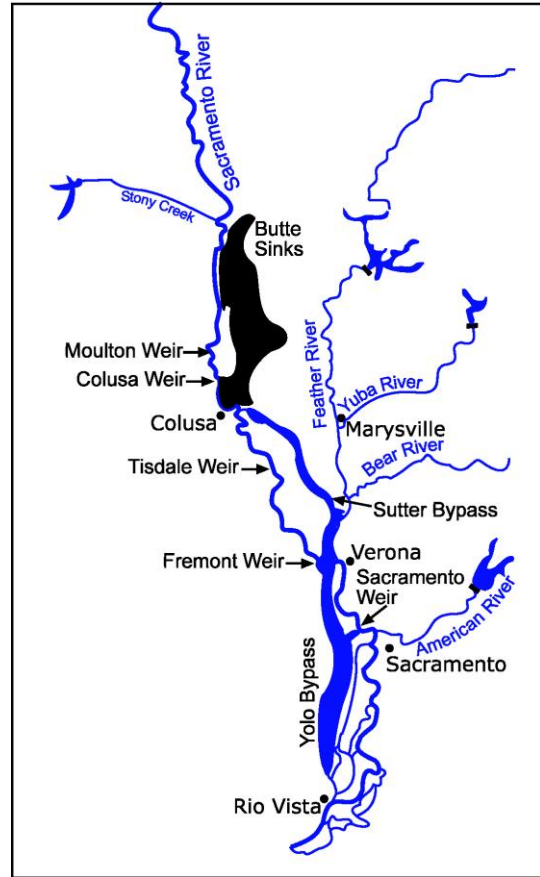
Like the juveniles, adult Chinook are widely distributed around the Delta, based on old tagging studies (Hallock et al. 1970) and the gill net fishery that existed until the 1950s. Presumably, steelhead are also distributed throughout the Delta, again with a concentration along and near the Sacramento River, but data are few.

Figure 8. Dams on Central Valley rivers. All major Central Valley rivers are blocked by large, impassable dams. Comanche Reservoir is on the Mokelumne River, and Friant Dam impounds Millerton Lake. The Red Bluff Diversion Dam is just upstream from Coyote Creek. Note that the rivers without dams are drawn ending at arbitrary points, not the upstream limit for anadromous fish. Copied from Williams (2006).



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., Mattern et al. 2002). Fry use moderately saline (15-20 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. NMFS has collected larger juveniles in the channels in April to June (MacFarlane and Norton 2002), but overall, data on distributions in the bay are sparse.

Figure 9. The flood bypass system along the Sacramento River. Water passes from the river through several weirs into the Butte Sinks, from which it flows into the Sutter Bypass, and then across the Sacramento River to the Yolo Bypass, which flows into the Delta. Copied from Williams (2006).



The distribution and production of hatchery salmon are summarized in Table 4. Hatchery Chinook returning as adults probably occur in all salmon streams, since hatchery fish stray more often than naturally produced fish. For example, five or six percent of the fall Chinook examined during carcass surveys on Mill and Deer creeks in 2003 and 2004 lacked adipose fins, and since only a small fraction of hatchery fall Chinook were marked at the time, a large proportion of the runs in those streams must have been straying hatchery fish (Williams 2006). The Joint Hatchery Review Committee (JHRC 2001) estimated that the straying rate of hatchery fish trucked around the Delta is over 70%, which helps explain the lack of detectable genetic variation among Central Valley populations of fall Chinook, described by Banks et al. (2000) and by Williamson and May (2005).

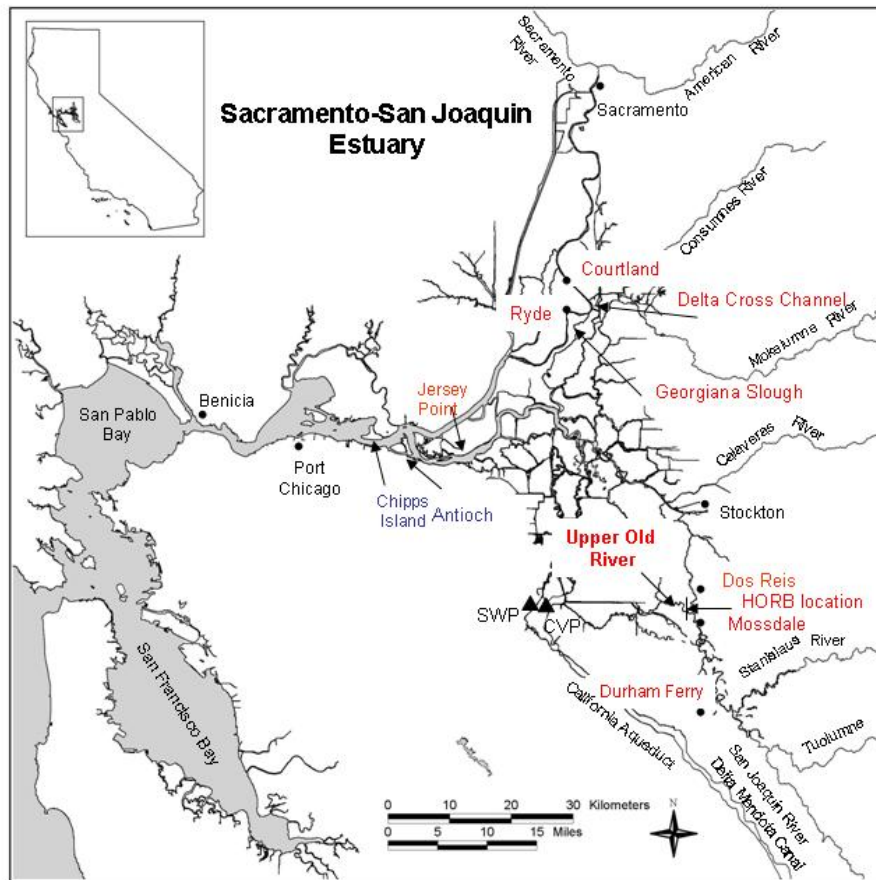


Figure 10. The Delta and bays. Locations marked in red figure importantly in IEP coded-wire tag studies. Sherwood Harbor, mentioned in the text, is not shown but is close to Sacramento. Copied from Newman (2008).

Table 4. Production and release data for salmon and steelhead in the Central Valley, data from JHRC (2001, Appendix V) and Brown et al. (2004). (JHRC) M = mitigation, E = enhancement. Coleman National Fish Hatchery is on Battle Creek, and Livingston Stone is on the Sacramento River near Keswick Dam. Fish with coded-wire tags (cwt) also are marked by removing the adipose fin.

Hatchery	Species or Run	Production Goal (millions)	Maximum Egg Take (millions)	Tag or Marks	Size and Time of Release	Release Location
Coleman	Fall	12, smolts		25% cwt BY 06 +	90/lb. Apr.	Battle Creek ¹
Coleman	Late-Fall	1, smolts		100% cwt	13-14/lb. Nov.-Jan	Battle Creek
Coleman	Steelhead	0.6, smolts		100% ad-clip, some cwt	~4/lb Jan.	75% Balls Ferry; 25% Battle Creek
Livingston Stone	Winter	0.2, smolts		100% cwt	~85 mm Jan.	Sac. R. at Redding
Feather River	Spring	5, smolts	7	100% cwt	May-June	50% F. R., 50% S. P. Bay
Feather River	Fall	M 6, smolts E 2, post-smolts	12	25%% cwt BY 06 +	April-June	San Pablo Bay
Feather River	Steelhead	0.45, yearlings		Ad-clip		
Nimbus	Fall	4, smolts				San Pablo Bay
Nimbus	Steelhead	0.43, yearlings		100% ad-clip		
Mokelumne River	Fall	M 1, smolts M 0.5 post smolts E 2, post-smolts		25% cwt BY 06 +	May-July Sept.-Nov. May-June	various Lower M. R. San Pablo B.
Mokelumne River	Steelhead	0.1	0.25	100% ad-clip	Jan.	Lower M. R.
Merced River	Fall	0.96, smolts or yearling		100% cwt	Apr. – June Oct. – Dec	Merced R. + exper. releases elsewhere

C. Population Trends

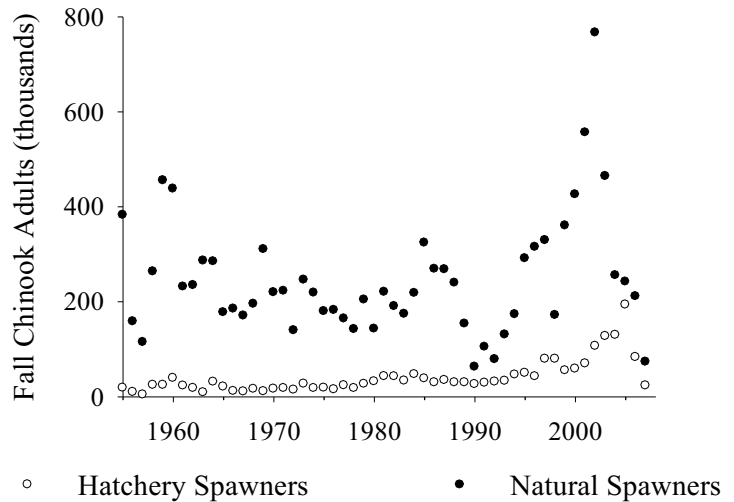
1. Fall Chinook

Returns of fall Chinook have fallen sharply from very high levels a few years ago (Figure 11). The decline is particularly striking because ocean harvest was well below normal levels for several years, and was shut done entirely in 2008. Poor ocean conditions have been identified as the proximate cause of the collapse by Lindley et al. (2009), in a report to the Pacific Fishery Management Council. However, the report also noted that “Degradation and simplification of freshwater and estuary habitats over a century and a half of development have changed the Central Valley Chinook salmon complex from a highly diverse collection of numerous wild

¹ A million fall Chinook from Coleman were trucked past the Delta in 2008.

populations to one dominated by fall Chinook from four large hatcheries.” Figure 10 understates hatchery influence, since many of the natural spawners are hatchery fish. A recent haphazard sample of about 100 from the party-boat fishery was 90% hatchery fish (Barnett-Johnson et al. 2007).

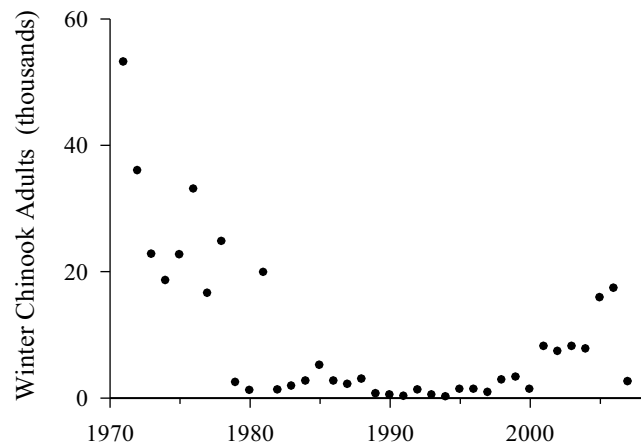
Figure 11. Returns of fall Chinook to Central Valley rivers (filled circles) and to Central Valley hatcheries (open circles). Data from CDFG. Recent years are preliminary.



2. Winter Chinook

After several years of increases, the number of winter Chinook returning to the Sacramento River declined sharply in 2007, although not as much as fall-run (Figure 12).

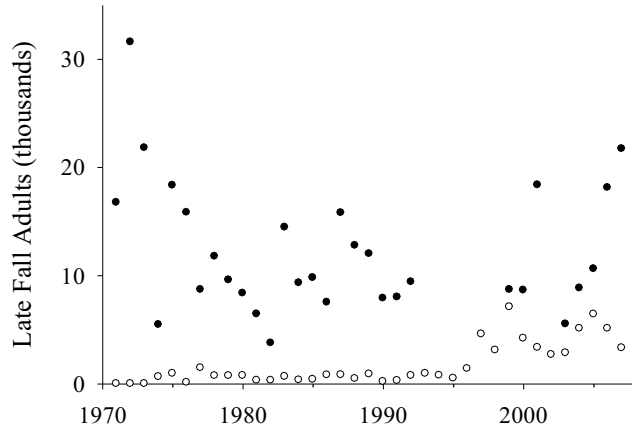
Figure 12. Returns of Winter Chinook to the Sacramento River. Data from CDFG. Recent years are preliminary.



3. Late fall Chinook

Returns of late fall Chinook have increased in recent years, in marked contrast to fall Chinook (Figure 13). As with fall Chinook, hatchery returns increased sharply after 1995. As discussed in the next chapter, late fall Chinook enter the ocean in winter, at a much larger size than fall Chinook, and this may explain why they responded differently to ocean conditions than fall Chinook.

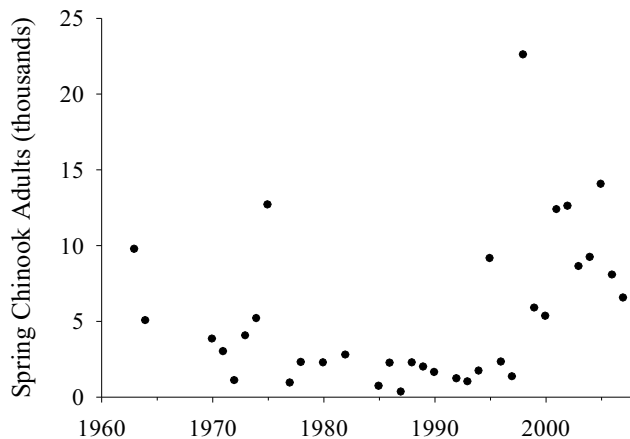
Figure 13. Returns of late fall Chinook to the upper Sacramento River (filled circles) and to Coleman Hatchery (open circles). Data from CDFG. Recent years are preliminary.



4. Spring Chinook

Spring Chinook have declined in recent years, especially in Mill and Deer creeks, but not as severely as fall Chinook (Figure 14). Spring-run from Butte Creek leave the Delta at about the same time and size as fingerling-migrant fall Chinook (see below), but for unknown reasons the spring Chinook suffered less from poor ocean conditions than did fall Chinook. There is essentially no hatchery influence on the Butte, Mill and Deer creek populations. Curiously, returns of hatchery-dominated Feather River spring Chinook were up in 2007, as were returns to the Sacramento River mainstem, which may be largely Feather River hatchery strays.

Figure 14. Returns of spring Chinook to the Mill, Deer, and Butte creeks. Data from CDFG. Recent years are preliminary.



5. Steelhead

There are few data on the abundance of wild or naturally produced adult steelhead in the Central Valley, now that they are no longer forced to pass a ladder at the Red Bluff Diversion Dam, and it is very hard to distinguish anadromous steelhead from large resident *O. mykiss* on the spawning grounds. Based on the number of unmarked juveniles captured at Chipps Island, however, the number of spawning females may average three or four thousand (Williams 2006).

IV. Ecology

A. Adult life history patterns

Chinook in the Central Valley usually are classified into four separate runs, named for the season in which adults enter fresh water: fall, late-fall, winter, and spring. Central Valley steelhead now enter fresh water mainly in fall, although a few adults of both species migrate up the Sacramento River even in the summer (Williams 2006). Winter Chinook are listed as endangered under the federal Endangered Species Act (ESA), and spring Chinook and steelhead are listed as threatened.

Fall Chinook generally enter fresh water as temperatures decline in the fall, in an advanced state of sexual maturation, and begin spawning when the water temperature declines to 15 or 16°C (Williams 2006). The timing of spawning varies somewhat from river to river and year to year (Table 5). Late-fall Chinook follow the fall-run into the rivers, but also spawn fairly soon after arriving on the spawning grounds. Winter and spring Chinook, however, typically hold in fresh water for several months to complete sexual maturation before they spawn. These different patterns are sometimes called “ocean maturing” and “stream maturing.”

Genetic evidence (Figure 15) 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. Steelhead in the American and Mokelumne rivers are descended from a coastal stock brought to Nimbus Hatchery after the native run failed to thrive in hatchery culture (McEwan 2001).

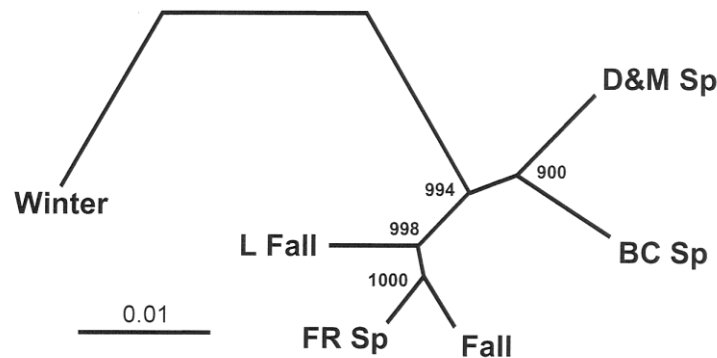


Figure 15. Genetic relationships among runs of Central Valley Chinook, based on distances (Cavalli-Sforza and Edwards) calculated from 12 microsatellite loci. The clustering analysis (UPGMA) distinguishes spring-run from Deer and Mill creeks (D&M Sp) and Butte Creek (BC Sp). Numbers next to nodes show the number of bootstrap trees, out of 1,000, showing this node. Nominal spring-run from the Feather River (FR Sp) group close to fall-run. Other genetic studies, reviewed by Hedgecock et al. (2001) have produced similar results. Copied from Hedgecock 2002.

Table 5. The estimated range in the time of spawning by Chinook salmon in various Central Valley rivers, summarized from tables 6-1 to 6-4 in Williams (2006).

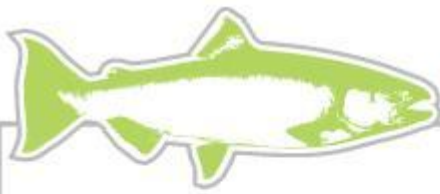
Run:	5% by	Peak	95% by
Fall	mid-Sep. to late Oct.	Mid-Oct to late Nov.	early Nov. to late Dec.
Late-fall	early to late Dec.	late Dec. to late Jan.	late March to early April
Winter	early to mid-May	early June to early July	early to mid-August
Spring	late Aug. to early Sept.	Sept. to early Oct.	mid to late Oct.

Like genetic lineages, management units of Chinook correspond generally but not exactly with the four named runs. In particular, for Endangered Species Act (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”, which ignores fall Chinook in the San Joaquin system and in the Mokelumne and Cosumnes rivers, which flow directly to the Delta.

