Factors Affecting Chinook Salmon Spawning in the Lower Feather River

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Abstract

We review the status of chinook salmon in the lower Feather River and examine factors affecting chinook salmon spawning since the construction of Oroville Dam. Spawning occurred in depths from 0.4 to 4 ft with the central 50% of observations in the 1.6 to 2.6 ft range. Depth used was slightly higher at increased flows. Velocities of 0.4 to 4.8 ft/s (central 50% = 1.5 to 2.7 ft/s) were used at all flows. Redds were constructed in substrate containing less than 60% fines in 0.2- to 1-inch to 6- to 9-inch gravel size classes.

Redd surveys showed that spawning occurred in twice as much area below Thermalito Afterbay Outlet than the low flow channel (LFC). However, in most recent years, about 75% of fish spawned in the LFC. Superimposition indices calculated from these results suggest that there was insufficient spawning area in the LFC to support the number of spawning pairs, but adequate area below Thermalito Afterbay Outlet. Spawning activity was highest in the upper three miles of the LFC, whereas spawning area was relatively evenly distributed below Thermalito Afterbay Outlet. Historical results suggest superimposition significantly reduces egg survival.

Statistical analysis of historical data showed that there has been a highly significant increase in the number of salmon spawning in the LFC. In-channel escapement explained a significant additional portion of the variability in spawning distribution. The significant increase in the proportion of spawners using the LFC over time may be at least partially attributable to an increasing proportion of river flow from this channel. Substrate composition based on Wolman counts and bulk samples do not explain trends in spawning distribution as LFC gravel has become progressively armored over the past 16 years, whereas downstream substrate composition has not changed detectably. Temperature trends were not significantly correlated with spawning distribution. We hypothesize that hatchery stocking location and genetic introgression between fall-run and spring-run chinook stocks also account for spawning activity in the LFC. Spawning simulations using an egg production model based on these statistical analyses yielded very different results than a PHABSIM instream flow model.

Introduction

The Feather River supports one of the largest runs of chinook salmon (*Onchorhychus tshawytcha*) in California's Central Valley. Unfortunately, relatively little information has been published about the status of salmon in the lower Feather River. The river was studied intensively by Painter and others (1977), who examined the effects of the construction of Oroville Dam on Feather River fish. In 1981 the California Department of Water Resources (DWR) conducted gravel studies in the river with emphasis on chinook salmon spawning riffles (DWR 1982). Dettman and Kelly (1987) and Cramer (1992) conducted analyses of the contribution of Central Valley salmon hatcheries (including Feather River) to ocean harvest and escapement. In the mid-1990s, DWR, in cooperation with the California Department of Fish and Game (DFG), conducted several unpublished fish studies that focused on the effects of flow on salmon. These results were later used by Williams (1996) for a theoretical analysis of the effects of variability on instream flow modeling results.

The following paper summarizes our understanding about the status of chinook salmon in the Feather River including a portion of their life history, abundance trends, and physical habitat. This information is used as the basis for detailed analyses of spawning, which we believe is probably more important to in-river salmon production than either adult holding, juvenile rearing, or emigration. Specific objectives were to:

- Describe the physical conditions for chinook salmon spawning in the Feather River.
- Identify the factors that affect spawning distribution and success.
- Develop models to simulate spawning in the Feather River.

Chinook Salmon Life History in the Feather River

The lower Feather River has two runs of chinook salmon, the fall-run and spring-run. Adult fall-run typically return to the river to spawn during September through December, with a peak from mid-October through early December. Spring-run enter the Feather River from March through June and spawn the following autumn (Painter and others 1977). However, the spring-run are genetically uncertain as a result of probable in-breeding with the fall-run (Yoshiyama and others 1996; Brown and Greene 1994; Hedgecock and others, this volume). Genetic studies are presently underway to examine this issue. Fry from both races of salmon emerge from spawning gravels as early as November (Painter and others 1977; DWR unpublished data) and generally rear in the river for at least several weeks. Emigration occurs from December to June, with a typical peak during the February through April period. The vast majority of these fish emigrates as fry (DWR unpublished data), suggesting that rearing habitat is limiting or that conditions later in the season are less suitable. Risks for late migrating salmon include higher predation rates and high temperatures. The primary location(s) where these fish rear is unknown, however in wetter years it appears that many young salmon rear for weeks to months in the Yolo Bypass floodplain immediately downstream of the Feather River before migrating to the estuary (Sommer and others 2001).

Historical distribution and abundance of chinook salmon in the Feather River is reviewed by Yoshiyama and others (this volume). They note that fall-run historically spawned primarily in the mainstem river downstream of the present site of Lake Oroville, while spring-run ascended all three upstream branches. Fry (1961) reported fall-run escapement estimates of 10,000 to 86,000 for 1940–1959, compared to 1,000 to about 4,000 for spring-run. Recent fall-run population trends continue to show annual variability, but are more stable than before Oroville Dam was completed (Figure 1). Pre-dam escapement levels have averaged approximately 41,000 compared to about 46,000 thereafter (see also Reynolds and others 1993). This increase appears to be a result of hatchery production in the system. The pre- and post-dam levels of spring-run are similar, however the genetically uncertain stock is now dominated by hatchery operations (Figure 2).

Hatchery History and Operations

Feather River Hatchery was opened in 1967 to compensate for the loss of upstream habitat by the construction of Oroville Dam. The facility is operated by the California Department of Fish and Game and typically spawns approximately 10,000 adult salmon each year (see Figure 1). Until the 1980s, the majority of the young hatchery salmon was released into the Feather River (Figure 3). However, the release location was shifted to the Bay-Delta Estuary to improve survival.

Hydrology

The Feather River drainage is located within the Central Valley of California, draining about 3,600 square miles of the western slope of the Sierra Nevada (Figure 4). The reach between Honcut Creek and Oroville Dam is of low gradient. The river has three forks, the North Fork, Middle Fork, and South Fork, which meet at Lake Oroville. Lake Oroville, created by the completion of Oroville Dam in 1967, has a capacity of about 3.5 million acre-feet (maf) of water and is used for flood control, water supply, power generation, and recreation. The Lower Feather River below the reservoir is regulated by Oroville Dam, Thermalito Diversion Dam, and Thermalito Afterbay Outlet. Under normal operations, the majority of the Feather River flow is diverted at Thermalito Diversion Dam into Thermalito Forebay. The remainder of the flow, typically 600 cubic feet per second (cfs), flows through the historical river channel, the "low flow channel" (LFC). Water released by the forebay is used to generate power before discharge into Thermalito Afterbay. Water is returned to the Feather River through Thermalito Afterbay Outlet, then flows southward through the valley until the confluence with the Sacramento River at Verona. The Feather River is the largest tributary of the Sacramento River.

The primary area of interest for salmon spawning is the low flow channel (see Figure 4), which extends from the Fish Barrier Dam (river mile 67) to Thermalito Afterbay Outlet (river mile 59), and a lower reach from Thermalito Afterbay Outlet to Honcut Creek (river mile 44). There is little or no spawning activity in the Feather River below Honcut Creek.

