A Comparison of Growth Rates of Wild Rainbow Trout (*Oncorhynchus mykiss*) in the Upper Sacramento River Before and After the Cantara Spill of 1991

by

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A COMPARISON OF GROWTH RATES OF WILD RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) IN THE UPPER SACRAMENTO RIVER BEFORE AND AFTER THE CANTARA SPILL OF 1991

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ABSTRACT

In July of 1991, a train car filled with metam-sodium pesticide fell into the upper Sacramento River, California, killing more than 300,000 wild rainbow trout and all aquatic life in the 38-mile stretch of river below the spill. I compared growth of wild rainbow trout prior to and following the spill based on analysis of scale samples collected by California Department of Fish and Game in 1978, 1980 and 1986 (pre-spill) and 1994, 1996 and 1997 (post-spill). Scale analyses were supplemented by diet analysis of wild trout collected in 1998-2001. Back-calculated lengths at age were determined using a natural log-transformed Fraser-Lee equation, and specific growth rates before and after the spill were compared using analysis of covariance (ANCOVA). Back-calculated lengths and specific growth rate comparisons between pre-spill and post-spill periods provided strong evidence that growth of trout decreased following the spill, but the effect apparently was not immediate. Back-calculated trout lengths and specific growth rates from 1994 scale samples were not significantly different from pre-spill scale samples, but analysis of 1996 and 1997 scale samples showed significant decreases in both length at age and specific growth rates for age 3 and 4 trout. Specific growth rates of rainbow trout were lowest in 1995, when a severe winter occurred and high winter and spring flows were recorded. Diet analysis revealed that wild rainbow trout were consuming a diverse selection of macroinvertebrates. Large trout were getting most of their consumed energy from *Dicosmoecus* sp., a large caddisfly larva, but showed no evidence of sculpin consumption. The upper Sacramento River trout population may have been more susceptible to the effects of natural disturbances in the process of recovery following the spill, as trout growth rates appear to partially reflect winter severity.

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INTRODUCTION

Until 1991 the upper Sacramento River was renowned for its wild rainbow trout fishery, and fishermen from across the country would come to catch trophy-size trout from its waters. On the night of July 14, 1991, a Southern Pacific train tanker car derailed and fell into the river at the Cantara Loop Bridge, spilling an estimated 19,000 gallons of metam-sodium pesticide into the river. The resulting chemical plume killed all aquatic life, including all species of fish, amphibians, and invertebrates in a 60km stretch of the river from the site of the spill downstream to Shasta Lake (Allen 1994). Species of fish killed included rainbow trout (*Oncorhynchus mykiss*), riffle sculpin (*Cottus gulosus*), Sacramento sucker (*Catostomus occidentalis*), Sacramento pike-minnow (*Ptycocheilus grandis*), spotted bass (*Micropterus punctulatus*), smallmouth bass (*Micropterus dolomieui*), and hardhead (*Mylopharodon conocephalus*) (Turek 1998).

Actual numbers of fish killed will never be definitely known, but an effort was made immediately after the spill by California Department of Fish and Game (CDFG) to estimate the numbers of fish killed by performing shoreline and instream counts of fish carcasses on about 15% of the river. These counts were expanded to estimate the total number of fish killed within the total area of the river affected by the spill (Hankin and McCanne 2000). Final estimates of total fish killed were well over one million fish, including an estimated 312,500 rainbow trout, 655,000 sculpin, 74,000 pikeminnow/hardhead, 34,000 suckers, and 3,000 bass (Hankin and McCanne 2000).

After the spill occurred, the river and all its tributaries were closed to fishing until 1994 to foster the recovery of the river ecosystem and rainbow trout population.

This was not the first time a chemical spill had occurred on the Upper Sacramento River. A less damaging spill occurred on 10 April 1976, again caused by a Southern Pacific train derailment at the Cantara Loop bridge (Hankin and McCanne 2000, Turek 1995). Chemical spills and associated negative impacts on fish populations have been widely reported in the literature and are not uncommon (Olmsted and Cloutman 1974, Johnson and Cheverie 1980, Moyle et al. 1983, Ensign et al. 1997). Due to the magnitude of the 1991 spill, a vigorous effort to aid and monitor the recovery of the trout fishery was undertaken by CDFG and several U.S. Government agencies, with the help of private fisheries consultants and Humboldt State University. Through this effort, the Cantara Spill Recovery-Monitoring Program was formed.

As part of the monitoring program, CDFG performed electrofishing surveys of the wild rainbow trout populations nearly every year from 1993 through 1998. During these surveys, scale samples from rainbow trout were collected from seven locations along the upper Sacramento River. A length at age analysis performed on rainbow trout scales from the 1994 surveys suggested that lengths at ages 3, 4, and 5 were much less than those reported in an earlier study (from 1978) prior to the spill (Turek 1995). A significant reduction in growth rates of wild rainbow trout on the upper Sacramento River following the spill would have important implications for recovery and management of the wild trout fishery.

Although the evidence of reduction in trout growth rates based on data from these two years seemed compelling, there were substantial uncertainties involved with comparing the 1978 scale analyses to the 1994 scale analyses. One problem was that differences in methodologies used to back-calculate length at age may have produced apparent differences in growth that are not real, but instead simply reflect differences in analysis methods. A second problem is that the 1978 scale data originated from a period thirteen years prior to the 1991 spill. Within such a long time period it is possible that naturally fluctuating environmental conditions could cause differences in trout growth rates that would then be misinterpreted as being caused by the spill. A third problem is that the 1978 scale samples were from creel surveys, while the 1994 samples were from electrofishing surveys. Scale samples taken from creel surveys can produce back-calculated lengths at age that are larger than back-calculated lengths from scale samples taken by electrofishing surveys of the same fish populations (Miranda et al. 1987). All of these possibilities warranted further investigation.

In a preliminary length at age investigation that I performed in 1998, back-calculated lengths from scale samples from the 1996 CDFG electrofishing surveys were compared with back-calculated lengths from scale samples collected from dead rainbow trout killed during the Cantara spill in 1991. Although the 1996 scales provided a good sample for back calculation, the regression of fish length vs. scale radius from the rainbow trout collected following the 1991 spill produced a wide scatter of points and a poor R^2 value of 0.58. Consequently, the body-scale relation from this sample of rainbow trout was judged not good enough for performing back-calculations. In the

Spring of 1998, however, archived upper Sacramento River rainbow trout scale samples from 1978, 1980, and 1986 were acquired from CDFG, thereby allowing for a more valid comparison of growth rates of rainbow tout prior to and following the 1991 spill.

The objective of this investigation was to make a more definitive comparison of wild rainbow trout growth rates in the upper Sacramento River prior to, and following the 1991 Cantara spill. The primary objective was to analyze all scale samples from pre-spill years and post-spill years with similar methodology, using modern back-calculation methods with computer-assisted identification and measurement of annular marks on scales. Comparison based on multiple years of pre and post-spill data would reduce the chance of incorrectly attributing a reduction in trout growth rates to the spill, when in fact it could have been caused by some other occurrence.

A secondary objective of the current study was to perform a diet study of the wild rainbow trout in the upper Sacramento River to determine if a change in growth rates could be related to a change in the trout prey community. Because riffle sculpin were the most abundant fish in the upper Sacramento River before the spill, it was speculated that the elimination of this species from the system could reduce growth rates of larger trout if sculpin were a major part of their diet prior to the spill (Turek 1995). Thus, a possible factor responsible for reduced growth rates might be identified through diet analysis, at least for the larger trout.

STUDY SITE

The upper Sacramento River is a 62km reach located in Northern California between Lake Siskiyou (Siskiyou County) and Shasta Lake (Shasta County, Figure 1). At its headwaters, the upper Sacramento River receives water from 4,316m Mount Shasta in the east and 2743m Mount Eddy in the west. These headwaters drain into Lake Siskiyou, a small lake (174 hectares) that was formed by the construction of Box Canyon Dam, built in 1969 for flood control and power generation (Turek 1998). Box Canyon Dam is effectively the upper boundary of the upper Sacramento River. The lower boundary is Shasta Lake, created by the construction of Shasta Dam in 1944. These two reservoirs act as complete barriers to historical migrations of anadromous salmonids, which included steelhead (*Oncorhynchus mykiss*) and chinook salmon (*Oncorhynchus tchawytcha*). The upper Sacramento River immediately below Box Canyon Dam is a fourth order stream with a drainage area of 316 km^2. At the confluence of Campbell Creek near Lake Shasta, the river is a fifth order stream with a drainage area of approximately 1100 km^2 (Allen 1999).

The main channel of the upper Sacramento River is bordered by steep mountainous terrain on both banks, and extensive channel migration is effectively restricted for the majority of the study site. There is a 610m drop in elevation between the upper reaches and the lower reaches. The river is paralleled for most of its length by a major interstate highway (I-5), and a railroad. The railroad berm essentially forms the

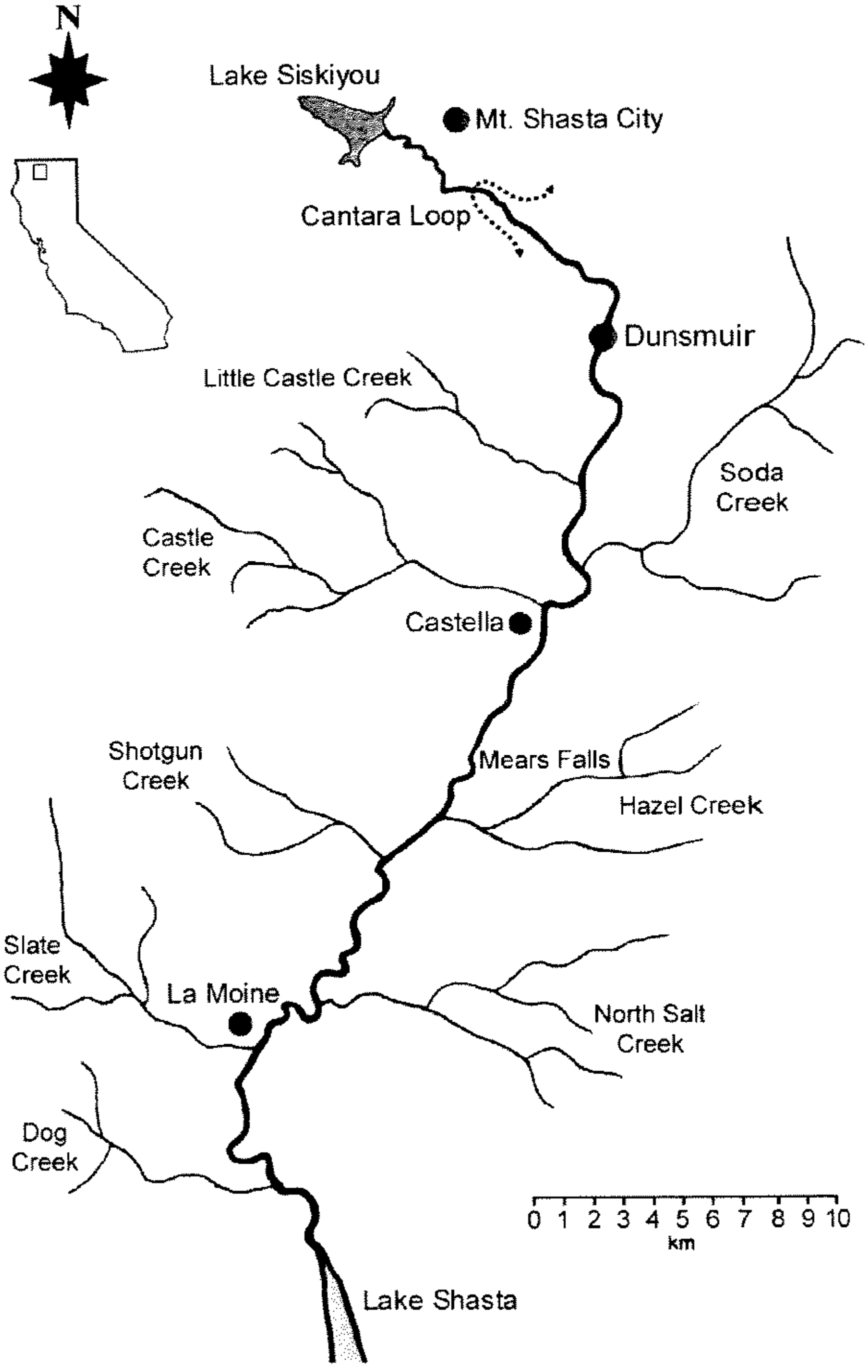


Figure 1. Map of the upper Sacramento River between Lake Siskiyou and Lake Shasta shown with major tributaries. The spill occurred at the Cantara Loop.

stream bank for a significant portion of the study area, and is frequently armored with rip-rap (Allen 1999). Stream gradient is highest in the upper reaches above Cantara Loop (1.7%) and decreases in the lower reaches near Lake Shasta to about 0.7% (Turek 1998). River flows are partially controlled at Box Canyon Dam, but a number of springs located in the upper reaches above Dunsmuir add substantial quantities of clear, cold water that help maintain good conditions for trout. Numerous large tributaries, which drain off the surrounding mountains, also add significant quantities of water to the river, especially during the spring snowmelt period. Annual mean flows are around 1,200 cubic feet per second (cfs) at the Delta gauging station near Shasta Lake, but winter and spring flows are quite variable and can be exceptionally high (> 15,000 cfs) for extended periods during wet years. During a recent eighty-year flood event (1 January 1997), peak streamflow exceeded 62,000 cfs and caused extensive changes to the channel (Allen 1999). During wet years, runoff from snowmelt may elevate streamflows well into July (Allen 1999).