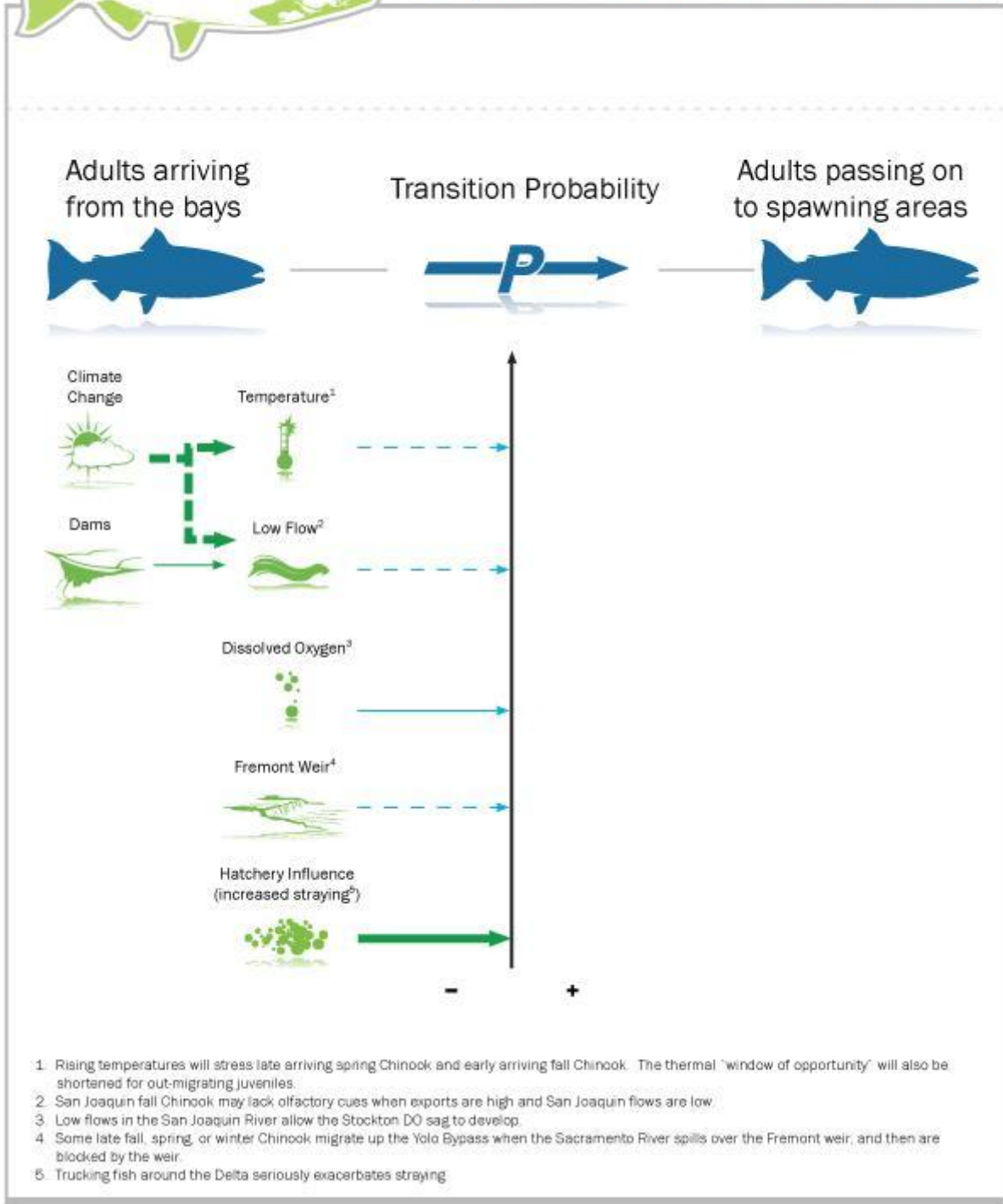
Steelhead migrate up the Sacramento River mainly from August through November, but some do so in all months (Hallock et al. 1961; McEwan 2001), and a summer-run may have existed historically (McEwan 2001). Although steelhead enter freshwater mainly in the fall, they are often called winter-run. The fall or winter-run steelhead spawn mainly from late December through April (Hallock et al. 1961; Hannon et al. 2003). Only few steelhead now migrate into San Joaquin River tributaries (Williams 2006).

B. Navigation by adults

Although the details remain uncertain, maturing salmon apparently find their way back to the vicinity of their natal stream using celestial and magnetic cues, and then shift mainly to their sense of smell to guide the rest of their migration (Quinn 2005). Maturing Chinook and steelhead migrating back to Central Valley rivers must pass through the Delta. Tagging studies showed that Chinook may spend weeks in the Delta (Hallock et al 1970), as they do in other estuaries (Olson and Quinn 1993), but some pass through quickly. Given the extent to which fish linger in the Delta, delays of a day or two at the Montezuma Slough gates or the Delta Cross Channel seem unlikely to be significant (Williams 2006). On the other hand, adult winter-run that try to migrate up the Yolo Bypass may find themselves trapped there. Factors reducing the survival of adults migrating through the Delta are summarized in Life Stage Transition Figure 3.



Transition Matrix: Chinook Salmon



Life Stage Transition 3

C. Juvenile life history patterns:

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 late fall and winter Chinook migrate downstream and into the bays during the fall and winter, and spring and fall Chinook may remain near the spawning areas for only a few days or for several months. Accordingly, juvenile Chinook of widely different sizes can be found in different Central Valley habitats (Figure 16). Although they are really points on a continuum, 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. Similarly variable patterns have been described in other rivers (Burke 2004). Life history patterns can also be distinguished in terms of the habitats in which juveniles mainly rear (Figure 16).

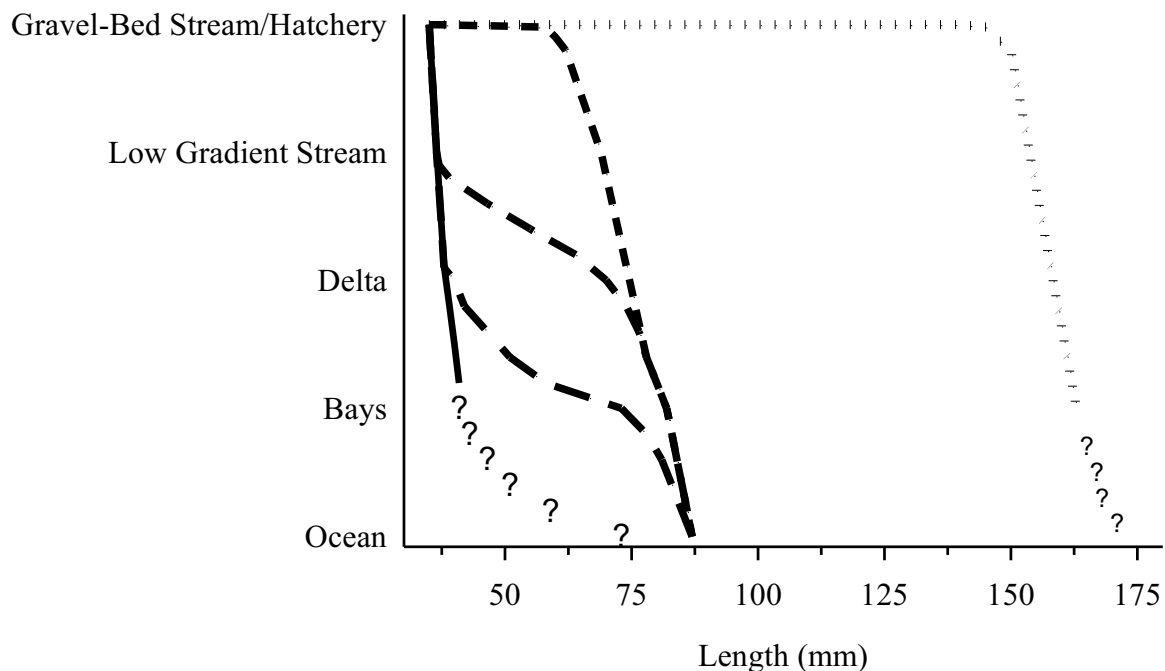


Figure 16. Conceptual “juvenile life-history space”. Lines show representative trajectories of growth and migration for juvenile Chinook. Fry emerge at ~35 mm, and may migrate directly to the bays; what they do when they get there is poorly understood. Many fish migrate directly to the Delta and rear there (long dashed line); if they survive, they migrate through the bays to ocean. Some fry migrate to the lower rivers and rear there before migrating through the Delta and bays (medium dashed line). Other fry emerge and remain in the gravel-bed reaches of the stream until they migrate, generally in spring, as fingerlings (short dashed line), while others remain in the gravel-bed stream through the summer and migrate as larger juveniles. 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.

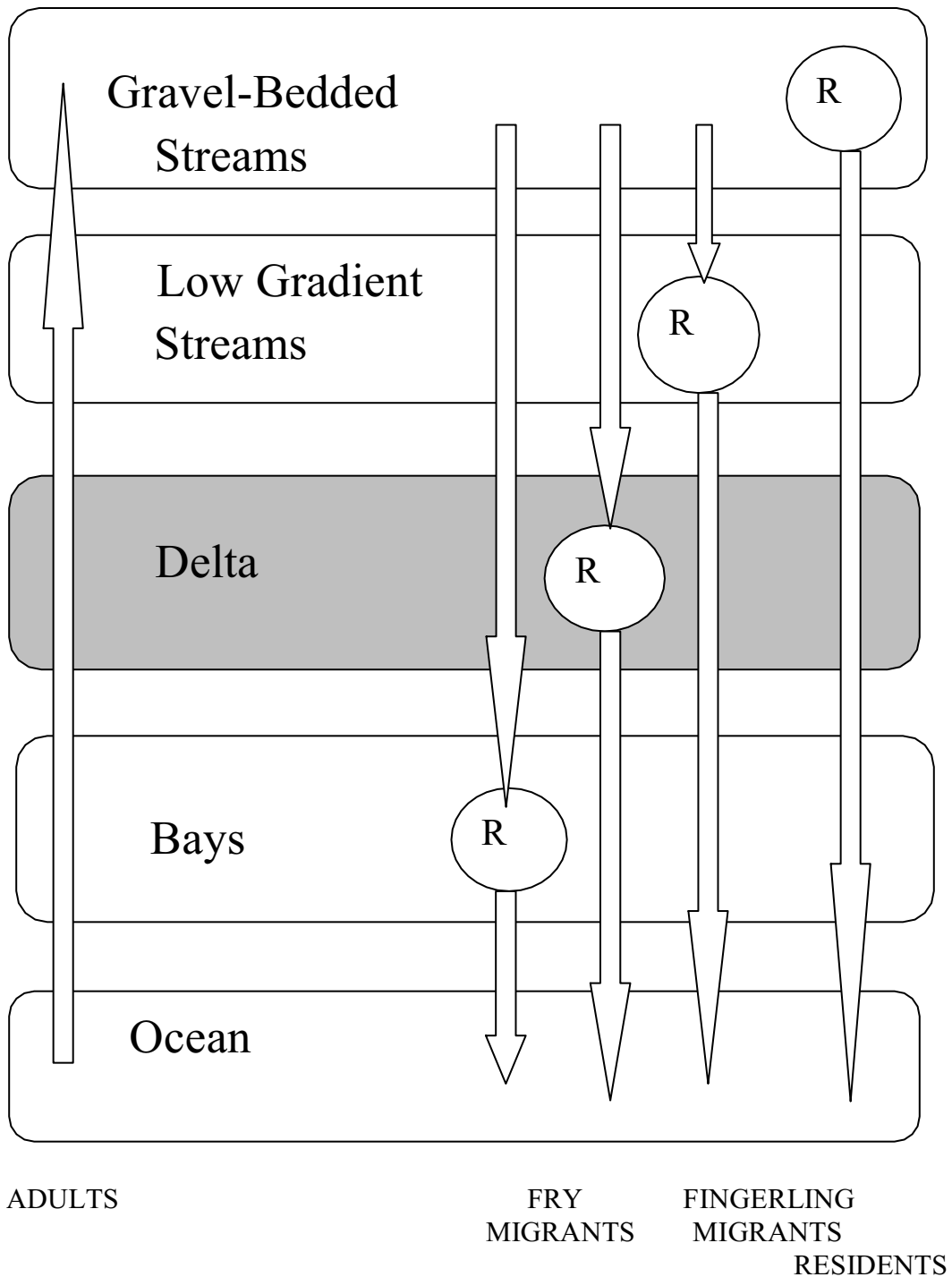


Figure 17. Schematic of the Chinook life-cycle, with arrows indicating migration and circles indicating the habitat in fish following different life-history patterns primarily rear.

Fry migrants to the bays migrate to brackish water soon after emerging from the gravel. Hatton and Clark (1942) captured significant numbers of ~40 mm juveniles at Martinez 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, 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 et al. 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. This life history may have been more common in the past, when more brackish tidal marsh habitat was available to them.

Fry migrants to the Delta also migrate downstream soon after emergence, but remain in the Delta and rear there before migrating into the bays. This is probably the most common life history pattern among juveniles, based on monitoring passage into the lower rivers (e.g. Figure 18), but the percentage that survive is unknown. Presumably, Chinook following this life history historically reared in the then-abundant tidal habitat in the Delta (Williams 2006).

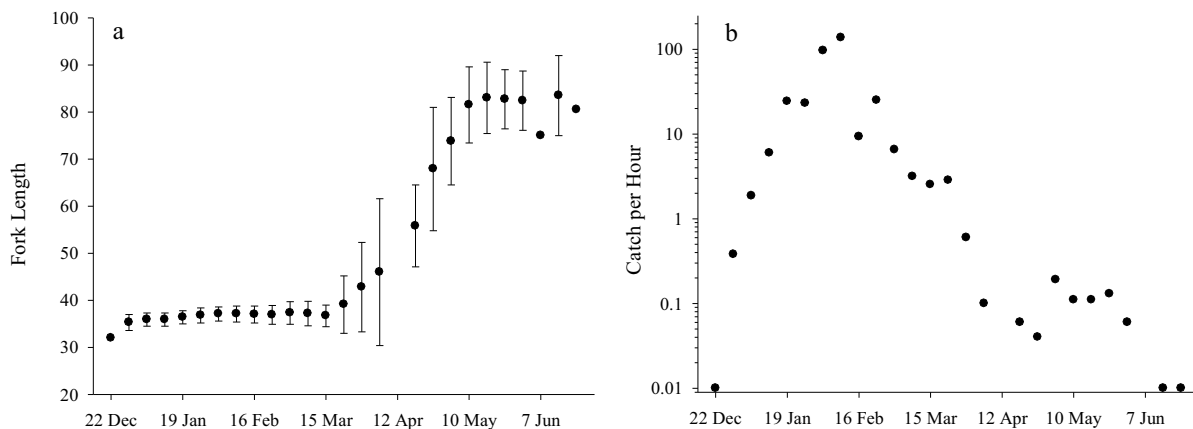
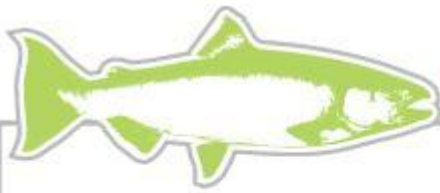
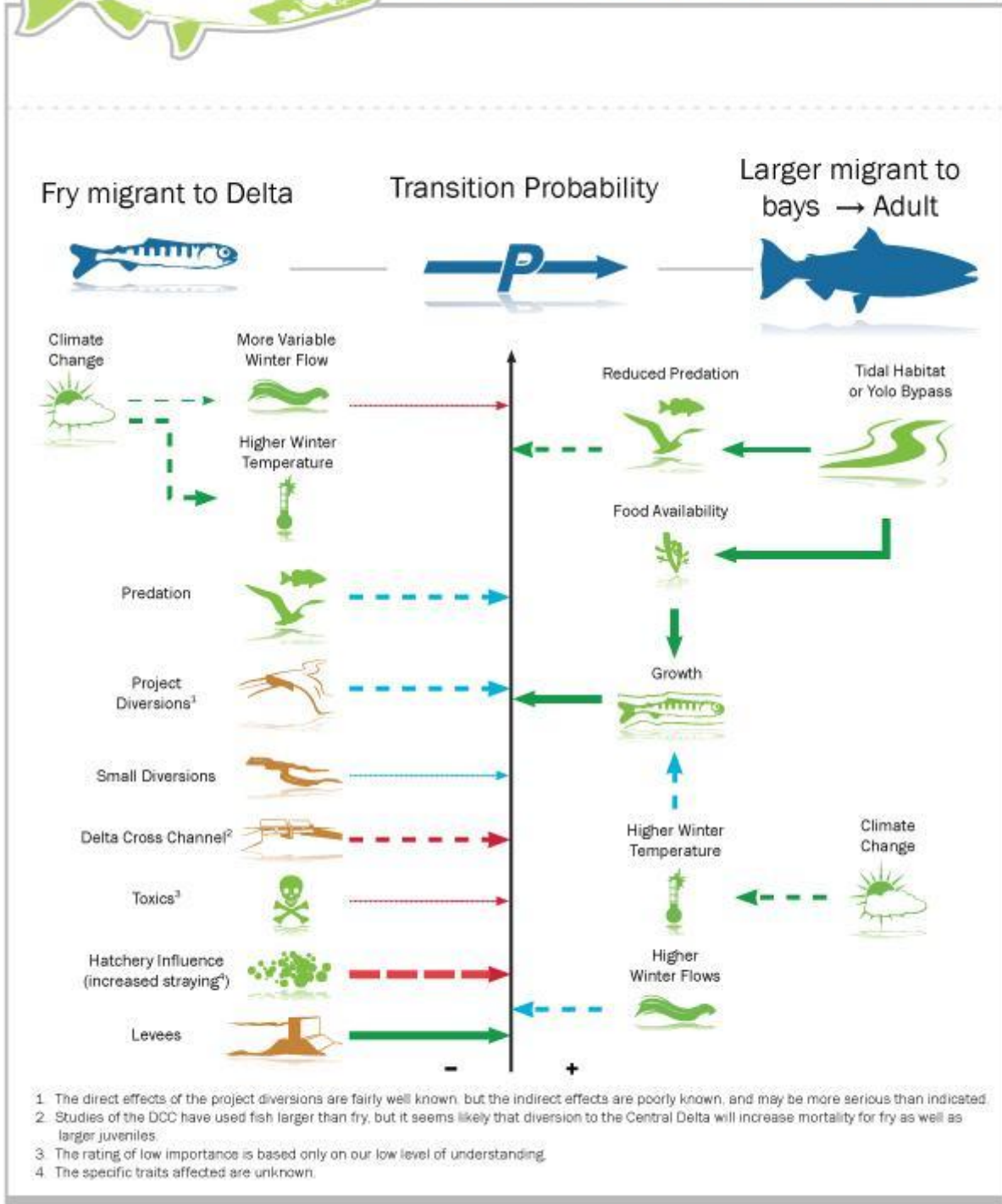


Figure 18. Mean length (a) and catch per hour (b) of juvenile fall Chinook salmon sampled in screw traps in 1999-2000 on the lower American River near the downstream limit of spawning habitat. Error bars show standard deviations. Note log scale in (b); the catch dropped sharply as size increased in March. Dates are approximately the middle of the sampling period. Data from Snider and Titus (2001); figure copied from Williams (2006).

Various factors influence the survival of fry migrants in the Delta, as summarized in the Life Stage Transition Figure 4. The negative factors (stressors) are discussed in Ch. 5; evidence for the positive effect of tidal or overbank habitat is discussed later in this chapter.