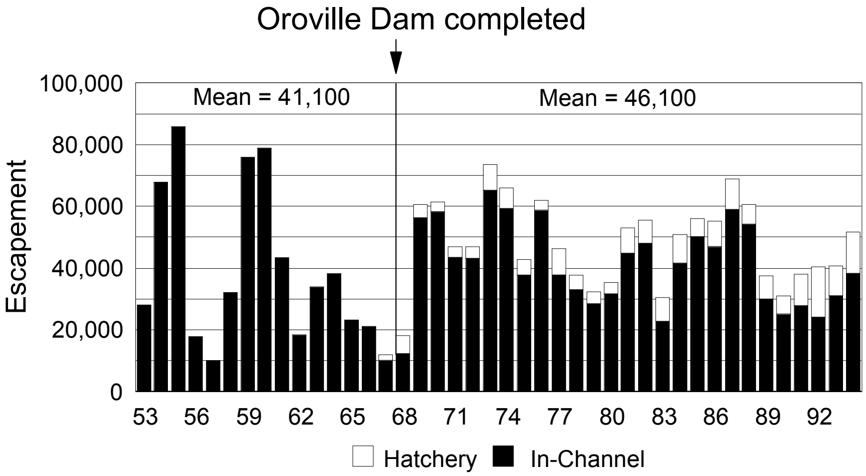

Figure 1 Escapement of fall-run chinook salmon (1953–1994) in the Feather River Hatchery and channel

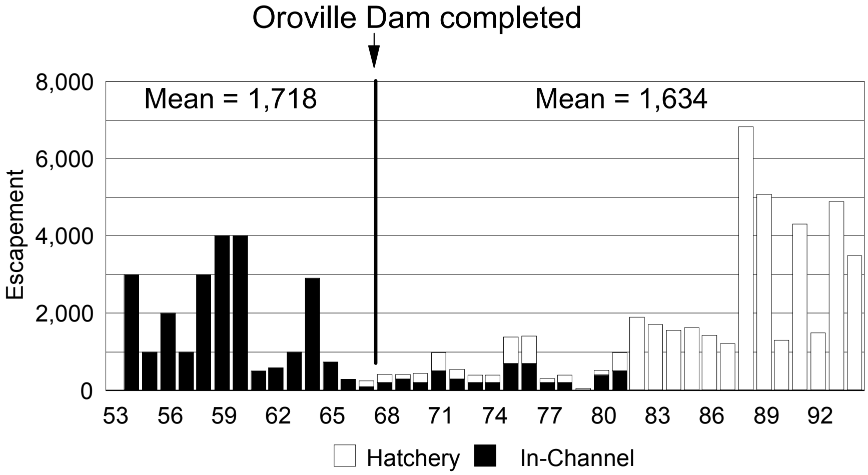

Figure 2 Escapement of spring-run chinook salmon (1953–1994) in the Feather River Hatchery and channel

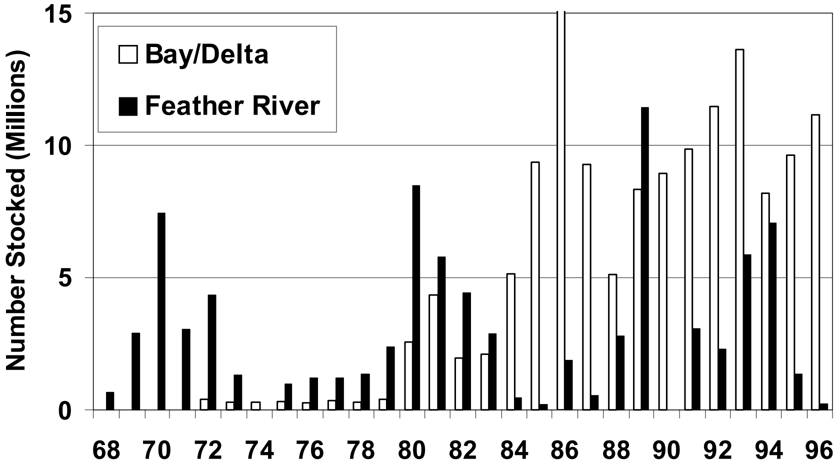

Figure 3 Stocking rates of juvenile salmon from the Feather River Hatchery into river and Bay-Delta locations

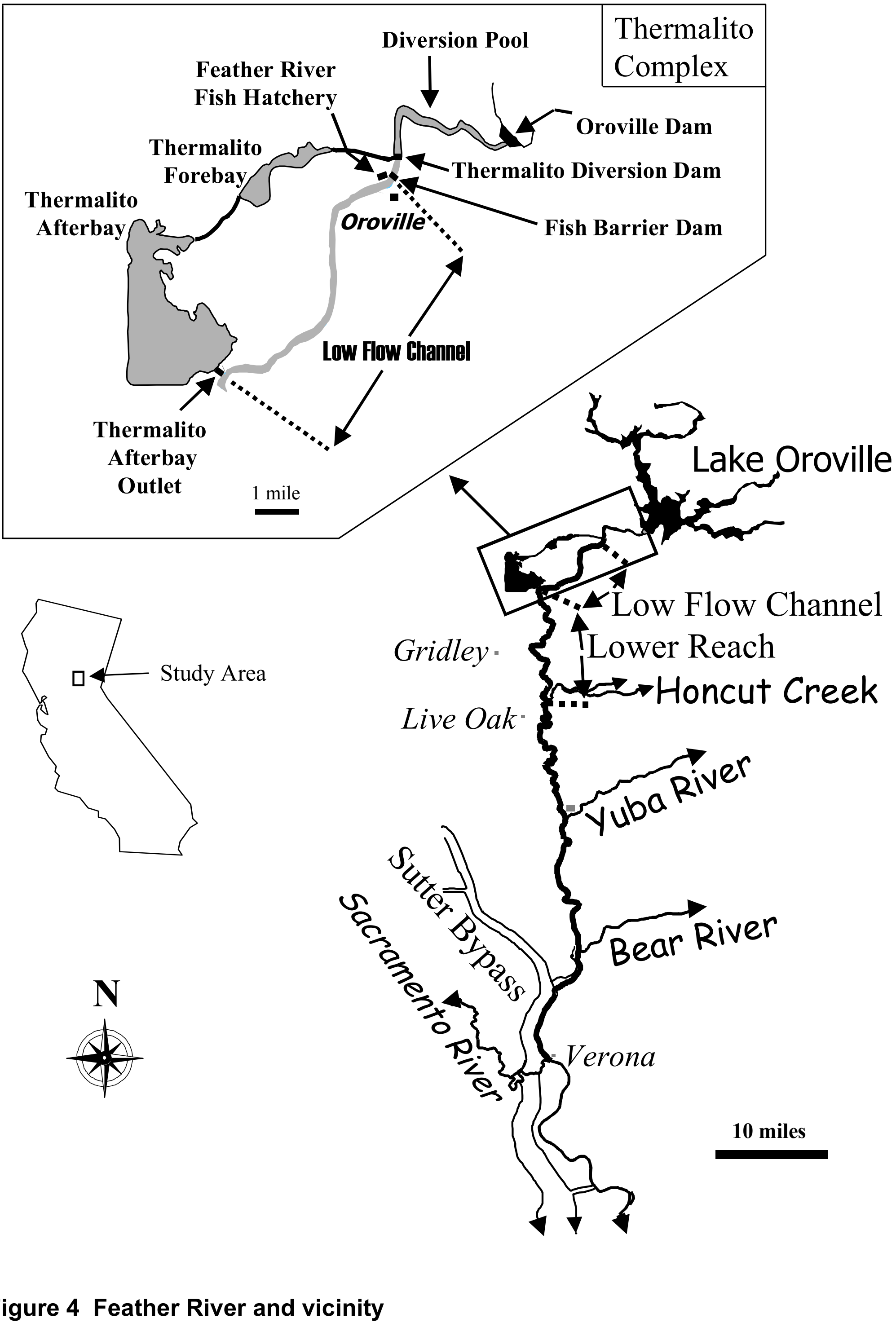

Figure 4 Feather River and vicinity

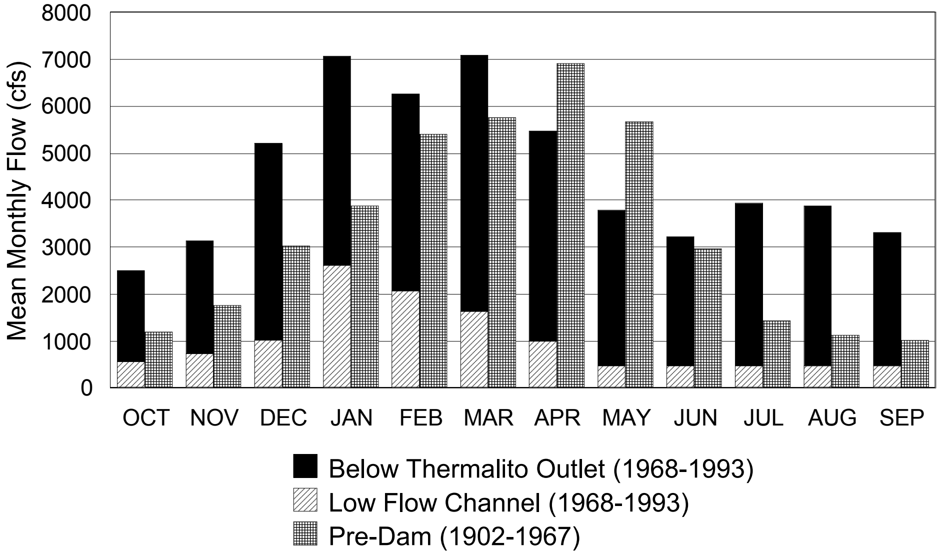

Figure 5 Mean monthly flows (cfs) in the Feather River for the pre-Oroville dam (1902–1967) and post-Oroville dam (1968–1993) periods. Total flow in the post-dam period includes the portion from the low flow channel and the portion diverted through the Thermalito complex.