Hot summers and cold winters typify the climate of the upper Sacramento River region. Summer water temperatures range from 9.0°C to 13.5°C in the upper river and from 12.5°C to 26°C in the lower river (Turek 1998). Decreased input from cold springs, and increased insolation are the main causes for the difference in temperature between the upper and lower river. Winter water temperatures do not differ much between the upper and lower portions of the river, and range from about 4-8°C from November through March (Turek 1998).

The upper reaches are characterized by a high percentage of deep and shallow pools connected by short runs and riffles. The mid-reaches between Cantara Loop and Sims contain more frequent and longer runs and riffles, and fewer pools. The lower reach below Sims is typified by the greatest percentage of deep pools, which are linked by extensive runs and few riffles (Turek 1998). The length and width of habitat units increase as one goes from the upper end to the lower end of the river. The substrate of the upper and mid-reaches is predominantly round cobbles and boulders (of granite, quartz, serpentine, and basalts), most of which have been worn down due to migration in the channel. There are also extensive areas of bedrock along the banks and in the channel. The lower reaches have generally smaller substrates of sand, pebbles and small cobbles, with some boulders still occurring. Bedrock is still common in the lower reaches and forms many of the deep pools in this area of the river.

A lush riparian forest is present along most of the river, and the upper reaches are moderately shaded due to the relatively small width of the channel. The riparian zone is dominated by trees such as white alder (*Alnus rhombifolia*), black cottonwood (*Populus trichocarpa*), big-leaf maple (*Acer macrophyllum*), Oregon ash (*Fraxinus agrifolia*), Canyon live-oak (*Quercus chrysolepsis*), and Ponderosa pine (*Pinus ponderosa*). Shrub-like species that occur along the river are willows (*Salix sp.*), poison oak (*Rhus diversiloba*) and Himalayan blackberry (*Rubus discolor*), with herbaceous species along the river's edge being mostly Indian rhubarb (*Peltiphyllum peltatum*), horsetail (*Equisetum hymale*), and sedges (*Carex* sp.). The shading effect of the riparian vegetation becomes minimal as the river widens in the mid and lower reaches. The river is an important resource for the diverse and abundant wildlife that lives in the riparian zone and adjacent conifer forest.

The fish community present in the upper Sacramento River changes between the upper and the lower reaches. The differences in fish species are due mostly to changes in water temperature, and a barrier to fish migration that occurs at Mears Falls. The upper sections of the river are dominated by wild rainbow trout and riffle sculpin, with riffle sculpin being the more abundant (Allen 1999). Hatchery rainbow trout are stocked by the CDFG in the Dunsmuir area annually and are more abundant in the upper portions of the river (personal observations from snorkel surveys). Studies have shown that the overwhelming majority (90-95%) of rainbow trout in the study area are wild fish (Hankin and McCanne 2000). Sacramento suckers begin to be present a few kilometers above Mears Falls, along with a few Sacramento pike-minnow. Below Mears Falls, rainbow trout numbers decline, and the numbers of Sacramento sucker and Sacramento pike-minnow increase substantially. Fish species diversity increases in the lower reaches, as non-native spotted bass and smallmouth bass, and native hardhead and speckled dace (*Rhinichthys osculus*) become common. The conditions become less favorable for rainbow trout in these lower areas because of high summer water temperatures and increased threat of predation on the smaller trout from pike-minnow and bass. Trout fry are most abundant in the upper reaches above Mears Falls, while non-game fry are most abundant in the lower reaches. Some migration of native and non-native fish species to and from Shasta Lake occurs in the lower river (Nielsen et al. 2000).

Prior to the spill (1983-1990), the upper Sacramento River was managed as part put-and-take fishery, and part wild trout catch-and-release fishery. The upper 40.7 km of the river was stocked with catchable size trout, and there was a 10-fish bag limit with no special gear restrictions. The lower 22 km of river was managed as a "wild trout" area, in which no hatchery fish were stocked (Rode and Zuspan 1993). There was a 2-fish bag limit imposed in this section to encourage a catch-and-release attitude among fishermen, since it had been determined that about 90% of all rainbow trout in this area were wild, including all trout of trophy size (>35.6 cm total length, Hankin and McCanne 2000).

Following the Cantara Spill, a moratorium on fishing was implemented for the upper Sacramento River until April of 1994, when the river was reopened to angling under special regulations. Under these regulations the river was split into three sections. The upper 10 km and the lower 42 km have been opened to catch-and-release angling only (0-fish limit), with artificial lures and barbless hooks required. In between the catch-and-release zones there is a 10 km section in the Dunsmuir area where there is a 5-trout bag limit, and the use of bait is allowed. In this section stocking of hatchery rainbow trout has taken place during the fishing season at a rate of around 20,000-25,000 catchable size trout per year (Turek 1998).

METHODS

Scale Analysis

Rainbow trout scale samples that were analyzed came from two different sources. The first source consisted of archived upper Sacramento River trout scale samples from 1978, 1980, and 1986 (from Michael Rode, CDFG, Mt. Shasta; and Dave Lentz, CDFG, Rancho Cordova). The 1978 and 1986 scale samples were from creel surveys that took place during spring and summer, and the 1980 samples were from an electrofishing survey that took place in late fall. In all three years, scale samples were taken from a variety of sites on the upper and lower river. Each scale sample envelope was labeled with the fish fork length, date, and location where the fish was collected. The pre-spill scale samples had been previously mounted between glass slides, but because of their age the tape holding many of the slides together had become loose, and the scales were often falling out. All of the pre-spill scale samples, therefore, were remounted; scales were rearranged neatly in rows, and glass slides were re-taped. Scale samples were labeled with sequential numbers and the year of collection. Numbers of scale samples for 1978, 1980, and 1986 were 116, 120 and 113 respectively.

Post-spill scale samples from 1994, 1996, and 1997 were acquired from Steve Turek (CDFG, Redding). The post-spill scale samples were collected during CDFG electrofishing surveys from late October through November at 7 different sites ranging from the upper river area of Ney Springs (1.5km downstream of Lake Siskiyou), to the lower river area of Dog Creek. Numbers of scale samples for 1994, 1996, and 1997 were 585, 695, and 676 respectively. Post-spill scale samples were collected mostly from smaller size classes but, according to Ricker (1992), it is important to include approximately equal numbers of all size classes for the regression of fish length on scale radius to determine the appropriate y-intercept for the back-calculation equation. To insure that approximately equal numbers of scales for each size category were selected for the analysis, all post-spill scale samples were sorted by fish length. Then a systematic sample of size n = 7 was taken within each 10mm length interval (bin) up to 320mm. If a 10mm interval contained less than 7 samples, then all the scale samples within that interval were selected. All scale samples from fish longer than 320mm were selected due to small sample sizes (<10) within the 10mm intervals.

The 1994 scale samples had been previously mounted on glass slides by CDFG. For mounting of the selected samples from 1996 and 1997, scales were removed from scale envelopes, placed in a glass dish with a mild soap solution, and allowed to soak for a few minutes. The scales were then agitated and rinsed. If available, at least 10 scales from the sample were placed on a microscope slide and arranged with the aid of a dissecting microscope. Any excess dirt, epidermis, and mucous was removed by scrubbing with a small paintbrush to insure that all circuli were clearly visible. A second glass slide was placed over the first, and slides were attached with pieces of tape. Slides were labeled with sequential numbers and the year of scale collection, and allowed to dry for several days before analysis.

All annuli and distances between annuli were determined without knowledge of fish length using a microscope that was connected to a TV monitor and a computer with

Image-Pro Plus (MediaCybernetics Inc.) optical imaging software installed. The actual scale measurements were made within the computer after an image of the scale had been imported via the imaging software. The Image-Pro Plus program was calibrated to read distances in mm and was accurate to approximately 10^{-3} mm. An annulus was identified on the scale where the inter-circuli spacing became small, and where there was a distinct convergence or "cutting-off" of circuli along the sides of this area. To verify the identification of an annulus, all scales on the sample slide were examined to make sure that the same annular marking patterns were present on every scale in the sample. If all scales of the same sample did not show identical numbers of annuli then the sample was excluded from the analysis because of the uncertainty that would exist in any age designation. Measurements of distances between annuli were made sequentially from the focus (center) to the outer margin of each annulus, and to the outer edge of the scale, all at a 20° angle from the central axis. Scale samples that consisted of all regenerated scales, or that had ambiguous or unidentifiable annuli were eliminated from the analysis. After all scales had been aged, they were re-examined two more times to double check the ages and make sure they were consistent over repeated readings.

Back-Calculation

After scale measurements were taken, separate linear regressions of trout fork length at capture (*L*) against scale radius at capture (*S*) were performed for each sample year. Plots of residuals from fitted regression lines suggested that the body-scale relations for upper Sacramento River rainbow trout were non-linear. In contrast, the regressions of natural log (ln) L on ln S appeared linear and lack of homoscedasticity in the regressions was no longer a problem.

Slopes and y-intercepts (elevations) of regression lines of ln L on ln S for all sample years were compared following Snedecor and Cochran (1967, sec. 14.6). Slopes of all ln L-ln S regressions from pre and post-spill were not significantly different from one another ($P = 0.24$). Fitting a common slope, elevations between the six years were compared. Elevations were found to be significantly different between the post-spill and the pre-spill regressions ($P = 0.0025$), with the elevations for the pre-spill regressions being significantly greater than the post-spill regressions ($P < 0.0001$). Elevations of all pre-spill regressions were judged equal to one another ($P = 0.18$), however, as were elevations of all post-spill regressions ($P = 0.26$). Therefore, a single pooled intercept value was used for all pre-spill groups and a single (but different) pooled intercept value was used for all post-spill groups in the Fraser-Lee back-calculation equations.

Back-calculations of fish length at annulus formation were performed for each trout scale sample using the natural log transformed Fraser-Lee method (Bartlett et al. 1984, DeVries and Frie 1996)

$$\widehat{\ln L_i} = \hat{a} + (\ln L_c - \hat{a})\frac{\ln S_i}{\ln S_c} \ , \qquad (1)$$

where L_i = the estimated length of fish at age ; L_c= the length of fish at time of capture; S_i = distance from scale focus to ith annulus; S_c = distance from scale focus to scale margin (scale radius) at time of capture; $\hat{a}$ = y-intercept value of the regression of the natural logarithm of fish length at capture (L_c) on the natural logarithm of scale radius (S_c). Back-calculated lengths produced from equation (1) were in logarithmic form, and were exponentiated to give fork lengths in millimeters. Then, mean back-calculated lengths at age ($\bar{x}_{ij}$), and their standard errors were calculated at age i for each cohort (age class) j (j =1+, 2+, 3+, 4+) present in a given year's data set. Due to the low occurrence of 5+ age fish in the scale samples, 4+ was the oldest cohort included in the back-calculations and growth rate determinations. Finally, for each year of scale collection, weighted grand means (WGM) were calculated for length at annulus i (i = 1,2,3) for all scale collection years following Seber (1982, section 1.3.2). Let

$\bar{x}_{ij}$ = mean length at age (annulus) i (i = 1, 2, 3, 4)
for each age class j (j = 1+, 2+, 3+, 4+), and

$\bar{\bar{x}}_i$ = weighted grand mean length at age i. Then

$$\bar{\bar{x}}_i = \frac{\sum_{j=1}^{m} w_{ij}\bar{x}_{ij}}{\sum_{j=1}^{m} w_{ij}}, \tag{2}$$

where the sum is over the m cohorts (j = 1, 2,…,m)) for which length at age i can be calculated. Variances of the $\bar{x}_{ij}$ ($\hat{V}(\bar{x}_{ij})$) were estimated using

$$\hat{V}(\bar{x}_{ij}) = s_{ij}^2 \;/ n_j \,, \tag{3}$$

where

$$s_{ij}^2 = \frac{\sum_{k=1}^{n_j}(x_{ijk} - \bar{x}_{ij})^2}{(n_j - 1)} \tag{4}$$

where n_j = the sample size for cohort *j*, and x_{ijk} = back-calculated length of the kth fish (k = 1, 2, …, n_j) at age *i* from cohort *j*. Finally, variance of the weighted grand means [$\hat{V}(\bar{\bar{x}}_i)$] was estimated using

$$\hat{V}(\bar{\bar{x}}_i) = \frac{1}{\sum_{j=1}^{m} w_{ij}} \frac{\sum_{j=1}^{m} w_{ij} (\bar{x}_{ij} - \bar{\bar{x}}_i)^2}{(m-1)}, \tag{5}$$

where

$$w_{ij} = \frac{1}{\hat{V}(\bar{x}_{ij})} \quad , \tag{6}$$

and where *m* = the number of cohorts over which the grand means are calculated.