Transition Matrix: Chinook Salmon



Life Stage Transition 4

Fry migrants to low gradient streams 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 Butte Creek spring-run fry are captured and tagged near Chico as they migrate into the Central Valley. The size of fish recaptured at Sherwood Harbor, near Sacramento, indicates that they mainly rear upstream of the Delta, presumably in the Butte Sinks or the Sutter Bypass, until they are > 70 mm; then they move rapidly through the Delta (Figure 19). The Yolo Bypass offers similar habitat to Sacramento River populations when water spills into it over the Freemont Weir, and several studies indicate that fish do well there (Sommer et al. 2001, 2005)

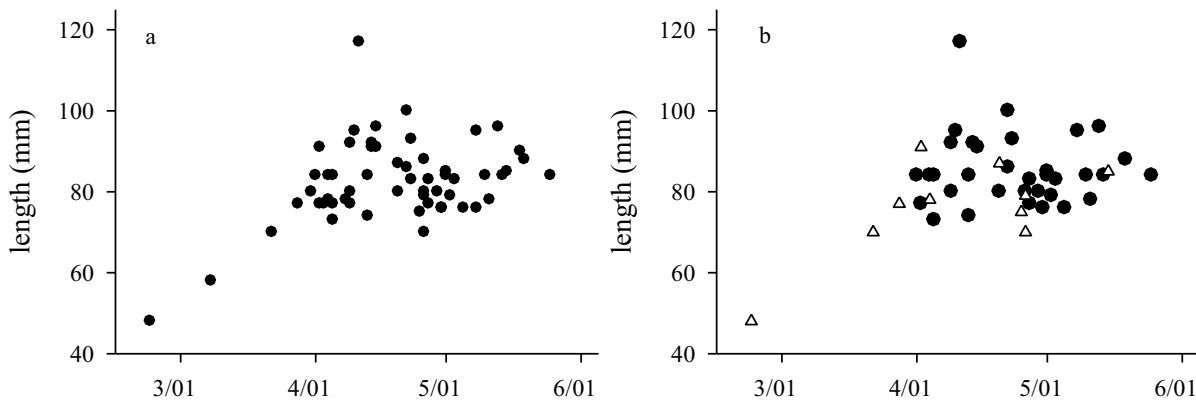
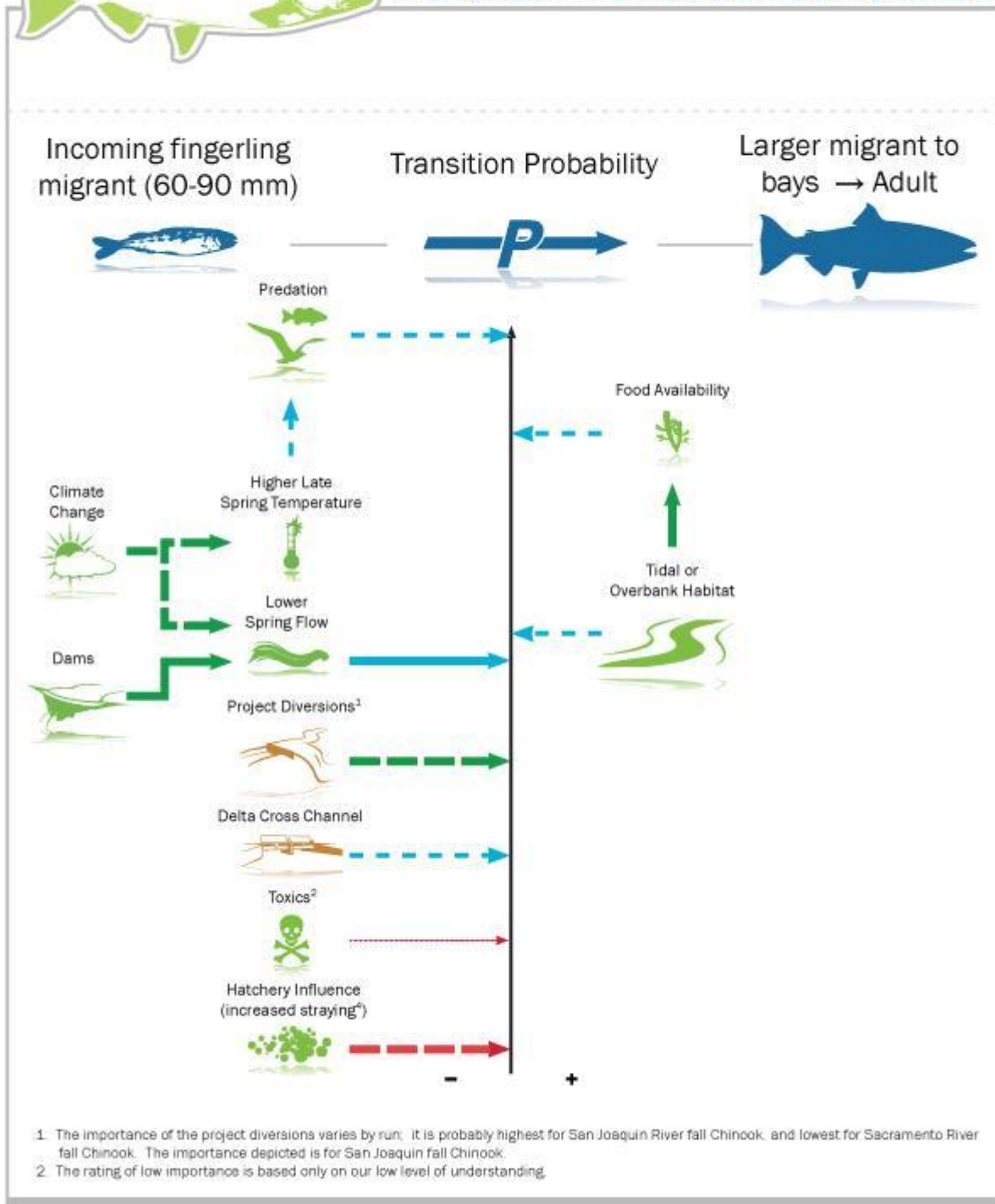


Figure 19: A. Size at date of capture of coded-wire tagged Butte Creek spring Chinook (n = 57), for all capture locations from Knights Landing to Chipps Island. B. As above, for Chipps Island (circles, n = 34) and Sherwood Island (triangles, n = 10). Data from USFWS, Stockton.

Fingerling migrants 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 May mode in Figure 18b 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, Figure 20). The larger migrants are often called smolts, although few of them have reached this stage physiologically (e.g., Snider and Titus 2001). This life history pattern has received the most attention from managers. For example, most of the USFS coded-wire tag survival studies apply to this group. The life history of hatchery fall Chinook released into the river also approximates this pattern, since the hatchery fish are released at generally > 65 mm and most move rapidly downstream. Some move downstream very rapidly, in hatchery trucks, and are released into the bays, to avoid mortality in the Delta (Williams 2006). Factors influencing the survival of fingerling migrants to the Delta are shown in Life Stage Transition Figure 5.



Transition Matrix: Chinook Salmon



Life Stage Transition 5

Winter Chinook seem mainly to have a somewhat different juvenile life history, although the data are too sparse to support strong statements on the matter. Most of the naturally produced fish begin migrating as fry, but they seem to migrate slowly, reaching the lower Sacramento River in November (Figure 21), and generally not reaching the Delta pumps until February. More is known about the migration of hatchery winter-run, discussed below, since they are tagged, but their behavior seems to be different.

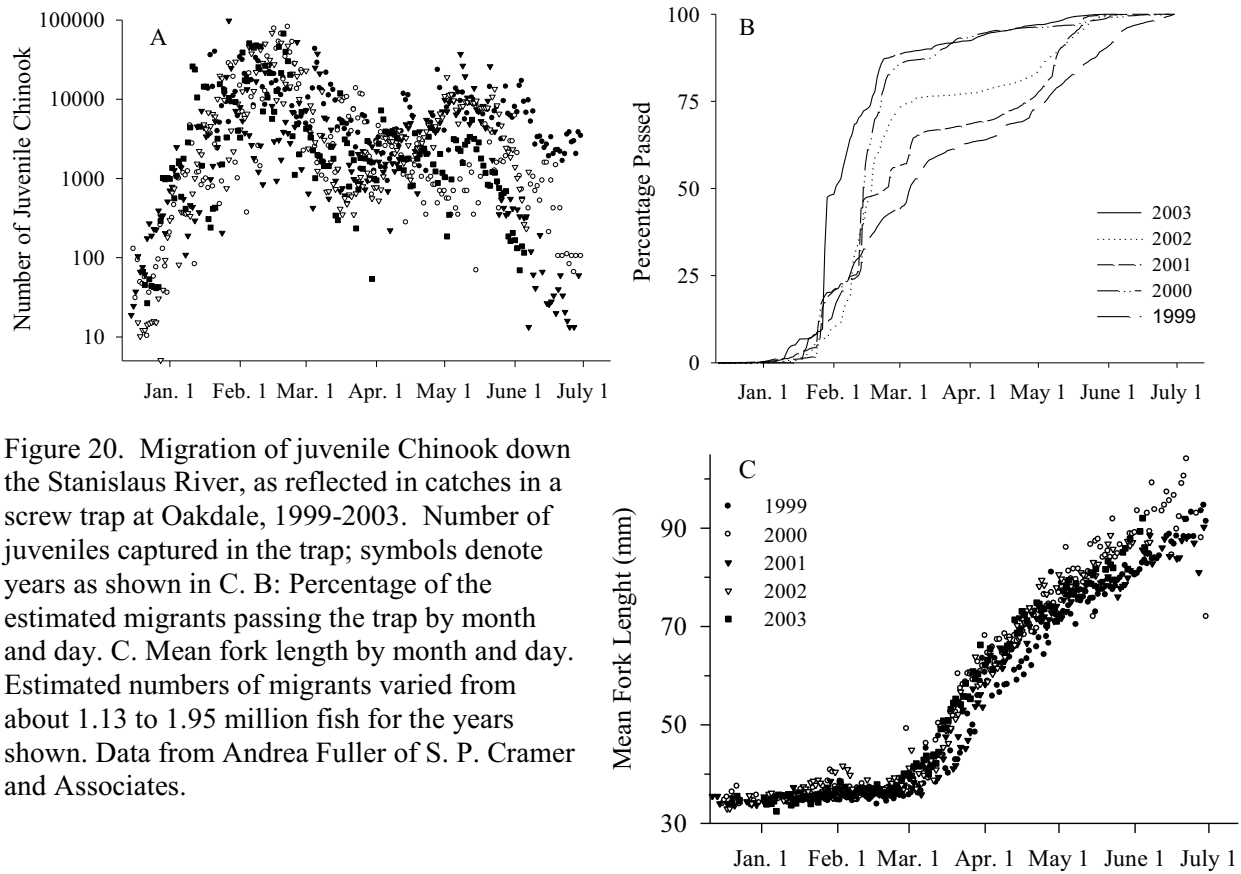
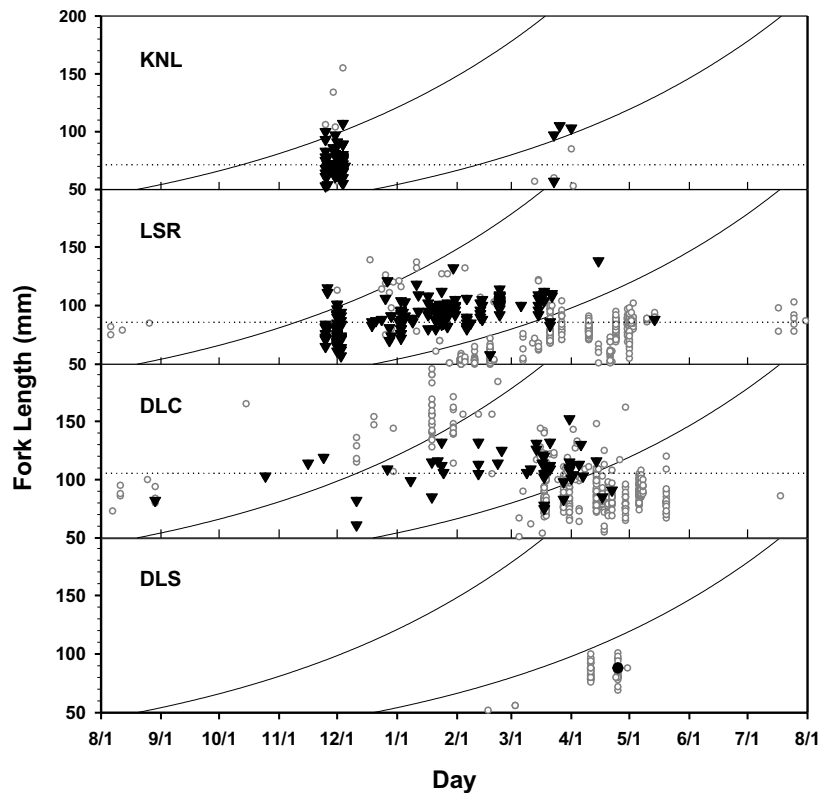


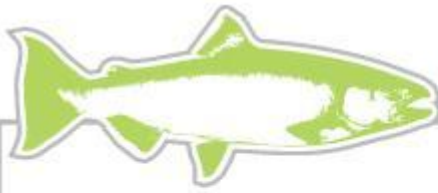
Figure 20. Migration of juvenile Chinook down the Stanislaus River, as reflected in catches in a screw trap at Oakdale, 1999-2003. Number of juveniles captured in the trap; symbols denote years as shown in C. B: Percentage of the estimated migrants passing the trap by month and day. C: Mean fork length by month and day. Estimated numbers of migrants varied from about 1.13 to 1.95 million fish for the years shown. Data from Andrea Fuller of S. P. Cramer and Associates.

Figure 21. Fork length and day of capture for juvenile Chinook assigned to runs by Hedgecock et al. (2002) for four areas from the IEP monitoring: Knights Landing (KNL), 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).



Fingerling residents remain in the gravel-bed reaches of the streams through the summer, and then migrate in fall or winter, generally at a length of 90 mm or more. This is probably the typical life history of late fall Chinook, and apparently it is being adopted by some fall Chinook below dams such as Keswick Dam on the Sacramento River that release cool water through the summer (Williams 2006). Many spring-run also follow this pattern; even in Mill and Deer creeks, most older juvenile spring-run migrate into the valley in November to January (Williams 2006).

Classic stream-type Chinook hatch in the spring, remain in the gravel-bed reaches of the stream through the winter, and migrate the following spring as smolts. This life history may have been more common before dams blocked most high elevation habitat, where low winter temperatures inhibit growth. Life Stage Transition Figures 6 shows the factors affecting the survival of the fingerling resident and stream-type juveniles in the Delta.



Transition Matrix: Chinook Salmon

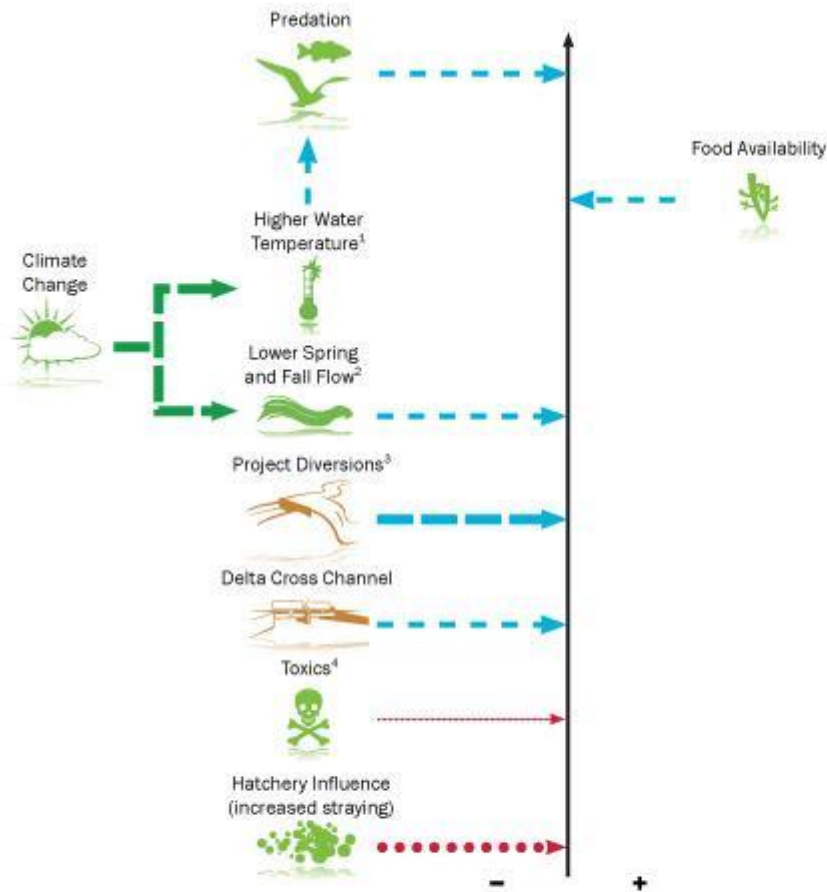
Incoming larger migrant (~ 90+ mm)



Transition Probability



Larger migrant to bays → Adult



1. Higher temperatures in the spring and fall will shorten the thermal "window of opportunity" for juvenile Chinook.
2. The influence of flow on the survival of these larger fish is less well known than for the somewhat smaller fish used in the coded-wire tag studies. It may be equally important, especially for ~ 90-110 mm that migrate through the Delta in the spring.
3. Project diversions probably affect these juvenile late fall and winter Chinook more than Sacramento fall-run fingerling migrants: see text.
4. The rating of low importance is based only on our low level of understanding.

Life Stage Transition 6

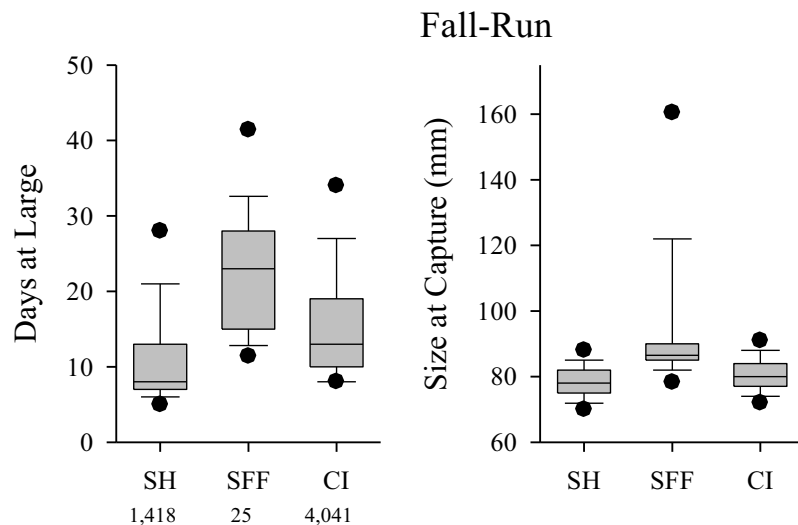
D. Juvenile migration rate

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. It is sometimes obvious that fry are being swept downstream (Williams 2006), but the downstream movement of large numbers of fry even during periods of low flows has seemed deliberate to most Central Valley 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, (Williams 2006), not enough to provide good estimates, except for Butte Creek spring Chinook (Figure 19). 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 for some time, as have fall Chinook from the Merced River Hatchery, and about 8% of fall Chinook from Coleman Hatchery were tagged from 1995-2002; 25% of fall Chinook are now marked, so more data are accumulating rapidly.

Fall Chinook released from Coleman Hatchery migrate rapidly, with median travels time of 8 days to Sherwood Harbor, near Sacramento, and 13 day to Chipps Island (Figure 22). This suggests that the migration rate slows as the fish approach the Delta, since it is about 365 km from the hatchery to Sherwood Harbor, and only about 80 more to Chipps Island. The change from riverine flow to bi-directional tidal flow may account for the change in pace. Remarkably few of the fall Chinook released at Coleman have been recovered at the pumps (34 compared to 4,041 at Chipps Island), but those that do take longer to get there. Either they were larger to begin with, or they grew well ($\sim 0.8 \text{ mm d}^{-1}$) along the way.

Figure 22. Days at large, size at capture, and release date 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. Data from USFSW.



Coleman late fall Chinook do not migrate quite as rapidly to Sherwood Harbor as Coleman fall-run, despite their greater size (Figure 23). However, they appear to move more rapidly from Sacramento to Chipps Island. More Coleman late fall have been recovered at the pumps than at Chipps Island (3,898 v 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.

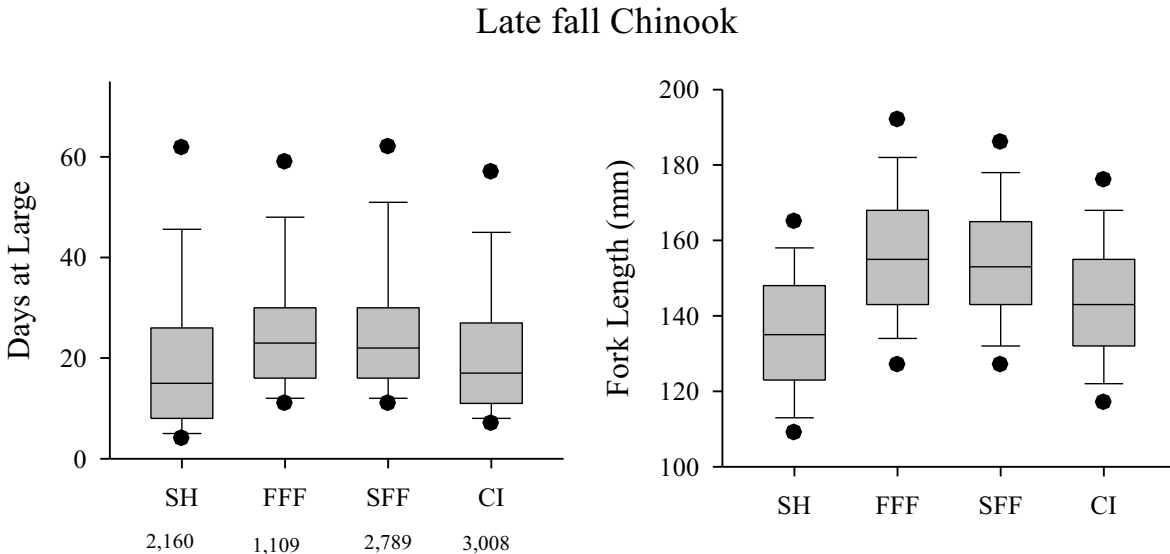


Figure 23. Days at large and size at capture of tagged late fall Chinook released at Coleman Hatchery, and recaptured at Sherwood Harbor (SH), the federal fish facilities (FFF), the state fish facilities (SFF), and Chipps Island (CI). Sample sizes are given below the labels on the X-axis, left panel. Data from USFWS.