The hydrology of the river has been considerably altered by the operation of the Oroville complex. The major change is that flow that historically passed through the LFC is now diverted into the Thermalito complex. Mean monthly flows through the LFC are now 5% to 38% of pre-dam levels (Figure 5). Mean total flow is presently lower than historical levels during February through June, but higher during July through January. Project operations have also changed water temperatures in the river. Compared to historical levels, mean monthly water temperatures in the LFC at Oroville are 2 to 14 °F cooler during May through October and 2 to 7 °F warmer during November through April. Pre-project temperature data are not available for the reach below Thermalito Afterbay Outlet, but releases from the broad, shallow Thermalito Afterbay reservoir probably create warmer conditions than historical levels for at least part of the spring and summer.

Methods

Data for the present study were obtained from three sources: annual carcass surveys, instream flow studies conducted during the early 1990s, and recent detailed studies on spawning. The major field measurements are summarized below.

Physical Conditions for Spawning

Our analysis of spawning conditions focused on depth, velocity, and substrate conditions. Initial field measurements were made October 1991, representing early-peak spawning activity. Sampling was concentrated in the vicinity of 36 transects selected to represent historical spawning areas (DWR 1982) and habitat types (see below). Further details about the transects are available in Williams (1996). Individual redds within approximately 100 ft of each transect were located by three field crew by wading or boat observations.

The ground level survey was verified using aerial photography of the area between Fish Barrier Dam and Honcut Creek. Photographs were taken on 16 October 1991 from an elevation of approximately 1000 ft. Comparison of color prints from the flyover with ground-level redd mapping confirmed that the field survey was reasonably comprehensive.

Field measurements of depth, substrate, and velocity were performed using wading methods. Depth and velocity were measured using a Price AA flow meter in undisturbed gravel approximately two feet upstream of each redd at an angle of 45 degrees to the direction of flow. The dominant gravel type was evaluated for the surface substrate using a modified Brusven classification (Platts and others 1983). A visual estimate of the amount of fines in the surface layer was recorded separately as a percentage of the total substrate. A single field observer was used throughout the study to minimize subjective variation.

Additional field measurements were made in 1995 based on concerns that the 1991 data were collected under unusually low flow conditions. Flows in the river during the 1995 spawning season (October to December) were experimentally increased in the low flow channel and reach below Thermalito Afterbay Outlet to 1,600 and 2,500 cfs, respectively, compared to the 600 and 1,000 cfs levels studied in 1991. Similar techniques were used in 1995 sampling, although substrate was not analyzed. Depth and velocity data from 1991 and 1995 were compared using Mann-Whitney U tests.

The quality of gravel in the major spawning riffles was examined in more detail from samples collected in 1982 and 1996. The 1996 samples were taken as close as possible to the original 1982 sites. Bulk samples weighing between 400 and 700 pounds were collected using shovels at the head of point bars adjacent to most of the major salmon spawning riffles. The surface and subsurface portions were sampled separately. Bulk samples were sieved on site and the sand to silt portion was taken to the laboratory for further analysis. The laboratory sieves ranged from 0.019 to 1.2 inches. The results were analyzed based on the geometric mean of the particle size distribution by river mile.

Surface samples were also taken at twenty riffles using a modified Wolman (1954) grid method. Although the Wolman counts do not adequately sample the finer sediments, we selected the technique because of its relative simplicity and common usage. The area sample included or was adjacent to the bulk sample site. Statistical analysis of the Wolman counts was similar to the bulk samples.

Spawning Distribution

Our basic approach to analyzing Feather River spawning distribution was to prepare a map of the available aquatic habitats, then use aerial photographs and ground-based observations to identify the spawning areas.

The major habitat types were classified using a system similar to Beak Consultants, Inc. (1989). Channel features delineated using aerial photographs (1 inch:400 feet) from October 1990 and US Geological Survey topographical maps indicated that the majority of the study area consisted of island bar complex and straight flatwater habitat. Field studies were then conducted to further refine site maps to include specific habitat components: riffles, pools and run-glide areas. Field observations were made at a flow rate of 600 cfs above Thermalito Afterbay Outlet and at approximately 4,500 cfs below the outlet.

The maps were analyzed by recording the linear distance (ft) of each habitat type. In complex areas with overlapping habitats or multiple channels, the relative abundance of each habitat type was estimated as a percentage of the total channel area. Note that actual habitat boundaries for "riffles", "pools" and "run-glide" areas changes relative to flow conditions. However, the maps we prepared provide a useful baseline to identify sampling areas and changes in spawning distribution. Another consideration is that there have been changes to some areas as a result of subsequent high flows in 1993 and 1995. However, site visits in 1995 indicated that there was no major change in the relative proportions of the different habitat types.

Aerial photographs were taken of the entire study reach in November 1995 to examine redd distribution. Ground-based observations were made within 24 hours of the date of the flight to check the accuracy of the methods. However, we were unable to identify individual redds because of the large numbers of fish spawning in relatively few areas. As an alternative, we quantified spawning activity based on the total area disturbed by spawning activity. Because some disturbed areas do not represent redds, we consider the results an estimate of the maximum amount of area used for spawning. The 1:3000 scale photographs were prepared using a yellow filter to minimize glare. The negatives were reviewed before printing to identify the sites containing redds that needed to be enlarged to a scale of 1:600. Total disturbed area, referred to as "total spawning area," was delineated on the prints relative to habitat boundaries from the previously described habitat map. The area estimates were calculated by digitizing these maps using AUTOCAD. The results were quantified by river mile, river reach, and habitat type.

We examined carcass count data from Painter and others (1977) to provide a historical perspective on spawning distribution. Carcass recoveries were recorded by river mile for 1971 through 1974. Although these data are biased because many carcasses would have drifted downstream of the riffle or run-glide where spawning occurred, we believe the results are a useful approximation of actual distributions.

Field observations of spawning suggested that superimposition of redds was a major problem in the Feather River. We developed indices from the 1995 data to examine superimposition rates by river reach as follows:

$$\text{Superimposition Index} = \frac{(\text{Escapement Estimate} \times 0.5)(\text{Spawning Area in ft}^2)}{55\text{ft}^2}$$

The escapement estimate is from DFG's fall carcass survey and is multiplied by 0.5 to represent the number of spawning pairs. The 55 ft^2 value is the average surface area for an average size fall-run chinook salmon (Bell 1986). The spawning area estimate was calculated from previously described aerial photography methods. We emphasize that the result should be considered an index rather than an actual measure of superimposition rates. As described in Healey (1991) there is considerable variability in the surface area of redds, which could have a major effect on the amount of superimposition in the Feather River.

Analysis of Factors Affecting Spawning Distribution

The superimposition and redd distribution analyses showed that there were major differences in the distribution of spawning activity between study reaches. We addressed this issue by examining the proportion of fish that spawned in the LFC relative to different environmental conditions. Historical escapement data were obtained from DFG for the LFC and from Thermalito Afterbay Outlet to Gridley. Data were available for 1969 through 1974, 1977, 1979 through 1987, 1989, and 1991 through 1996. We calculated the percentage of spawners in the low flow channel as:

$$\text{Percent Spawners in Low Flow Channel} = 100 \times \frac{\text{Escapement in Low Flow Channel}}{\text{Total Escapement Oroville to Gridley}}$$

As will be discussed in further detail, we found strong time trend in spawning distribution. We used regression analysis to determine whether total escapement, temperature, flow, and flow distribution had similar time trends that might explain the apparent changes in spawning distribution. In addition, we regressed each variable against the residuals from the spawning distribution-time relationship to determine whether the variable explained a significant additional portion of the variability. We calculated average maximum daily temperature for October and November of each year (1969–1991) using data from US Geological Survey records for Thermalito Afterbay Outlet. USGS data for 1969–1996 were obtained to estimate average October and November flow in the LFC and flow distribution, calculated as the percentage of total river flow that was released through the LFC. The normality of each variable was tested with a Shapiro-Wilks W test and log-transformed where necessary.