To test for significant differences between weighted grand mean lengths at age for both pre and post-spill years, 95% confidence intervals for the differences between means were constructed following Zar (1996, ch. 8). Because of bias that is created from exponentiation (Hayes et al., 1995), means were compared in logarithmic form. If such constructed intervals exclude the value zero, then one can state, with 95% confidence, that the means are different; otherwise, there is no significant difference between the means at the chosen α = 0.05 level.

Growth Rates

Estimated mean lengths at ages 2, 3, and 4 derived from the scale samples reflect accumulated growth of rainbow trout over periods of two to four years. These calculated mean lengths, therefore, do not isolate the actual rate of fish growth in a particular year for a given cohort. Thus, it may be difficult to determine if the Cantara Spill had an effect on rainbow trout growth unless growth rates in the years immediately following the spill can be isolated and statistically compared to growth rates of pre-spill years. To address this problem, I calculated daily specific growth rates (g) of individual fish at ages 2, 3, and 4 following Ricker (1975):

$$g = \frac{\ln L_{i+1} - \ln L_i}{t} \times 100 \qquad (7)$$

where L_i = back-calculated length at age i, and t = 365 days. Mean specific growth rates ($\overline{g}_{ij}$), and their estimated variances ($\hat{V}(\overline{g}_{ij})$) for age i (i = 2, 3 ,4) for each cohort j (j =2+, 3+, 4+) present in a given year's data set were calculated as follows:

$$\overline{g}_{ij} = \sum_{k=1}^{n_j} g_{ijk} / n_j \qquad (8)$$

and

$$\hat{V}(\overline{g}_{ij}) = s_{ij}^2 \ / n_j , \qquad (9)$$

where

$$s_{ij}^2 = \frac{\sum_{k=1}^{n_j} (g_{ijk} - \overline{g}_{ij})^2}{(n_j - 1)} \qquad (10)$$

where the sum is over the $k = 1,\ldots, n_j$ fish of age i in cohort j.

Mean growth rates by year and associated confidence intervals were plotted and compared for all years present on the scale samples. The graphs of the growth rate data revealed a great deal of variation for all cohorts. Upon further investigation, it appeared that one of the main sources of variation in calculated growth rates within cohorts was the effect of initial fish size on growth rate. Regressions of specific growth rate on fish size at beginning of growth year (all years combined) revealed a significant negative relationship between specific growth rates and initial fish size because fish growth rates decrease as fish size increases. Removing the variation in growth rates due to the "size effect" would make it easier to quantify and compare variation in growth rates due to environmental conditions in a particular year ("year effects", see Weisberg 1993).

I used analysis of covariance (ANCOVA) to adjust for variation in growth rates due to initial fish size, and to allow for a better comparison of possible differences in growth rates caused by environmental ("year") effects (Underwood 1997). Tests of assumptions of ANCOVA were carried out, including tests for normality, tests for equality of variance in growth rates between years (within cohorts), and tests for equality of slopes of the individual regressions of fish growth rate on fish length. Also tested was the significance of the growth rates versus fish length regression using the common slope for all years within each cohort. A few years of growth rate data did not meet the assumptions of the ANCOVA analysis and were not in included in the calculations. After the ANCOVA was performed, the adjusted mean growth rates were compared across years using a Fisher's LSD multiple comparison procedure following a Bonferroni adjustment of the α value (Dowdy and Wearden 1991, Day and Quinn 1989).

Diet Analysis

A small-scale diet analysis was performed to achieve a better understanding of the bioenergetics of the upper Sacramento River rainbow trout population. The main questions of interest were: 1) Which prey were providing trout with most of their consumption energy? 2) Were there differences in prey selection between age classes? 3) Could differences in rainbow trout growth before versus after the Cantara spill be attributable to changes in trout food base that resulted from the spill?

Fish were sampled at sites from Dog Creek to Ney Springs via electrofishing or hook-and-line between June and November in 1998-2001. A total of 71 trout stomachs were collected during this period, of which 22, 28, 16, and 5 were collected in 1998, 1999, 2000, and 2001 respectively. A conscious effort was made to collect a full range of age classes of rainbow trout for the diet study. Fish sampled ranged in size from 215mm – 483mm. All fish were sampled in the late afternoon or evening to insure that their stomachs were full with items that were eaten during the day.

For the 1998 collections, gut contents were extracted from the fish with the use of a stomach pump (Bowen 1996) and then placed in 90% ethanol. Ten fish were sacrificed after the stomach was pumped to determine if all the stomach contents had been evacuated. It was found that there was some retention of the stomach contents after stomach pumping, so in the 1999-2001 collections all fish were sacrificed, and stomachs of trout were frozen after they were dissected from the fish.

To sort diet constituents, stomachs were first removed from the ethanol or thawed. Then the stomach contents were placed in a sorting dish in small portions that could be separated and observed easily. Each portion was thoroughly separated and studied using a dissecting microscope, a probe tool, and forceps. Identifiable intact stomach contents were separated and categorized. Stomach contents that were digested and not identifiable were placed in a miscellaneous category. Macroinvertebrates were identified to order, and in some cases to family and genus, based on Merritt and Cummings (1996). The order Diptera was separated into two families, Chironomidae and Simulidae, and the genus *Dicosmoecus* sp. was separated from other Trichoptera because they were large and easily separated from other stomach contents. Wet weight of macroinvertebrates in each category was measured with an OHAUS electronic scale (± 0.001g) for the 2000-2001 collections. A few riffle sculpin sampled from the river were boiled and skeletal parts were removed and cleaned for comparison to any skeletal parts that could be found in the rainbow trout stomachs.

Frequency of occurrence of all diet items was determined for all fish sampled to see what the general diet trends were. Percentage by weight of categorized diet items was determined for trout sampled in 2000 and 2001. It became apparent that large caddisflies *Dicosmoecus* sp. were making up a major proportion of the diet for larger (>240mm) trout, so this species was weighed separately from the other Trichoptera. Since the *Dicosmoecus* sp. were found consumed with their protective cases, a sample of 30 were weighed first with the case and then without the case to determine the average percent of insect weight that consisted of digestible matter.

Otolith analysis

Although direct validation of age designations could not be done for this study, I compared the number of identified annular marks between scales and otoliths for the same rainbow trout to check agreement of age determinations between different hard structures (Beamish and McFarlane 1983, Kruse et al. 1993, DeVries and Frie 1996, Chilton and Bilton 1986).

Otoliths were extracted from 46 fish collected in the diet study during 1998-2000, and scales were collected from these same fish for comparison. The largest otolith (sagitta) was used for the age comparisons. For the majority of trout collected, both otoliths were extracted from the head, but in a few trout only one otolith was found. The otoliths were small, only a few millimeters long, and were brittle, which made grinding and polishing difficult. Both otoliths were mounted on glass slides (except when only one was found), and then were ground to the sagittal mid-plane and polished following Boiano (2000) and Hall (1991). The otolith with the clearer rings was used for aging. Examination of otoliths was performed with the same microscope/computer setup used for the scale analysis. Clove oil was brushed on the otoliths prior to examination to accentuate the annuli. Of the 46 trout sampled, 24 showed clear annuli that were appropriate for aging. The low proportion of readable otoliths was partially due to excessive bleaching of the first batch during the cleaning process, which made most of the otoliths from this group impossible to age.

An otolith annulus was identified as the thin hyaline zone present in the annual growth patterns of the otoliths, which represents the period of reduced growth for the fish (Chilton and Beamish 1982). Otoliths and scales were read independently without knowledge of the fish of origin, and both structures were aged similarly by counting the annuli from the center (nucleus), to the anterior edge. Age estimates from scales and otoliths of the same fish were then compared, and results were expressed as the percentage of age estimates of corresponding hard parts that were identical, also termed "percent agreement" (Chilton and Beamish 1982).

RESULTS

Scale Analysis

The majority of scales from the upper Sacramento River wild rainbow trout had well-defined annuli that were easily identified (Figure 2). There were always identical numbers of annuli for all scales examined in a sample, and the annuli were always located in the same relative position on each scale. A small percentage of scale samples (around 5-10% depending on sample year) contained scales that were all regenerated, or did not exhibit identifiable annuli. These scales were not included in the analysis, because of the uncertainty that would exist in any age designation. The pre-spill creel survey scale sampled consisted exclusively of older age classes (2+ thru 5+). The post-spill scales samples, collected by electrofishing, contained all age classes (0+ thru 5+), including a large number of scales from the 0+ age group which had not yet formed an annulus. Study of the circuli patterns on these scales aided in locating the first annulus on the scales of older fish, which increased confidence in the validity of the age designations. Fish over five years of age (5+) were few (5 or less) for all years sampled and were not be included in the back-calculation results because of small sample sizes. Only two age 6+ fish were found.

Body-Scale Regressions

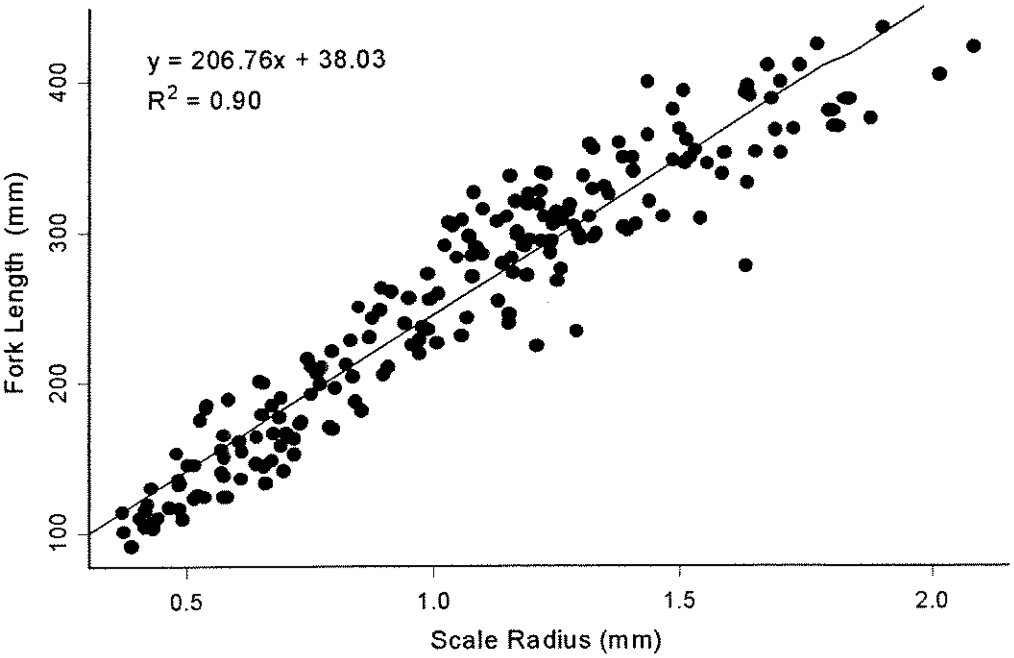
Plots of *L* on *S* before and after natural log transformation, and corresponding residual plots are shown for 1996 and 1997 data to illustrate lack of linearity and

Figure 2. Image of scale from Upper Sacramento River rainbow trout showing three clearly defined annular marks. Scale shows large amounts of growth for first three years of life.

heteroscedasticity before log transformation, as compared to approximate linearity and homoscedasticity after log transformation (Figures 3-6). The residuals plots before natural log transformation exhibited distinct non-linearity and increased variability as values of fork length get larger, but not after natural log transformation (Figures 4 and 6). Comparisons of ln *L* on ln *S* regressions showed that slopes of all pre-spill (1978, 1980, 1986), and post-spill (1994, 1996,1997) data were not significantly different ($P = 0.24$). Y-intercepts were not significantly different among pre-spill regressions ($P = 0.18$), and among post-spill regressions ($P = 0.26$), respectively, but pre-spill y-intercepts were significantly greater ($P < 0.0001$) than post-spill y-intercepts. Therefore, two separate ln *L* on ln *S* regressions were calculated, and the distinct y-intercepts were used in the back-calculations for the pre-spill as compared to post-spill data sets. Regression plots of *L* on *S*, and ln *L* on ln *S* from the pooled data of the two groups are shown in Figures 7 and 8.

