Chinook Salmon in the Lower American River, California's Largest Urban Stream

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Abstract

The American River now supports a mixed run of hatchery and naturally-produced fall-run chinook averaging about 30,000 spawners; the spring-run was lost to dams. Salmon in the river have been much studied over the last 20 years, largely because of litigation over proposed diversions, but much uncertainty remains about various aspects of their biology and about the environmental conditions needed to support them. This paper briefly reviews what is known and not known about salmon in the American River and makes recommendations for future work.

Introduction

The American River is the second largest tributary of the Sacramento and supports a mixed run of hatchery and naturally produced fall-run chinook salmon. Salmon in the American River have been intensively studied, largely because of litigation challenging a proposed diversion of water, but much remains to be learned. Here I review what is known about chinook salmon in the American River and give suggestions for future work.

Folsom Dam, a Central Valley Project facility completed in 1955 about 30 miles upstream from the Sacramento River, creates a 975,000 acre-foot reservoir and regulates flows in the reach now accessible to salmon. Salmon migration is blocked at river mile 23 by Nimbus Dam, a regulating facility for Folsom hydropower operations that also diverts a small amount of water into the Folsom-South Canal. Below Nimbus Dam, the lower American River flows through a parkway, surrounded by urban development and is a major recreational area for the Sacramento region. The American River is designated as a recreational river in the state and federal wild and scenic river systems. On average, tens of thousands of hatchery or naturally produced chinook salmon return each year to spawn in California's largest urban stream.

In natural conditions the American River supported spring, fall, and perhaps late fall chinook. Historical data on the upstream extent of salmon migrations are summarized in Yoshiyama and others (Volume 1). Salmon runs were devastated by hydraulic gold mining, and in 1886 the California Fish Commission reported that:

The American River is a shallow, muddy stream and empties into the Sacramento River at Sacramento City. But few fish are found in the lower parts of the stream. Trout are found in some of its branches above the mining districts—notably Silver River and the Rubicon. This river, prior to placer mining, was one of the best salmon streams in the state. Of late years no salmon have ascended it.

Salmon can be resilient, however; 44 years later, G. H. Clark (1929) wrote that although the old Folsom Dam blocked passage for salmon the area downstream supported a large run.

The run of salmon into the American River has always been a late fall migration[1] *and like the other rivers has known great runs. In 1927–1928 there was a very good run in the river, which has shown the inhabitants no noticeable decrease in the last twenty years. It was reported that the run of salmon in this river had been destroyed by the early mining operations. Such may have been the case, but since then the run has returned and has remained fairly constant, according to the observations of local residents.*

Clark reported that the old Folsom Dam, constructed in the late 1890s, effectively blocked salmon passage although it had a ladder that passed steelhead. Subsequent ladder counts showed a few spring-run chinook, but any prospect for restoring that run were dimmed considerably by construction of Folsom and Nimbus dams.

Physical Setting

The American River drains a roughly triangular watershed of about 1,900 square miles that is widest at the crest of the Sierra and narrows almost to the width of the river at its confluence with the Sacramento River at Sacramento. As described in USACE (1991):

The American River drainage basin above Folsom Dam is very rugged, with rocky slopes, V-shaped canyons, and little flat valley or plateau area. Elevations range from 10,400 feet at the headwaters to about 200 ft at Folsom Dam, with an average basin slope of 80 feet per mile. The upper third of the basin has been intensely glaciated and is alpine in character, with bare peaks and ridges, considerable areas of granite pavement, and only scattered areas of timber. The middle third is dissected by profound canyons, which have reduced the inter-stream areas to narrow ribbons of relatively flat land. The lower third consists of low rolling mountains and foothills.

Below Folsom, the watershed flattens into the Central Valley, but the river remains confined or semi-confined by resistant Pleistocene fan deposits or by

1. Presumably these were fall-run chinook that spawned later than runs in some other rivers, like the current run, rather that late fall-run fish.

levees and has only a narrow flood plain that has been aggraded by debris from hydraulic mining. The channel of the lower American River is described in Snider and others (1992), and Beak Consultants and others (1992). Generally, the gradient of the river decreases over the 23 miles between Nimbus Dam and the Sacramento River, and the size of the particles making up the bed decreases from cobble and gravel to sand. This transition is not smooth, however, and there are large pools separated by steeper reaches along much of the lower river.

Snider and others (1992) divided the lower American River into three reaches (Figure 1). Reach 1, the 4.9 miles from the Sacramento confluence to Paradise Beach, has a very low gradient and sand bed. Depth is normally controlled by the stage in the Sacramento River, rather than discharge, and varies with the tide. Reach 2 includes the 6.7 miles of channel from Paradise Beach to Gristmill, with some slope (average gradient about 0.0005). The bed is mainly sand, but includes some gravel riffles. Reach 3 covers 11.1 miles from Gristmill to the weir at Nimbus Hatchery with more slope (average gradient about 0.001). The bed is mainly gravel, but the river is still characterized by long pools separated by riffles. The average width of the river at a flow of 1,000 cfs in the three reaches is 350, 375, and 275 feet.

The annual discharge in the river averages about 3,750 cfs, or about 2,710,000 acre-feet per year, but has varied from 730 to 7,900 cfs. Runoff comes from winter rains at lower elevations and from spring snowmelt at higher elevations, but very high flows all result from winter storms. Discharge is regulated by various dams, of which Folsom is the largest, with past and present direct diversions being relatively minor. The main hydrological effect of the dams has been to dampen variance in winter runoff and to store snowmelt for release in the spring to meet irrigation demand, mainly in the San Joaquin Valley, with the variance and timing of runoff being changed more than the total amount.

"Natural" mean monthly flows have been estimated by the Bureau of Reclamation (Figure 2A), and on average rise to a peak in May and drop to low levels in August through October. Flows reflecting diversions, regulations, and operating practices in effect in 1993 have been estimated by the Sacramento Area Flood Control Agency (Figure 2B) and show less variation over the year and within winter and spring months, but more variation within summer and early fall months. Comparison of daily flows from the moderately dry years 1908 and 1992 shows these effects in more detail (Figure 3). Because Folsom Reservoir is relatively small compared to the mean annual flow in the river; however, reductions in peak flows in wet years have been moderate (Figure 4), and geomorphically effective flows still occur with some frequency.

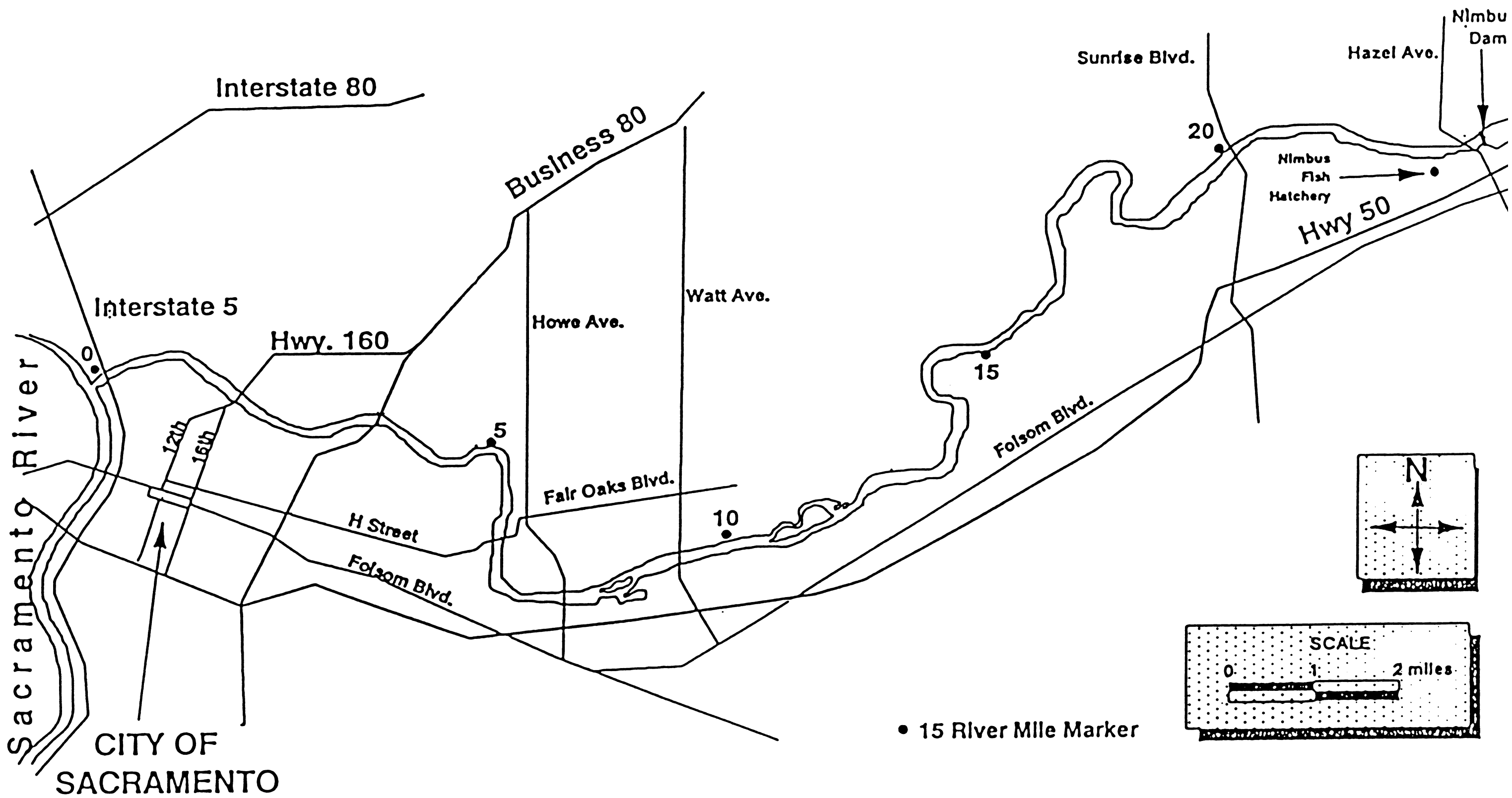

Figure 1 Map of the lower American River taken from Snider and others (1992)