Modeling

Two different approaches were used to model spawning in the lower Feather River. The first was to use simulate the effect of flow on spawning using the instream flow model Physical Habitat Simulation System (PHABSIM). As an alternative, we simulated egg production using a simple mechanistic model developed from statistical relationships for factors affecting spawning distribution and egg survival.

Instream Flow Model

PHABSIM methods and models were developed by the US Fish and Wildlife Service Instream Flow Group (Bovee 1982). To summarize briefly, a habitat mapping approach (Morhardt and others 1984) was used to select and model the previously described transects. A hydraulic model was developed based on physical data collected at each transect to simulate depth, velocity, and substrate at a range of river flows for each reach. Weighted Useable Area (WUA), an index of habitat, was simulated by combining the hydraulic model results with binary suitability curves developed from data collected on conditions used for spawning. Details about the modeling approach are provided below and in Williams (1996).

Physical data collection procedures followed the methodology of Trihey and Wegner (1981). Permanent headstakes and benchmarks were established between autumn 1991 and summer 1992 at all transects following surveys of the study reach. Stage-discharge measurements were attempted at three to four different flows between autumn 1991 and spring 1993. For most lower reach transects, stage data were collected at 1,000, 2,500 and 3,000 cfs. In the LFC, stage measurements were performed at 400, 600 and 1,000 cfs.

During July 1992 cross-sectional coordinates and mean column velocity (one to three depths) were collected on at least 15 points across the wetted width of each transect. At pool and glide sites, Price AA flow measurements were made from a ten-foot aluminum boat attached to aircraft cable stretched across the channel. Similar measurements were made at riffle sites by wading using a top-setting rod.

The hydraulic data were calibrated using the methods of Milhous and others (1989). Water surface elevation and velocity data for most transects were calibrated using the IFG4 option of PHABSIM, although MANSQ was used as an alternative to calibrate elevations for some riffle and glide habitats. When at least four stage-discharge measurements were available, calibration was often improved using separate low- and high-flow range models to simulate elevations. Following calibration, water surface elevations and velocities were simulated using IFG4 within the maximum extrapolation range recommended by Stalnaker and Milhous (1983): 200 to 2,500 cfs in the LFC and 500 to 7,500 cfs in the lower reach.

Habitat suitability curves were developed using previously described data on depth, velocity, and substrate. For modeling purposes, the results were simplified into binary curves. The central 50% of observations for each depth, velocity, and dominant substrate were assigned a value of "1" and the remaining observations were assigned a value of "0." In addition, any substrate with greater than 50% fines was assigned a value of "0." Although we also considered modeling suitability based on more complex curve-fitting techniques (Bovee 1982), the resulting curves are often biologically questionable (Bovee, personal communication, see "Notes"). The binary curve approach seems reasonable for the Feather River, where spawning activity is concentrated in suitable gravel on a relatively small number of riffles and glides.

The amount of microhabitat available for different discharge rates was simulated using the PHABSIM program HABTAT (Milhous and others 1989). Habitat availability was calculated in terms of WUA by combining hydraulic simulation data and binary habitat suitability curves. The WUA in each reach was obtained by weighting transects modeled for each habitat type using habitat abundance data collected during site selection.

Egg Production Model

As further described in the results, statistical analyses suggest that flow and escapement have a significant effect on the proportion of salmon that spawn in the LFC. However, egg survival is reduced in the LFC as a result of superimposition. We developed a spreadsheet model which simulates egg survival based on flow and escapement. The basic structure of the model is that spawning distribution between the two river reaches is simulated using a regression equation based on the proportion of flow from the LFC and escapement. Initial egg production for each reach is calculated from the number of spawning pairs. Egg survival rates are then assigned separately to the two study reaches based on historical observations.

The regression equation for spawning distribution came directly from previously-described analyses of variables affecting the proportion of LFC spawners. Other variables such as hatchery practices that may result in time trends in spawning distribution were assumed to be constant. Total flow was assumed to be constant at 2,500 cfs, which is typical for the spawning period. Total egg production was calculated for each reach by multiplying the number of spawning pairs by an assumed fecundity of 5,000 eggs.

Egg survival was simulated based on the results of Painter and others (1977), who examined the proportion of live and dead eggs for several years over different spawning densities. They found a significant inverse relationship between egg survival (S) and escapement of salmon in the LFC (L): $S = -0.00292L + 111.2$, ($r^2 = 0.575$, $P < 0.05$). We assumed that this regression relationship represented egg survival in the LFC, but set a minimum survival limit of 30%, the lowest rate observed in the Painter and others (1997) study. The upper limit was set at 100% based on maximum survival estimates from Healey (1991). There was no such relationship or strong indication of density dependence for the study reach below Thermalito, so we used the average egg survival rate for 1968 through 1972 (84%) for all simulations.

As evidence that the highest egg survival rates measured by Painter and others (1977) are reasonable, survival estimates for undisturbed chinook salmon eggs to hatching stage range from 82% (Briggs 1953) to 97% (Vronskiy 1972). We also used the method of Tappel and Bjornn (1983) to calculate "ideal" Feather River egg survival rates based on the particle size distribution of several spawning riffles. The key particle sizes needed for the model were estimated by linear interpolation from combined bulk surface and subsurface samples. The survival estimate for gravel in three spawning riffles using the Tappel and Bjornn (1983) method was 83% (SD = 5), close to the 84% average (SD = 8) for below Thermalito Afterbay Outlet, but lower than the highest survival rate observed in the LFC (93%). Although these results suggest that the highest Feather River survival rates measured by Painter and others (1977) are reasonable, we were unable to verify the shape of the inverse relationship with LFC escapement. The Painter and others (1977) results were from observations of eggs pumped from redds using a McNeil sampler, which does not measure mortality of eggs lost to the water column through superimposition. However, Fukushima and others (1998) found that the number of pink salmon eggs lost into the channel was roughly proportional to spawner abundance, indicating that water column losses can at least be expected to follow the same trend as intergravel mortality. For modeling purposes, we assumed that the slope of the Painter and others (1977) relationship would not change substantially if water column losses were included.

Results

Physical Conditions for Spawning

A total of 205 depth measurements and 198 velocity measurements was made in riffles, pools and glides in the low flow channel. Spawning occurred in depths from 0.4 to 4.0 ft with the central 50% of observations ranging from 1.6 to 2.6 ft (Figure 6). Salmon spawned at velocities of 0.4 to 4.8 ft/s with a range of 1.5 to 2.7 ft/s for the central 50% of observations (Figure 7). The data suggest that the velocities used in 1992 were similar to 1995, but spawning occurred at somewhat greater depths in 1995 (see Figure 6). These hypotheses were confirmed using a Mann-Whitney U test, which showed that there were no significant differences for velocities, but highly significant differences for depth ($P < 0.0001$).

The dominant substrate used by spawners ranged from the 0.2- to 1-inch size class to the 6- to 9-inch class (Figure 8). Spawning was not observed in substrate with greater than 50% fines. The Wolman samples show that the largest substrate was at the top of the LFC, with a trend towards smaller material to Thermalito Afterbay Outlet (Figure 9). Gravel size increased at most sampling sites in the LFC from 1982 to 1996, but decreased below Thermalito Afterbay Outlet, suggesting armoring of the LFC as smaller gravel was transported downstream. Armoring is also evident in the surface bulk samples, with similar spatial trends and changes between the two years in the samples (Figure 10). Subsurface gravel size was somewhat larger in the LFC and showed an increase in size in the uppermost riffles.