Winter Chinook from Livingston Stone Hatchery at Keswick migrate more slowly, with median travel times of 24 days to Sherwood Harbor and 45 days to Chipps Island (Figure 24), again suggesting that migration slows approaching the Delta. Travel time to the pumps is not as long as to Chipps Island, different from the case with fall or late fall Chinook, although the hatchery winter-run collected at the pumps are larger on average than those at Chipps Island, as with fall and late fall. It seems likely that some biology that we do not understand is involved here.

L.S. Winter-Run

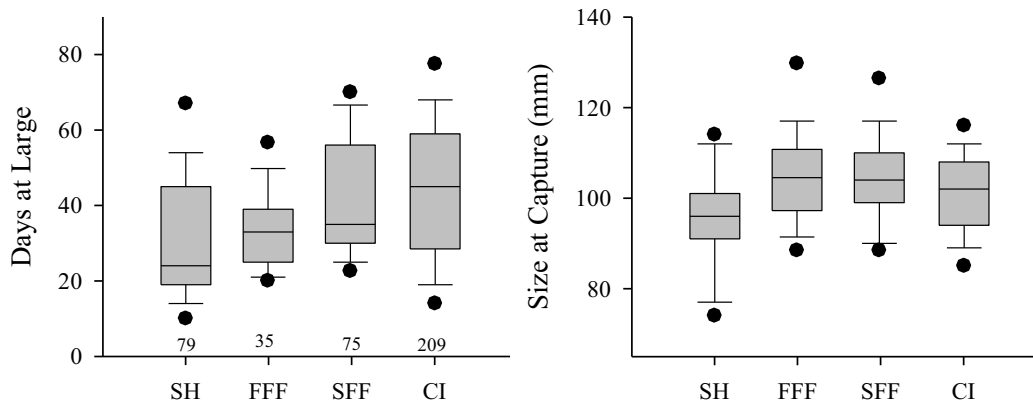


Figure 24. Days at large and size at capture of tagged winter Chinook released at Livingston Stone, and recaptured at Sherwood Harbor (SH), the federal fish facilities (FFF), the state fish facilities (SFF), and Chipps Island (CI). Sample sizes are given above the labels on the X-axis, left panel. Data from USFWS.

It is tempting to study the migratory behavior of hatchery fish because we have data with which to work, but we should remember that wild or naturally produced fish may behave differently. Hedgecock et al. (2002) analyzed tissue samples from juvenile Chinook at the pumps, and reported the length and capture date of 711 fish identified as winter-run using microsatellite DNA; they were intermediate in size between the hatchery late fall and winter Chinook, and arrived at the pumps slightly later in the year than hatchery winter-run (Figure 25), although they began migrating downstream sooner. Fortunately, it is now possible to obtain a good deal of information about the migratory history of wild and naturally produced Central Valley Chinook and steelhead by microchemical analyses of their otoliths (Barnett-Johnson et al. 2008; Phillis et al. 2008; Malamud-Roam et al. 2008). Such information is needed if we are to manage the Delta for the benefit of wild and naturally produced fish, rather than hatchery fish.

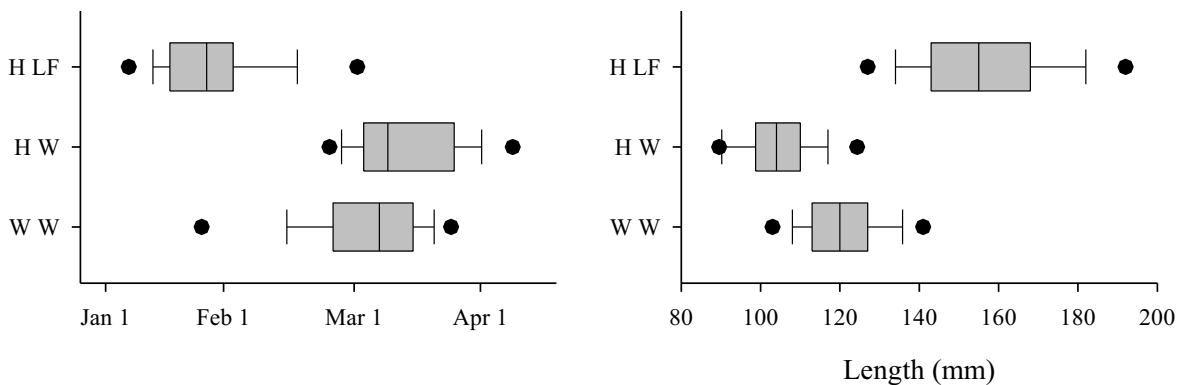


Figure 25. Distributions of dates of capture and length at capture for hatchery late fall-run (H LF), hatchery winter-run (H W), and wild winter-run (W W) at the state and federal fish facilities. Data from USFWS and Hedgecock (2002).

E. Navigation by juveniles

The sequential odor hypothesis (Harden Jones 1978) is the current 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. There is also evidence that other genetic factors may affect homing in fresh water (Quinn 2005), but these seem to be secondary. The sequential odor hypothesis implies that hatchery fish that are trucked to the bays should stray more often than fish that swim there, and this is observed (SRFCRT 1994). This raises the concern that staying hatchery fish may interbreed with locally adapted natural populations and reduce their fitness, as may have happened with fall Chinook in Mill and Deer creeks (Williams 2006).

The mechanisms by which juveniles 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 a sufficient mechanism, but in other cases, such as the complex migration of juvenile sockeye through 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 seems necessary for navigation, especially for rapid migration through the Delta.

F. Steelhead juvenile life history patterns

The life histories of *O. mykiss* are even more variable than those of Chinook, but not much information is available on Central Valley populations; Lindley et al. (2007) described the status of populations on streams that do not have hatcheries as "data deficient." Figure 1 applies for anadromous *O. mykiss*, steelhead, but it seems that many *O. mykiss* in Central Valley streams either do not migrate, or else do not migrate beyond the large rivers or the Delta (Williams 2006). This is a recent development that may reflect evolutionary as well as environmental change. In rivers such as the Sacramento, Yuba, or Stanislaus, populations of large resident *O. mykiss* have developed where summer releases of cool water from dams provides good habitat for them.

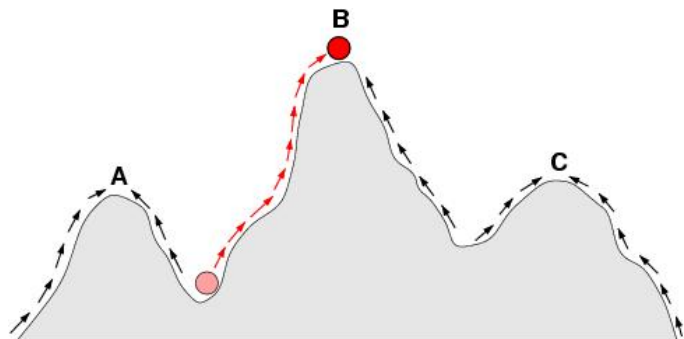
As far as is known, steelhead in the Central Valley follow a stream-type life history. Most naturally produced steelhead from the native lineage migrate to sea after two winters in fresh water, although fish from the American River grow rapidly, and migrate after one winter. Some American River fish, called "half-pounders" by anglers, may migrate only as far as the Delta or bays and then return. Hatchery steelhead also grow rapidly and migrate when released, after one winter in fresh water, but there is evidence from the sex ratios of steelhead captured at Knights Landing and Chipps Island that some hatchery males may not migrate beyond the Delta. (Rob Titus, DFG, pers. comm. 2008).

G. The adaptive landscape

Hatchery culture modifies the natural life cycle in several important ways: mates are selected by hatchery personnel rather than the fish, mortality during the egg and alevin stages are sharply reduced, and fish are canalized into a single juvenile life history pattern. 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. 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 et al. (2007) demonstrated a rapid loss of fitness for natural reproduction.

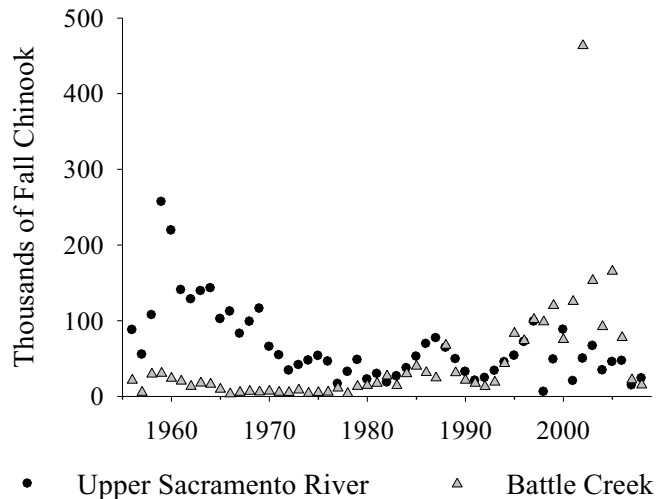
The ‘adaptive landscape’ is a conceptual model that helps explain this. For an organism in a given environment, there is a level of fitness associated with each combination of genes, or more specifically, of alleles (think of fitness as the propensity to have descendents). This can be visualized for 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 shows the frequency of an allele in a population. Then, 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 26).

Figure 26. Cartoon of an adaptive landscape, in for 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. Copied from Wikipedia.



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. This can be modeled; Figure 3 is from a paper describing such a model, and it shows that a shift toward one peak or the other can happen suddenly. Data on fall Chinook in the upper Sacramento River suggests that such a shift may have occurred in that population, perhaps in the generations from the late 1970 to the early 1990s (Figure 27). Neither natural nor artificial selection can maximize the fitness of a population for both environments.

Figure 27. Number of adult fall Chinook returning to the upper Sacramento River (above Red Bluff) and to Battle Creek, including Coleman Hatchery. Assuming that these represent the naturally reproducing and hatchery components of the run, the run is now dominated by hatchery fish.



H. Local adaptation

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. 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 et al. 2006). As a local example, coded-wire tag studies suggest that juvenile Chinook from the Merced River survive better when released into the San Joaquin River than juveniles from the Feather River (Newman 2008). Traits related to juvenile migration seem a logical target for selection leading to local adaptation; for example, it seems likely that juvenile Chinook from the Sacramento River would benefit from an inherent tendency to bear to the right when they sense tidal flow reversals.

Estuaries are generally places of high biological productivity, and also provide habitat where juvenile salmon can rear and grow. For Chinook and steelhead, the importance of estuaries as juvenile rearing habitat varies inversely with the size at which the fish enter the estuaries, as indicated by the review of life history patterns above. This conceptual model is so simple that it seems unnecessary to render it in a graphic, but it is basic for assessing the importance of restoration activities in the Delta for the various runs. Spring Chinook, or at least the Butte Creek population, pass quickly through the Delta, so habitat restoration there seems unlikely to do much for them. The same is probably true for late fall Chinook, and for steelhead. Fall Chinook, however, probably would benefit strongly from tidal marsh restoration. The case for winter Chinook seems equivocal.

The life cycle of anadromous salmonids requires that the fish pass through estuaries at least twice in their lives. Navigating through a large estuary is not a simple matter, so it is important

that human activities not interfere with the navigational abilities by which salmon find their way. There is concern that various contaminants may do that, as discussed below.

I. Understanding salmonid life history diversity

There is great variability in the timing with which salmonids pass through the various stages shown in Figure 1, even within single species such as Chinook and steelhead, as discussed above. This variation is best understood for Atlantic salmon, for which a conceptual model has been developed by John Thorpe and colleagues (e.g., Thorpe et al. 1998).

The basic facts of Atlantic salmon life-history that the model seeks to explain are these. Atlantic salmon spawn in the fall, with fry emerging in the spring. The distribution of fry sizes is approximately normal at emergence, but then becomes bimodal, at least in some conditions (Thorpe 1977; Thorpe et al. 1998). In such conditions, all surviving fry feed actively early in their first summer, but the slower-growing ones restrict feeding in late summer and spend most of the winter hiding in the gravel in the streambed, while others continue actively feeding through the winter. Fish that continue feeding typically migrate in the spring, after one year in freshwater. Most of the slower-growing group then feeds actively through their second year, and then migrates to the sea, but a fraction again restricts feeding, and spends a third year in freshwater. After migrating, the fish spend a variable number of years in the ocean before returning to spawn.

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 photoperiodically-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 (Shapovalov and Taft 1954; Thorpe 1989). Marc Mangel has developed this conceptual model into a numerical model (e.g., Mangel 1994), and with support from CALFED is currently extending and developing it for steelhead, in a form that also allows assessment of evolution in response to altered environmental conditions (Mangel and Satterthwaite 2008; Satterthwaite et al. 2009a, b). This helps explain the shift toward a resident life history in some populations of Central Valley *O. mykiss*.

The typical steelhead life-history is similar to that of Atlantic salmon, except that steelhead spawn in the late winter or spring, and some fish follow a resident life-history, especially in coastal California streams (Satterthwaite et al. 2009b). The reason this can be advantageous is sometimes obvious; for example, the Carmel River did not reach the ocean for three years during the drought of the late 1980s, and fish that probably would have been anadromous if they had had the chance were observed spawning in the upstream reaches where flow persisted. A resident life-history also seems to be developing in some Central Valley rivers where releases of cool water from reservoirs maintain good habitat for large trout through the summer (Williams

2006). However, the optimal life-history for a steelhead depends on the interactions among several environmental factors and the attributes of the particular fish (Satterthwaite et al. 2009a), so simple generalizations are hazardous.

Many Chinook salmon migrate downstream shortly after emergence, so it is clear that this model must be modified before it can be applied to them, but the fundamental insight remains that a fairly simple developmental program, 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. At least for some spring-run Chinook, a photoperiod-sensitive switch determines whether fish follow an ocean-type or stream-type juvenile life-history pattern (Clarke et al. 1992). Typically, these fish spawn at high enough altitude that 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 until the following winter. This causes them to grow slowly, and as suggested by the model they do not migrate. If the fry are exposed experimentally to a short-day photoperiod, however, they will grow rapidly and adopt an ocean-type life history, migrating in their first year. This would explain why Spring Chinook in Butte Creek, which are restricted to < 350 m elevation, mostly migrate in their first spring.

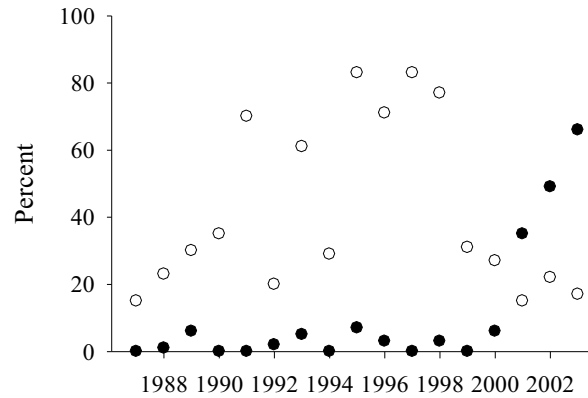
J. Use Of habitats:

1. Gravel-bed streams:

Apart from hatcheries, salmon reproduce and spend their early life in gravel-bed streams. Generally, the fish select redd sites where water flows through the gravel, such as at the tail of a pool where water downwells into the gravel, or where it upwells in the gravel bar below (Williams 2006). Water flowing through the gravel carries oxygen to the developing embryos or alevins, and carries away metabolic wastes. Some gradient in the stream is needed for suitable spawning habitat, but not much. For example, Rutter (1904) mapped fall Chinook spawning beds as far downstream as Tehama, near the Mill Creek confluence, although early commercial vessels could navigate beyond Tehama to Red Bluff.

Current distributions of spawning habitat for major Central Valley Chinook populations are well known from spawner surveys that are conducted to estimate adult returns (Low 2005; Pipel 2005), and uncertainly about most of the others is constrained by terminal dams or natural barriers. Although spawning extends well downstream, it tends to be concentrated near the barriers (Williams 2006). This is nicely illustrated by the upstream shift in the distribution of spawning by winter Chinook after passage was improved over the Anderson-Cottonwood Irrigation District (ACID) dam at Redding (Figure 28). Steelhead spawning is harder to observe, since the fish and their redds are smaller, they spawn in the winter when the water is often turbid, and it is very difficult to distinguish spawning by steelhead and similarly sized resident *O. mykiss*.

Figure 28. Percentage of winter-run redds observed above the ACID Dam (filled circles) between the dam and the Highway 44 bridge (open circles) in CDFG aerial surveys. Data from Doug Killam, CDFG, Red Bluff; copied from Williams (2006).



Redds occupy an area, and the area of suitable spawning habitat in a stream is limited. Females compete for spawning sites, and after spawning defend them for as long as they can. This limits the population that a given stream can support, and is one mechanism for the more general phenomenon of density-dependent mortality. That is, except at very low numbers, the survival or reproduction of members of a population tends to decrease as abundance increases. It is likely that density-dependent mortality among salmon occurs during other life-stages besides spawning, but not much is known about this for Central Valley populations (Williams 2006). One possibility is competition between hatchery and naturally produced Chinook in the Delta, bays, and Gulf of the Farallones. Kjelson et al. (1982:409) noted that “The problem of exceeding estuarine rearing capacity [through hatchery releases] is of some concern in the Sacramento-San Joaquin (hatchery releases total about 26 million smolts annually), but as yet has not been studied.” Many hatchery fish are now trucked around the Delta, but the point remains valid, especially for the bays.

Juvenile salmon can live at high densities if food is abundant, as demonstrated by hatcheries, but the rearing capacity of streams is more limited. Especially in smaller streams, fry tend to establish and defend territories, unless they migrate. The size of the territories increases with the size of the fish, imposing a limit on the number of fish that an area of stream can support that decreases as the fish grow. To what extent migratory fish in Central Valley are pushed out of some upstream habitat is unclear, since juveniles in larger rivers tend to form schools (Williams 2006), but density-dependent migration has been incorporated into models of salmon populations in rivers, for example Greene and Beechie (2004). It is clear, however, that a stream-type life history cannot support as large a population in a given stream as an ocean-type life history (Quinn 2005). This makes it unlikely that steelhead were ever as abundant as Chinook in the Central Valley.

2. Low gradient streams:

As juvenile Chinook or steelhead 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). This graded almost imperceptibly into the Delta, so

there was not a clear distinction between the Delta and flooded overbank habitat farther upstream, especially in the Sacramento Valley (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 unleeved reaches of the Cosumnes River.

When the Cosumnes River spreads out over its floodplain, juvenile fall Chinook do so as well (Moyle et al. 2007). The fish grow rapidly there (Figure 29), and most move back into the river as the water level declines and floodplain drains. Similarly, juvenile salmon pass into the bypasses, and also grow well there (Sommer et al. 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 et al. 2005; Jeffres et al. 2008).



Figure 29. Comparison of juvenile Chinook from one enclosure on the Cosumnes River floodplain and from another in the river downstream, which is tidal in this reach and so part of the Delta. Copied from Jeffres et al. 2008.

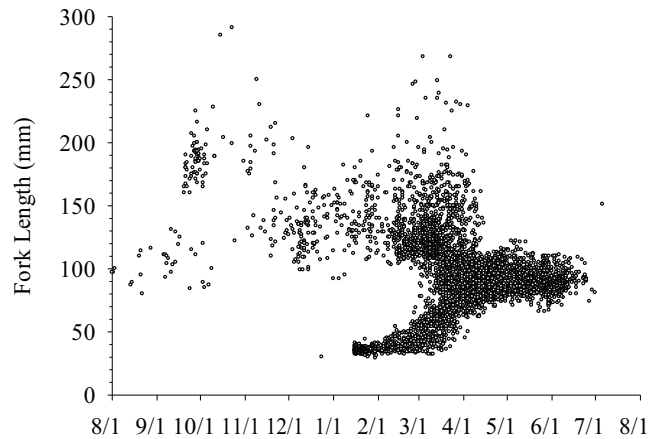
3. The Delta:

Geographical boundaries are usually more discrete on maps than on landscapes, as exemplified by the boundary of the Delta, defined here on the upstream side by the limit of tidal influence. Historically, the Delta was a vast tidal wetland (Atwater et al. 1979; TBI 1998), but most Delta channels are now confined by levees and have steep banks, like the low gradient river reaches upstream.

The diversity of juvenile Chinook in the Delta is reflected in the size at date of fish captured at the state and federal pumps (Figure 30). 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; it is unclear where a line should be drawn here between fingerling residents and classic stream-type. 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 through June, when the Delta becomes too warm for juvenile salmon.