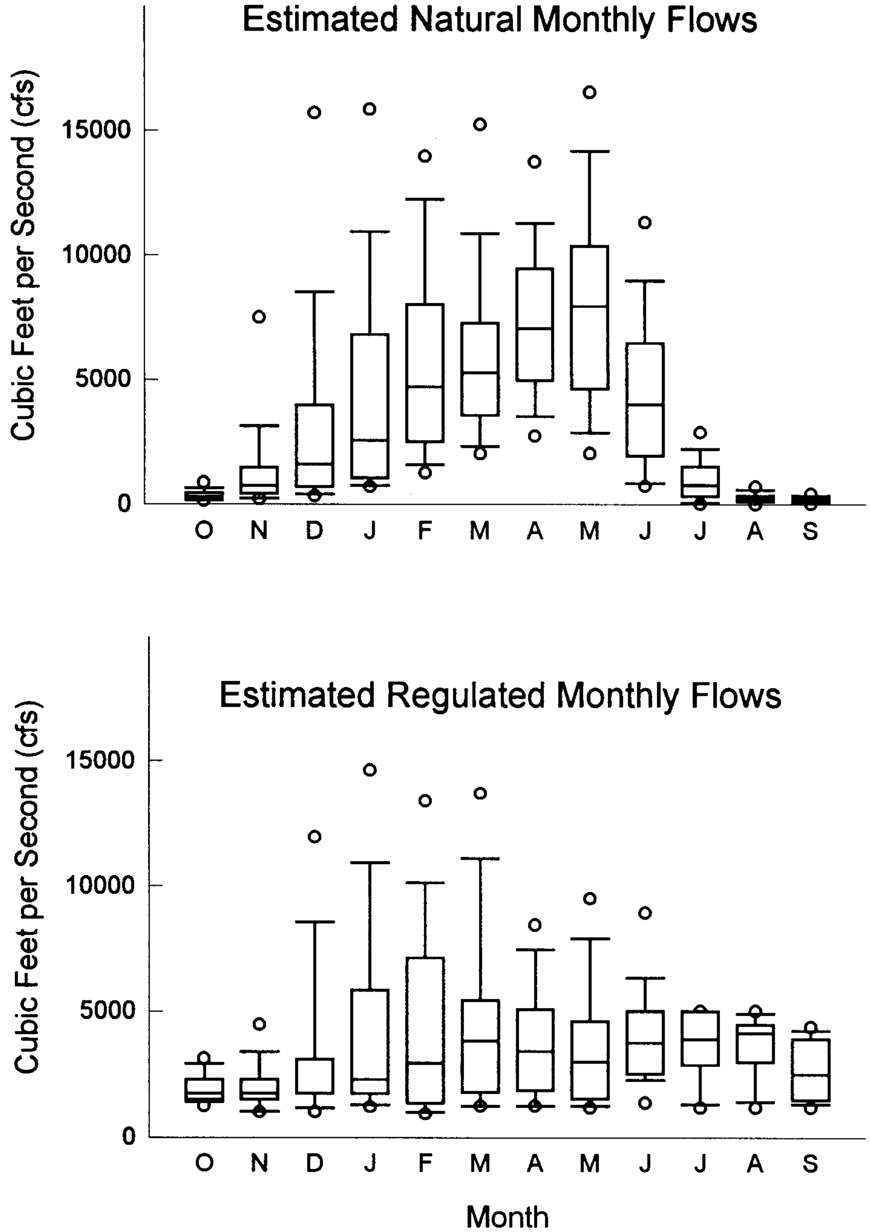

Figure 2 Comparison of the distributions of mean monthly flows in the lower American River for natural conditions (upper panel) and simulated 1993 conditions, assuming the same climatic conditions (lower panel). In the box plots for each month, the "box" covers the central 50% of the data, from the 25th to the 75th percentiles, the solid line across the box shows the median, and the dashed line shows the mean. The "whiskers" extend to the 10th and 90th percentiles, and the circles show the 5th and 95th percentiles. Note that the 1993 simulated flows do not reflect recent corrections to PROSIM, the operations model used for the simulations, or recent changes in CVP operations.

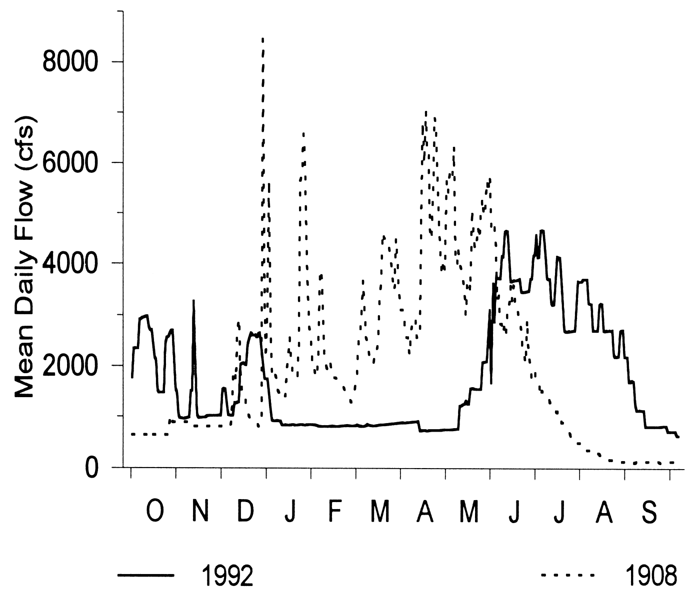

Figure 3 Comparison of flow in the American River in two dry years with approximately equal total discharge, illustrating the effects of regulation on the seasonality and variability of flow

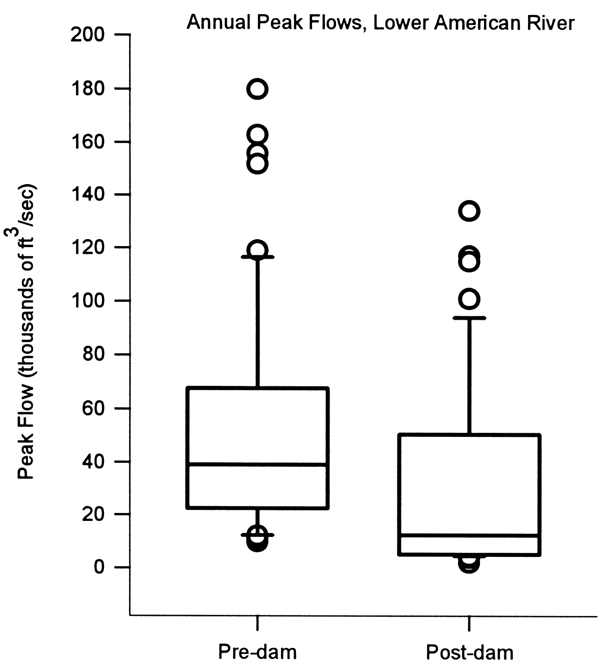

Figure 4 Comparison of the pre- and post-Folsom distributions of peak flows in the lower American River. Box plot conventions are as in Figure 2, except that circles show all values beyond the 5th and 95th percentiles. Data from USGS Fair Oaks gage.

The Hodge Decision

In 1970, the East Bay Municipal Utility District (EBMUD) negotiated a contract with the Bureau of Reclamation to take up to 150,000 acre-feet of water annually from the American River, through the Folsom-South Canal. The Environmental Defense Fund (EDF), Save the American River Association (SARA), and Sacramento County sued to block the contracts in 1972. Over the next 17 years, the California Department of Fish and Game (DFG) and the State Lands Commission (SLC) joined the litigation, the case went to the California Supreme Court twice, to the United States Supreme Court once, and to the State Water Resources Control Board (SWRCB) for a report of referee, before coming to trial in the Alameda County Superior Court of Judge Richard Hodge in 1989.

Simply put, the question was whether EBMUD could divert water through the Folsom-South Canal, or whether it must divert the water at some point farther downstream, so that the water could also serve instream uses. EBMUD wanted to divert through the canal because water quality decreases downstream. In its Report of Referee, the SWRCB recommended that EBMUD could divert through the canal, provided that certain instream flow standards were met. These standards were acceptable to EBMUD, but not to the plaintiffs. When the case went back to the Alameda County Superior Court, the substantive issues concerned the relation between water quality and public health on one hand and instream flow needs on the other.

Judge Hodge ruled that EBMUD could take water through the Folsom-South Canal, provided that enough water remained in the river to protect public trust resources. Based on the evidence in the record, Judge Hodge determined that "enough" meant: October 16 through February, 2,000 cfs; March through June, 3,000 cfs; July through October 15, 1,750 cfs. These flow standards, which apply to the whole 23-mile reach from Nimbus Dam to the Sacramento River confluence, are to remain in effect unless evidence is developed that justifies changes. The conditions apply only to diversions by EBMUD or by other parties to the litigation. Because the Bureau of Reclamation was not a party, the standards do not control the Bureau's operation of Folsom.

Judge Hodge emphasized that the evidence presented was inadequate to support a final determination of the flows necessary to protect public trust resources, however, so he retained jurisdiction, ordered the parties to cooperate in scientific studies to reduce the uncertainty regarding the necessary flows, and appointed the author as special master to supervise the continuing jurisdiction (Hodge 1990):

Perhaps the most salient aspect of the fishery/hydrology testimony consists of its large area or remaining uncertainty. …The task for this court is to recognize the fundamental inadequacy of existing studies as they relate to the American River, to extract from the 'consensus' and from the testimony those factors which can provide a guide for protecting fishery values, and significantly, to retain jurisdiction until the scientific community can provide definitive answers. (p 88, 95).