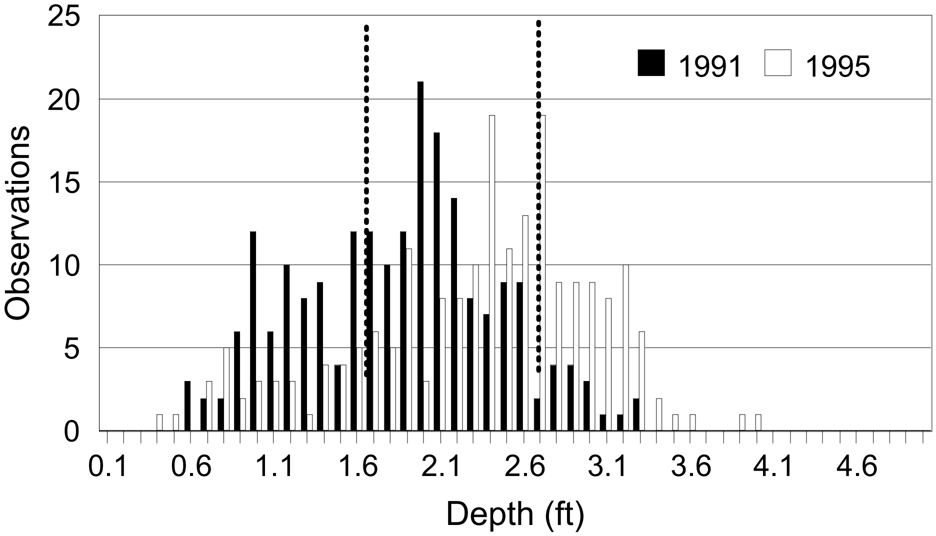

Figure 6 Histogram of spawning observations at different depths for 1991 and 1995, when flows were higher. The central 50% of observations are bracketed by dashed lines.

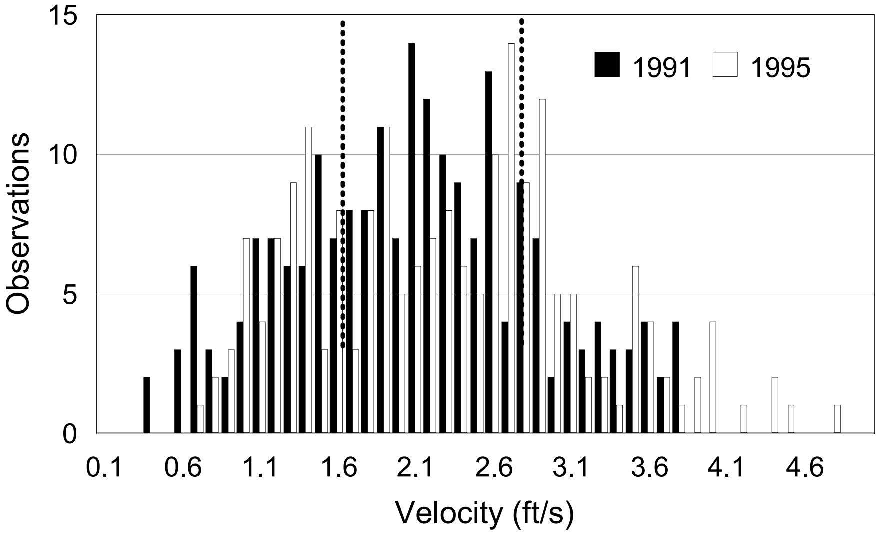

Figure 7 Histogram of spawning observations at different velocities for 1991 and 1995, when flows were higher. The central 50% of observations are bracketed by dashed lines.

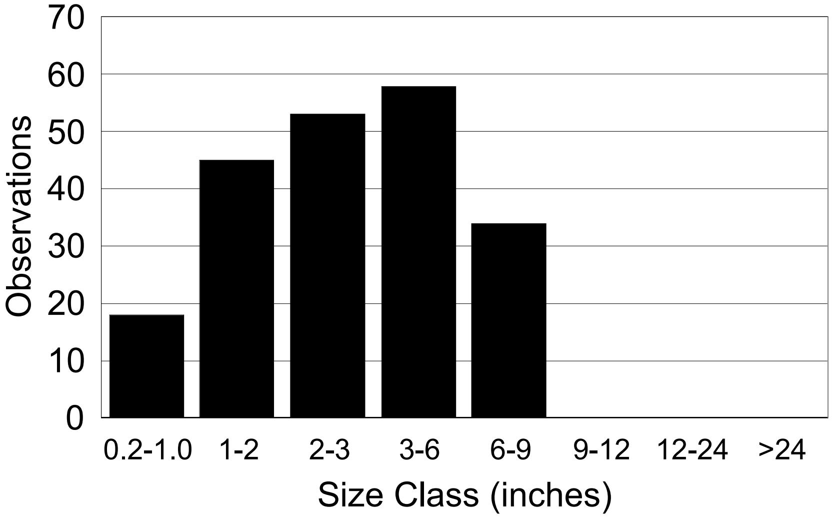

Figure 8 Size classes of spawning gravel used by Feather River salmon

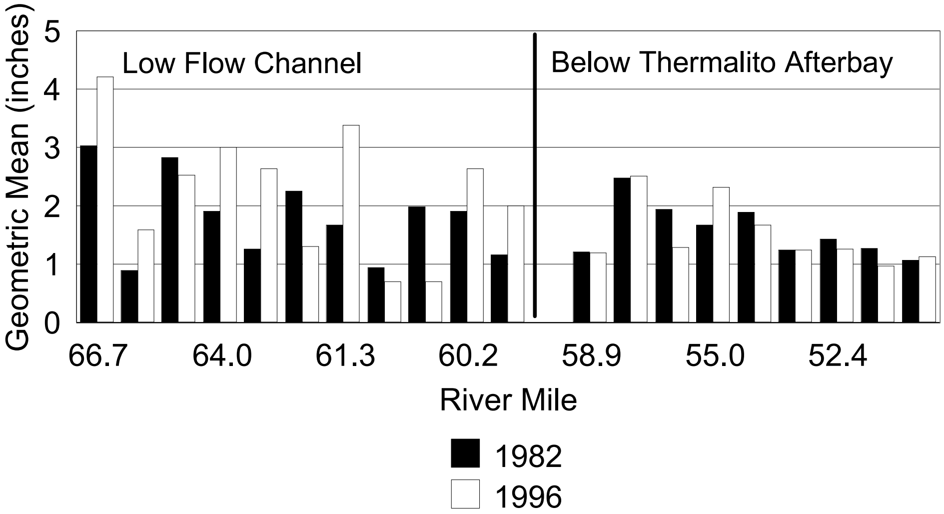

Figure 9 The geometric mean (inches) of Wolman gravel samples collected by river mile for 1982 and 1996

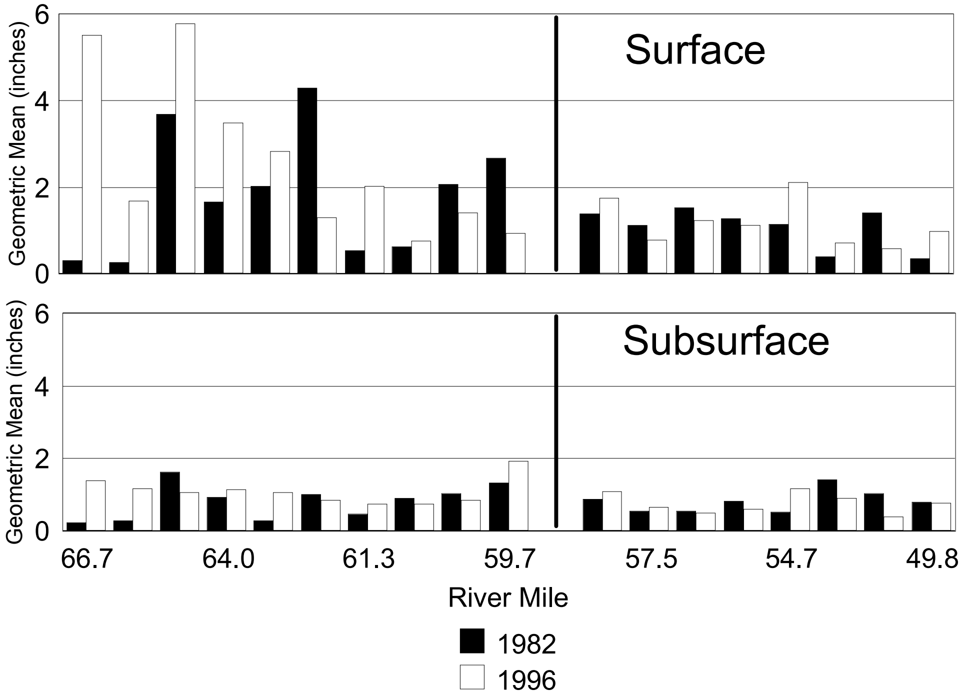

Figure 10 The geometric mean (inches) of bulk surface and subsurface gravel samples collected by river mile for 1982 and 1996

Spawning Distribution: In 1995 a total of 773,732 ft^2 of the LFC was used for spawning, with the greatest area concentrated in upper few kilometers of the reach (Figure 11). The majority of spawning occurred in the "riffle" and "glide" areas (Table 1). The upper three miles contained more than 60% of the total spawning area. A similar trend for the LFC is also evident in the historical data (Figure 12).