Back-Calculation

Mean back-calculated lengths at age are summarized by sample year in Tables 1-6. There was no clear evidence of Lee's Phenomenon (decreasing length for successive age classes at a particular annulus) in the back-calculation tables. Yearly increases in length for upper Sacramento River rainbow trout were large, averaging nearly 100mm per year for the first two years of growth, and about 75mm per year for the third and fourth years of growth (Table 7). Averaged mean lengths for combined pre-spill years



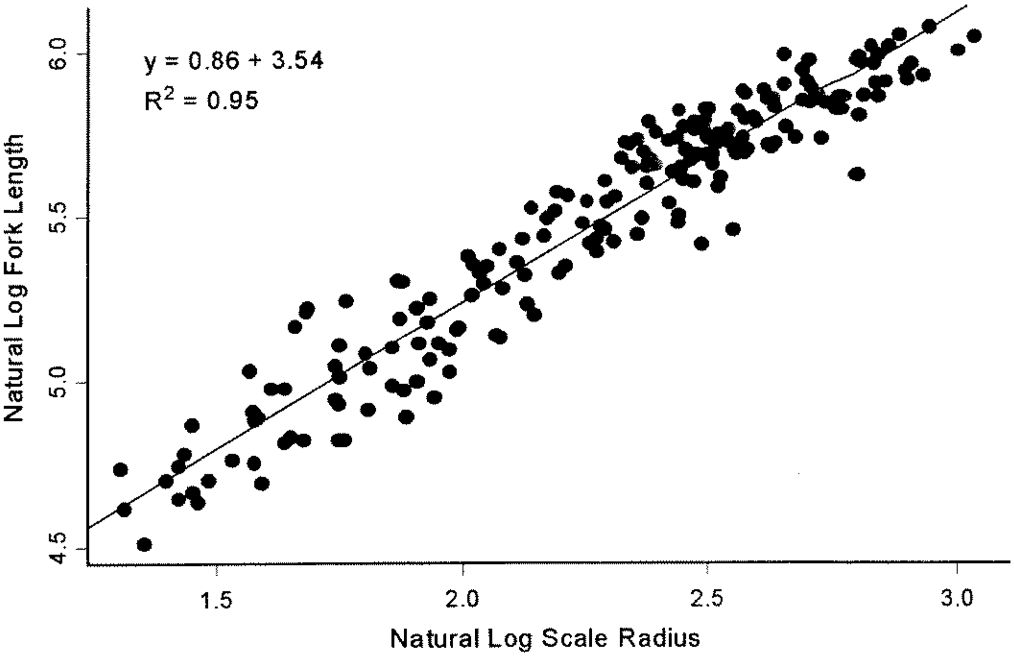
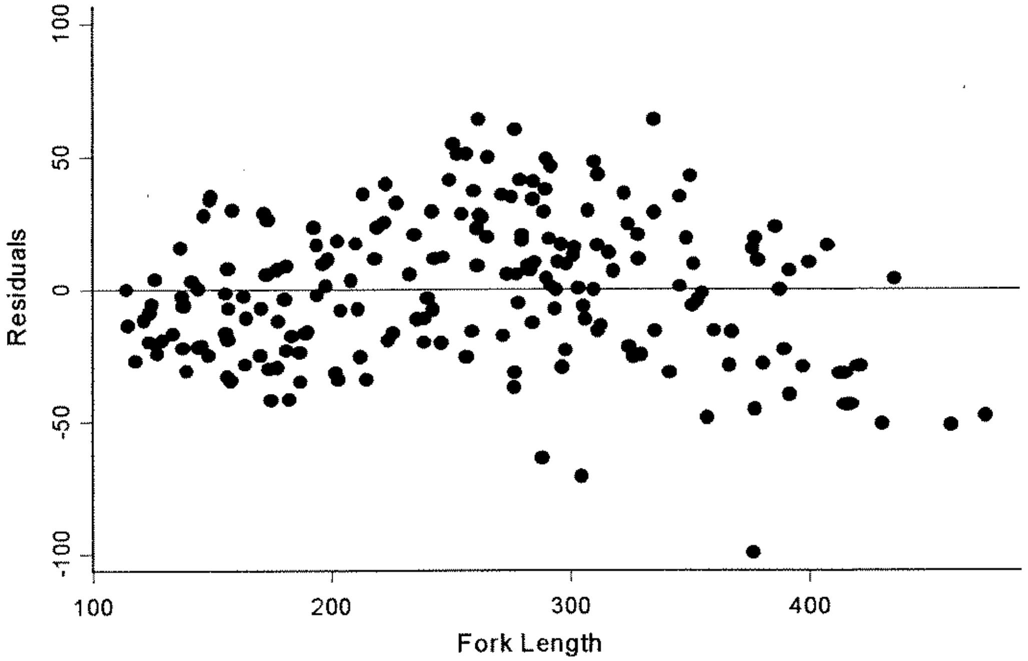


Figure 3. Fork length vs. scale radius regression plots before and after natural log transformation for upper Sacramento River rainbow trout from 1996 electrofishing survey scale samples.



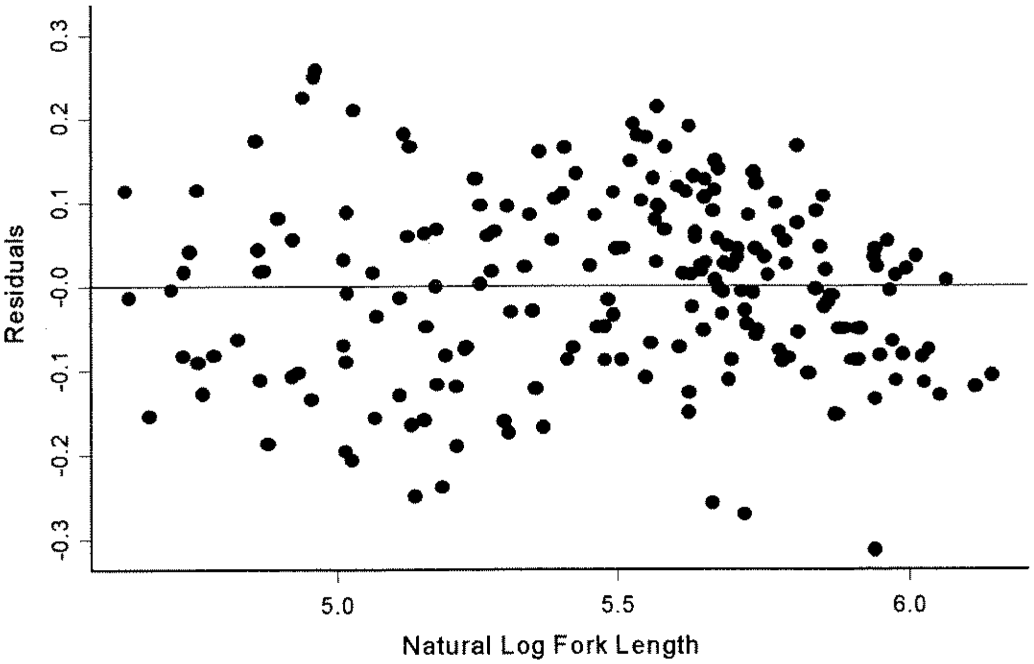
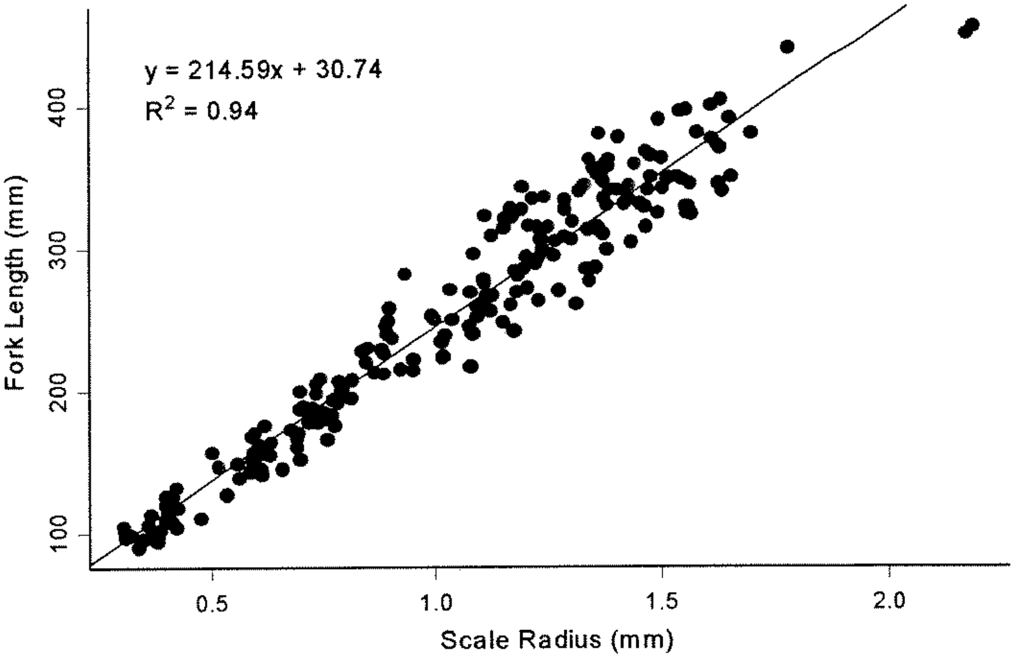


Figure 4. Residual plots for fork length vs. scale radius regressions before and after natural log transformation for upper Sacramento River rainbow trout from 1996 electrofishing survey scale samples.