Figure 30. 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. Data from Hedgecock (2002).



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 more 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 (e.g., Levy and Northcote 1982). The juveniles tend to move into deeper water and down the estuary as they grow (Healey 1980; 1991). Juvenile Chinook are opportunistic feeders, and reports on diet vary from study to study, but broad patterns are evident. Smaller juveniles occupying marsh channels often feed heavily on larval and pupal chironomids (e.g., Shreffler et al. 1992; Lott 2004). This has been observed in a remnant tidal marsh in the Delta (Simenstad et al. 2000), as well as in overbank habitats close to the Delta (Sommer et al. 2001, 2005; Jeffres et al. 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.

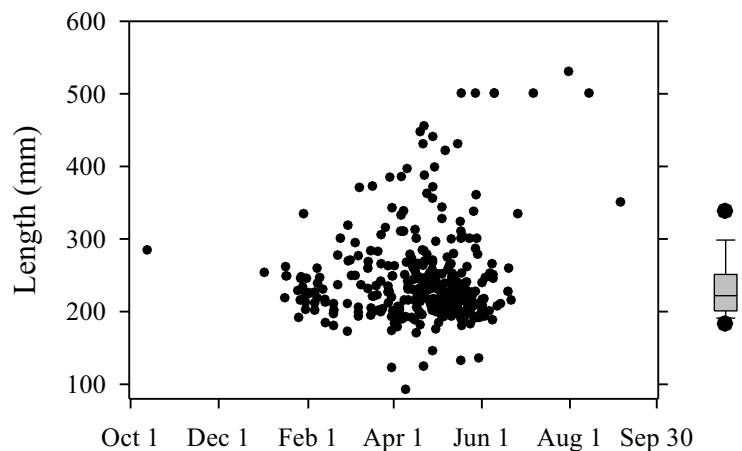
Most habitat in the Delta is now subtidal, because most channels are leveed with steep banks, and the prey available for fry reflect this. The best data are from Kjelson et al. (1982), who summarized their own and earlier studies as follows:

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 (1966), and Sasaki (1966).

Kjelson et al. (1982) called fish < 70 mm fry, but their samples included many fish < 50 mm. Larger juveniles sampled at Chipps Island more recently fed mainly on amphipods (*corophium*), but also postlarval crabs, flies, shrimp, and (non-fly) insects (MacFarlane and Norton 2002).

Naturally produced juvenile steelhead from the Sacramento system move past Knights Landing into the lower river in winter and spring, but mainly in April and May (Titus et al. 2004). Naturally produced juvenile steelhead are captured in the Chipps Island trawl are about the same size, mostly 200 to 250 mm long (Figure 31), suggesting a rapid migration. There are no data on the rate at which they move through the bays or how much they grow there. A few steelhead also migrate out of the Mokelumne River and San Joaquin River tributaries (Williams 2006).

Figure 31. Size and date of capture of 346 unmarked juvenile steelhead from the Chipps Island Trawl from 1999-2008. The box plot at right summarizes the size distribution. The larger fish may be kelts. Data from USFWS.



Studies on coastal streams (e.g., Bond 2006) show that lagoons can be very important habitat for juvenile steelhead. However, steelhead entering the Delta are older and much larger than the fish entering the lagoons in the coastal streams, so it is unlikely that these findings apply to the Delta.

4. The bays:

Habitat use in the bays probably is like that in the Delta, with larger juveniles mainly using deeper water farther from shore, and smaller juveniles mainly using shallower water and marsh channels around the margins. More small juveniles are captured in or entering the bays in wet years (Kjelson et al. 1982, Brandes and McLain 2001), but they have also been found there in dry years (Hatton and Clark 1942). A few are found in Suisun Marsh (e.g., Mattern et al. 2002).

Juvenile Chinook migrating through the bays from April through June were sampled in open water with trawls by NMFS, from 1995 to 2005. Most of these were fall Chinook, but some could have been ocean-type spring Chinook, which migrate at the same time (Fig. 19). On average, fish captured near the Golden Gate were 18 days older than fish captured near Chipps Island, and about 6 mm longer, but hardly any heavier (B. MacFarlane, NMFS, pers. comm.).

2008, Figure 32). The slow growth may reflect anthropogenic changes in the bays, as noted above, 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.

Figure 32 Size and condition of juvenile fall Chinook in the bays and ocean during 2005. Copied from Lindley et al. (2009). Note that “Estuary Entry” refers to Suisun Bay.

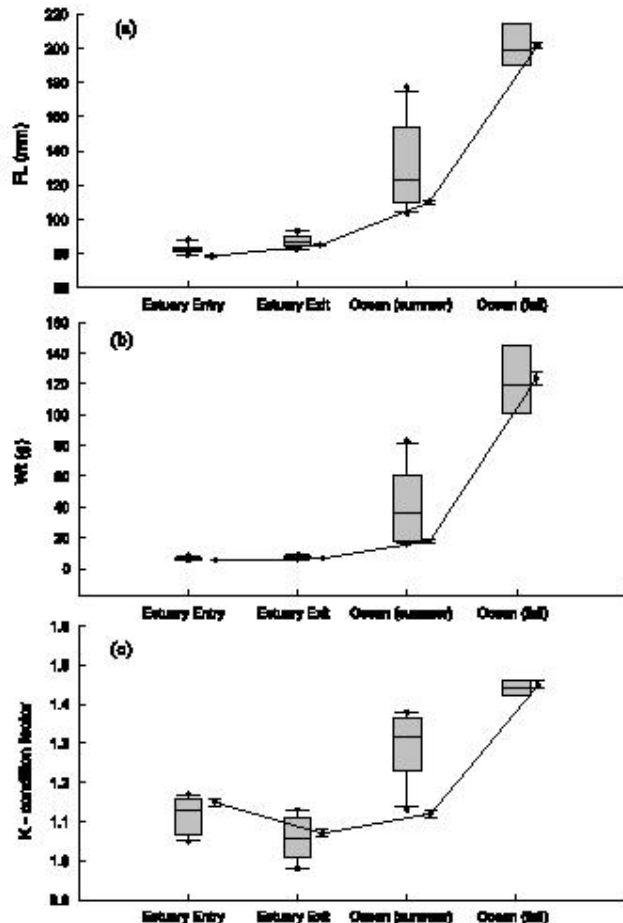
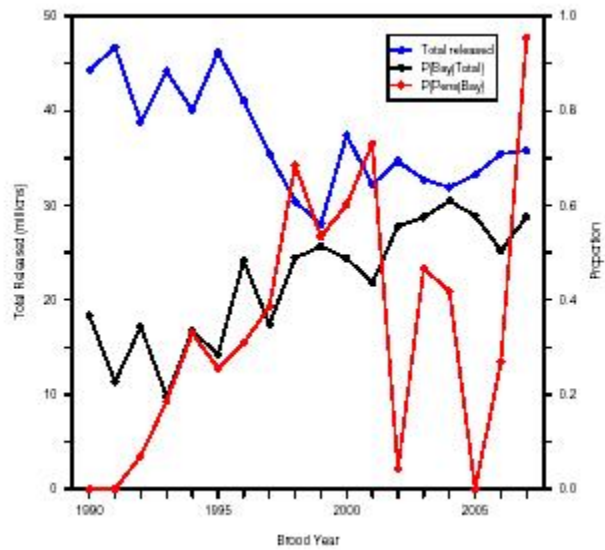


Figure 16: Changes in (a) fork length, (b) weight, and (c) condition (K) of juvenile Chinook salmon during estuarine and early ocean phases of their life cycle. Boxes and whiskers represent the mean, standard deviation and 90% central interval for fish collected in San Francisco Estuary (entry = Suisun Bay, exit = Golden Gate) during May and June and coastal ocean between 1998-2004; points connected by the solid line represent the means (± 1 SE) of fish collected in the same areas in 2005. Unpublished data of B. MacFarlane.

Poor growth in the bays also implies a strong potential for density-dependent mortality or reductions in growth, since many millions of hatchery smolts are released into the bays (Figure 33). This should be regarded as a serious problem unless new evidence suggests otherwise.

Figure 33: Total releases of hatchery fall Chinook, proportion of releases made to the bay, and the proportion of bay releases acclimatized in net pens. Unpublished data of CDFG and USFWS. Copied from Lindley et al. 2009.



5. The ocean:

Juvenile Chinook and steelhead leaving the bays enter the Gulf of the Farallones, a shallow and somewhat protected area, where they grow rapidly. From an eleven years study by NMFS, the mean and standard deviation of the length of fish entering the gulf were 87.1 and 10.4 mm; the same statistics for age (since hatching) were 153 and 22 days. Initially, the density of juveniles Chinook is highest in eddies on either side of the Golden Gate, but by September most have moved northward along the coast (B, MacFarlane, NMFS, pers. comm. 2008).

Data on the size and condition of juvenile fall Chinook in 2005 show that conditions in the ocean during the summer probably were responsible for the poor survival returns in 2007, since the size and condition of the fish were unusually small and poor (Figure 32). A statement to the contrary in Williams (2006) is mistaken. Unfortunately, such data have not been collected since 2005.

Most Central Valley Chinook, and probably steelhead as well, remain over the coastal shelf, rather than moving out into the open ocean as many salmon do at higher latitudes. Central Valley Chinook range mainly between Monterey Bay and the Columbia River, although a few go farther north or as far south as Point Conception (Williams 2006).

Juvenile steelhead from Scott Creek, on the San Mateo County coast, survive very poorly if they enter the ocean smaller than 140 mm (Bond 2006). Why smaller juvenile Chinook can successfully enter the ocean is uncertain, but higher biological productivity in summer and the protected conditions in the Gulf of the Farallones probably explain it. Conditions in the gulf can differ from conditions along the open coast farther north, which could weaken the correlation between the abundance of Chinook in the Central Valley and in coastal rivers.

K. Habitat use by run

Winter Chinook spawn in the summer, and because embryos are the most temperature sensitive life stage, winter Chinook require summer water temperatures $< \sim 14^{\circ}\text{C}$. Historically, this limited them to upper Sacramento River tributaries that drain basalt or porous lava terrain, and receive large amounts of cool water in the summer from springs (Lindley et al. 2004). Currently, winter-run spawn in the Sacramento River, downstream from Keswick Dam, where releases of water from Lake Shasta keep temperatures cool. Passage of juvenile winter-run past the Red Bluff Diversion Dam (RBDD) is well documented (Figure 34); most juveniles pass the dam as fry, in August and September. The size of the fish increases beginning in October, but the numbers drop off. The fish here are classified to runs by size and date, and so assignment involves some error, but the method is more reliable here than farther downstream, at least for smaller fish (Williams 2006).

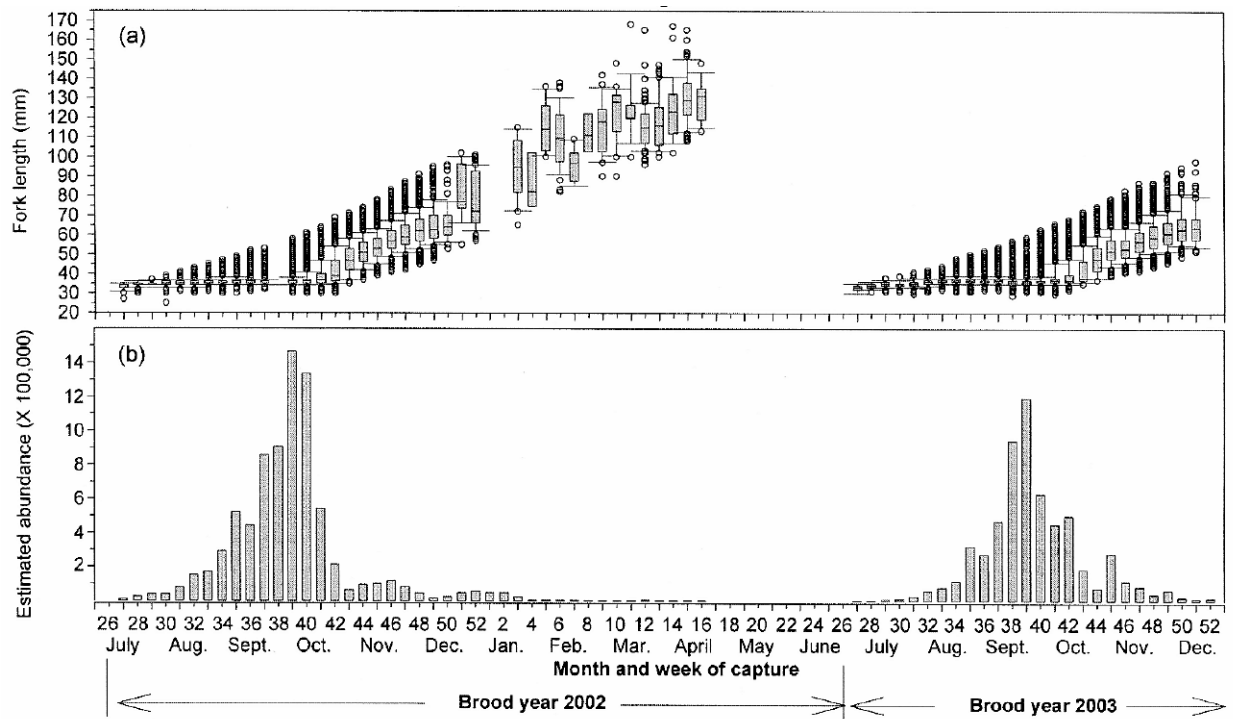


Figure 34. Size distributions (a) and numbers (b) of winter-run size juvenile Chinook salmon captured in screw traps at the RBDD in July 2002 through December 2003. Box plots in (a) show the 10th, 25th, 50th, 75th, and 90th percentiles, plus outliers. Note that the outliers simply trace the size criteria when abundance is high. Classification accuracy is probably better for smaller fish. Copied from Gaines and Poytress (2004).

What juvenile winter-run do once they pass the RBDD is less well known, because the size-at-date criteria for assigning fish to runs do not work so well, and because monitoring farther downstream is less intensive. Based on a relatively small sample identified genetically, only a few winter-run reach the lower Sacramento and the Delta before late November (Figure 21). Winter-run appear at the pumps mostly in February and March, at an average length of 121 mm

(Figure 35). Generally, the data suggest a slow migration, but the relative survival of the smaller and larger migrants past the RBDD is unknown, so inferences about the migration rate and timing of the survivors are highly uncertain. Work in progress at UC Berkeley using microchemical analyses of adult otoliths (Ingram 2008) may clarify this. Tissue samples from fish captured at Chipps Island are now being analyzed to assign fish to runs, so more information should soon be available about the size and time at which winter Chinook move into the bays.

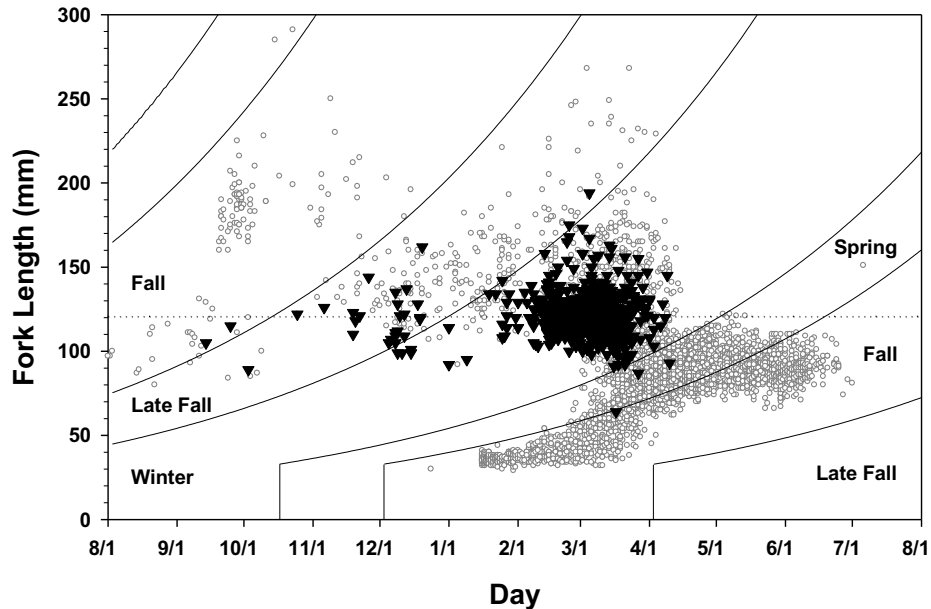


Figure 35. Distribution, by fork length and day of capture, of 6,752 juvenile Chinook salmon with assignable genotypes over a six-year period, from August 1995 through July 2001. The 711 juveniles assigned to winter-run are shown by dark inverted triangles; fish assigned to other runs are shown by open circles. Note that each symbol may represent more than one fish, and that many non-winter-run are obscured by the tight cluster of winter-run. Mean fork length of winter run juveniles (121 mm) is shown by the dotted line. The figure and most of the caption are copied from Figure 1 in Hedgecock (2002).

Adult spring Chinook hold over in streams during the summer, but do not spawn until the water temperature is declining in the fall (Table 4). They can tolerate summer water temperatures up to $\sim 20^{\circ}\text{C}$ daily average, as documented by careful monitoring in Butte Creek, although this presumably involves considerable stress. There is some evidence that gametes are less tolerant than the adults, so temperature stress may lead to reproductive failure even if spawning occurs (Williams 2006). Juveniles that remain in the stream over the summer must tolerate at least the same and perhaps higher temperatures.

Particularly in Butte Creek, most juveniles move down into the valley in spring, mainly as fry but also as larger (50 -100 mm) juveniles (Figure 36). Even larger juveniles migrate into the valley in fall, winter, and spring, but their numbers are very low by late winter. (Note that the X-

ax2s on this figure are logarithmic.) Tagging studies show that fry migrants from Butte Creek rear for some time in the Butte Sinks or Sutter Bypass before they migrate through the Delta (Figure 18). Similar information is not available for spring Chinook from Mill and Deer creeks, but it could be developed by studies of otolith microchemistry.

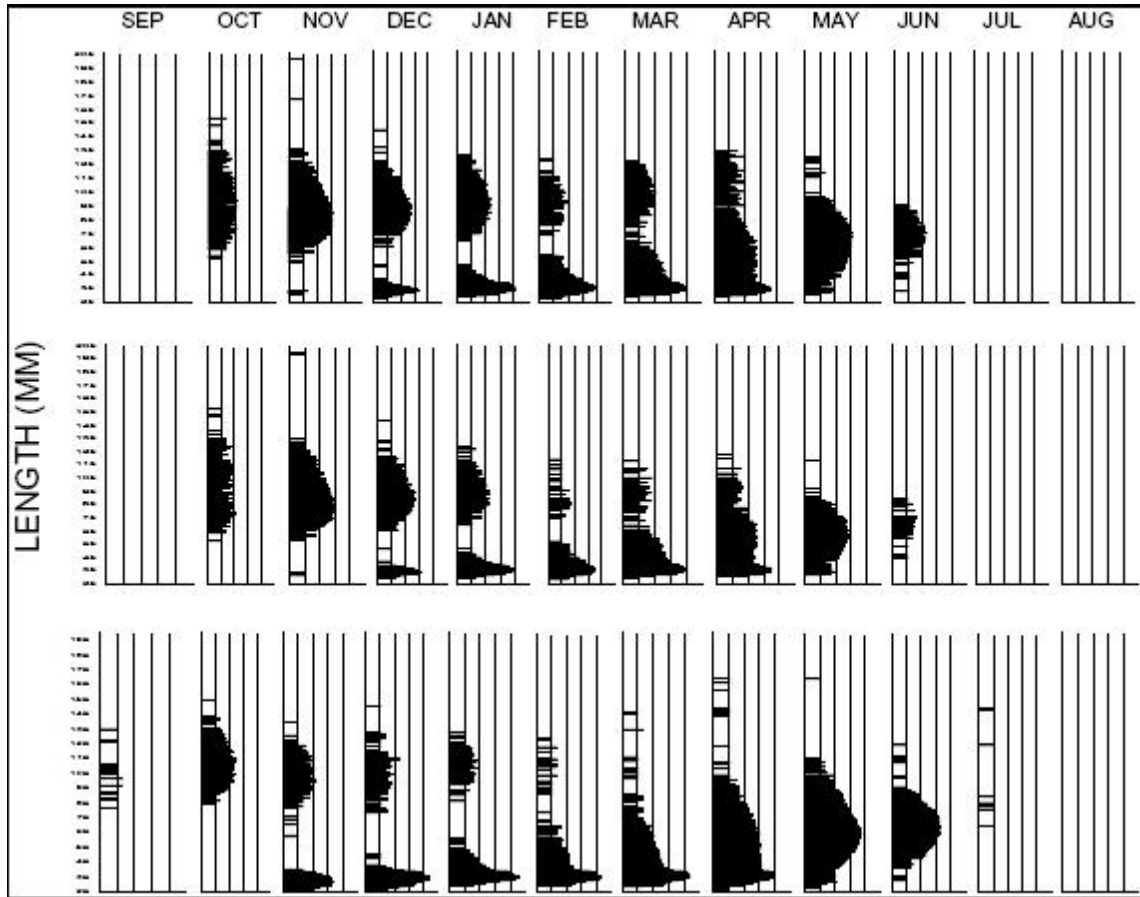


Figure 36. Length and time distribution of juvenile spring Chinook in Mill (top), Deer, and Butte (bottom) creeks. The scale of the x-axis is \log_{10} , from 1 to 10,000; the length scale is linear from 25 to 195. Copied from Lindley et al. 2004

Late-fall Chinook are present only as juveniles in the summer, and probably can tolerate about the same temperatures as the other runs. The historical distribution of their spawning habitat is not documented, but it may have been a lower elevation subset of the spring-run distribution. Naturally produced late-fall Chinook juveniles are thought to migrate to the Delta in the fall; the Chipps Island genetic sampling should clarify the timing of their migration into the bays.