The estimate of total spawning area for the reach below Thermalito Afterbay was 1,480,085 ft^2 (see Figure 11). The "glide" areas showed the greatest amount of spawning activity and the "riffle" and "pool" areas had approximately equal levels (see Table 1). In contrast to the LFC, spawning area below Thermalito showed no obvious trend by river mile—spawning areas were relatively evenly distributed across the reach. The historical data below Thermalito Afterbay suggest a similar pattern, although there is some indication of increased spawning activity near river mile 57 at the upper end of the reach (see Figure 12).

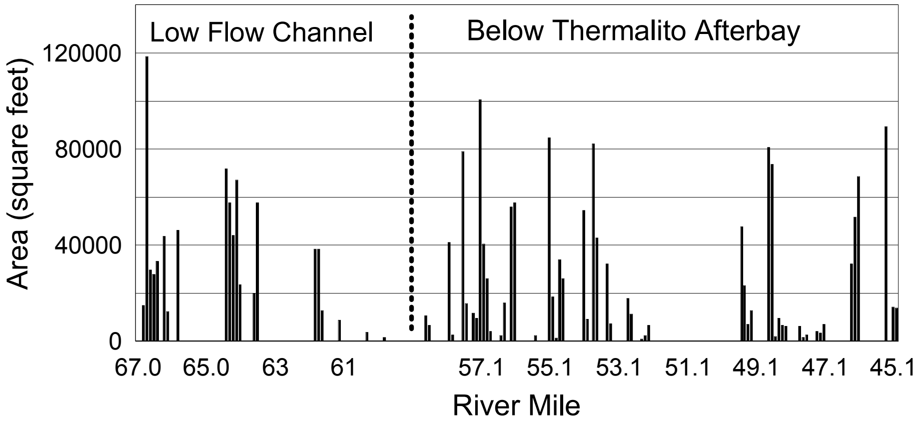

Figure 11 Spawning area (ft^2) by river mile for 1995

Table 1 Spawning areas relative to boundaries set in a baseline habitat map

Habitat	*Area (ft^2)*	*Percent*
Low Flow Channel		
“Riffle”	276,078	40
“Glide”	141,486	20
“Pool”	280,845	40
Total	698,409	100
Below Thermalito Afterbay		
“Riffle”	508,607	34
“Glide”	517,340	35
“Pool”	468,531	31
Total	1,494,478	100

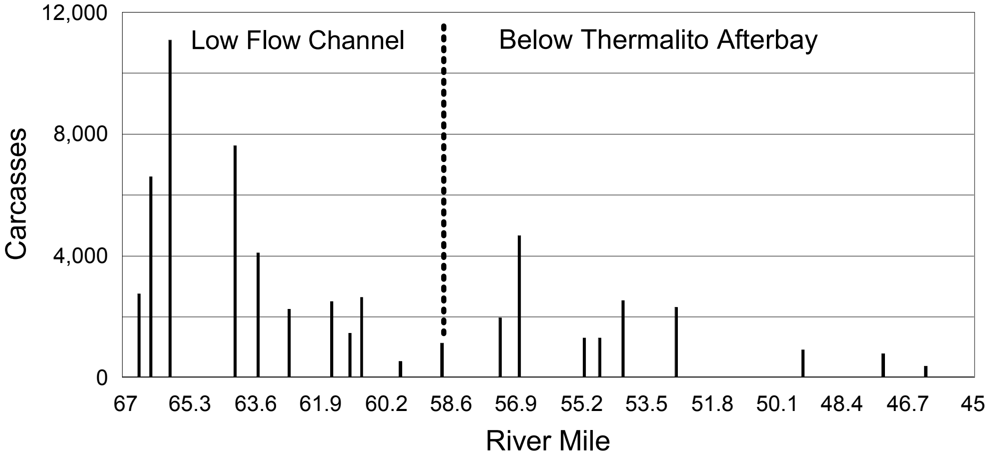

Figure 12 Salmon carcass numbers collected by river mile for 1971–1974

The 1995 DFG carcass surveys estimated that the total number of spawners for the low flow channel and the reach from Thermalito Afterbay Outlet to Gridley (see Figure 1) was 44,111 and 15,572, respectively. However, spawning area showed the opposite trend with estimates of 773,732 ft^2 and 915,089 ft^2, respectively. Based on these results, the estimated superimposition index for the LFC was 1.57 and the index for the lower reach was 0.47.

Factors Affecting Spawning Distribution

Time had a highly significant effect on the percentage of fish spawning in the LFC, explaining 72% of the variability (Figure 13). LFC flow ($r^2 = 0.02$, $P > 0.05$), October water temperature ($r^2 = 0.12$, $P > 0.05$), November water temperature ($r^2 = 0.02$, $P > 0.05$) and annual escapement ($r^2 = 0.09$, $P > 0.05$) showed no such time trend. However, flow distribution had a similar significant but weaker trend ($r^2 = 0.33$, $P < 0.001$) (Figure 14). Flow distribution ($r^2 = 0.10$, $P > 0.05$), total LFC flow ($r^2 = 0.02$, $P > 0.05$), October water temperature ($r^2 = 0.15$, $P > 0.05$) and November water temperature ($r^2 = 0.02$, $P > 0.05$) were not significantly related to the residuals from the spawning distribution-time relationship, but escapement had a weak significant relationship ($r^2 = 0.19$, $P < 0.05$) (Figure 15).

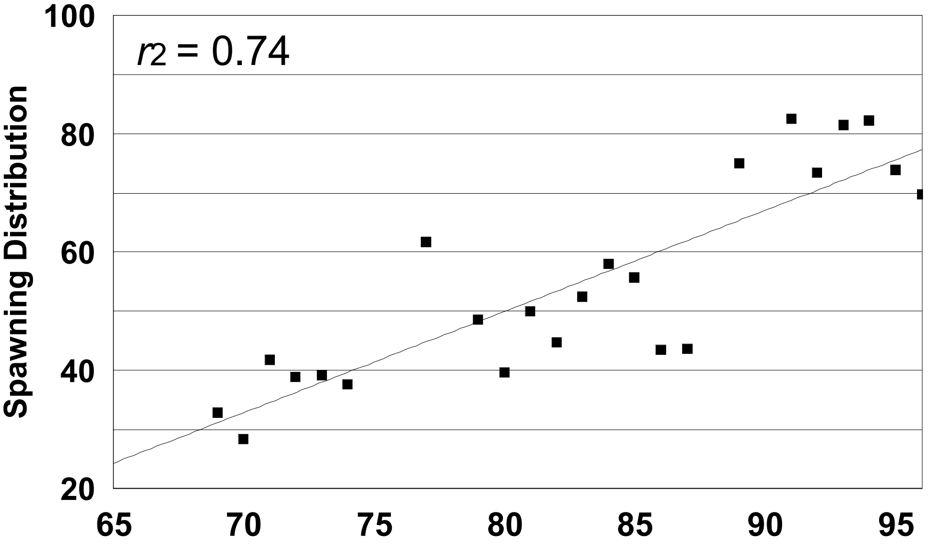

Figure 13 The percentage of salmon spawning in the LFC for 1969–1996. The increase is significant at the $P < 0.001$ level.