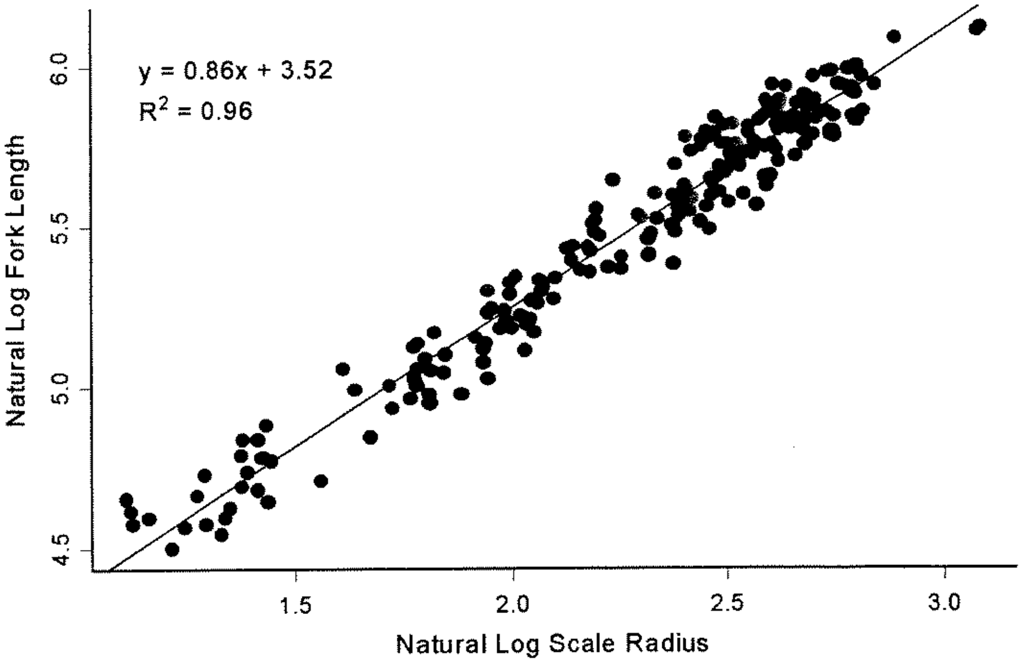
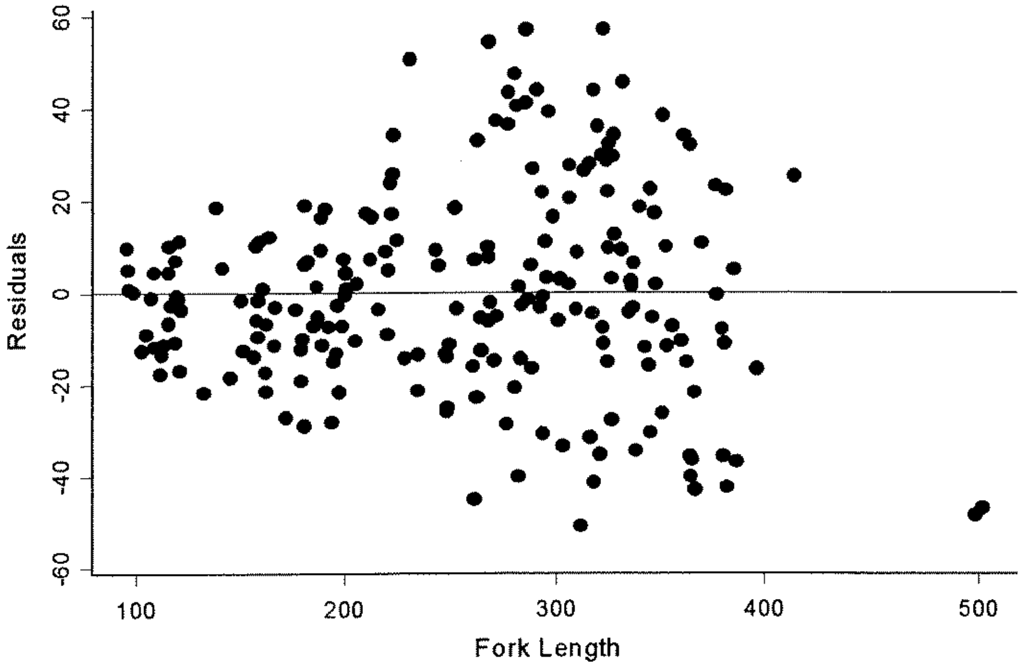


Figure 5. Fork length vs. scale radius regression plots before and after natural log transformation for upper Sacramento River rainbow trout from 1997 electrofishing survey scale samples.



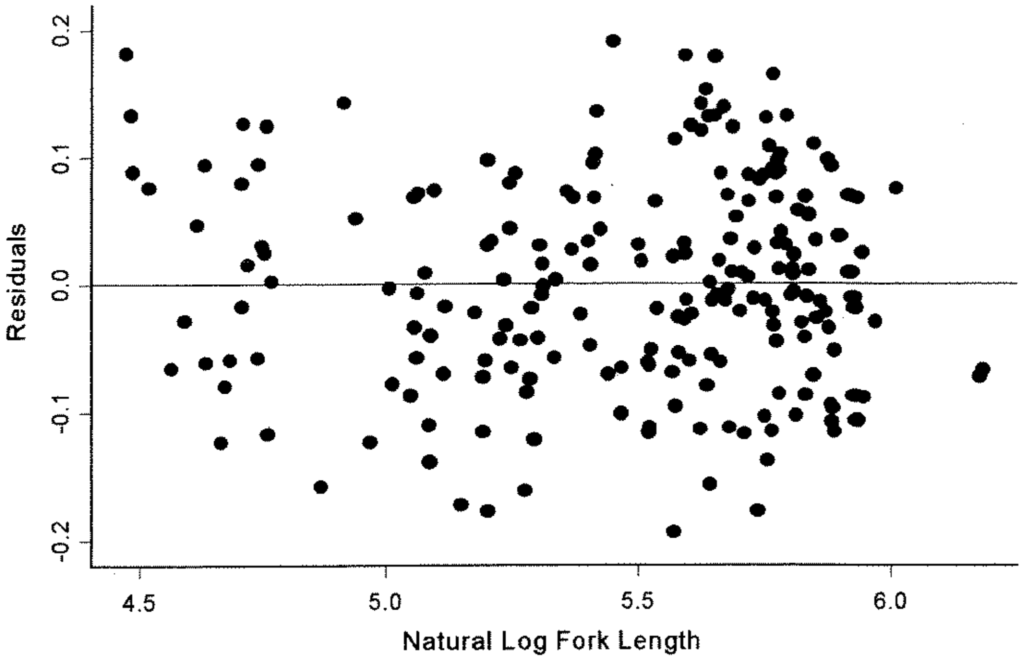


Figure 6. Residual plots for fork length vs. scale radius regressions before and after natural log transformation for upper Sacramento River rainbow trout from 1997 electrofishing survey scale samples.

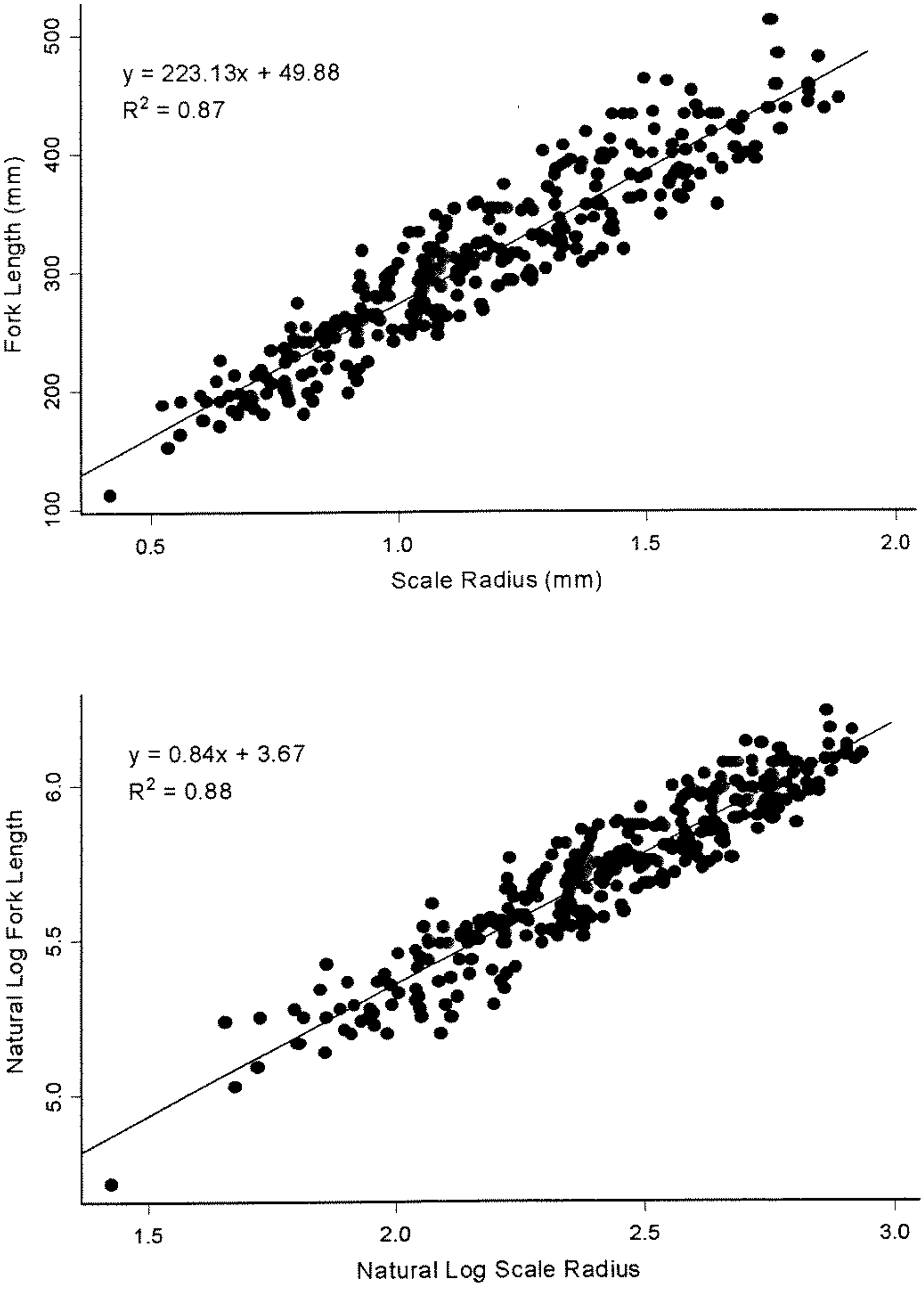


Figure 7. Fork length vs. scale radius regression plots before and after natural log transformation for upper Sacramento River rainbow trout for pooled data from 1978, 1980, and 1986 scale samples.

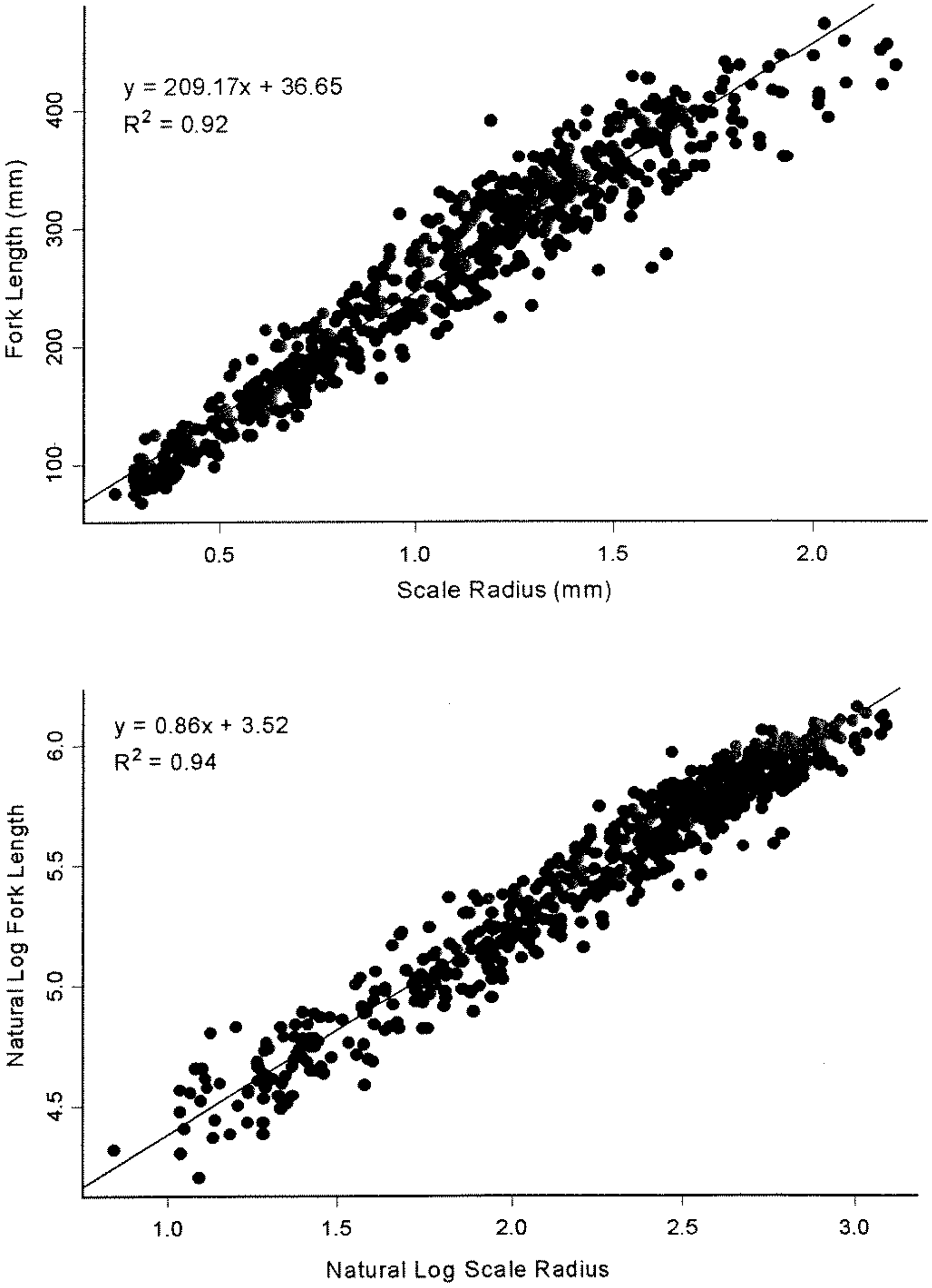


Figure 8. Fork length vs. scale radius regression plots before and after natural log transformation for upper Sacramento River rainbow trout for pooled data from 1994, 1996, and 1997 scale samples.