By emphasizing scientific uncertainty and framing a course of action that protects public trust resources while taking uncertainty into account, the Hodge Decision provides a good example of adaptive management (Castleberry and others 1996; Williams 1998).

Instream Flow Standards

In 1958, the SWRCB issued Decision 893, which granted the Bureau of Reclamation a permit for Folsom Dam, and set very low instream standards for the lower American River: 500 cfs from mid-September through October and 250 cfs otherwise. These remain the nominal state standards. The SWRCB set higher standards in Decision 1400, regarding Auburn Dam (for fish, 1,250 cfs from mid-September through June, 800 cfs otherwise), but since Auburn has not been constructed, these have not been binding. Nevertheless, the Bureau typically managed the lower American River to meet an approximation of the D-1400 standards called the "modified" D-1400 standards. [Why the SWRCB has never made the D-1400 standard applicable to Folsom is a fair question, but it has not. And as noted above, the Hodge standards only apply to diversions by the parties.] Since late 1997 the Bureau has operated Folsom with flow objectives set by the Anadromous Fish Restoration Plan (AFRP) (Table 1), developed under the Central Valley Project Improvement Act (CVPIA) which became law in 1992. Besides operating Folsom to meet the AFRP flows, the Bureau now meets regularly with the resource agencies and other interested parties to review details of dam operations.

Table 1 AFRP flow objectives for the lower American River

Month	*Wet*	*Above and below normal*	*Dry and critically dry*	*Critical relaxation*
October	2,500	2,000	1,750	800
November to February	2,500	2,000	1,750	1,200
March to May	4,500	3,000	2,000	1,500
June	4,500	3,000	2,000	500
July	2,500	2,000	1,500	500
August	2,500	2,000	1,000	500
September	2,500	1,500	500	500

As the AFRP flow objectives suggest, the amount of water available in the American River is limited in many years, and allocation of water to instream flows involves trade-offs among seasons, life-stages, and species, especially chinook and steelhead. Hence there is a need to understand the expected benefits of different seasonal flow regimes, typically in the face of uncertainty about future inflows to Folsom Reservoir and so about the amount of water that will be available to allocate in subsequent seasons. For example, a decision about how much water to allocate for spawning flows requires more than an understanding of the relation between flow and spawning habitat; it also requires an understanding of the importance of flows for juveniles and of the probability that water will be available for rearing flows, which will depend on post-spawning weather. One recent attempt to address this problem depended on the subjective assessment of biologists and did not spell out the rationale for the recommended allocation rules (Bratovich and others 1995), making it impossible to test the assumptions underlying the rules and to revise them in light of new information. A more transparent framework based on explicit assumptions and hypotheses is needed for guiding allocation decisions. Decision analysis (Peterman and Anderson 1999) seems well suited for this purpose.

Salmon in the American River

The EDF vs. EBMUD "Consensus"

With the agreement of the parties, Judge Hodge had the fish experts for both sides in the trial meet in closed session, without attorneys, to see how much agreement they could reach among themselves. The result was a "Report on Agreements and Recommendations," referred to elsewhere in the decision as the "consensus," that provides a useful summary of the understanding of chinook salmon at the time.

Life History Periodicities

1. Adult fall run chinook salmon are known to enter the lower American River from approximately mid-September through January. There is a high year-to-year variability; however, the bulk of the migration occurs from approximately mid-October through December.

2. Adult chinook salmon are known to spawn in the lower American River from approximately mid-October through early February. There is high variability from year to year; however, the bulk of the spawning occurs from approximately mid-October through December.

3. Chinook salmon egg and alevin incubation is known to occur in the lower American River from approximately mid-October through April. There is high variability from year to year; however, most incubation occurs from approximately mid-October through February.

4. Chinook salmon fry emergence is known to occur in the lower American River from January through mid-April.

5. Chinook salmon young-of-the-year juvenile rearing is known to occur in the lower American River from January to approximately mid-July. There is high year-to-year variability; however, the bulk of the rearing occurs from February through May. During March 1989, a few yearling chinook salmon were collected in the lower American River, suggesting that some fish may rear year round.

Water Temperature

1. Based on the scientific literature, the range of water temperatures for highest survival of incubating chinook salmon eggs appears to be between 43 °F to 58 °F. Prolonged (that is, more than a few days) exposure of eggs to temperatures in excess of 58 °F results in high egg mortality. 62 °F should be avoided.

2. Any definition of an “optimum” water temperature or temperature range for juvenile chinook salmon should include a synthesis of information on the effects of temperature on (a) growth rates; (b) effects on and availability of food supply ration; (c) predation; (d) disease; (e) stimulation of emigration; (f) physiological transformation to endure seawater; and (g) acclimation to the waters of the Lower Sacramento River and Delta when warmer than the American River.

Consensus on the optimum temperature range could not be reached.

Flow Needs

1. SWRCB Decisions 893 and 1400 are inadequate to meet the chinook salmon spawning habitat management objective for the lower American River.

2. The group could not reach consensus on the optimum spawning flow (or range of flows) needed to meet the fishery habitat management objective for chinook salmon in the lower American River.

3. Consensus could not be reached on the levels of flow required to provide optimum rearing habitat needed for juvenile chinook salmon in the lower American River.

4. SWRCB Decision 893 does not provide adequate rearing flows to meet the fish habitat management objective of maximizing the in-river production of juvenile chinook in the lower American River.

Recent Escapement Data

Both naturally and hatchery produced chinook salmon now spawn in the lower American River. Escapement has been estimated for several decades (Figure 5) and is highly variable but averages around 30,000. The data need to be regarded with considerable caution (Williams 1995). Returns to the hatchery are counts, but escapement to the river is estimated from mark-recapture methods applied to carcasses. Rich (1985) detailed problems with early estimates, and even recent estimates based on intensive carcass surveys involve great uncertainty, arising both from sampling errors and from the methods used to make estimates from the observations. Since 1976, DFG has used a modification of the Schaefer method, a multi-sample version of the Peterson method, but recently has reported estimates based on the Jolly-Seber method (e.g., Snider and Reavis 1996). For 1995, for example, the Schaefer estimate of escapement to the river was 70,096, while the Jolly-Seber estimate was 42,973, or 61% of the Schaefer estimate. The methods have been evaluated on Bogus Creek, a small tributary of the Klamath River for which weir counts are also available (Sykes and Botsford 1986; Boydston 1994; Law 1994), but conditions are less favorable for mark-recapture studies on larger rivers where a smaller percentage of marked fish are recaptured (Boydston 1994). Mark-recapture methods are also used to estimate escapement on other large rivers in the Central Valley and an evaluation by a competent statistician of their use on such rivers is sorely needed, as is a method for developing confidence intervals for the estimates.

The percentage of hatchery-produced fish among spawners in the American River is unknown, but presumably is large. Dettman and Kelley (1986) tried to evaluate this percentage; but as demonstrated by Hankin (1988) their calculations used so many approximate numbers and assumptions that it is hard to assign meaning to their results. Cramer (1992) applied a more sophisticated approach to the same question but the basic problem arises from the nature of the available data rather than the particular approach taken, so his estimates are also highly uncertain. For example, the results would depend on whether one used Schaefer or Jolly-Seber estimates of escapement. Cramer (1992, p 99) acknowledges this uncertainty:

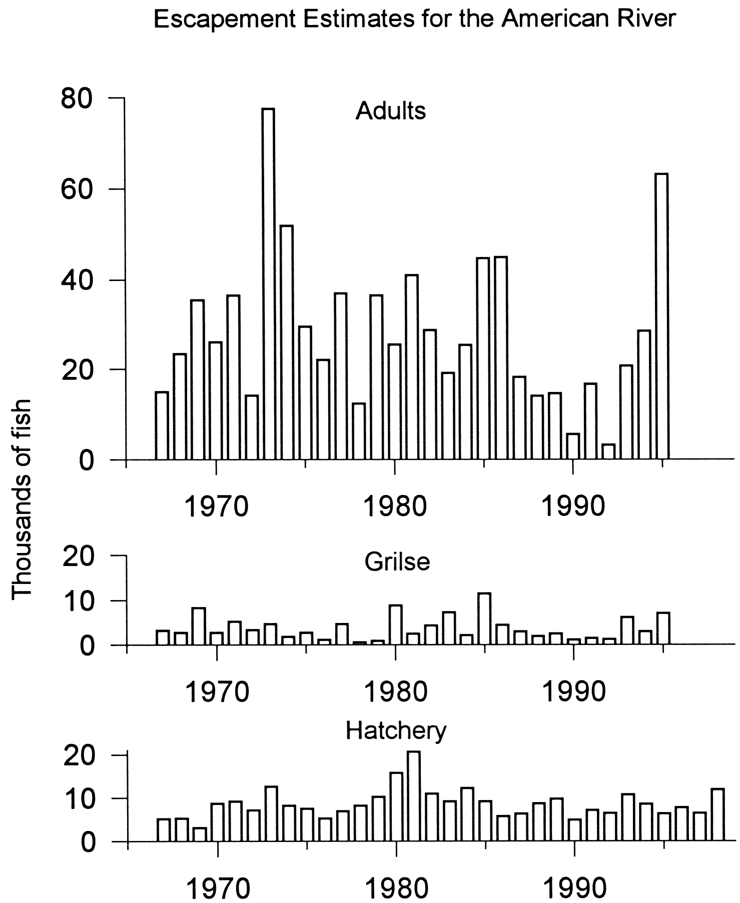

Figure 5 Escapement estimates for the lower American River from carcass surveys for "adults" and grilse, and counts at Nimbus Hatchery. Note that criteria for distinguishing grilse are not consistent and are of uncertain biological meaning (Williams 1995, p 100).