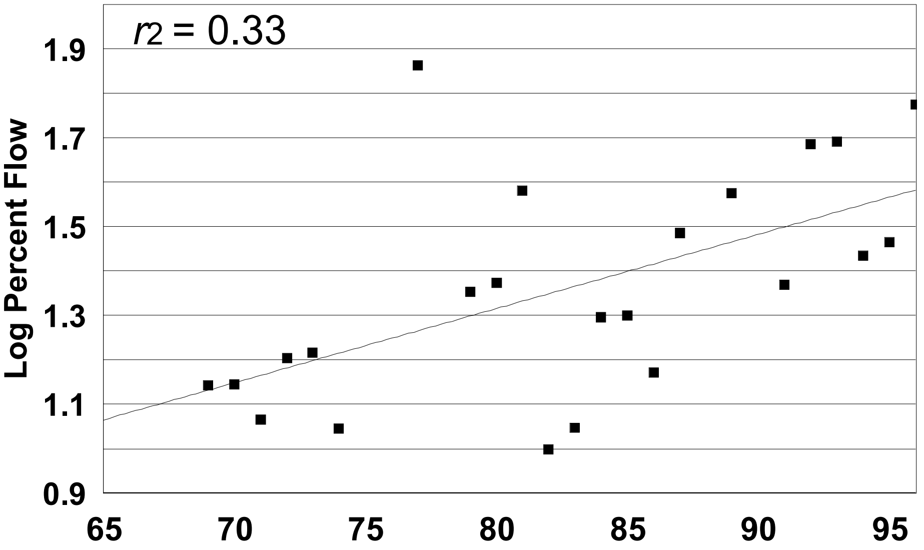

Figure 14 Log percentage of river flow from the LFC for 1969–1996. The increase is significant at the $P < 0.05$ level.

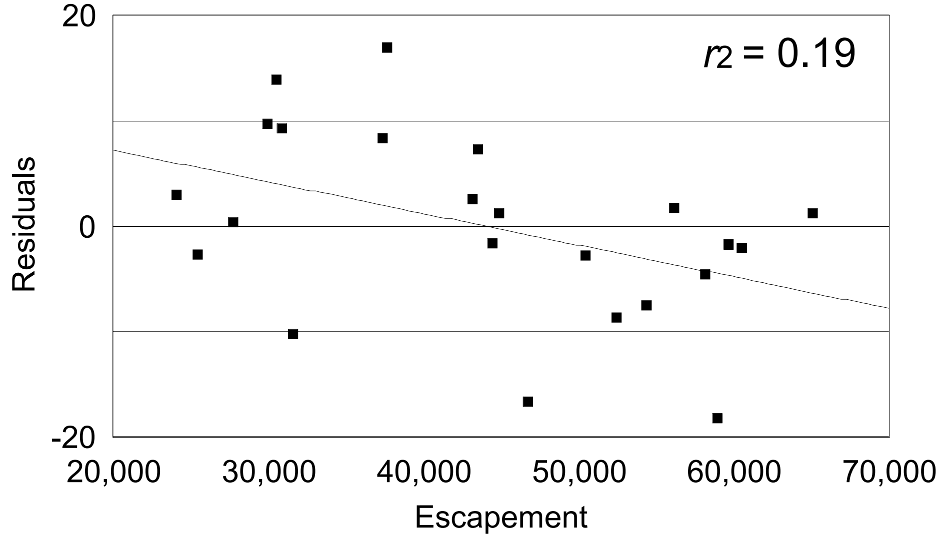

Figure 15 Relationship between in-channel escapement and the residuals from the time-LFC flow distribution relationship (see Figure 11). The decrease is significant at the $P < 0.01$ level.

These results suggested that escapement in the river and flow distribution were the key variables analyzed that could explain trends in spawning distribution. The two variables were combined in a multiple regression analysis, which showed that total escapement in the river and flow distribution explained about 47% of the variability in the percentage of salmon spawning in the LFC. However, the combined effects of flow and escapement explain less variability in spawning distribution than a model using time and escapement (multiple $r^2 = 0.77$, $P < 0.001$).

Modeling

The PHABSIM model predicted that WUA would be maximized in the LFC at 1,000 cfs and at 3,250 cfs in the reach below Thermalito Afterbay Outlet (Figure 16). The results for the egg survival model were quite different (Figure 17). Egg production increased roughly in proportion to the number of spawners. Flow had relatively little effect on predicted egg production at low escapement levels (20,000), but at higher escapement levels total egg production improved with decreasing flow.

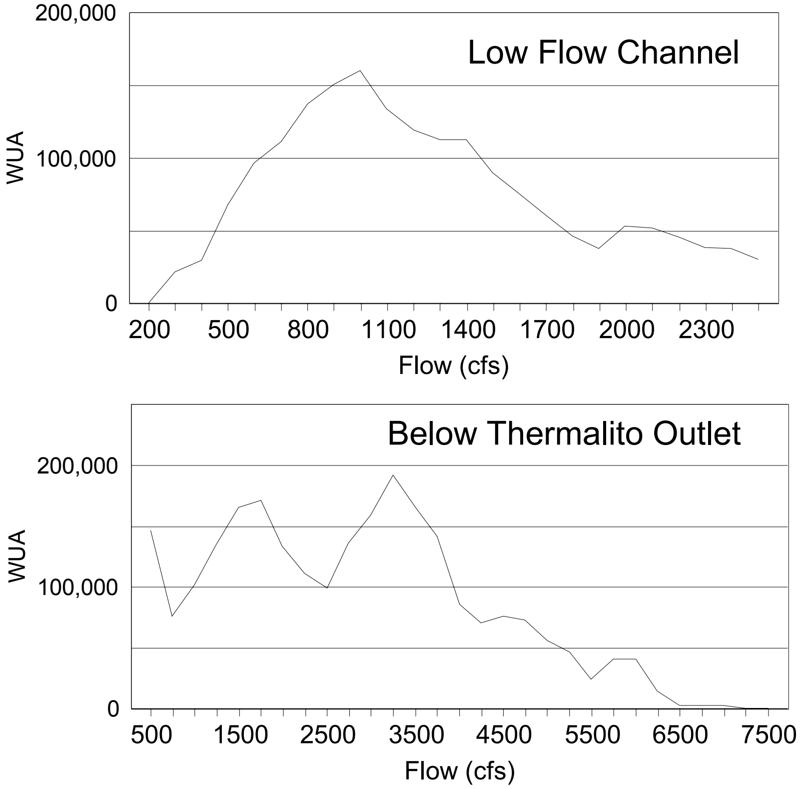

Figure 16 Simulation of spawning Weighted Useable Area (WUA) against flow (cfs) for two reaches of the lower Feather River using a PHABSIM model

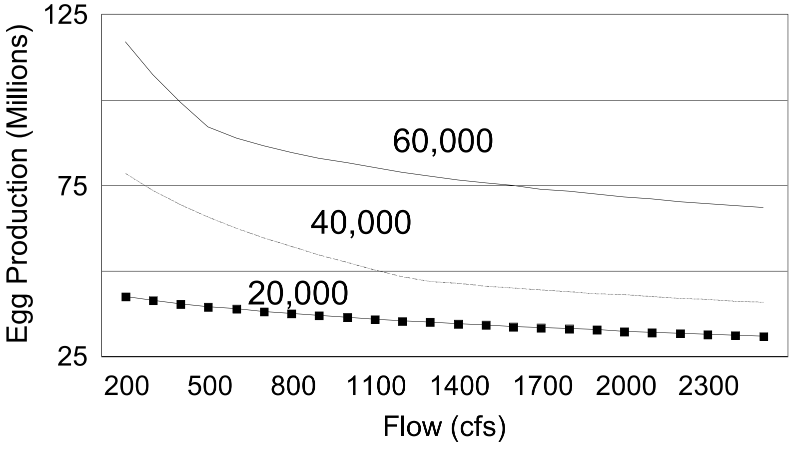

Figure 17 Simulation of egg production against flow (cfs) for three different levels of in-channel escapement

Discussion

This study documents a marked shift in the spawning distribution of chinook salmon in the lower Feather River. Since the construction of Oroville Dam and Feather River Hatchery, salmon have shifted their spawning activity from predominantly in the reach below Thermalito Afterbay Outlet to the LFC (see Figure 13). An average of 75% of spawning activity now occurs in the LFC with the greatest portion crowded in the upper three miles of the LFC (see Figure 11). While there is evidence that this upper section of the LFC was also intensively used after the construction of the dam and hatchery, the shift in the spawning distribution has undoubtedly increased spawning densities. The high superimposition indices we calculated for the LFC suggest that spawning habitat in this reach is limiting. Moreover, the results of Painter and others (1977) indicate that increased escapement will result in high egg mortality from superimposition.