Table 1. Back-calculated mean lengths at annulus for upper sacramento river rainbow trout determined from scale samples taken during 1978 creel surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means. There were no fish from the 1+ age group because the scale samples came from large fish (>190mm) from creel surveys.

Age		Mean Fork Length at Annulus (mm)							
Group	n	1	S.E.	2	S.E.	3	S.E.	4	S.E.
2+	30	99.71	(2.36)	202.46	(4.47)				
3+	39	92.18	(2.23)	182.25	(4.63)	279.99	(5.81)		
4+	25	100.21	(2.32)	193.01	(5.77)	278.08	(8.15)	369.60	(8.04)
Weighted Grand Mean Length in mm		97.20		192.78		279.33		369.60	
Standard Error		2.64		6.24		1.00		-	

Table 2. Back-calculated mean lengths at annulus for upper Sacramento River rainbow trout determined from scale samples taken during 1980 electrofishing surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means.

Age		Mean Fork Length at Annulus (mm)							
Group	n	1	S.E.	2	S.E.	3	S.E.	4	S.E.
1+	41	97.40	(2.07)						
2+	33	98.26	(2.31)	195.97	(4.49)				
3+	19	101.27	(2.52)	199.35	(6.06)	280.06	(6.34)		
4+	10	106.76	(4.20)	196.30	(6.36)	293.02	(6.87)	364.12	(7.95)
Weighted Grand Mean Length in mm		99.45		196.97		286.03		364.12	
Standard Error		1.59		1.02		6.48		-	

Table 3. Back-calculated mean lengths at annulus for upper sacramento river rainbow trout determined from scale samples taken during 1986 creel surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means. There were no fish from the 1+ age group because the scale samples came from large fish (>190mm) from creel surveys.

Age		Mean Fork Length at Annulus (mm)							
Group	n	1	S.E.	2	S.E.	3	S.E.	4	S.E.
2+	25	97.58	(2.87)	206.98	(5.79)				
3+	39	103.22	(2.53)	207.42	(3.70)	297.31	(4.56)		
4+	34	104.68	(2.76)	195.74	(3.59)	276.65	(5.82)	352.41	(4.96)
Weighted Grand Mean Length in mm		102.01		202.33		289.45		352.41	
Standard Error		2.08		4.05		9.86		-	

Table 4. Back-calculated mean lengths at annulus for upper Sacramento River rainbow trout determined from scale samples taken during 1994 electrofishing surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means.

Age Group	n	Mean Fork Length at Annulus (mm)							
		1	S.E.	2	S.E.	3	S.E.	4	S.E.
1+	45	99.59	(1.97)						
2+	58	103.89	(1.87)	197.90	(3.51)				
3+	56	96.77	(1.83)	187.93	(3.76)	278.18	(3.41)		
4+	39	97.41	(1.82)	191.82	(4.28)	284.68	(3.69)	356.65	(3.83)
Weighted Grand Mean Length in mm		99.35		192.60		281.17		356.65	
Standard Error		1.62		3.06		3.24		-	

Table 5. Back-calculated mean lengths at annulus for upper Sacramento River rainbow trout determined from scale samples taken during 1996 electrofishing surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means.

Age		Mean Fork Length at Annulus (mm)							
Group	n	1	S.E.	2	S.E.	3	S.E.	4	S.E.
1+	40	90.91	(2.36)						
2+	31	96.47	(2.24)	181.19	(3.85)				
3+	70	95.38	(1.58)	188.20	(3.49)	255.71	(3.75)		
4+	26	100.53	(3.04)	195.82	(6.52)	270.42	(4.48)	329.49	(4.46)
Weighted Grand Mean Length in mm		95.35		186.50		261.77		329.49	
Standard Error		1.59		3.48		7.24		-	

Table 6. Back-calculated mean lengths at annulus for upper Sacramento River rainbow trout determined from scale samples taken during 1997 electrofishing surveys. Reported means given in millimeters are averages of exponentiated natural logarithm values. See text for explanation of methods used to calculate weighted grand means.

Age		Mean Fork Length at Annulus (mm)							
Group	n	1	S.E.	2	S.E.	3	S.E.	4	S.E.
1+	46	93.59	(2.17)						
2+	38	94.64	(1.93)	176.68	(3.80)				
3+	75	95.95	(1.58)	183.32	(3.12)	264.34	(3.10)		
4+	31	99.42	(2.49)	187.61	(4.33)	266.78	(5.81)	333.94	(5.87)
Weighted Grand Mean Length in mm		95.67		182.30		264.88		333.94	
Standard Error		1.06		2.90		1.26		-	

Table 7. Highest and lowest back-calculated non-weighted mean lengths for upper Sacramento River rainbow trout from pre-spill and post-spill scale samples. Overall means were derived using a simple average of all non-weighted means for each age class.

	Age	1	2	3	4
Mean Fork Length in mm					
Pre-Spill					
	Lowest	92	182	277	352
	Highest	107	207	297	370
	Overall Mean	100	198	284	362
Post-Spill					
	Lowest	91	177	256	330
	Highest	104	198	285	357
	Overall Mean	97	188	270	340

were greater than averaged mean lengths for post-spill years for all cohorts, and the difference in mean lengths became greater with each older age class (Table 7).

Graphs of weighted grand means (WGM) and associated 95% confidence intervals from sample years are shown for cohorts 1-4 in Figures 9-12. Graphs of natural log mean lengths, and exponentiated lengths in millimeters are both provided to show actual fish sizes. Because of bias that results from exponentiation, only back-calculated means in log units were compared (see Methods). Results of the statistical comparisons between means are shown in Table 8.

WGMs for trout at age 1 were generally similar, with the majority being about 100mm (Figure 9, Table 8). Pre-spill mean lengths were not statistically different from one another, and post-spill mean lengths were not statistically different from one another. There was no significant difference between the 1978 and 1980 mean lengths, and all post spill mean lengths. The 1986 mean length was significantly greater than the 1996 and 1997 mean lengths ($P < 0.05$) but was not greater than the 1994 mean length. There was an apparent decrease in length at age for the 1996 and 1997 mean lengths compared to 1994, but it was not significant.

For age 2 trout, back-calculated mean lengths increased from 1978 to 1986 (Figure 10), but there were no statistical differences between the pre-spill mean lengths (Table 8). The 1978 mean length had a large confidence interval, and was not significantly different from mean lengths of any post-spill year. There was an apparent decreasing trend for the post-spill mean lengths, but there was no statistical difference between 1994 and any pre-spill year. There was a decrease in mean lengths between

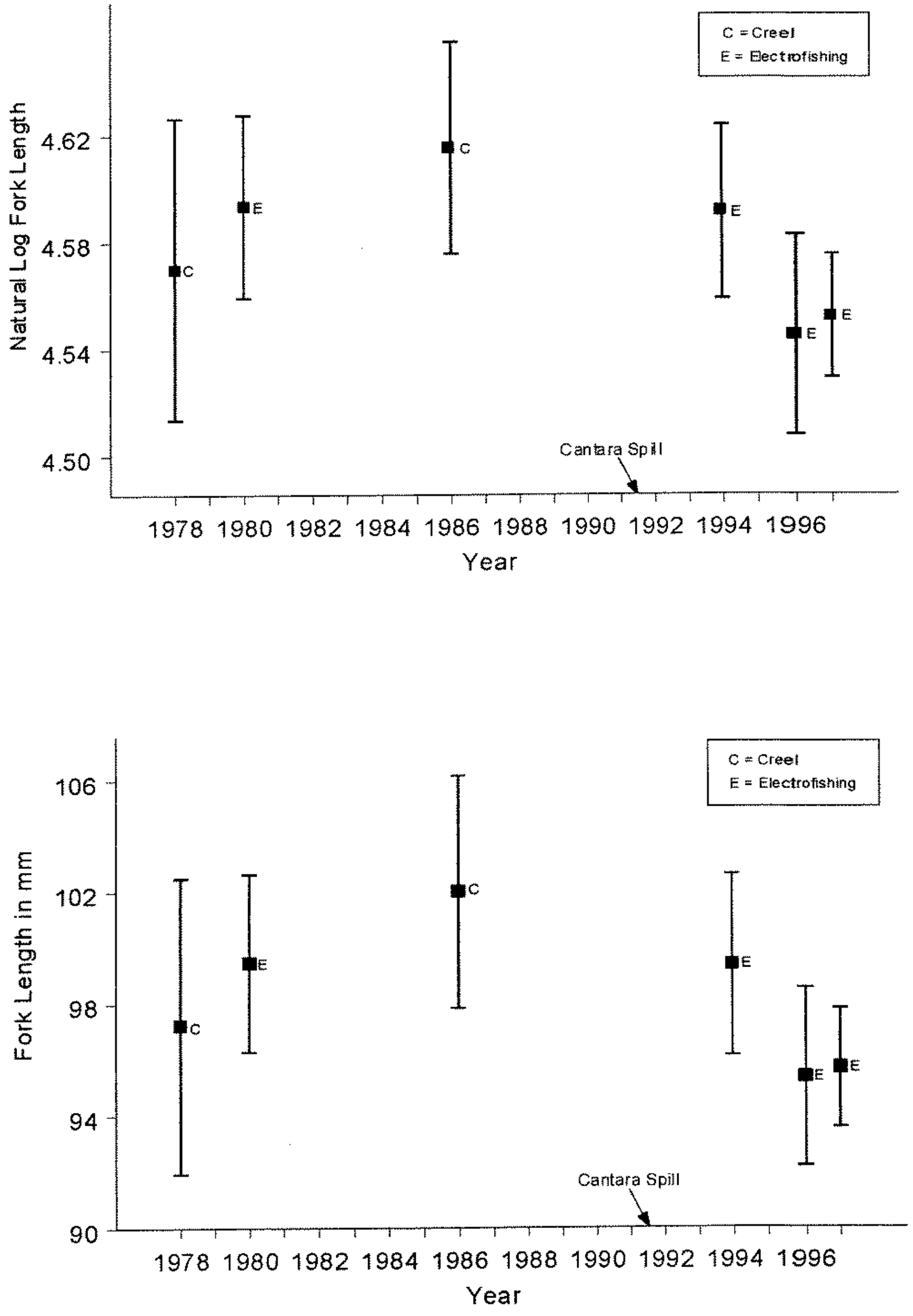


Figure 9. Weighted grand mean back-calculated lengths at age and associated 95% confidence intervals for age 1 rainbow trout from the upper Sacramento River. Based on CDFG scale samples.