> *I conclude from these comparisons that Dettman and Kelley's predications of the escapement of hatchery fish are too high. However, evidence cited in this chapter also indicates escapement of hatchery fish predicted by run reconstruction may be too low. Clearly, hatchery and natural contributions cannot be estimated with confidence until a well designed marking program of hatchery fish and wild fish, extended to all release types, is initiated and systematic sampling is begun for all major spawning areas and river fisheries.*

It is remarkable that almost eight years after passage of the CVPIA, which calls for doubling the number of naturally produced anadromous fishes, the proportion of the salmon spawning in Central Valley rivers that are of hatchery origin remains unknown.

Hatchery Production

About half the chinook spawning habitat below Folsom was inundated by Nimbus Dam and Lake Natoma (USFWS and DFG 1953). Nimbus Hatchery was constructed to mitigate only for the spawning and rearing habitat inundated by Nimbus Dam and Lake Natoma, since passage of salmon was largely blocked by the Old Folsom Dam [loss of the opportunity to build a successful ladder over that dam apparently was not considered]. Nimbus now operates with a target of producing 4 million smolts for release in the estuary from May to July, for which it may collect up to 8 million eggs, distributed over the spawning season. The target size at release is 60 per pound (7.6 grams) or larger. Nimbus hatchery production of fingerlings for recent years is given in Table 2[2].

In the past, Nimbus Hatchery typically hatched more fry than it could rear, and over the period 1955–1967 released an average of almost 14 million fry annually. Emphasis then shifted toward producing larger juveniles, and average production of fry dropped to 3 million annually for 1968–1984 (Dettman and Kelley 1987). After 1990, fry were released into the Sacramento River at Garcia Bend so not to interfere with studies in the American River. But this too has recently ended; beginning with brood year 1998, DFG policy has been to rear to smolts all eggs hatched, and to limit egg take to meet smolt production goals (Bruce Barngrover, DFG, 1999, personal communication).

Table 2 Production of chinook salmon by Nimbus Hatchery [a]

Brood year	*Fingerlings (≤ 7.6 grams, 90 mm)*	*Advanced fingerlings (> 7.6 grams)*
1985	5,241,020	3,139,240
1986	3,167,680	3,040,375
1987	1,257,770	4,278,750
1988	---	3,210,570
1989	7,437,911	4,092,000
1990	6,069,505	1,244,800
1991	9,218,652	1,734,200
1992	7,930,390	1,988,700
1993	7,940,000	1,183,900
1994	8,103,143	1,378,100

[a] Data from California Department of Fish and Game.

2. Data for earlier years are available in Dettman and Kelley (1986) or Cramer (1992), but are given in different size categories.

The biological consequences of hatchery production for chinook salmon in the American River are unclear, but merit more attention. (General concerns about the effects of hatchery production on salmon populations are reviewed in NRC [1996]; see also Hilborn [1999]). Recent studies in New Zealand have shown that hatchery fish can replace naturally produced chinook rather than supplement them (Unwin 1997), probably because of density-dependent mortality in early ocean life, and some biologists believe that the same is true here (Walters 1997; Hilborn 1999). Hatchery production can lead to changes in life history patterns (Unwin and Glova 1977). Unwin (1997) also found that the size-adjusted mortality rates of hatchery fish were much higher than naturally produced fish, even though many of the naturally produced fish were progeny of hatchery fish.

One possible consequence of hatchery production on American River chinook may be decreased fecundity (discussed in the following paragraphs). Another possible indication of detrimental biological effects of hatchery production involves the composition of otoliths. The calcium carbonate in salmonid otoliths normally occurs as aragonite, which is opaque, and all the juvenile salmon sampled from the American River by Castleberry and others (1991, 1993) had opaque otoliths. However, some transparent otoliths were noted in juveniles from Nimbus Hatchery during supplemental work on marking otoliths with oxytetracyline (D. Castleberry, USFWS, 1995, personal communication). In transparent otoliths, the calcium carbonate occurs as vaterite. Such otoliths have been observed in high frequencies in some hatcheries in British Columbia, and there is concern that vaterite otoliths reflect inbreeding. Additionally, in British Columbia some of vaterite otoliths are also misshapen, raising concerns about how well they function (Blair Hotlby, June 1992, personal communication).

Life History Patterns

Chinook salmon remaining in the American River are fall-run, ocean-type fish that migrate to the ocean within a few months of emerging. Fish of this life history pattern simply avoid the period when flows in Central Valley rivers are naturally low and warm. Although late summer flows in the lower American River are now much higher and somewhat cooler than in natural conditions (Williams 1995), conditions are still unsuitable for chinook rearing, and water temperature in the lower Sacramento River often becomes very warm for juvenile chinook in late May or early June. Juveniles that fail to emigrate before the Sacramento River gets too warm probably have little chance of survival.

Spawning

Adult salmon appear in the American River in July, but many local biologists and fishermen believe that these early arrivals are hatchery strays from the Feather River, where spawning begins earlier than in the American. Spawning in the American River begins in October or November, typically when the water cools to about 15.5 °C (60 °F), approximately the temperature at which egg survival is possible. Facilities for controlling the temperature of releases from Folsom Dam were improved in 1996, and salmon responded by starting to spawn about two weeks sooner than had been common in the past. In 1997 water remained above 15.5°C until mid-November, however, and spawning was similarly delayed (Kris Vyverberg, DFG, 1999, personal communication). This variation in timing supports the hypothesis that water temperature rather than some correlated variable such as day length mainly controls the initiation of spawning.

Chinook redds normally show up well in aerial photographs of the American River because the water is usually clear and undisturbed gravel has a darkening surface layer of algae. Aerial photographs have been taken at intervals throughout the spawning season since 1991, producing a good record of where and when salmon spawn, at least for the early part of the season (Figure 6). Later, the popular areas are dug up so thoroughly that it is no longer possible to see individual redds or estimate the numbers of spawning fish from the photographs (Snider and Vyverberg 1996). Nevertheless, the approach should allow development of an empirical relation between flow and spawning habitat. The aerial photography also shows that spawning sites are related to geomorphic features in the channel that promote subsurface flow, as reported for the Columbia River by Geist and Dauble (1998).

Snider and Vyverberg (1996) report data on redd size, which is substantially smaller when measured on the ground (average 62 ft^2) than when measured from aerial photographs (average 196 ft^2). They discuss possible reasons for the difference, but until the matter is further clarified estimates of superimposition based on aerial photography should be viewed with some caution. Nevertheless, superimposition data (Table 3) indicate that density-dependent mortality can occur during spawning, and tends to vary inversely with flow (Snider and Vyverberg 1996).

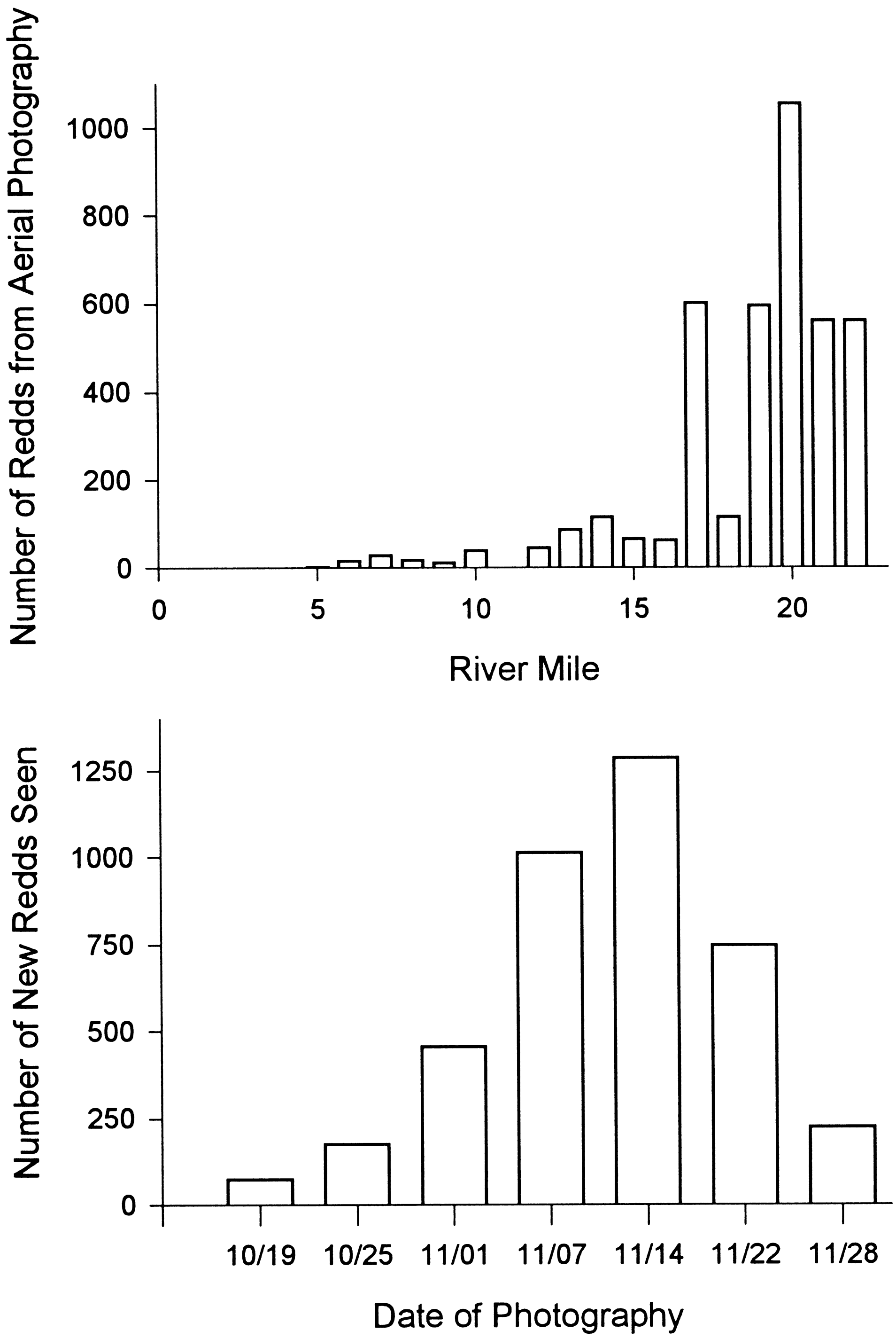

Figure 6 The spatial and temporal distribution of spawning in the lower American River in 1995. Data from Snider and Vyverberg (1996).