Fall Chinook typically are not present during the summer, since adults normally enter fresh water as temperatures are declining, and the juveniles normally out-migrate in the spring. Some juveniles now hold over through the summer and pass through the Delta in the fall, for example

the group around 160 to 210 mm in September in Figure 30 (Williams 2006). It may be that some fall-run have always followed this life history, but summer releases of cool water from some dams make it more viable. Because fall Chinook are the most abundant run, and the only run in San Joaquin system and Delta tributaries, the traditional monitoring programs provide much more information about their behavior than about the other runs (e.g., Figure 34).

L. Environmental constraints on life history patterns:

There are at least three significant constraints on salmon life history patterns in the Central Valley. High summer water temperature is the most serious, since Chinook and steelhead one way or another must avoid thermally unsuitable habitat in the lower elevation rivers and the Delta. For example, juvenile Chinook in the Central Valley do not migrate to the Delta during the summer, although juvenile Chinook do migrate into estuaries in other rivers during that season. Similarly, as noted above, adult winter and spring Chinook are restricted to habitats that are thermally suited to spawning or holding during the summer. This constraint will become more serious as the climate warms. Butte Creek spring Chinook are most at risk; they are restricted to elevations below 350 m, and already suffer significant mortality in some years (Williams 2006).

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 make currents shift to predominantly southward flow, which induces upwelling of nutrient-rich water from the coastal shelf and slope (Ainley 1990; Williams 2006). The timing of this spring transition varies from year to year, and can strongly affect factors such as the nesting success of seabirds. Although direct evidence is lacking, it seems reasonable to expect that the survival rate of juvenile salmon increases with increasing biological productivity in the gulf, and Roth et al. (2007) have reported a relationship between seabird nesting success, which also depends on the productivity of the gulf, and the subsequent abundance of fall Chinook. Thus, juvenile Chinook that enter the ocean during times of lower productivity may be less likely to survive, especially if they are small. 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 et al. 2009).

M. Predation:

Many juvenile Chinook and steelhead are eaten in the Delta by other fishes, but high juvenile mortality is normal, so simply showing that significant predation occurs does demonstrate that something is “wrong.” Given that on average a female produces over a thousand fry (Table 1), we should expect that in natural conditions most will be eaten.

There is good evidence that predation in the Delta is significant. For example, studies of the survival of tagged hatchery fish show that fish released into Georgiana Slough survive ~45% as well as fish released into the Sacramento River nearby (Newman 2008), and acoustic tag studies indicate that increased predation there is probably the main reason for the difference, although fish released into the slough are also much more likely to be entrained at the pumps (K.

Newman, USFS, pers. comm. 2008). Similarly, Baker et al. (1995) found that the survival of tagged juvenile fall Chinook decreased as temperature rose above about 18°C. This is well within the physiological tolerance of the fish, so it seems likely that a decrease in survival results from the increased appetite of predators at temperatures that are not directly lethal for the salmon (Williams 2006). Similar increases in mortality at relatively low temperatures have been observed in the Columbia River (Anderson 2003).

The actual extent of predation remains uncertain, however, especially for smaller juveniles. The tagging studies were done with hatchery fish, and hatchery fish, especially those recently released, may be more susceptible to predation than naturally produced fish. In a modeling study, Lindley and Mohr (2003) found that the influence of striped bass predation on winter Chinook abundance probably was small, although more significant influence could not be ruled out. Nobriga et al. (2003) found relatively few Chinook in the stomachs of black and striped bass in shallow water, where small Chinook are more likely to occur, and Nobriga et al. (2006) did not find them in the stomachs of Sacramento pikeminnow.

V. ANTHROPOGENIC STRESSORS IN THE DELTA

Anthropogenic stressors in the Delta and current understanding of them are summarized in tables 7 and 8, and described below.

A. Climate Change

High water temperature is a major stressor for Chinook and steelhead in the Delta as well as in Central Valley rivers and streams. Temperature in late spring is an important predictor of the survival juvenile Chinook (Baker et al. 1995; Newman and Rice 2002; Newman 2003; Figure 32). The Delta is too warm in the summer for salmon, and Central Valley salmon have life history patterns that largely keep them out of the Delta during that season. This is a natural condition that was noted over a century ago (Rutter 1904). Water temperature in the Delta is determined primarily by atmospheric conditions, so anthropogenic climate change is already making the Delta warmer, and continued climate warming will increase the seasonal periods when the Delta is unfavorable or unsuitable for salmon.

Climate change in the Central Valley will affect different runs and life histories differently. Populations or life histories that remain in fresh water over the summer are most obviously at risk, but even ocean-type Chinook that rear upstream for some period before migrating will face a shorter period of favorable thermal conditions. Fry migrants may fare better by comparison, but may also face worsened ocean conditions. Climate change is the greatest long-term challenge facing Central Valley salmon (Williams 2006).

B. Levees

Levees impose a major stress on juvenile Chinook by blocking their access to tidal habitat (or to overbank habitat farther upstream), and confining them to habitat in the channels. This problem has been compounded in the Delta by subsidence of the Delta islands, so that in most

cases removing the levees would create subtidal ponds rather than restore the marsh habitat that used to exist there. The severity of this stress is greatest for fall Chinook, since it obstructs what was probably their predominant life history pattern. That is, the levees impose a greater stress on the fry migrant life histories that seem best able to tolerate climate change.

C. Diversions

1. Project diversions

Entrainment of juveniles in diversions at the state and federal pumps in the Delta is an obvious problem, but also a difficult one to assess. Samples of the fish that are collected for salvage are counted, providing an estimate of the total number collected, but an unknown number of fish are lost to predation near the pumps or bypass the collection facilities. Mark-recapture studies have been conducted to try to estimate mortality in the forebay at the state pumps, but these have used hatchery fish that may suffer higher mortality than naturally produced fish or hatchery fish that have been at large for some time (Williams 2006). The uncertainty in these estimates of “pre-salvage survival” compromises direct assessments of the harm done by the pumps. As a further complication, there is additional but poorly known “indirect” mortality farther from the pumps, but attributable to modification of Delta circulation patterns or other conditions associated with the pumps.

As an alternative to sampling at the pumps, the USFWS has conducted a long series of experimental releases of tagged hatchery fish that were recovered by trawling at Chipps Island or in the ocean fishery. Then, estimates were made of the effects of export pumping and other variables on the survival of the tagged fish. Two major analyses of these data have been published (Newman and Rice 2002, Newman 2003), and the results of these studies are compared in Figure 37. The magnitude of the coefficients shows the estimated strength of the influence of the associated variable, and the error bars show the associated statistical uncertainty. The effects of the exports/flow ratio is clearly strong using one analytical approach, and almost strong using the other. (See Williams 2006, Ch. 10 and Appendix B, for a more extensive comparison of these analyses).

Table 7. Summary of anthropogenic stressors in the Delta.

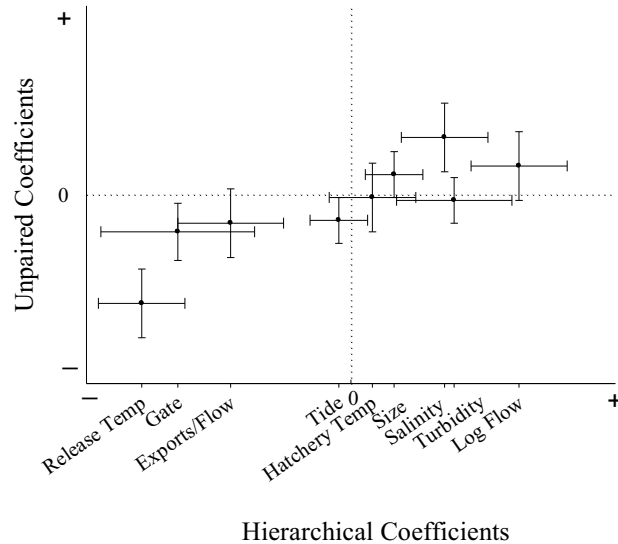
Life Stage	Stressors in the Delta						
	Levees	Water Temperature	Project Diversions	Smaller Diversions	Toxics	Hydrograph Modification	Gates and Barriers
Fry	Block access to tidal habitat	Increase predation	Entrainment, Indirect mortality	Entrainment (probably minor)	Inhibit imprinting, homing	Delay migration, change migration timing	Divert fish to Central Delta (SR fish) or South Delta (SJR fish)
Fingerlings	Block access to tidal habitat	Increase predation, physiological stress	Entrainment, Indirect mortality		Inhibit imprinting, homing	Increase late spring water temperature	Divert fish to Central Delta (SR fish) or South Delta (SJR fish)
Smolts (90+ mm)		Increase predation, physiological stress	Entrainment, Indirect mortality		Inhibit imprinting, homing	Increase late spring water temperature	Divert fish to Central Delta (SR fish) or South Delta (SJR fish)
Adults		Physiological stress	Delay migration to San Joaquin tribs		Inhibit homing?		Delay migration?

Life Stage	Stressors in the Delta		
	Hatchery Influence	Predation by introduced fishes	Dissolved Oxygen
Fry	Genetic effects from naturally spawning hatchery fish	Increases with water temperature	
Fingerlings	Genetic effects from naturally spawning hatchery fish, completion with hatchery fish	Increases with water temperature	
Smolts (90+ mm)	Genetic effects from naturally spawning hatchery fish, completion with hatchery fish	Increases with water temperature	
Adults	Genetic effects from naturally spawning hatchery fish, completion with hatchery fish, mortality from hatchery supported fishery		Low DO can delay migration of adults into the San Joaquin River.

Table 8. Summary of understanding of anthropogenic stressors in the Delta. U, I, and P are the estimated understanding, importance, and predictability of the stressors, with ranges from 1 (low) to 4 (high).

	Levees	Water Temperature	Project Diversions	Smaller Diversions	Toxics	Hydrograph Modification	Gates and Barriers	Hatchery Influence	Predation by introduced fishes	Dissolved Oxygen
Fry	U = 4 I = 4 P = 4	U = 3 I = 3 P = 3	U = 3 I = 3 P = 3	U = 3 I = 2 P = 2	U = 2 I = ? P = 1	U = 4 I = 4 P = 4	U = 2 I = 3 P = 2	U = 2 I = 4 P = 4	U = 3 I = 3 P = 3	U = 4 I = 1 P = 4
Fingerlings	U = 4 I = 3 P = 4	U = 4 I = 4 P = 4	U = 4 I = 4 P = 4	U = 3 I = 2 P = 2	U = 2 I = ? P = 1	U = 4 I = 4 P = 4	U = 3 I = 3 P = 3	U = 3 I = 4 P = 4	U = 3 I = 3 P = 3	U = 4 I = 1 P = 4
Smolts (90+ mm)	U = 3 I = 3 P = 4	U = I = P =	U = 3 I = 4 P = 3	U = I = P =	U = 2 I = ? P = 1	U = 3 I = 3 P = 4	U = 4 I = 3 P = 4	U = 3 I = 4 P = 4	U = 3 I = 3 P = 3	U = 4 I = 1 P = 4
Adults	U = 4 I = 1 P =	U = 3 I = 3 P = 3	U = I = P =	U = I = P =	U = 2 I = ? P = 1	U = I = P =	U = 4 I = 3 P = 3	U = 4 I = 4 P = 4	U = 4 I = 1 P = 4	U = 3 I = 2 P = 3

Figure 37.. Comparison of estimated coefficients plus/minus two standard errors for the unpaired analysis of Newman and Rice (2002) and the hierarchical analysis of Newman (2003) with release-specific capture probabilities. Copied from Williams 2006.



More recently, Newman (2008) has analyzed the results of several coded wire tag studies designed to address more specific questions, and summarized his results as follows:

For the most part, the substantive conclusions from the [Bayesian hierarchical model] analyses, summarized below, were consistent with previous USFWS analyses.

Delta Cross Channel: There was modest evidence, 64 to 70% probability, that survival of Courtland releases, relative to the survival of Ryde releases, increased when the gate was closed.

Interior: Survival for the interior Delta releases was estimated to be about 44% of the survival for the Sacramento River releases.

Delta Action 8: There was a negative association between export volume and relative survival, i.e., a 98% chance that as exports increased, relative survival decreased. Environmental variation in the relative survival was very large, however; e.g., for one paired release the actual relative survival at a low export level could with high probability be lower than relative survival at a high export level for another paired release.

VAMP: (a) The expected probability of surviving to Jersey Point was consistently larger for fish staying in the San Joaquin River (say passing Dos Reis) than fish entering Old River, but the magnitude of the difference varied between models somewhat; (b) thus if the HORB effectively keeps fish from entering Old River, survival of out-migrants should increase; (c) there was a positive association between flow at Dos Reis and subsequent survival from Dos Reis and Jersey Point, and if data from 2003 and later were eliminated from analysis the strength of the association increased and a positive association between flow in Old River and survival in Old River appeared; (d) associations between water export levels and survival probabilities were weak to negligible. Given complexity and number of potential models for the VAMP data, however, a more thorough model selection procedure using Reversible Jump MCMC is recommended

A shift in survival studies is underway. The studies described above used coded-wire tags, which identify batches of fish rather than individual fish, and require that fish be sacrificed for recovery of the tag. In the last few years, acoustic tags have largely replaced coded-wire tags for experimental studies, although coded-wire tags are still used to mark production releases of hatchery fish. Fish with the acoustic tags are individually marked and can be tracked remotely, which allows for addressing questions at much finer spatial and temporal scales, and for multiple detections of the same fish.

Results of acoustic tag studies in the Central Valley are beginning to appear in journals (e.g., Perry et al. In press), but have been reported mainly in talks. Unpublished work at the Delta Cross Channel indicates that the tidal and day/night cycles strongly influence the percentage of fish that pass into the central Delta through the Delta Cross Channel in the fall, which suggests that careful operation of the gate might reduce the effect of diversions through the gate on late fall and winter Chinook (Brau et al. 2007). The acoustic tag studies confirm that survival in the interior Delta is lower than in the Sacramento River. However, although visualization techniques make the data from these studies compelling, the acoustic tag studies are unlikely to be a panacea. Perry et al. (In press) and Perry and Skalski (2009) found that the survival of tagged late fall Chinook varies considerably among years and Delta channels, which suggests that considerable data will be needed before results can be relied upon, and the survival of fish with acoustic tags (e.g., those reported by Lindley et al. 2008) seems too low to be representative of a self-sustaining population. Most importantly, all studies to date have used hatchery fish, which may behave differently than naturally produced fish.

Yet another approach to analyzing the effects of the state and federal diversions uses data from the non-experimental releases of coded-wire tagged fish, usually at or near the hatchery. This approach has the advantage that fish may be exhibiting more natural migratory behavior than fish released in or near the Delta. By comparing recoveries of tagged fish at the pumps and at Chipps Island, Kimmerer (2008) estimated the percentage of fish from Coleman and Livingston Stone hatcheries leaving the Delta that are collected in the salvage facilities at the pumps, as a function of export flow (Figure 38). The analysis required some strong assumptions, so the detailed results should be regarded with due caution. One problem is that the Coleman Hatchery data include both fall and late fall Chinook, and it appears that late fall Chinook have a greater propensity to turn up at the pumps (Figure 39, Table 7). Nevertheless, the percentages of winter and especially late fall Chinook that are salvaged during periods of high exports is surely significant, especially if pre-screen mortality is high.

Figure 38. Relationship of estimated proportional salvage of tagged smolts at the fish facilities, PS, to export flow. Small symbols represent data based on six or fewer fish caught, which were not used in determining the line. Lines are from a generalized linear model with log link function and variance proportional to the mean ($p < 0.0001$, 57 df), with source of fish as a categorical variable. Thick lines are predictions for fish from each hatchery; thin lines are upper 90% confidence limits of the predicted mean values. Copied from Kimmerer 2008.

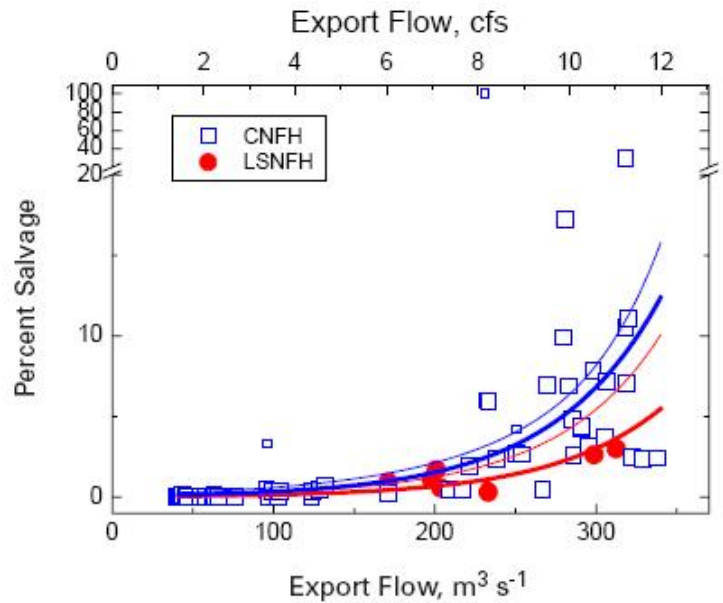
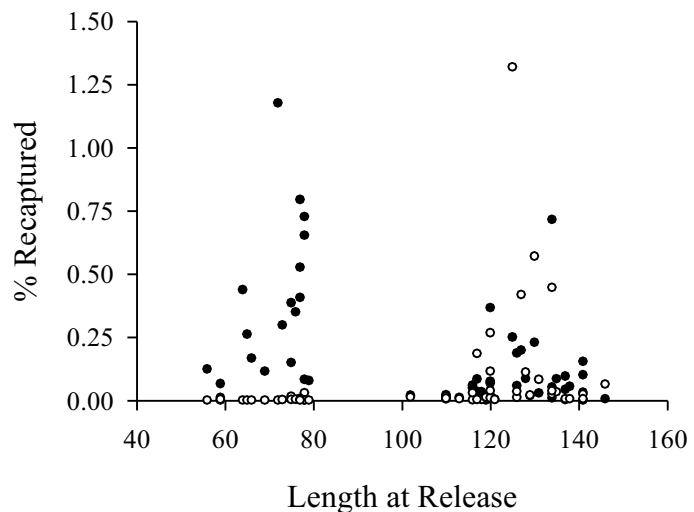


Figure 39. Recaptures of tagged juvenile fall and late fall Chinook at Chipps Island (filled circles) and the state and federal pumps (open circles). Fall Chinook (< 80 mm) are taken at the pumps much less frequently than late fall-run. Note that recaptures are not expanded to account for the limited duration of sampling, as was done for Figure 38). Data from Table 2 in Kimmerer (2008).



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 captures at Chipps Island; few Butte Creek spring-run show up at the pumps, and even fewer fall Chinook released from Coleman Hatchery do so (Table 9). Geography probably explains the 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 it seems likely that behavioral differences among the runs are also involved. The data deserve more analysis.