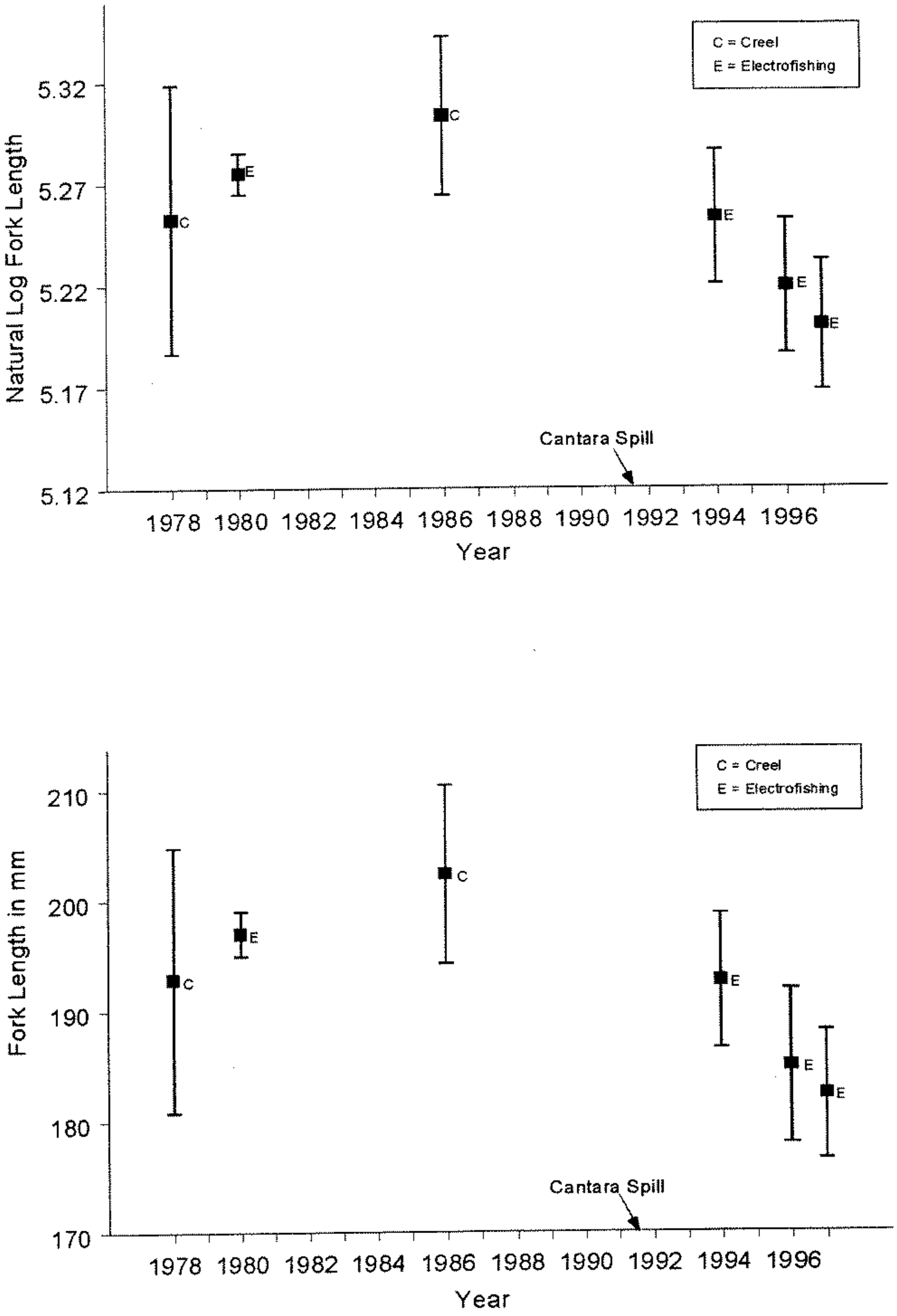
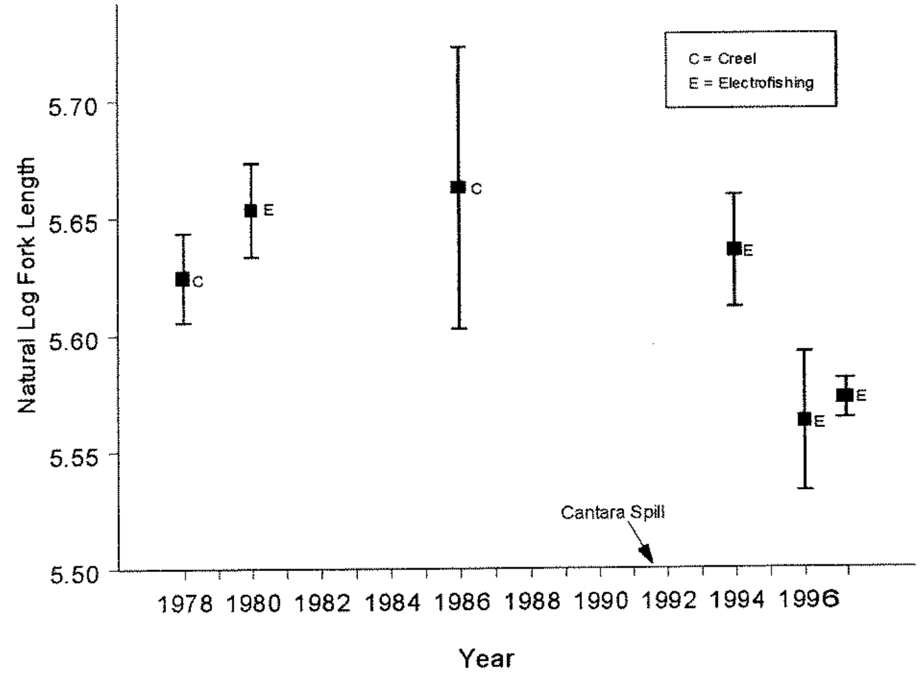


Figure 10. Weighted grand mean back-calculated lengths at age and associated 95% confidence intervals for age 2 rainbow trout from the upper Sacramento River. Based on CDFG scale samples.



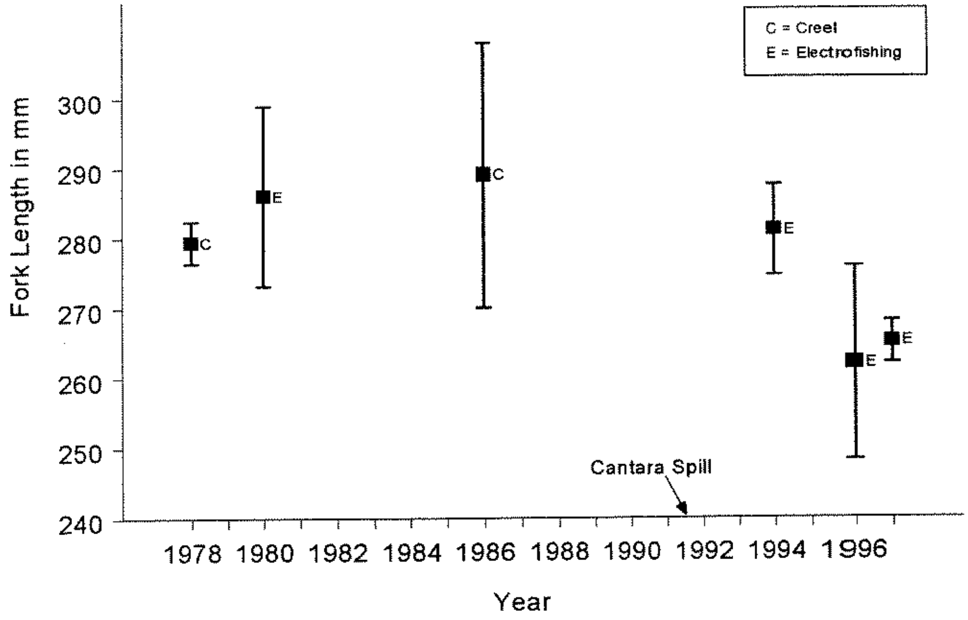


Figure 11. Weighted grand mean back-calculated lengths at age and associated 95% confidence intervals for age 3 rainbow trout from the upper Sacramento River. Based on CDFG scale samples.

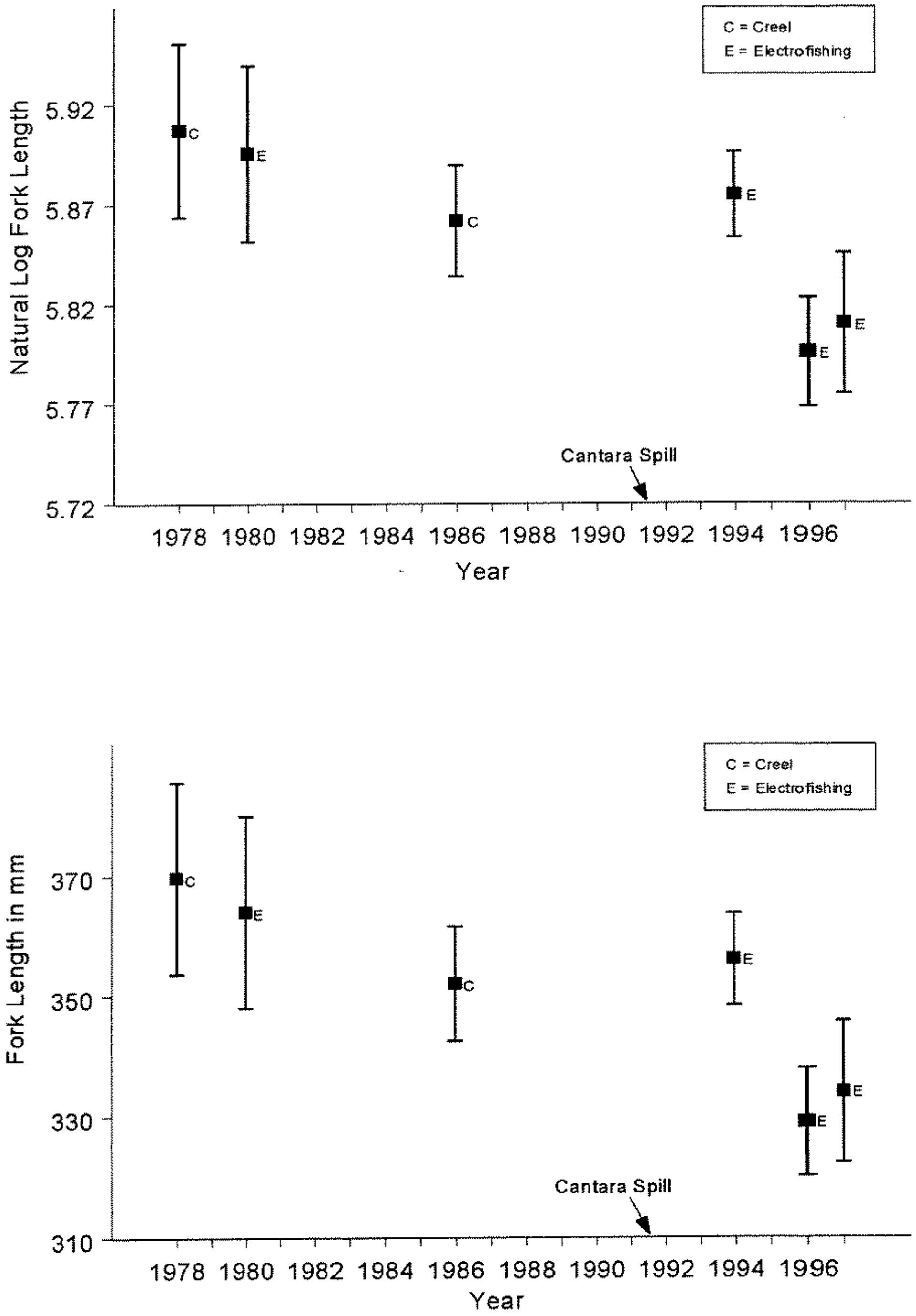


Figure 12. Weighted grand mean back-calculated lengths at age and associated 95% confidence intervals for age 4 rainbow trout from the upper Sacramento River. Based on CDFG scale samples.

Table 8. Results of comparisons of back-calculated weighted mean fork lengths for rainbow trout scale samples from the upper Sacramento River. Means are given in log units and millimeters for size reference. Log means that are not significantly different are indicated by similar superscripts. Comparisons are based on constructed confidence intervals of the differences between means of log lengths (Zar 1996).

Year of Collection	Age 1		Age 2		Age 3		Age 4	
Prespill	mm	Log	mm	Log	mm	Log	mm	Log
1978	97	4.570 ^{ab}	193	5.253 ^{abc}	279	5.624 ^{a}	370	5.907 ^{a}
1980	99	4.593 ^{ab}	197	5.275 ^{a}	286	5.653 ^{a}	364	5.895 ^{a}
1986	102	4.615 ^{a}	202	5.303 ^{a}	289	5.663 ^{a}	352	5.862 ^{a}
Postspill								
1994	99	4.591 ^{ab}	193	5.253 ^{ab}	281	5.635 ^{a}	357	5.875 ^{a}
1996	95	4.546 ^{b}	187	5.220 ^{bc}	262	5.563 ^{b}	329	5.796 ^{b}
1997	96	4.552 ^{b}	182	5.197 ^{c}	265	5.572 ^{b}	334	5.806 ^{b}

1994, and 1997, with the difference between 1994 and 1997 being significant ($P < 0.05$) (Figure 10, Table 8). Mean lengths from 1996 and 1997 were significantly lower ($P < 0.05$) than the 1980 and 1986 lengths.

Back-calculated mean lengths for age 3 trout were very similar for the first four sampled years (Figure 11). There were no significant differences between pre-spill years. Comparing pre to post spill years, the mean length for 1994 was not significantly different from to any of the pre-spill years, and was slightly greater than 1978 (Table 8). Like the age 1 and age 2 cohorts, there was a noticeable decrease in mean length for 1996 and 1997, compared to 1994 and all pre-spill years, with mean lengths for 1996 and 1997 being significantly less ($P < 0.05$) than all pre-spill years, and 1994 (Figure 11, Table 8).