Table 3 Observed superimposition of redds, 1991–1995 [a]

Year	*Percent of redds superimposed*	*Number of redds affected*	*Escapement estimate*	*Average flow (cfs)*
1991	8	137	18,145	1,200
1992	42	474	4,472	500
1993	19	1,156	20,820 – 26,786	1,750
1994	17	450	26,881 – 31,333	1,500
1995	1.3	51	42,924 – 69,892	2,625

[a] Data from Snider and Vyverberg (1996); where two escapement estimate are given the first is a Jolly-Seber estimate, others are Schaefer estimates. There is a slight discrepancy between population estimates for 1995 given here for 1995 and those in Snider and Reavis (1996).

Spawning gravels in the lower American River are well described by Vyverberg and others (1997), who used both bulk sampling and pebble counts to estimate gravel size distributions and characterized intragravel conditions in terms of dissolved oxygen, water temperature, and hydraulic permeability. Gravel conditions are generally good but there are subsurface layers of coarse gravels that inhibit redd construction in some areas. These coarse gravels probably are deposits of stones too large for salmon to move during spawning in previous years. Vyverberg and others (1997) proposed that substrate conditions in these areas probably could be improved by "ripping" the gravel to break up the subsurface layers and to reduce compaction, which was done in late summer 1999 with an experimental design that includes pre- and post-project data collection in both treatment and control areas. Gravel was also added to the river as part of this project, funded through the CVPIA, despite a finding by Vyverberg and others (1997) that addition of gravel may not be necessary.

Vyverberg and others (1997) also showed that there is a good relation between the areas where salmon spawn and the permeability of the gravel and the estimated rate of subsurface flow, but the traditional microhabitat variables of depth and velocity do not distinguish areas that are used from those that are not (Figures 7 and 8). This should not be a surprise. According to Healey's review of chinook salmon life history (Healey 1991):

> *Provided the condition of good subgravel flow is met, chinook apparently will spawn in water that is shallow or deep, slow or fast, and where the gravel is coarse or fine.*

Nevertheless, the data provide further evidence that weighted usable area (WUA), the statistic calculated by the Physical Habitat Simulation Model (PHABSIM), is not a good measure of chinook spawning habitat because it ignores subsurface flow, the factor that seems most important to the fish. Gallagher and Gard (1999) reported statistically significant relations between WUA and the number of redds in PHABSIM "cells" in the American and Merced rivers, but the relations are not strong (r^2 = 0.40 and 0.38 respectively) and the study was conducted in areas that salmon were known to favor for spawning, and so presumably had good subsurface flow. Whether there is much of a relation between WUA and number of redds in randomly chosen areas of the river is unknown but doubtful in light of the results in Vyverberg and others (1997) on the American River and Geist and Dauble (1998) on the Columbia River.

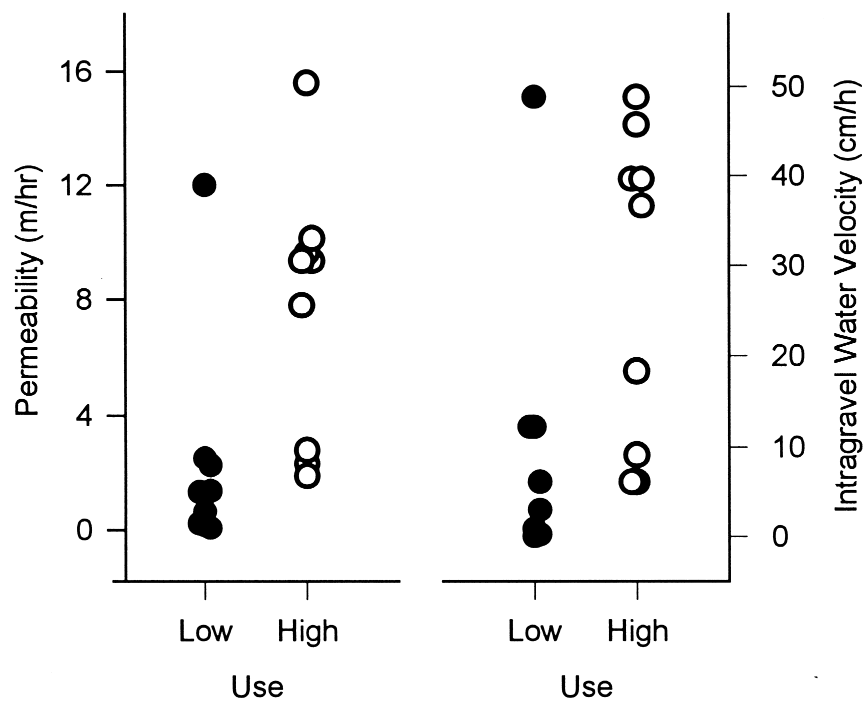

Figure 7 Permeability and estimated intragravel water velocity at ten sites that are selected (open circles) or avoided (closed circles) for spawning by chinook salmon. Data from Vyverberg and others 1997).

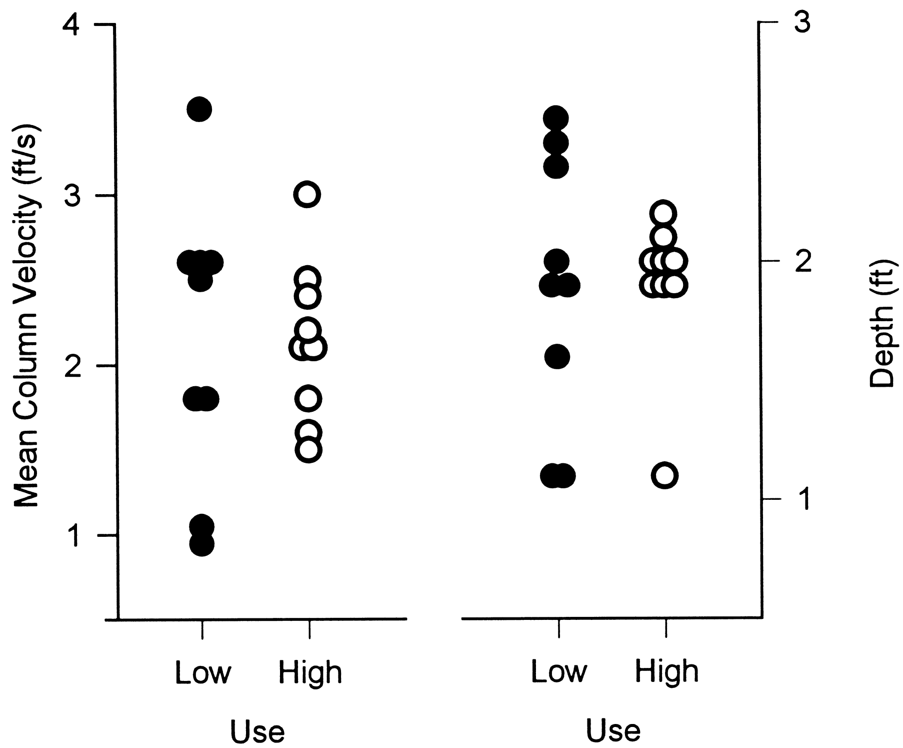

Figure 8 Mean column water velocity and depth at ten sites that are selected (open circles) or avoided (close closed circles) for spawning by chinook salmon. Data from Vyverberg and others (1997).

Pre-Spawning Mortality

The percentage of females that spawn completely before dying varies from year to year, ranging from 94% in 1993 to 68% in 1995 in samples of several hundred fish examined during DFG escapement surveys (Table 4) (Snider and others 1993, 1995; Snider and Bandner 1996; Snider and Reavis 1996). The reasons for the variation are not obvious; high proportions of unspawned carcasses were found in 1995 well into the spawning season, when water temperature should not have been a problem, and effective density as measured by redd superimposition was low. These data also illustrate the danger of drawing quick conclusions from short-term studies.

Table 4 Observed pre-spawning mortality (percent) from 1992 to 1995[a]

	1992	*1993*	*1994*	*1995*
Fully spawned	92%	94%	74%	68%
Partially spawned	3%	3%	9%	13%
Unspawned	5%	3%	17%	19%

[a] Data from Snider and Reavis (1996).

Incubation

Incubation is relatively rapid for fall-run chinook salmon in Central Valley streams because the water is warm compared to more northerly streams; in the lower American River water temperature usually averages between 6 and 9 °C in January, the coldest month. There are no available data on mortality during incubation on the American River. Emergence traps deployed in 1996 and 1997 were destroyed by high flows. However, Vyverberg and others (1997) estimated mortality using published relations between survival and gravel size (Tappel and Bjornn 1983) and between survival and intragravel water velocity (Gangmark and Bakkala 1960). There was no clear relation between the two estimates, which varied from 66% to 100% at 18 sites based on gravel size, and from 54% to 79% based on intragravel water velocity, except that estimates based on gravel size were always higher. Intragravel water velocity is directly related to the supply of oxygen to the eggs and alevins and the removal of metabolic wastes and seems a sounder basis for estimating survival.