The combined effects of time and escapement explained the greatest proportion of variability in spawning distribution. The effect of run size is biologically reasonable because spawning adults are highly territorial. Increased escapement levels could be expected to “push” more fish into the reach below Thermalito Afterbay Outlet.

Possible factors responsible for the time trend in spawning distribution include changes in total LFC flow, flow distribution, temperature, substrate, escapement, and hatchery practices. Of the first three variables, only flow distribution had a significant time trend. Three reasons may account for the increase in the proportion of flow from the LFC over the past three decades: (1) the minimum required LFC flow increased from 400 to 600 cfs in 1983; (2) drought conditions during 1987–1992, when total river flows were low; and (3) LFC high flow tests in 1995 and 1996. It is biologically reasonable that increasing percentage of flow from the LFC resulted in higher spawning activity in that reach—there is a well documented effect of “attraction flows” on the movements of salmon (Banks 1969).

Although changes in flow distribution explain much of the time trend in spawning distribution, it is likely that other changes may be of equal or greater importance. The combined effects of time and escapement explain 77% of the variability in spawning distribution, whereas flow distribution and escapement explain only 47%. Other potential explanations for increased use of the LFC over time include changes in gravel quality and hatchery operations. If substrate were responsible we would expect to see the greatest decline in gravel quality below Thermalito Afterbay Outlet. Yet our Wolman counts and bulk samples show that the gravel quality has deteriorated to the greatest extent in the LFC, not downstream. The increase in the gravel size at the surface of the upstream riffles in the LFC shows that substantial armoring has occurred (see Figure 10) as smaller material has been transported downstream. Note, however, that our analyses do not account for possible changes in gravel permeability. It is possible that reduced use of the lower reach is a result of decreased gravel permeability.

Spawners seem most attracted to the heavily armored riffles at the upstream end of the reach, suggesting that hatchery operations may be at least partially responsible. We suggest two possible mechanisms for hatchery effects: (1) changes in stocking location of hatchery salmon and (2) genetic introgression between fall-run and spring-run chinook stocks.

Before 1983, most hatchery fish were stocked in the river, but after most were released downstream in the Sacramento-San Joaquin Estuary (see Figure 3). This change in operations probably increased survival rates of the hatchery fish (Cramer 1992), perhaps increasing the proportion of hatchery salmon in the stock. Salmon of hatchery origin are likely to have a stronger behavioral attraction to the LFC riffles closest to the hatchery than wild fish. Juvenile tagging studies initiated in the 1970s and more intensively in the 1990s may help to address this issue. As an indication that the proportion of hatchery fish has increased in the population, the mean escapement of fall-run at Feather River Hatchery was 4,600 adults during the first ten years of the operation of the hatchery as compared to a mean of 9,200 adults for 1983–1994 (see Figure 1). There is also evidence from other locations that hatchery salmon can displace natural stocks. Unwin and Glova (1997) found that the proportion of naturally produced chinook salmon steadily declined after the construction of a hatchery on a New Zealand stream. Like the Feather River fall-run (see Figure 1), operation of the hatchery resulted in no major change in total run strength. There is also good local evidence that operation of a hatchery can cause major changes in the distribution of chinook salmon stocks. Coleman National Fish Hatchery was built in 1942 on Battle Creek, a small tributary of the Sacramento River, to mitigate for the construction of Shasta Dam (Leitritz 1970; Black, this volume). Data for 1967–1991 show that there has been a major increase in the number of spawners using Battle Creek, while escapement in the mainstem Sacramento River had no obvious trend (Figure 18). The likely cause is that the Battle Creek population has been augmented by, or perhaps even replaced by, salmon from Coleman Fish Hatchery.

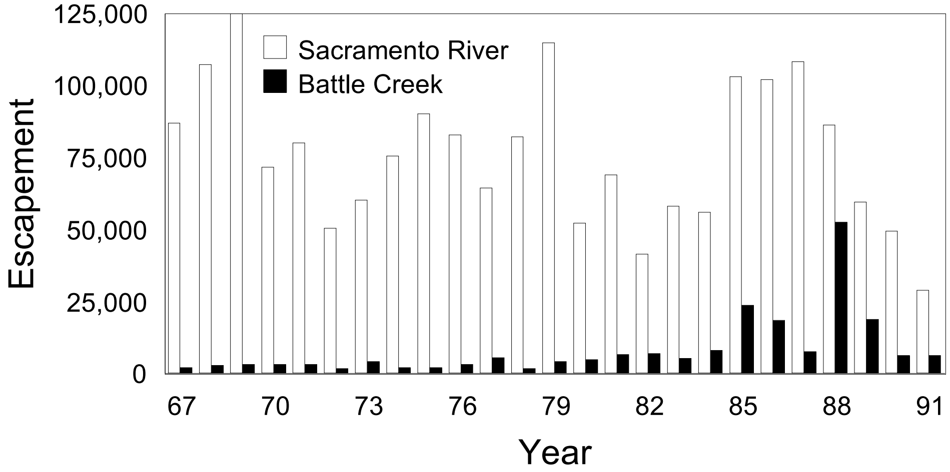

Figure 18 Salmon escapement trends in the Sacramento River compared with Battle Creek, a small tributary where Coleman National Fish Hatchery was constructed

An alternative hypothesis is that genetic introgression between fall-run and spring-run chinook salmon increased spawning in the LFC. The spawning periods for these two races historically overlapped in late summer and early fall. Genetic integrity was maintained by differences in spawning location; fall-run spawned on the valley floor, while spring-run migrated into higher gradient reaches and tributaries (Yoshiyama and others 1996). However, the construction of several dams on the Feather River blocked spring-run access to historical spawning areas. Since the construction of Oroville Dam, DFG staff at the Feather River Hatchery attempted to maintain the genetic integrity of the two races by designating the earliest-arriving spawners as spring-run. Unfortunately, this approach does not appear to have been successful. Brown and Greene (1994) describe coded-wire-tag studies on the progeny of hatchery fish identified as "fall-run" and "spring-run" and found evidence of substantial introgression. They report that significant portions of the offspring of each hatchery race returned as adults during the wrong period. For example, many of the "spring-run" group returned during months when hatchery operators designated all spawners as "fall-run." Based on historical spawning behavior, gradual introgression of spring-run traits into the Feather River population would be expected to result in an increasing preference for the uppermost riffles of the LFC.

The PHABSIM and egg survival models yielded dramatically different results. Whether either model is a useful management tool is open to debate. The PHABSIM model is based on instream flow methodology, which is the most widely used system to develop flow recommendations (Reiser and others 1989). It predicts that increasing minimum flows in the LFC by 50% should result in the maximum amount of spawning area (see Figure 16). However, the egg survival model indicates that increasing flow to the LFC could make conditions worse by attracting more spawners, resulting in high egg mortality through superimposition (see Figure 17). Another concern is the PHABSIM model for the reach below Thermalito Afterbay Outlet produced polymodal results, which is biologically questionable (see Figure 16). An advantage of the egg survival model is that it is based on field data collected over many years in the Feather River. While superimposition has been shown to be a major source of mortality in other locations (Fukushima and others 1998), additional studies are needed to determine whether egg supply is actually a limiting factor in the Feather River and to verify the shape of the egg survival-escapement relationship developed by Painter and others (1977). The egg survival model also does not incorporate potentially important effects of hatchery operations and is particularly questionable at low flows in the LFC, when river temperature and egg aeration could result in egg mortality.

We do not recommend either model to manage river flows at this time. Although the models yielded different results, both may reflect actual processes in the river. Given the many additional factors that could affect salmon survival in the river, we recommend the development of a more comprehensive life history model which may include aspects of the PHABSIM and egg survival models, as well as features to describe the effect of hatchery operations. In the absence of a quantitative model of salmon production in the Feather River, the results of this study could still be used as the basis for a conceptual model to test different hypotheses in the river. For example, it is possible that superimposition problems could be reduced by shifting more of the spawning activity to the reach below Thermalito Afterbay, where armoring is low and spawning habitat is more abundant. Testable alternatives to achieve this include varying the proportion of flow from the LFC or reducing the hatchery component of the stock, which are more likely to spawn in the uppermost reach of the LFC close to Feather River Hatchery.

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Notes

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