Table 9: The number of marked or tagged fish recorded at the state and federal pumps and at Chipps Island: winter Chinook from Livingston Stone Hatchery, late fall Chinook from Coleman Hatchery, wild Butte Creek spring Chinook, fall Chinook from Merced River Hatchery, and steelhead from all hatcheries. 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
Steelhead	507	177	2.86

Finally, based simply on the numbers of fish that are recovered at the pumps compared to the numbers that migrate into the Delta, the direct effects of the pumps seem not to be a major hazard for fry migrants to the Delta, at least when they are small.

2. Smaller diversions:

There are thousands of smaller diversions on Central Valley rivers and the Delta, most unscreened or poorly screened. These entrain some Chinook or steelhead, but the effects of these on salmon populations is uncertain (Moyle and Israel 2005). A recent study in the Delta by Nobriga et al. (2004) found that large numbers of larval and postlarval fishes were entrained in an unscreened diversion, but most of these were small non-native species. Generally, smaller fish are more vulnerable to entrainment than larger fish, and small Chinook are in the Delta mainly during the winter and early spring when diversion rates are low. Diversions on smaller streams may take a significant fraction of the flow, even if the absolute amount is small, and these may have a greater effect on the local populations. In light of the equivocal evidence for effects on populations, Moyle and Israel (2005) recommended that public money not be spent on screens “unless the projects have a strong evaluation component to them, including intensive before and after studies.”

D. Hatchery influence

Hatchery salmon can have negative effects on naturally reproducing salmon for various reasons, reviewed in Williams (2006). For example, hatchery Chinook presumably compete with naturally produced fish, in the Delta and especially in the bays, as noted above. Large numbers of hatchery fish may also attract predators that reduce the survival of naturally produced fish, as has occurred in streams (Nickelson 2003), and probably occurs with the ocean fishery. The presence of hatchery fish may also conceal or divert attention from the condition of wild or naturally reproducing fish. This is particularly the case when few hatchery fish are marked, as with fall Chinook until a few years ago. We will learn more about the extent of this problem this

year and next, when hatchery broods of fall Chinook with 25% marking return to spawn. In a related problem, conducting survival experiments with hatchery fish will tend to encourage management of the Delta to benefit fish that behave in the same way. If wild or naturally produced behave differently (figures 28, 29 and 36), this may be to their detriment. Similarly, attention to hatchery fish may need to neglect of fry migrants to the bays and Delta.

More serious and persistent are genetic changes, resulting from selection for a life cycle that involves reproduction in a hatchery, rather than a stream (Myers et al. 2004; Araki et al. 2007; 2008). In recognition of this, Lindley et al. (2007) included the degree of hatchery influence among criteria for viability of ESA-listed Central Valley salmon populations. Based on these criteria, Central Valley fall Chinook are at high risk of extinction.

Hatchery salmon tend to stray more than wild salmon (Williams 2006), and the practice of trucking juveniles around the Delta strongly increases straying (JHRC 2001). Straying presumably magnifies the harm from hatchery fish spawning in rivers by extending the effects of domestication selection into populations in streams that do not have hatcheries, such as fall Chinook in Mill and Deer creeks.

E. Toxics

Toxics in the Delta are a potential stressor for salmon, but the extent of the problem is unknown (I. Werner, UCD, pers. comm. 10/08). The main potential problems are ammonia, pyrethroid pesticides, and copper. Besides direct effects, ammonia reduces resistance to disease (Ackerman et al. 2006). The most likely effects from pyrethroid, organophosphate and copper pesticides are damage to the olfactory system (Schulz et al. 2000; Sandahl et al. 2004; Hecht et al. 2007) that can impair homing and predator avoidance. Past sources of acute toxicity, such as the Iron Mountain Mine, have been mostly abated.

F. Dissolved Oxygen

Dissolved oxygen concentrations on the San Joaquin River near Stockton can be low enough to block migration of adult salmon (Hallock et al. 1970; Alabaster 1989). This is a continuing problem, resulting from complex interactions among factors such as diversion of San Joaquin River water toward the Delta pumps, modifications of channel morphology to allow shipping, and wastewater discharge, that is the subject of considerable recent work (e.g., Lee and Jones-Lee 2003; Jassby and Van Nieuwenhuyse 2005) and a current test mitigation project by DWR (http://baydeltaoffice.water.ca.gov/sdb/af/index_af.cfm). Usually this problem eases in late October.

G. Water temperature

Hallock et al. (1970) reported that water warmer than 21°C blocks migration of Chinook into the San Joaquin River and water warmer than 19°C inhibits it. However, data from the new weir on the Stanislaus River indicate that in 2003 over 500 Chinook passed through water 21°C daily average, or warmer, in the lower San Joaquin River (SRFG 2004). The role of temperature in blocking migration should be clarified as data from this weir or others that may be installed on

other tributaries accumulate. Whether migration through such warm water harms gametes should also be considered.

H. Predation

Predation is natural, but human modification of the Delta can increase it, for example through increased predation associated with the pumps and the Delta Cross Channel. Striped bass and black bass, introduced species, are important predators on juvenile salmon in the Delta. Predation seems the most likely reason for the lower survival of migrating juvenile salmon in the interior Delta, discussed above. Tidal channels are thought to provide protection from predatory fishes (Lott 2004 and citations therein), so the loss of tidal habitat may increase predation. Predation by humans, harvest, is usually a serious stressor on Central Valley Chinook populations, but not in the Delta. See Chapter 13 in Williams (2006) for a discussion of ocean harvest of Central Valley Chinook.

VI. Outcomes

A logical desired outcome for Chinook and steelhead is recovery of the fish listed under the Endangered Species Act, or, more specifically, that winter and spring Chinook and steelhead should meet the viability criteria given in Lindley et al. (2007), and that the unlisted fall and late-fall Chinook should also meet these criteria. These criteria deal mainly with abundance and hatchery influence at the population level, and also with spatial diversity at the ESU or DPS level. However, for several reasons, these outcomes are only marginally useful for assessing management of the Delta. First, some of these criteria, such as the need for additional independent populations of winter Chinook, are unrelated to management of the Delta. Second, because so much of the life cycle of Chinook and steelhead occurs away from the Delta, and survival in these other habitats can be highly variable, even major improvements in Delta conditions would be unlikely to give a clear signal in abundance data until many years had passed (Bradford et al. 2005). The boom and bust of Central Valley fall Chinook over the last fifteen years illustrate the problem with using abundance alone as an indicator of success. Nevertheless, abundance and the viability criteria are surely important for assessing the overall effects of salmon and steelhead management and restoration efforts, of which Delta activities are an important part.

For assessing management of the Delta, monitoring the abundance of juveniles leaving the Delta and the bays seems more useful, but also seems very difficult to do well. Kimmerer (2008) used the Chipps Island trawl data to try to estimate the abundance of juvenile Chinook leaving the Delta, but the estimates depend on a number of strong assumptions and are of unknown accuracy and precision, and the trawl captures smaller fish less efficiently (Williams 2006). Trying to estimate the numbers coming into the Delta would face the same problems, at least downstream from the Red Bluff Diversion Dam, which presents an unusually favorable site for monitoring. Estimating the number of juveniles leaving the bays seems impossible.

Focusing on estimates of growth, growth rate and condition of juveniles rearing in and leaving the Delta should be more useful, particularly because data already exist from an 11-year NMFS program that sampled juveniles in the bays and the Gulf of the Farallones from 1995 to 2005 that provide a baseline, and allowed Lindley et al. (2009) to reach a much more robust conclusion about the collapse of the fall Chinook population than would have been possible otherwise (see Figure 32). Results from early years of the study have been published (MacFarlane and Norton 2002; MacFarlane et al. 2005), and a summary paper is in review (B. MacFarlane, pers. comm., April. 2009). There are also data on size at date from the USFWS trawling at Chipps Island. These data could be used to set quantitative targets for size at date and condition of juvenile Chinook leaving the Delta, and also to test whether there is a relationship between size at date and condition of juveniles leaving the Delta and subsequent adult returns.

Given that sublethal exposure to pesticides or other contaminants in the Delta can disrupt the olfactory system of juvenile salmon and interfere with normal imprinting, a natural rate of straying would be a desirable outcome of management of contaminants. However, straying is difficult to measure, and the natural rate of straying is not precisely known, so setting an outcome for management of toxics in terms of straying does not seem feasible. Setting targets in terms of concentrations of toxics that affect olfaction of fishes in the laboratory, or cause other harm, seems more realistic.

VII. Future Research

The suggestions below for future research try to go beyond the usual questions about the survival of tagged hatchery fish. They are based on the notion that we cannot do a good job of managing something unless we know how it works, and there are still major gaps in our understanding of how Chinook and steelhead populations work.

What are the life-history patterns followed by naturally produced juveniles from different Chinook lineages and populations? When and at what size do they enter and leave the Delta? What are the relative contributions of the different life history patterns to adult returns?

These questions can be addressed regarding lineages through genetic assignment of juveniles sampled in existing monitoring programs. This is currently underway for the sampling at Chipps Island, but it also seems important to clarify when and at what sizes the different lineages of Chinook come into the Delta, by genetic assignment of samples of fish collected in the Sherwood Harbor trawling. This seems especially important for winter Chinook, and would clarify to what extent hatchery late fall-Chinook can be used as surrogates for wild winter Chinook in survival and migration studies.

Genetic assignment should also be effective for spring Chinook, assuming that the Mill and Deer creek populations can be treated as one. It would not suffice for fall Chinook, which are too homogenous genetically to distinguish populations. However, the major populations of fall Chinook can be distinguished by microchemical analysis of otoliths (Barnett-Johnson et al. 2005; 2008), which takes advantage of geological variation along the Sierra Nevada and Cascade

Mountains. Analyses of the microstructure of otoliths collected from adults would provide information on the contributions of the different juvenile life history patterns to returns.

What determines the life-history patterns followed by Chinook and steelhead?

A modeling study to address this question for steelhead is already underway at UCSC, with funding by CALFED (Satterthwaite 2009a). However, even if the approach taken in this study is successful, much more information on the condition of juvenile steelhead and Chinook in the Central Valley will be needed to apply it fully. Fortunately, the data on growth and condition of juveniles suggested as appropriate for measuring the outcome of management of the Delta, from the point of view of salmon, will also be useful for developing the modeling approach.

How do juveniles navigate through the Delta?

Juvenile salmon may use celestial or magnetic cues to find their way through the Delta, as discussed above. Learning more about this may be useful, not from the point of view of installing giant magnets or search lights in the Delta to try to steer fish away from the pumps, but rather for understanding whether and how different groups of fish behave differently, and how hatchery practices, such as trucking fish around the Delta, might affect selection for such behavior. As a related question:

How do ATPase activity or other physiological variables correlate with or modify migratory behavior among Central Valley salmon?

There is a large and inconclusive literature on salmonids regarding this general topic, reviewed by Høgåsen (1998), but much of it is related to hatchery practices, rather than naturally produced fish, and it seems likely that the relations between physiological variables and migration will differ among different life-history types.

Ewing et al. (2001) describe migratory behavior of spring Chinook in the Rogue River, Oregon, that may be a model for the behavior of winter Chinook, although with a seasonal offset. Ewing et al. (2001) found that the migrating juveniles can be roughly divided into one group that migrates slowing down the margins of the channel and another group that migrates more rapidly down the center of the channel, with individuals shifting from the more slowly to the more rapidly migrating group over time. They also found that the status of individuals in this dichotomy can be assessed in terms of changing levels of gill Na^+/K^+ ATPase activity. If this story or some modification of it holds true for winter or late fall Chinook, this knowledge might improve monitoring and management of facilities in the Delta. It could also help answer a very applied question: can hatchery late fall Chinook be used as surrogates for wild winter Chinook?

Is migration a self-reinforcing behavior?

If migratory behavior is self-reinforcing, if the act of migration strengthens the physiological signals that promote migration, then studies of hatchery fish released into the Delta may not be representative of fish released at the hatchery, or of naturally produced fish.

What traits are involved in selection for fitness in a hatchery-based life-cycle?

It now seems settled that hatchery culture involves selection for fitness in a hatchery-based life-cycle, and against fitness in a natural life-cycle (Araki et al. 2007, 2008; Myers et al. 2004).

However, the particular traits selected for or against are not known, although it seems likely that multiple traits are involved (Araki et al. 2008). Traits affecting survival during the egg-alevin part of the cycle are good candidates, since the associated environments are radically different in hatcheries and in streams. In this regard, it is important to realize that hatchery culture does not simply relax selection for or against traits that affect survival in the wild. One reason is that hatcheries canalize fish into particular life histories, and so subject them to different conditions than they might have experienced otherwise (Goodman 2005). For example, steelhead from Coleman Hatchery smolt a year younger than most naturally produced Sacramento River steelhead. This means that Coleman steelhead will experience life in the Delta, bays and the ocean differently than naturally produced fish. Similarly, fall Chinook from Coleman are canalized into a fingerling migrant life-history, and will be subjected to different selective regimes than naturally produced fry migrants.

Does the spring transition in the Gulf of the Farallones define the beginning of a “smolt window” for Central Valley salmon?

Studies of salmon populations elsewhere have suggested that the timing of ocean entry strongly affects smolt survival, and that the timing of ocean entry has evolved in response (e.g., Tallman and Healey 1994). For Central Valley salmon, the spring transition in the Gulf of the Farallones to a regime dominated by upwelling (Ainley 1990; Williams 2006) seems a logical candidate for the beginning of such a period of higher survival. It is easy to see how the migration timing of fall Chinook or fry-migrant spring Chinook would fit such a conceptual model, but the larger juveniles that migrate down the Sacramento River during late fall and winter would seem not to fit. However, if the timing with which wild juvenile winter Chinook appear at the pumps (Figure 18) reflects the timing with which they leave the Delta, and if their migration through the bays is slow, then winter-run might indeed fit this model. This might be tested by comparing the timing of an increase in growth rate from the otolith microstructure of returning adults with the timing of ocean entry estimated from otolith microchemistry. As an alternative hypothesis, it could be that survival of winter-migrant juvenile Chinook depends on reaching a large enough size, as appears to be the case with coastal steelhead (Hayes et al. 2008).

Does food availability in the estuary limit the growth and subsequent survival of juvenile salmon? Does competition with hatchery fish adversely affect naturally produced fish in the estuary?

Recent estimates of the growth rates of juvenile Chinook in the Delta and especially in the bays seem low (Figure 32). Data on size at date from the Chipps Island trawling records and from recoveries at the state and federal pumps could be compiled to check for year to year variation and longer term trends in size at date, and data from monitoring in the rivers could be used to try to separate the effects on size of conditions in the Delta and in the rivers. Similarly, an index of food availability for juvenile salmon might be constructed from the long IEP monitoring records in the Delta. The indices of growth or of food availability might be used as covariates in statistical analyses of survival. Data on growth and condition of fish from the 1995-2005 NMFS monitoring could be used for detailed assessments for those years. The NMFS samples could also be classified as hatchery or naturally produced based on otolith microstructure, so that these groups of fish could be analyzed separately.

VIII. References

- Ackerman, PA, Wicks, BJ, Iwama, GK, Randall, DJ. 2006. Low levels of environmental ammonia increases susceptibility to disease in Chinook salmon smolts. *Physiological and Biochemical Zoology* 79:695-707.
- Ainley, DG. 1990. Seasonal and annual patterns in the marine environment near the Farallones. In: Ainley, DG, Bockelheide, RJ, editors. *Seabirds of the Farallon Islands*. Stanford University Press.
- Alabaster, JS. 1989. The dissolved oxygen and temperature requirements of king salmon, *Oncorhynchus tshawytscha*, in the San Joaquin Delta, California. *Journal of Fish Biology* 34:331-332.
- Anderson, JJ. 2003. Toward a resolution of the flow/survival debate and the impacts of flow augmentation and water withdrawal in the Columbia/Snake River system. Seattle: Columbia Basin Research, School of Aquatic and Fishery Science, University of Washington.
- Araki, H, Berejikian, BA, Ford, MJ, Blouin, MS. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1:342-355.
- Araki, H, Cooper, B, Blouin, MS. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318:100-103.
- Atwater, BF, Conrad, SF, Dowden, JN, Hedel, CW, MacDonald, RL, Savage, W. 1979. History, landforms, and vegetation of the estuary's tidal marshes. In: Conomos, TJ, Editor. *San Francisco Bay, the urbanized estuary*. AAAS. p. 347385.
- Baker, PF, Speed, TP, Ligon, FK. 1995. Estimating the influence of temperature on the survival of Chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento - San Joaquin River Delta of California. *Canadian Journal of Fisheries and Aquatic Sciences* 52:855-863.
- Banks, MA, Rashbrook, VK, Calvaetta, MJ, Dean, CA, Hedgecock, D. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of Chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. *Canadian Journal of Fisheries and Aquatic Sciences* 57:915-927.
- Barnett-Johnson, R, Garza, JC, Grimes, CB, MacFarlane, RB. 2008. Linking freshwater sources of Chinook salmon to their ocean distributions using genes and otolith signatures of origin. Abstracts, 5th Biennial CALFED Science Conference; Sacramento, CA. p. p. 74.
- Barnett-Johnson, R, Grimes, CB, Royer, CF, Donohoe, CJ. 2007. Identifying the contribution of wild and hatchery Chinook salmon (*Oncorhynchus tshawytscha*) to the ocean fishery using otolith microstructure as natural tags. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1683-1692. doi:10.1139/Fo7-129
- Barnett-Johnson, R, Ramos, FC, Grimes, CB, MacFarlane, RB. 2005. Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2425-2430.
- Bond, MH. 2006. Importance of estuarine rearing to central California steelhead (*Oncorhynchus mykiss*) growth and marine survival. University of California Santa Cruz.
- Bottom, DL, Jones, KK, Cornwell, TJ, Gray, A, Simenstad, CA. 2005. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* 64:79-93.
- Bradford, MJ, Higgins, PS. 2001. Habitat-, season-, and size specific variation in diel activity patterns of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:365-374.
- Bradford, MJ, Korman, J, Higgins, PS. 2005. Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus* spp.) to experimental habitat alterations. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2716-2726.
- Brandes, PL, McLain, JS. 2001. Juvenile Chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin estuary. In: Brown, RL, editor. *Contributions to the biology of Central Valley salmonids, Vol 2*. Fish Bulletin No. 179. Sacramento: California Department of Fish and Game. p. 39-138.
- Brau, J., A. Blake, and R. Perry. 2007. Sacramento/San Joaquin River Delta regional salmon outmigration study plan: Developing understanding for management and restoration. Available: http://baydeltaoffice.water.ca.gov/ndelta/salmon/documents/RegionalSalmonStudyPlan_2008.01.07.pdf. (May 2009).
- Brett, JR, Shelbourn, JE, Shoop, CT. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363-2394.
- Brown, R, Cavallo, B, Jones, K. 2004. The effects of the Feather River Hatchery on naturally spawning salmonids.