Emergence

The timing of emergence depends on the timing of spawning and on water temperature, which strongly affects the rate of development of eggs and alevins. Chinook fry have been captured as early as late November in recent DFG studies (Snider and others 1998), earlier than suggested by the EDF vs. EBMUD “consensus.” This change may reflect new sampling methods (rotary screw traps), and perhaps the relatively warm water temperature in the fall and winter of 1995–1996. Fry usually begin to emerge in large numbers in January and continue to emerge until April, or even later in some years (Snider and Keenan 1994).

Juvenile Rearing

Although most juvenile chinook leave the American River shortly after emerging, some rear in the river for a few months before emigrating. Even of this group, however, most are gone by mid-May and relatively few remain in June based on both trap (Snider and Titus 1995; Snider and others 1997, 1998) and seine data (Brown and others 1992; Snider and McEwan 1993; Snider and Keenan 1994; Snider and Titus 1996). Snider and others (1998) note that juvenile chinook now emigrate earlier in the year than when the USFWS operated fyke traps on the river in 1945–1947 (USFWS and DFG 1953). Warmer water during the incubation period resulting from the thermal effects of Folsom Reservoir seems the most likely explanation for this change (Rob Titus, DFG, 1999, personal communication).

Jackson (1992) observed habitat use by juvenile chinook in late April or early May at two flows, 350 cfs in 1991 and 3,700 cfs in 1989. Although his efforts were hampered by poor visibility, he summarized his observations as follows (p 104–105):

> *Juvenile chinook salmon in the lower American River exhibited trends in habitat selection and behavior similar to what has been observed by other researchers in other rivers. Juvenile chinook salmon occurred in groups of two fish to schools of thousands and ranged from 50 to 120 mm (FL), but predominantly were 50 to 80 mm in length. Schools were always associated with cover which provided visual and/or velocity shelter, the latter was utilized most often. As the juvenile chinook salmon became larger (80 to 120 mm), a progression toward deeper and faster water was observed. The larger fish were either paired or more often alone utilizing large cobble/boulder substrate as velocity cover and would move quickly from their shelter to feed on drift organisms. Individual chinook salmon were aggressive and territorial.*
>
> *During the high flow period a considerable amount of terrestrial vegetation was submerged and utilized extensively by juvenile chinook salmon. Root wad/debris jams were limited in quantity in the upper two reaches of the lower American River. These were utilized extensively and provided a significant juvenile chinook salmon microhabitat niche. On all occasions where root wad/woody debris jams were available as a cover type, except [for one], large schools of juvenile chinook salmon were observed. No juvenile chinook salmon were observed at either flow utilizing the one area surveyed … with riprap. During high flow juvenile chinook salmon were observed utilizing eddies and small microniches within undulating sandy substrate.*

While in the river the juveniles feed mainly on drifting invertebrates. Chironomids (midges) are most frequently eaten, but the larger caddisflies and mayflies make up most of the diet by weight (Brown and others 1991; Merz 1993).

Castleberry and others (1991; 1993) evaluated the physiological condition of juvenile chinook in the lower American River in 1991 and 1992, years with moderately low flows and warm water in late winter and early spring[3]. They found that non-polar lipid percentages for juveniles increased with length and tended to decrease with distance downstream, averaging about 6% to 8% dry weight for 40 to 49 mm fish, and 10% to 14% dry weight for fish 60 to 69 mm. This is in the low range for hatchery fish, but there are few comparable data for wild fish. They found that activity levels for Na^+-K^+ ATPase, an enzyme found in special cells in the gills that remove excess sodium and chloride ions from the blood, were high compared to published values. These data indicate that conditions in the river in 1991 and 1992 did not hinder the development of sea-water tolerance by juvenile chinook.

Approximate ages were determined from otoliths (Castleberry and others 1991, 1993, 1994), and showed that juveniles were growing well, averaging about 0.38 mm per day at 50 mm fork length (Williams 1995; estimates given in Castleberry and others 1991, 1993 are incorrect). Data on length by month suggest that juvenile chinook grew more slowly in 1993, when flow was higher and temperature lower, but this remains to be confirmed by analysis of the otoliths of fish collected and archived in 1993. DFG has this work underway (Rob Titus, DFG, 1999, personal communication).

Emigration

It has long been known that some ocean-type juvenile chinook emigrate as fry, shortly after emerging from the gravel, while others rear in the river for a few months and emigrate as smolts or large parr (Healey 1991). Based on the poor survival of coded-wire tagged fry released in the Delta (USFWS 1983), many biologists have assumed that the parr or smolt emigrants account for most returning adults. For example, the following assertion in Kelley and others (1985) was unchallenged in the trial of EDF vs. EBMUD:

> *Many of the small salmon are either washed, or voluntarily move, down into the estuary soon after they emerge from the gravel of the river bottom. The survival of these fish is very small, and fish that remain in the river and grow to a larger size have a much better chance of becoming adults.*

Some biologists argued that fry emigrants have continued to produce good returns in wet years; however, and a different view was expressed in the past. In the SWRCB hearings on Folsom in 1957, George Warner, a DFG biologist, argued the importance of fry emigrants:

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3. See Williams (1995) for detailed temperature and flow data for 1991–1993.

Small fingerlings which are flushed rapidly out of the river to the rich feeding grounds in the Delta and in the ocean have a good chance of survival. A speedy downstream migration at high flows cuts down the loses from predation and losses in irrigation diversions. In addition these fish grow faster than fish which spend considerable time in the river. This has been amply proved in fingerling marking experiments and scale studies[4].

Recent investigations by DFG using screw traps near Watt Avenue (Snider and Titus 1995; Snider and others 1997, 1998) show that the overwhelming majority of fry leave the spawning areas in the lower American River shortly after emerging, with emigration usually peaking in February. Comparison of the size distribution of fish collected in the screw traps with that of fish collected with seines near the upstream limit of spawning suggests that this behavior has a temporal component, such that early emerging fry tend to emigrate directly (almost all fish are <50 mm before April), but later emerging fry are more likely to rear for some period before emigrating (Figure 9).

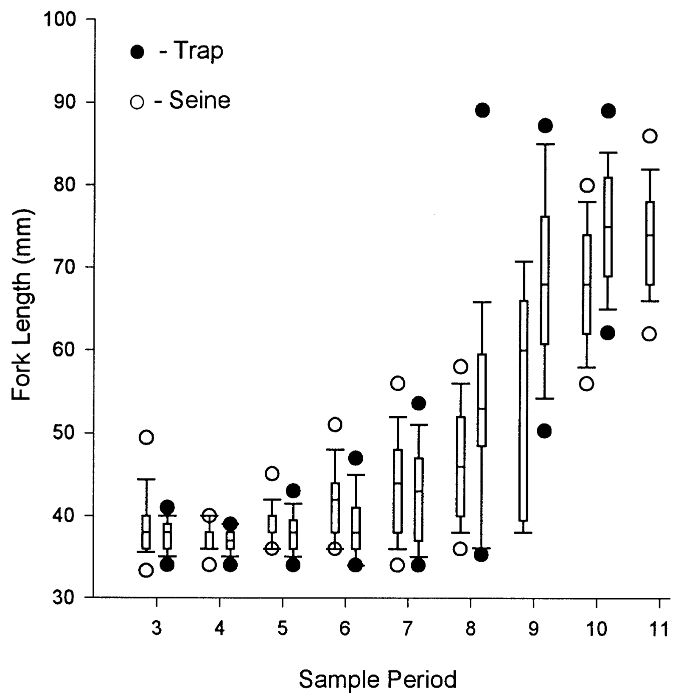

Figure 9 Size distributions of juvenile chinook salmon captured in the lower American River in screw traps (box plots with closed circles) and seines (plots with open circles) in 1995. Sample periods are two weeks: period 3 is 2/6–2/19, period 7 is 4/3–4/16, period 11 is 5/29–6/11. Box plot conventions are as in Figure 2. Data from DFG.

4. Unfortunately, he did not cite the studies; except for Clark's (1929) discussion of scale patters, I have not found any that fit his description.

There is controversy in the literature whether fry emigration is a forced, density-dependent behavior, or a volitional behavior (see Healey 1991 for a review). In the American River, the lack of larger juveniles in the seine samples early in the year when fish density is still low suggests early emigration is volitional, rather than a response to fish density or territorial behavior. Unpublished work relating length to otolith microstructure has developed no evidence that the fry captured in the traps are growing more slowly than others (Rob Titus, DFG, 1999, personal communication). More light could be shed on this issue by comparing the physiological condition of fry captured in the rotary screw trap with fry captured near the upper limit of spawning. Unfortunately, the traps were not effectively in service during the period that Castleberry and others (1991, 1993) were doing their work. Nevertheless, Castleberry and others (1993) found that ATPase activity increased downstream in fry <40 mm that were captured in seines, which is consistent with volitional emigration.

The large percentage of fry emigrants makes it seem likely that this is a viable life history pattern (Healey 1991). As noted by Snider and others (1998), the large proportion of fry emigrants emphasizes the importance of downstream rearing conditions for American River chinook salmon. Recent work by Sommer and others (2001) indicates that juvenile chinook in the Yolo Bypass grew more rapidly and had better survival to Chipps Island than fish in the Sacramento River, which supports the idea that natural floodplains along the lower Sacramento provided important habitat for juvenile chinook from the American River before the river was leveed.

Almost all juveniles leave the river before developing the full classic suite of smolt characteristics. DFG recently has classified juveniles collected in the screw traps as sac-fry, fry, parr, silvery parr, and smolts, (Snider and Titus 1995; Snider and others 1997, 1998) and reports less than 1% smolts and 74% or more fry or sac-fry (Table 5). Generally, however, the size distribution of fish collected in the screw trap is bimodal, with the great majority of the fish less than 45 or 50 mm, relatively few between 50 and 60 mm, and a second, much smaller group larger than 60 mm. The life stages. are not well correlated with length, however, in part because the length of parr and silvery parr tends to increase over the season (Snider and others 1998).

Table 5 Life stage statistics for emigrating chinook, 1994–1996 [a]

Life stage	*1994*	*1995*	*1996*
Yolk-sac fry	not distinguished	3.5%	22.6%
Fry	96.7%	70.5%	59.6%
Parr	1.6%	22.5%	17.4%
Silvery parr	1.4%	0.1%	4%
Smolt	0.3%	0.4%	0%

[a] Source: Data from Snider and others 1998.

Although the rotary screw trap data appear to provide good information on the timing of emigration and the nature of the emigrants, they do not provide good estimates of numbers of emigrants. Mark-recapture work by DFG shows that the capture efficiency of the rotary screw trap used by DFG is less than 1% (Snider and others 1998), and Roper (1995) argues that a capture efficiency of 10% or more is necessary for usefully accurate population estimates.

Age at Return

There are no data on the age or length at age of naturally produced chinook salmon returning to the American River, and very few data on hatchery fish, since fish from Nimbus are not normally coded-wire tagged. Recent information on length at age for Central Valley chinook generally is remarkably scarce, although it is commonly assumed that most spawners are three years old. Clark (1928) reported age data for salmon taken in the Delta gill net fishery in 1919 and 1921 (Figure 10), with ages determined by reading scales, showing more four- and five-year-old fish than three-year-old fish. However, chinook scales are hard to read (Godfrey and others 1968), and Clark may have overestimated ages (Frank Fisher, DFG, 1993, personal communication), but there is little doubt that the ocean troll fishery reduces that average age at return (Hankin and others 1994 and references therein). There is also good evidence that the size of returning adults has decreased from a comparison of the sizes reported by Clark and by a DFG survey in the American River (Figure 11). Hankin and others (1994) posit a genetically-influenced threshold size for maturation (see also Mangel 1994) that could be affected by inadvertent selection by the fishery and perhaps by hatchery practices.

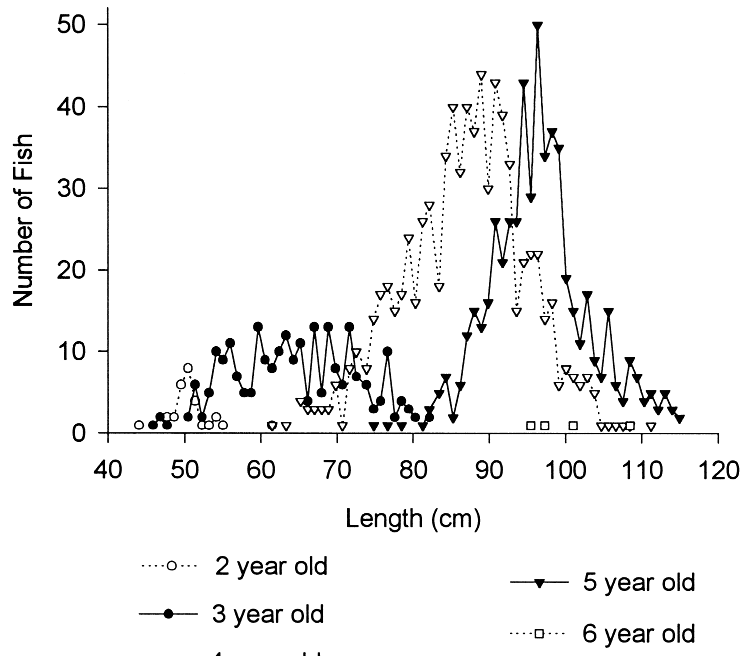

Figure 10 Ages of chinook salmon captured in the Sacramento gill net fishery in 1919 and 1921, estimated from scales. Data from Clark (1929).

Fecundity

There is substantial variation and a significantly declining trend in the average fecundity of females spawned at Nimbus Hatchery (Figure 12) from about 5,800 in the period 1955–1964 to about 5,100 for 1988–1997. Values for 1983 and 1984 stand out as low outliers, presumably reflecting poor ocean conditions associated with El Niño conditions. Unfortunately, the data were taken as the total number of eggs divided by the number of females, and there is information on the variance in fecundity among females and on the relation between fecundity and length for only one year, 1997. Fecundity of 135 individuals in 1997 varied from about 3,100 to 7,800 eggs, with length accounting for just over half the variation when fitted by fecundity = 6.385 (fork length)$^{1.564}$ (DFG 1998)[5]. Accordingly, the decline in average fecundity could reflect either a decline in fecundity at length, a decline in average length, or both. Fecundity is a basic biological parameter that deserves more attention.

5. A decline in average length probably accounts for the difference between the fecundity reported for Sacramento River chinook by McGregor (1923), which is cited by Healey and Heard (1984) and Healey (1991), and the fecundity at Nimbus in the late 1950s; in any event the fish measured by McGregor were large.

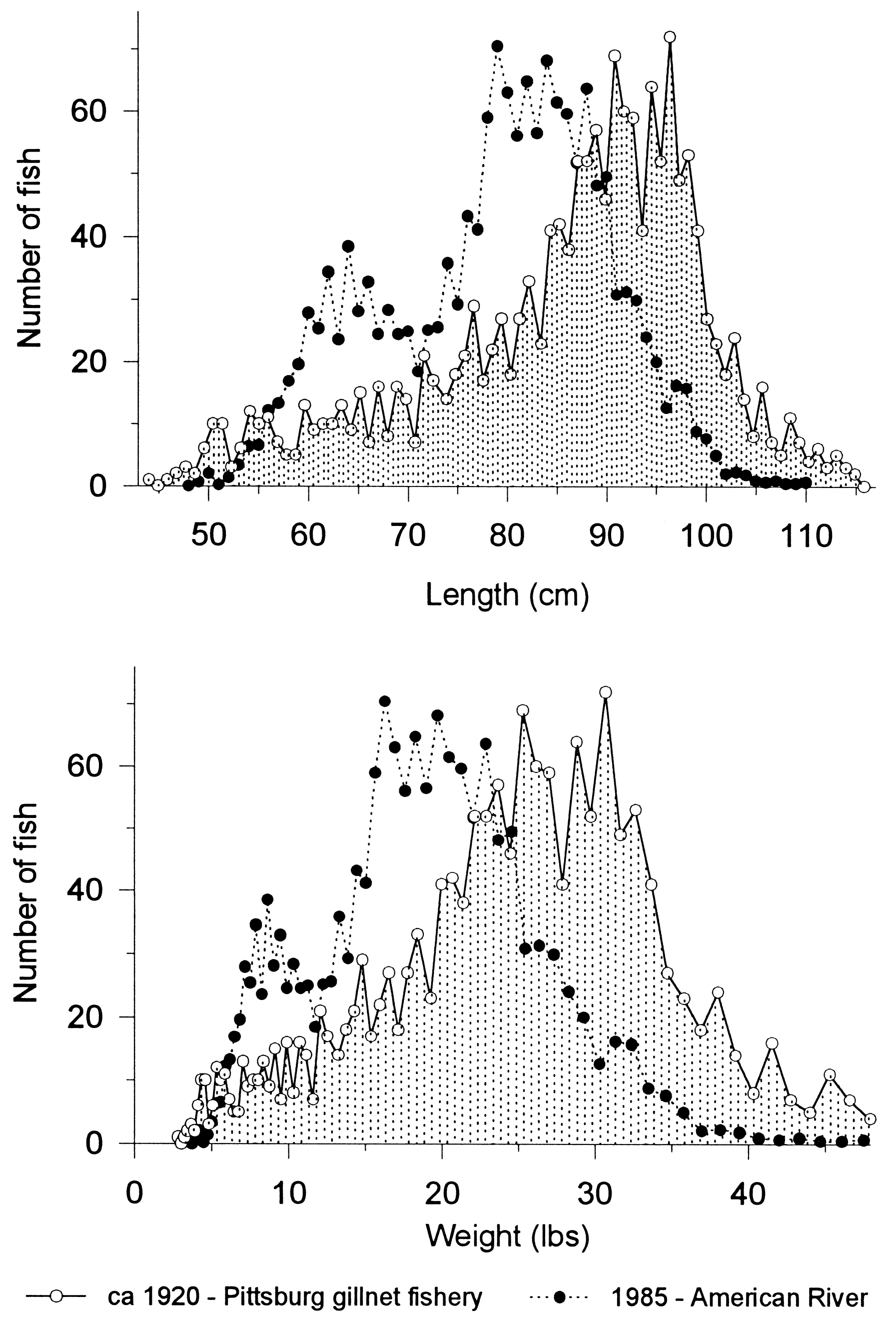

Figure 11 Length and weight distributions of chinook salmon captured in the Sacramento gill net fishery in 1919 and 1921, and from carcass surveys by DFG in 1985. Weights estimated with a length-weight relationship provided by Frank Fisher of DFG. Data from Clark (1929) and Fred Meyer of DFG.