- California Department of Water Resources.
- Burke, Jennifer L. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to the present: MS thesis, Oregon State University; 2004.
- Castleberry, DT, Cech, JJr, Saiki, MK, Martin, BA. 1993. Growth, condition and physiological performance of juvenile salmonids from the American River, February through July, 1992. Dixon, California: U. S. Fish and Wildlife Service.
- Clark, GH. 1928. Sacramento- San Joaquin salmon (*Oncorhynchus tshawytscha*) fishery of California. Fish Bulletin 17:1-73.
- Clarke, WC, Whithler, RE, Shelbourn, JE. 1992. Genetic control of juvenile life history pattern in Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 49:2300-2306.
- Clarke, WC, Hirano, T. 1995. Osmoregulation. In: Groot, C, Margolis, L, Clarke, WC, editors. Physiological ecology of Pacific salmon. Vancouver, British Columbia: UBC Press. p. 317-438.
- Erkkila, LF, Moffett, JW, Cope, OB, Smith, BR, Nielson, RS. 1950. Sacramento - San Joaquin Delta Fishery Resources: Effects of Tracy Pumping Plant and Delta Cross Channel. Sacramento, California: U.S. Fish and Wildlife Service. Special Scientific Report: Fisheries No. 56.
- Ewing, RD, Ewing, GS, Satterthwaite, TD. 2001. Changes in gill Na⁺, K⁺-ATPase specific activity during seaward migration of wild juvenile Chinook salmon. Journal of Fish Biology 58:1414-1426.
- Geist, DR, Abernathy, CS, Hand, KD, Cullinan, VI, Chandler, JA, Groves, PA. 2006. Survival, development, and growth of fall Chinook salmon embryos, alevins, and fry exposed to variable thermal and dissolved oxygen regimes. Transactions of the American Fisheries Society 135:1462-1477. doi:10.1577/T05-294.1
- Gilbert, CH. 1913. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. Bulletin of the Bureau of Fisheries.
- Goodman, D. 2004. Salmon supplementation: demography, evolution, and risk assessment. In: Nickum, MJ, Mazik, PM, Nickum, JG, MacKinley, DD, editors. Propagated fish in resource management. American Fisheries Society, Symposium 44. Bethesda, Maryland: American Fisheries Society. p. 217-232.
- Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences 62:374-389.
- Greene, CM, Beechie, TJ. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:590-602.
- Hallock, RJ, Elwell, RF, Fry, DHJr. 1970. Migrations of adult king salmon (*Oncorhynchus tshawytscha*) in the San Joaquin Delta as demonstrated by the use of sonic tags. Fish Bulletin 151. California Department of Fish and Game.
- Hallock, RJ, Van Woert, WF, Shapovalov, L. 1961. An evaluation of stocking hatchery-reared steelhead rainbow trout (*Salmo gairdnerii gairdnerii*) in the Sacramento River System. Fish Bulletin No. 114. California Department of Fish and Game.
- Hannon, J, Healey, M, Deason, B. 2003. American River steelhead (*Oncorhynchus mykiss*) spawning, 2001-2003. Sacramento, California: U. S. Bureau of Reclamation and California Department of Fish and Game.
- Hanson, HA, Smith, OR, Needham, PR. 1940. An investigation of fish salvage problems in relation to Shasta Dam. Special Scientific Report # 10. Washington, D. C.: U. S. Bureau of Fisheries.
- Harden Jones, FR. 1978. Fish Migration. London: Arnold.
- Hatton, SR, Clark, GH. 1942. A second progress report on the Central Valley fisheries investigation. California Fish and Game 28:116-123.
- Hayes, Sean A.; Hanson, Chad V.; Macfarlane, R. B., and Bond, Morgan H. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences.; 65: 2242-2252.
- Healey, MC. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In: Groot, C, Margolis, L, editors. Pacific salmon life histories. p. 311-394.
- Healey, MC. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. Fishery Bulletin 77:653-668.
- Hecht, SA, Baldwin, DH, Mebane, CA, Hawkes, T, Gross, SJ, Scholz, NL. 2007. An overview of sensory effects on juvenile salmonids exposed to dissolved copper. D. S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-83.
- Hedgecock, D, Banks, MA, Rasbrook, VK, Dean, CA, Blankenship, SM. 2001. Applications of population genetics to conservation of Chinook salmon diversity in the Central Valley. In: Brown, RL, editor. Contributions to the biology of Central Valley salmonids. Fish Bulletin .1. p. 45-70.

- Hedgecock, D. 2002. Microsatellite DNA for the management and protection of California's Central Valley Chinook salmon (*Oncorhynchus tshawytscha*). University of California, Davis, Bodega Marine Laboratory.
- Hill, MF, Botsford, LW, Hastings, A. 2003. The effects of spawning age distribution on salmon persistence in fluctuating environments. *Journal of Animal Ecology* 72:736-744.
- Høgåsen, HR. 1998. Physiological changes associated with the diadromous migration of salmonids. *Canadian Special Publication of Fisheries and Aquatic Sciences* 127.
- Ingram, L. 2008. The role of the San Francisco Bay-Delta in juvenile rearing for winter and spring run Chinook salmon, to be determined by otolith microchemistry. Supplemental proposal to CALFED, 2007 Supplemental PSP.
- Jassby, A, Van Nieuwenhuysse, EE. 2005. Low dissolved oxygen in an estuarine channel (San Joaquin River, California): mechanisms and models based on long-term time series. *San Francisco Estuary and Watershed Science* (online serial) 3:Article 2. <http://repositories.cdlib.org/jmie/sfews/vol2/iss2/art2>.
- Jeffres, CA, Opperma, JJ, Moyle, PB. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California River. *Environmental Biology of Fishes* In press: DOI: 10.1007/s10641-008-9367-1
- Joint Hatchery Review Committee (JHRC). 2001. Final Report on Anadromous Salmonid Fish Hatcheries in California, Review Draft. California Department of Fish and Game and National Marine Fisheries Service Southwest Region.
- Kelley, R. 1989. *Battling the inland sea*. Berkeley: University of California Press.
- Kimmerer, WJ. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological response. *San Francisco Estuary and Watershed Science* (online serial) 2:Article 1. <http://repositories.cdlib.org/jmie/sfews/vol2/iss1/art1>.
- Kimmerer, WJ. 2008. Losses of Sacramento River Chinook salmon and Delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 6:Article 2. <http://repositories.cdlib.org/jmie/sfews/vol6/iss2/art2/>
- Kjelson, MA, Raquel, PF, Fisher, FW. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary, California. In: Kennedy, VS, editor. *Estuarine comparisons*. New York: Academic Press. p. 393-411.
- Kostow, KE. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61:577-589.
- Lee, GF, Jones-Lee, A. 2003. Synthesis and discussion of findings on the causes and factors influencing low DO in the San Joaquin River deep water ship channel near Stockton, CA: including 2002 data. El Macero, CA: G. Fred Lee & Associates.
- Levy, DA, Northcote, TG. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 39:270-276.
- Lindely, ST, Schick Robert S., Agrawal, A, Goslin, M, Pearson, TE, Mora, E, Anderson, JJ, May, BP, Greene, S, Hanson, C, Low, A, McEwan, DR, MacFarlane, RB, Swanson, C, Williams, JG. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. *San Francisco Estuary and Watershed Science* Volume 4:Article 3. <http://repositories.cdlib.org/jmie/sfews/vol4/iss1/art3>
- Lindely, ST, Schick Robert S., Mora, E, Adams, PB, Anderson, JJ, Greene, S, Hanson, CMBP, McEwan, DR, MacFarlane, RB, Swanson, C, Williams, JG. 2007. Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento-San Joaquin Basin. *San Francisco Estuary and Watershed Science* Volume 5 :Article 4. <http://repositories.cdlib.org/jmie/sfews/vol5/iss1/art4>
- Lindley, ST, Michel, C, Sandstrom, PT. 2008. Estimating reach-specific smolt survival rates and the factors affecting them from acoustic tagging data. 5th Biennial CALFED Science Conference; Sacramento, CA.
- Lindley, ST, Mohr, MS. 2003. Modeling the effects of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*). *Fishery Bulletin* 101:321-331.
- Lindley, ST, Schick, R, May, BP, Anderson, JJ, Greene, S, Hanson, C, Low, A, McEwan, D, MacFarlane, RB, Swanson, C, Williams, JG. 2004. Population structure of threatened and endangered Chinook salmon ESUs in California's Central Valley Basin. NOAA-TN-NMFS-SWFSC-370.
- Lindley, S. T.; Grimes, C. B.; Mohr, M. S.; Peterson, W.; Stein, J.; Anderson, J. R.; Botsford, L. W.; Botton, D. L.; Busack, C. A.; Collier, T. K.; Ferguson, J.; Garza, J. C.; Grover, A. M.; Hankin, D. G.; Kope, R. G.; Lawson, P. W.; Low, A.; MacFarlane, R. B.; Moore, K.; Plamer-Zwahlen, M.; Schwing, F. B.; Smith, J.; Tracy, C.; Webb, R.; Wells, B. K., and Williams, T. H. 2009. What caused the Sacramento River fall Chinook stock collapse? National Marine Fisheries Service, Southwest Fisheries Science Center. NOAA_TM_SWFSC-447.

- Lott, MA. 2004. Habitat-specific feeding ecology of ocean-type juvenile Chinook salmon in the lower Columbia River estuary. MS Thesis, University of Washington, School of Aquatic and Fishery Science.
- Lotze, JK, Lenihan, HS, Bourque, BJ, Bradbury, RH, Cooke, RG, Kay, MC, Kidwell, SM, Kirby, MX, Peterson, CH, Jackson, JB. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806-1809.
- Low, A. 2005. Existing program summary: Central Valley salmon and steelhead monitoring programs . Sacramento, California: California Department of Fish and Game.
- Ludwig, D. 1994. Uncertainty and fisheries management. In: Levin, SA, editor. *Frontiers in Mathematical Biology*. Springer-Verlag. p. 516-528.
- MacFarlane, BR, Ralston, S, Royer, C, Norton, EC. 2005. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth on the Central California coast during the 1980 El Niño and the 1999 La Niña. *Fisheries Oceanography* 14:321-332.
- MacFarlane, RB, Norton, EC. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and the Gulf of the Farallones, California. *Fishery Bulletin* 100:244-257.
- Malamud-Roam, FP, Phillis, C, Ingram, L, Weber, PK. 2008. San Francisco Bay Estuary habitat use determined by otolith stable isotopes. Abstracts, 5th Biennial CALFED Science Conference; Sacramento, CA. p. p. 157.
- Mangel, M. 1994. Climate change and salmonid life history changes. *Deep-Sea Research II* 41:75-106.
- Mangel, M, Satterthwaite, WH. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Butte tin of Marine Science* 83:107-130.
- Marine, KR, Cech, JJr. 2004. Effects of high temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. *North American Journal of Fisheries Management* 24:198-210.
- Maslin, P, Kindopp, J, Storm, C. 1999. Intermittent streams as rearing habitat for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*): 1999 update. California State University Chico, Dept. of Biological Sciences.
- Mattern, SA, Moyle, PB, Pierce, LC. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. *Transactions of the American Fisheries Society* 131:797-816.
- McEwan, D, Nelson, J. 1991. Steelhead restoration plan for the American River. Sacramento, California: California Department of Fish and Game.
- McEwan, D. 2001. Central Valley Steelhead. In: Brown, RL, Editor. *Contributions to the biology of Central Valley salmonids*, Fish Bulletin 179. Fish Bulletin 179.1. California Department of Fish and Game. p. 1-44.
- McGregor, EA. 1923. Notes on the egg yield of Sacramento River king salmon. *California Fish and Game* 9:134-138.
- Moyle, PB. 2002. *Inland Fishes of California*. University of California Press.
- Moyle, PB, Crain, PK, Whitener, K. 2007. Patterns in the use of a restored California floodplain by native and alien fishes. *San Francisco Estuary and Watershed Science* vol. 5, issue 3, article 1:1-27. <http://repositories.edlib.org/jmi/sfews/vol5/iss3/art1>
- Moyle, PB, Israel, JA. 2005. Untested assumptions: effectiveness of screening diversions for conservation of fish populations. *Fisheries* 30:20-28.
- Myers, RA, Levin, SA, Lande, R, James, FC, Murdock, WW, Paine, RT. 2004. Hatcheries and endangered salmon. *Science* 303:1980.
- Myrick, CA, Cech, JJr. 2002. Growth of American River fall-run Chinook salmon in California's Central Valley: temperature and ration effects. *California Fish and Game* 88:35-44.
- Myrick, CA, Cech, JJr. 2001. Temperature effects on Chinook salmon and steelhead: a review focusing on California's Central Valley populations. <http://www.cwemf.org>: Bay-Delta Modeling Forum.
- Myrick, CA, Cech, JJr. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know. *Reviews in Fish Biology and Fisheries* 14:113-123.
- Myrick, CA, Cech, JJr. 2000. Temperature influences on California rainbow trout physiological performance. *Fish Physiology and Biochemistry* 22:245-254.
- Newman, KB. 2008. An evaluation of four Sacramento-San Joaquin River Delta juvenile salmon survival studies. Stockton, Ca: USFWS.
- Newman, KB. 2003. Modeling paired release-recovery data in the presence of survival and capture heterogeneity with application to marked juvenile salmon. *Statistical Modeling* 3:157-177.
- Newman, KB, Rice, J. 2002. Modeling the survival of Chinook salmon smolts outmigrating through the lower Sacramento River system. *Journal of the American Statistical Association* 97:983-993.

- Nichols, FH, Cloern, JE, Luoma, S, Peterson, DH. 1986. The modification of an estuary. *Science* 231:567-573.
- Nickleson, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1050-1056.
- Nobriga, M, Matica, Z, Hymnson, Z. 2004. Evaluating entrainment vulnerability to agricultural irrigation diversions: a comparison among open-water fishes. *American Fisheries Society Symposium* 39. p. 281-295.
- Nobriga, ML, Feyrer, F, Baxter, RD. 2006. Aspects of Sacramento pikeminnow biology in nearshore habitats of the Sacramento-San Joaquin Delta, California. *Western North American Naturalist* 66:106-114.
- Nobriga, ML, Baxter, R. 2003. Baby steps toward a conceptual model of predation in the Delta: preliminary results from the shallow water habitat predator-prey dynamics study. *IEP Newsletter* 16:19-27.
- Olson, AF, Quinn, TP. 1993. Vertical and horizontal movements of adult Chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. *Fishery Bulletin* 91:171-181.
- Perry, RW, Brandes PL, Sandstrom, PT, Ammann, A, MacFarlane, B., Klimley, AP, and Skalski, JR. Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin River Delta. In press. *North American Journal of Fisheries Management*.
- Perry, RW and Skalski, JR. 2009. Survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin River Delta during the winter of 2008-2009. Report to the USFWS, Stockton, Ca.
- Phillis, C, Ingram, L, Weber, PK. 2008. River and estuary rearing of successfully spawned adult Chinook salmon, determined by otolith Sr isotopes. Abstracts, 5th Biennial CALFED Science Conference; Sacramento, CA. p. p. 75.
- Pipel, KA. 2005. Summary of monitoring activities for ESA-listed salmonids in California's Central Valley. NOAA-TM-NMFS-SWFSC-373.
- Quinn, TP. 2005. The behavior and ecology of Pacific salmon and trout. Bethesda, Maryland: American Fisheries Society.
- Rich, AA. 1987. Report on studies conducted by Sacramento County to determine the temperatures which optimize growth and survival in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Sacramento, California: McDonough, Holland & Allen.
- Roth, JE, Mill, KL, Sydeman, WJ. 2007. Chinook salmon (*Oncorhynchus tshawytscha*) seabird covariation of central California and possible forecasting applications. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1080-1090.
- Rutter, C. 1904. Natural history of the Quinnot Salmon. *Bulletin of the United States Fish Commission* 22:65-142.
- Sacramento River Fall Chinook Review Team (SRFCRT). 1994. Sacramento River Fall Chinook Review Team Report. Portland, Oregon: Pacific Fishery Management Council.
- Sacramento-San Joaquin Estuary Fishery Resource Office (SSJEFRO). 2003. Abundance and survival of juvenile Chinook salmon in the Sacramento-San Joaquin Estuary. Stockton, California: U.S. Fish and Wildlife Service.
- Sandahl, JF, Baldwin, DH, Jenkins, JJ, Scholz, NL. 2004. Odor-evoked field potentials as indicators of sublethal neurotoxicity in juvenile coho salmon (*Oncorhynchus kisutch*) exposed to copper, chlorpyrifos, or esfenvalerate. *Canadian Journal of Fisheries and Aquatic Sciences* 61:404-413.
- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009a. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. *Evolutionary Applications*. doi: 10.1111/j.1752-4571.2009.00103.x
- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009b. Insights from a state dependent model of steelhead life history. *Transactions of the American Fisheries Society*. 2009b; 138:532-548.
- Scholz, NL, Truelove, NK, French, BL, Berejikian, BA, Quinn, TP, Casillas, E, Collier, TC. 2000. Diazinon disrupts antipredator and homing behaviors in Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:1911-1918.
- Scofield, NB. 1899. Notes on an investigation of the movement and rate of growth of the Quinnot salmon fry in the Sacramento River. Appendix to the Journals of Senate and Assembly of the thirty-third session of the legislature of the State of California .
- Scofield, N. B. A general report on a quinnat salmon investigation, carried on during the spring and summer of 1911. 1913. *Fish Bulletin* 1:35-41.
- Scofield, WL. 1920. King salmon marking experiment at Klamath River, 1919. *California Fish and Game* 6:101-103.
- Shapovalov, L, Taft, AC. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*). Sacramento: California Department of Fish and Game. *Fish Bulletin*

No. 98.

- Shreffler, DK, Simenstad, CA, Thom, RM. 1992. Foraging by juvenile salmon in a restored estuarine wetland. *Estuaries* 15:204-213.
- Simenstad, CTJ, Higgins, H, Cordell, J, Orr, M, Williams, P, Grimaldo, L, Hymanson, Z, Reed, D. 2000. Sacramento/San Joaquin Delta breached levee wetland study (BREACH). Preliminary Report. Seattle, Washington: University of Washington, School of Fisheries.
- Skinner, JE. 1962. Fish and wildlife resources of the San Francisco Bay Area. Sacramento, California: California Department of Fish and Game.
- Snider, B, Titus, RG. 2001. Lower American River emigration survey, October 1997-September 1998. Sacramento, CA: California Department of Fish and Game, Stream Evaluation Unit. Technical Report No. 01-6.
- Sommer, TR, Nobroga, ML, Harrell, WC, Batham, W, Kimmerer, WJ. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:325-333.
- Sommer, TR, Harrell, WC, Nobriga, M. 2005. Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. *North American Journal of Fisheries Management* 25:1493-1504.
- Stearns, SC, Hendry, AP. 2004. The salmonid contribution to key issues in evolution. *Evolution illuminated: salmon and their relatives*. New York: Oxford University Press.
- Stewart, DC, Middlemas, SJ, Youngson, AF. 2006. Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish* 15:552-558.
- Tallman, RF, Healey, MC. 1994. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta*. *Canadian Journal of Fisheries and Aquatic Sciences* 48:661-671.
- The Bay Institute (TBI). 1998. From the Sierra to the sea: the ecological history of the San Francisco Bay-Delta watershed. Novato, California: The Bay Institute. http://www.bay.org/sierra_to_the_sea.htm (2005)
- Thorpe, JE. 1977. bimodal distribution of lengths of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *Journal of Fish Biology* 11:175-184.
- Thorpe, JE. 1989. Developmental variation within salmon populations. *Journal of Fish Biology* 35(Supplement A):295-303.
- Thorpe, JE, Mangel, M, Metcalfe, NB, Huntingford, FA. 1998. Modeling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* 12:581-599.
- Titus, RG, Volkoff, MC, Snider, WM. 2004. Use of otolith microstructure to estimate growth rates of juvenile Chinook salmon from a Central Valley, California stock. In: Feyrer, FL, Brown, RL, Orsi, JJ, editors. *Early life history of fishes in the San Francisco Estuary and watershed*. American Fisheries Society Symposium 39. Bethesda, Maryland: American Fisheries Society. p. 181-202.
- Weatherley, AH, Gill, HS. 1995. Growth. In: Groot, C, Margolis, L, Clarke, WCC, editors. *Physiological ecology of Pacific salmon*. Vancouver, British Columbia: University of British Columbia Press.
- Werner, I, Smith, TB, Feliciano, J, Johnson, ML. 2005. Heat shock proteins in juvenile steelhead reflect thermal conditions in the Navarro River Watershed, California. *Transactions of the American Fisheries Society* 134:399-410.
- Williams, JG. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed Science* 4: <http://repositories.cdlib.org/jmie/sfews/vol4/iss3/art2>
- Williamson, KS, May, B. 2005. Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* 25:993-1009.
- Wilson, MF. 1997. Variation in salmonid life histories: patterns and perspectives. Portland, Oregon: USDA, Forests Service, Pacific Northwest Research Station. Research Paper.
- Yoshiyama, RM, Gerstung, ER, Fisher, FW, Moyle, PB. 2001. Historical and present distribution of Chinook salmon in the Central Valley drainage of California. In: Brown, RL, editor. *Fish Bulletin 179: Contributions to the biology of Central Valley salmonids*. 1. Sacramento: p. 71-176.
- Yoshiyama, RM, Gerstung, ER, Fisher, FW, Moyle, PB. 1996. Historical and present distributions of Chinook salmon in the Central Valley drainage of California. In: *Sierra Nevada Ecosystem Project, Status of the Sierra Nevada, Volume III. Final Report*. p. 309-362.