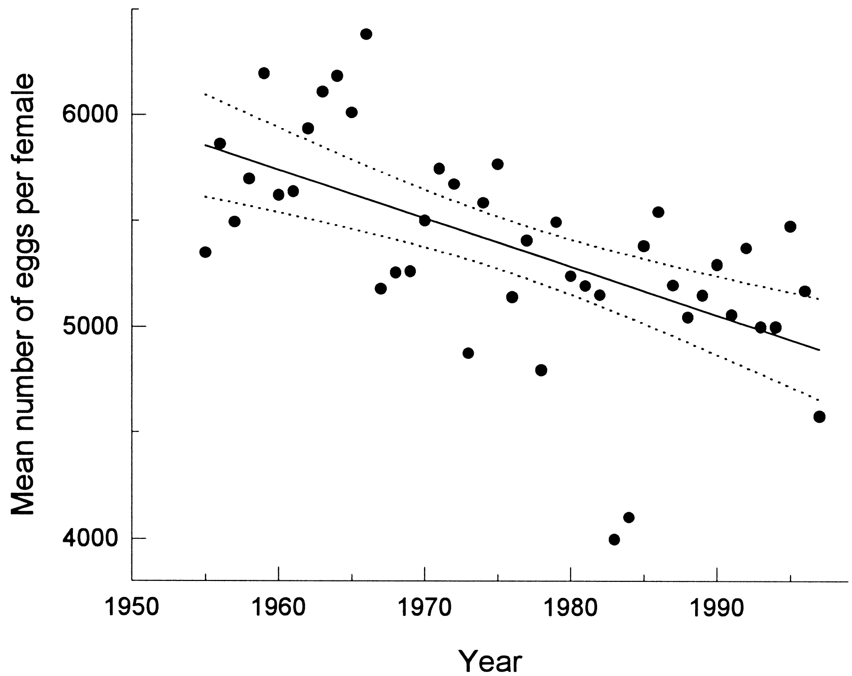

Figure 12 Declining trend in the average fecundity of chinook salmon at Nimbus Hatchery. Data from Fred Meyer and Terry West of DFG.

Salient Uncertainties and Research Needs

Several topics that deserve better understanding, such as fecundity and prespawning mortality, have been described above. Some additional topics follow.

Relation Between Flow and Rearing Habitat

The relation between flow and rearing habitat remains unclear. According to the consensus statement from a small workshop that discussed the American River at some length, "... currently no scientifically defensible method exists for defining the instream inflows needed to protect particular species of fish or ecosystems" (Castleberry and others 1996; Williams 1997). Methods such as PHABSIM suffer from measurement, statistical, and conceptual problems (Shirvell 1986, Shirvell 1994; Williams 1995, 1996; Campbell 1998; Bult and others 1999; Kondolf and others forthcoming). Simple empirical approaches that depend on measures such as smolts per spawner are confounded by measurement problems and density-dependent mortality (Williams 1999) and by the unknown percentage of hatchery fish. An adaptive approach that emphasizes measures of condition of juvenile fish, exemplified by the work of Castleberry and others (1991, 1993) on the American River, appears to be most promising, especially when linked to population-level responses by individual-based modeling (Osenberg and others 1994; Maltby 1999). More observations of habitat use like those of Jackson (1992) would be helpful, especially if they are directed toward developing a better understanding of the way juvenile chinook use habitat rather than "habitat suitability criteria" for PHABSIM studies. In any event, understanding the cause-and-effect relationships that underlie the responses of populations to habitat change seems crucial for effective management of habitats in regulated rivers (Jones and others 1996; Williams 1999).

The Importance of Fry Emigrants

The relative viability of fry that emigrate soon after emerging and fry that rear in the river for some time remains poorly known, as described above, but has important implications for management of the American River and investment in habitat restoration in the Delta. For example, there appears to be a trade-off between providing high flows for spawning in the fall and the risk of low carryover storage for flows the following spring, should the winter be dry. The optimal allocation of water to spawning probably depends on viability of fry emigrants, which in turn may depend upon habitat conditions in the lower Sacramento River and the Delta. DFG has work on otolith microstructure in progress that among other things aims to distinguish patterns associated with different juvenile life history patterns. If this can be done with even modest accuracy, then analysis of otoliths from adults should clarify the viability of fry emigrants. Monitoring the physiological condition of emigrating fry in the lower Sacramento River as well as in the American, and comparing these with fish remaining near upstream spawning areas in the American River, would be an alternative and complementary approach.

Density-dependent Mortality

Understanding the mechanisms of density-dependent mortality for chinook salmon in the American River should allow better management, even if measurement problems preclude quantifying the relationship accurately. As noted above, aerial surveys have provided some information on density-dependent mortality at spawning. Assuming that density-dependent mortality for juveniles works through mechanisms that also produce sub-lethal stress in juveniles, measures of condition such as lipids, otolith increment widths, or inter-renal distance (Castleberry and others 1991, 1993; Norris and others 1996) may be most useful. Otolith data on growth during early ocean life may provide evidence for density-dependence in that life stage, especially if combined with population data from streams where populations can be estimated more accurately than seems possible on the American River. Bold adaptive variation in hatchery production at a regional scale may be required to clarify this issue, however.

Temperature Tolerance of Juveniles

The temperature tolerance of juvenile chinook was much debated in the trial of EDF vs. EBMUD and despite recent progress remains unclear. Analyses of juvenile chinook and steelhead in the lower American River in 1991 and 1992 showed that they appeared to be growing well and be in good physiological condition, despite moderately low flows and warm water in late winter and early spring (Castleberry and others 1991, 1993; Williams 1995). Coded-wire-tagged fish in the Yolo Bypass grew more rapidly and showed better survival to Chipps Island than did paired releases of fish in the Sacramento River, where water temperature was lower (Sommer and others 2001). Juvenile chinook that move up relatively warm intermittent tributaries of the Sacramento River to rear grow rapidly (Moore 1997; Maslin and others 1997). Recent laboratory studies at the University of California at Davis (Marine 1999) showed that juvenile chinook from Coleman Hatchery grew as rapidly at 17 to 20 °C on full ration as they did at 13 to 16 °C. On the other hand, Clarke and Shelbourn (1985) described delayed mortality associated with scale loss in fish that were raised in freshwater at 16 or 17 °C, so freshwater growth and survival may not be the whole story. Paired coded-wire-tag releases like those of Sommer and others (2001), which will allow estimates of survival to catchable size from tag returns from the ocean fishery, could be especially useful in this regard. In any event, water temperature is an important predictor of the survival of coded-wire-tagged smolts, regardless of the statistical method used on the data (Ken Newman, University of Idaho, 1999, personal communication), while other variables such as flow seem important in some analyses but not in others. Assays for stress proteins (Iwama and others 1998) in fish collected at Chipps Island for the coded-wire tag studies could provide independent evidence of temperature stress. A literature review of the temperature tolerance of juvenile chinook that should clarify this issue is currently underway by Chris Myrick at the University of California at Davis.

The Importance of Hatchery Production

Intelligent management of chinook salmon in the American River depends on distinguishing fish of natural and hatchery origin. Hatchery fish can be marked easily and economically by manipulating water temperature in the trays in which larval fish (alevins) are reared. This creates visible bands of narrow and wide growth increments in otoliths (ear-stones) that mark fish as hatchery produced; the bands can even form bar-codes by which fish from different hatcheries or batches can be distinguished (Volk and others 1990, 1994). If all hatchery fish are marked, the proportion of naturally produced spawners could be estimated accurately from a relatively small sample, and the associated analysis of otoliths could also provide information on length at age of adults and perhaps information on year-to-year variation in ocean condition and on the life history patterns of fish that survive to spawn. A program for thermally marking the otoliths of hatchery fish is now being developed by DFG.

Quantitative Methods

Methods for analyzing biological data have developed rapidly in recent years (for example, Jongman and others 1987; Efron and Tibshirani 1991, 1993; Hilborn and Mangel 1997; Peterman and Anderson 1999). Unfortunately, these methods are unfamiliar to most Central Valley salmon biologists and even methods such as the bootstrap that are easy to implement are seldom used. Data analysis routinely should include the development and testing of models of the biological and sampling processes that generate the data (Elliott 1994; Hilborn and Mangel 1997). Besides guiding field studies to address the most relevant issues, this approach helps avoid the waste of resources on field studies that cannot generate useful information. The recent analyses of coded-wire tag data by Ken Newman and John Rice reveal a large gap between the quality of analysis that is possible and the quality that is typical in studies of salmon in the Central Valley, bearing out the observation of Effron and Tibshirani (1993) that "Statistics is a subject of amazingly many uses and surprisingly few effective practitioners."

Concluding Remarks

Much is known about chinook salmon in the American River and elsewhere, but much remains to be learned. Because of EDF vs. EMBUD, there have been many recent studies of chinook in the American River. In many respects, however, the American River is not a good study stream. Developing good population estimates for chinook salmon in the river does not seem to be practicable, especially for juveniles, mainly because the river is so big. The urban setting and heavy recreational use of the river create other problems, as does the heavy presence of hatchery fish. Efforts to understand density-dependent mortality or other aspects of chinook biology that require good population estimates probably should be focused on smaller streams such as Butte Creek or Clear Creek, or the Feather River side-channel where Castleberry and others (1994) confirmed that juvenile chinook form otolith increments daily. The low flow channel of the Feather River (see Sommer and others, Volume 1) probably is a better system than the American River for intensive studies on a larger scale because better experimental control of flows is possible.

Much could be gained by a regional perspective among salmon researchers that would allow a coordinated approach to addressing some questions and allow others to be addressed primarily in the parts of the system with the most favorable study conditions. Unfortunately, there is a tendency toward

Balkanization of salmon research in the Central Valley, with divisions among regions and agencies that discourages communication, let alone cooperation. Workshops such as the one giving rise to this publication are a step in the right direction, but much remains to be done to create an effective community of scientists in which the efforts and intelligence of those studying salmon in the Central Valley can realize their potential. (See also Kimmerer and others, this volume.)

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