Mean lengths for age 4 trout were lower in 1986 than in 1978, but differences among pre-spill years were not significant. There was some increase in length at age 4 between 1986 and 1994 (Figure 12). Like the age 2 and age 3 cohorts, there were no significant differences between mean length from 1994 samples, and any pre-spill mean lengths (Table 8). Similar to cohorts 2 and 3, there was a decrease in mean length for 1996 and 1997 samples of age 4 fish, with mean lengths being significantly less than mean lengths from 1994, and significantly less than all pre-spill years ($P < 0.05$) (Figure 12, table 8).

Growth Rates

Tests of the assumptions for the ANCOVA procedure allowed comparison of growth data from most years. A few years and cohorts of data (cohort 2: 1978, 1984, 1996; cohort 3: 1978, 1992) did not meet the ANCOVA assumptions and were excluded from this analysis. The results of the ANCOVA that compared mean growth rates across years (after adjusting for fish size) showed that growth rates varied significantly over years for cohort 2 ($F = 4.40$, $df = 10, 390$, $P < 0.0001$), cohort 3 ($F = 8.56$, $df = 8, 361$, $P < 0.0001$), and cohort 4 ($F = 9.54$, $df = 5, 154$, $P < 0.0001$). Plots of adjusted mean growth rates with 95% confidence intervals revealed that although there were growth rate differences between some years for individual cohorts, many of the mean growth rates prior to the Cantara spill were similar to those after the spill (Figure 13-15).

Adjusted mean growth rates for cohort 2 (2nd year growth) were more variable in the pre-spill year than in the post-spill years (Figure 13). The highest adjusted mean growth rate for age 2 trout occurred during the pre-spill years in 1985, while the lowest occurred after the spill, in 1995. Although two of the pre-spill adjusted mean growth rates were significantly greater ($P<0.005$) than post-spill growth rates, there were no significant differences between most of the pre-spill and post-spill growth rates for age 2 trout (Figure 13). Adjusted mean growth rates from post-spill sample years were fairly even for the first four years.

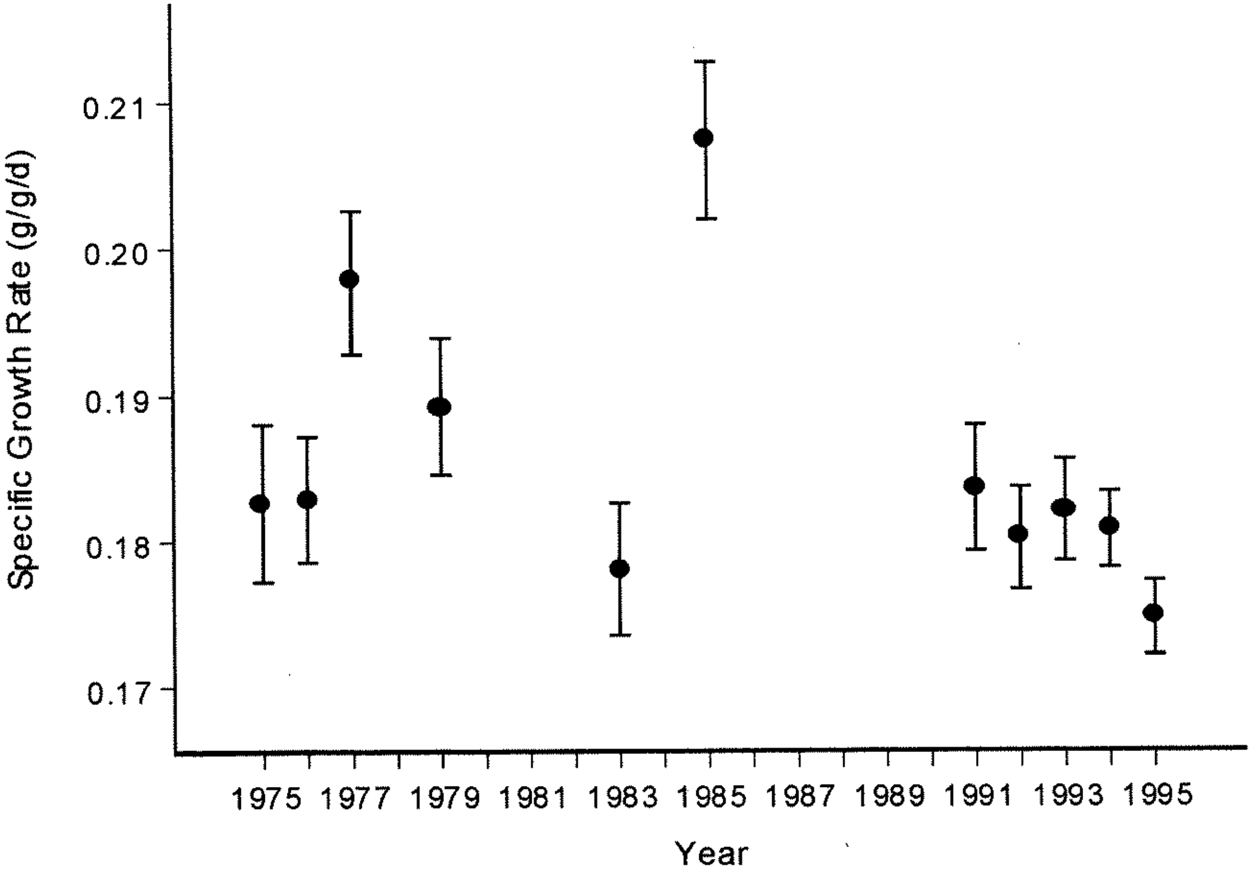


Figure 13. Adjusted specific growth rates and 95% confidence intervals for 2nd year growth of upper Sacramento River rainbow trout based on back-calculated lengths from CDFG scale samples.

Figure 14. Adjusted specific growth rates and 95% confidence intervals for 3rd year growth of upper Sacramento River rainbow trout based on back-calculated lengths from CDFG scale samples.

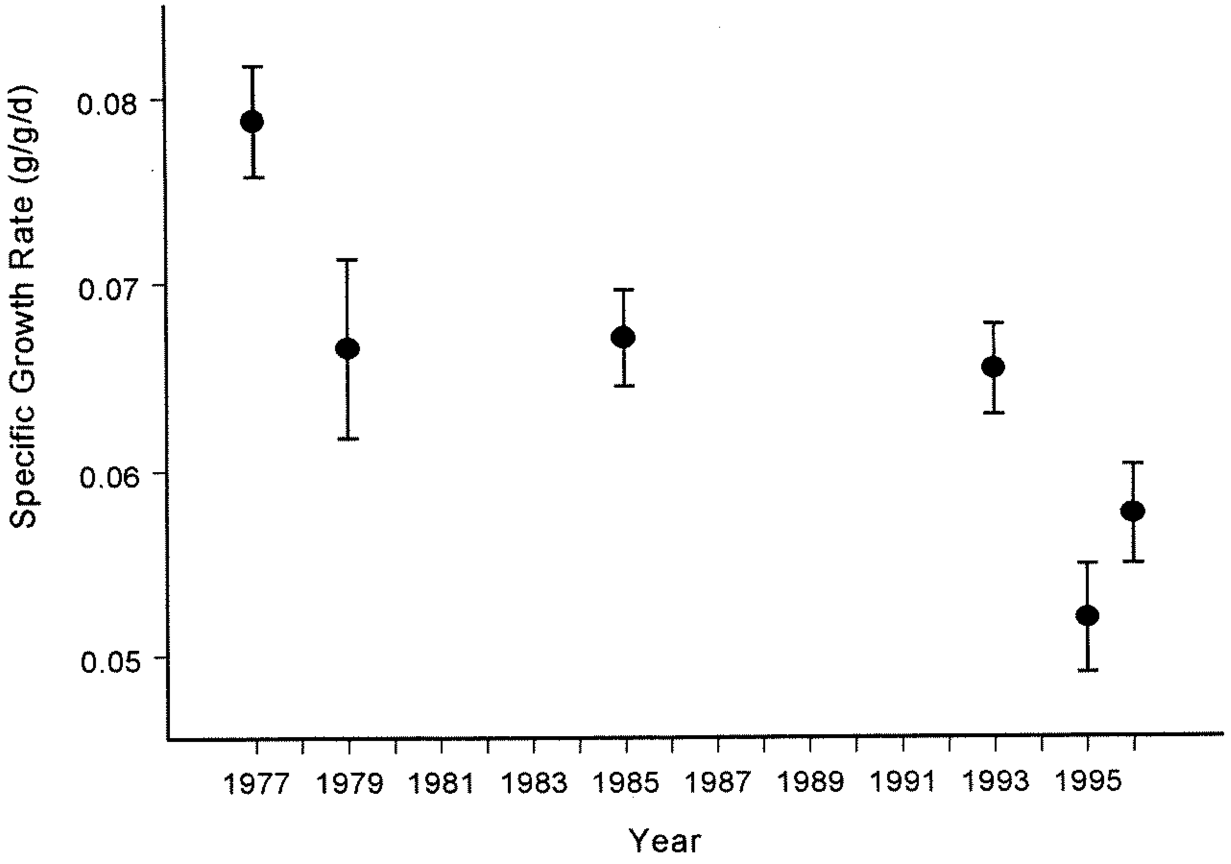


Figure 15. Adjusted specific growth rates and 95% confidence intervals for 4th year growth of upper Sacramento River rainbow trout based on back-calculated lengths from CDFG scale samples.

For cohort 3, adjusted mean growth rates varied, and followed a pattern similar to cohort 2; highest adjusted mean growth rates for age 3 trout occurred in pre-spill sample years, whereas the lowest growth rates occurred in the post-spill sample years. Although growth rates for 3rd year growth were variable, there were no significant differences among pre-spill years, and 1993, the first post-spill year in the samples (Figure 14). There was a decreasing trend after 1993, however, as adjusted mean growth rates decreased substantially in 1994 and again in 1995. Growth rates then rebounded to levels not significantly different than pre-spill levels in 1996 (Figure 14). Adjusted mean growth rates for 1995 were the lowest of all years sampled for cohort 3, being significantly lower ($P<0.005$) than all pre-spill sample years except for 1979, and all post-spill sample years except for 1994 ($P < 0.005$). The year with the highest growth rate for age 3 trout was 1977.

Adjusted mean growth rates for year 4 growth (cohort 4) followed the same general trend as cohorts 2 and 3, with the highest growth rates occurring in the pre-spill sampled years, and the lowest growth rates occurring in the post-spill sampled years (Figure 15). The highest adjusted mean growth rate for age 4 trout occurred in 1977 for all years sampled, being significantly greater than 1985 and all post-spill years ($P<0.005$). Comparing the other two pre-spill years to post-spill, growth rates from 1979 and 1985 were very similar to the growth rate for 1993, the post-spill sample year closest in time to the spill (Figure 15). In a trend similar to cohorts 2 and 3, a significant decrease in growth occurred in 1995, with the adjusted mean growth rate being significantly lower than 1977, 1985, and 1993 ($P < 0.001$). Growth rates increased some in 1996, but were still much lower compared to 1993 and all pre-spill years.

Diet Analysis

The majority of trout stomach contents were fully intact and easily identified. The diet of upper Sacramento River rainbow trout consisted mainly of aquatic invertebrates, with a portion being terrestrial flying insects. The nymph or larval stage was the most common life stage of aquatic invertebrate found in the trout stomachs, whereas the typical life stage for the terrestrial forms was the winged adult. The diversity of diet items found in the trout was high (Figure 16). In all, sixteen different orders of invertebrates were found in the stomach contents, with several different species present from each order. Algae, vegetation, and non-living debris like small rocks and stems were also found in the trout stomachs, and were fairly common (Figure 16).

The Frequency of Occurrence (FO) plot was divided into trout less than 265mm and trout greater than 265mm, since this was close to the size where noticeable differences in prey selection were observed. The most common diet items found in trout stomachs were aquatic invertebrates of the orders Diptera, Ephemeroptera, Trichoptera, and Plecoptera, more commonly known as midges, mayflys, caddisflys and stoneflys respectively (Figure 16). Aquatic dipterans were found in about 90% of the fish in both size classes, but when separated into taxonomic family groups, it was clear that smaller fish were consuming chironomids at a greater frequency than larger fish, while larger

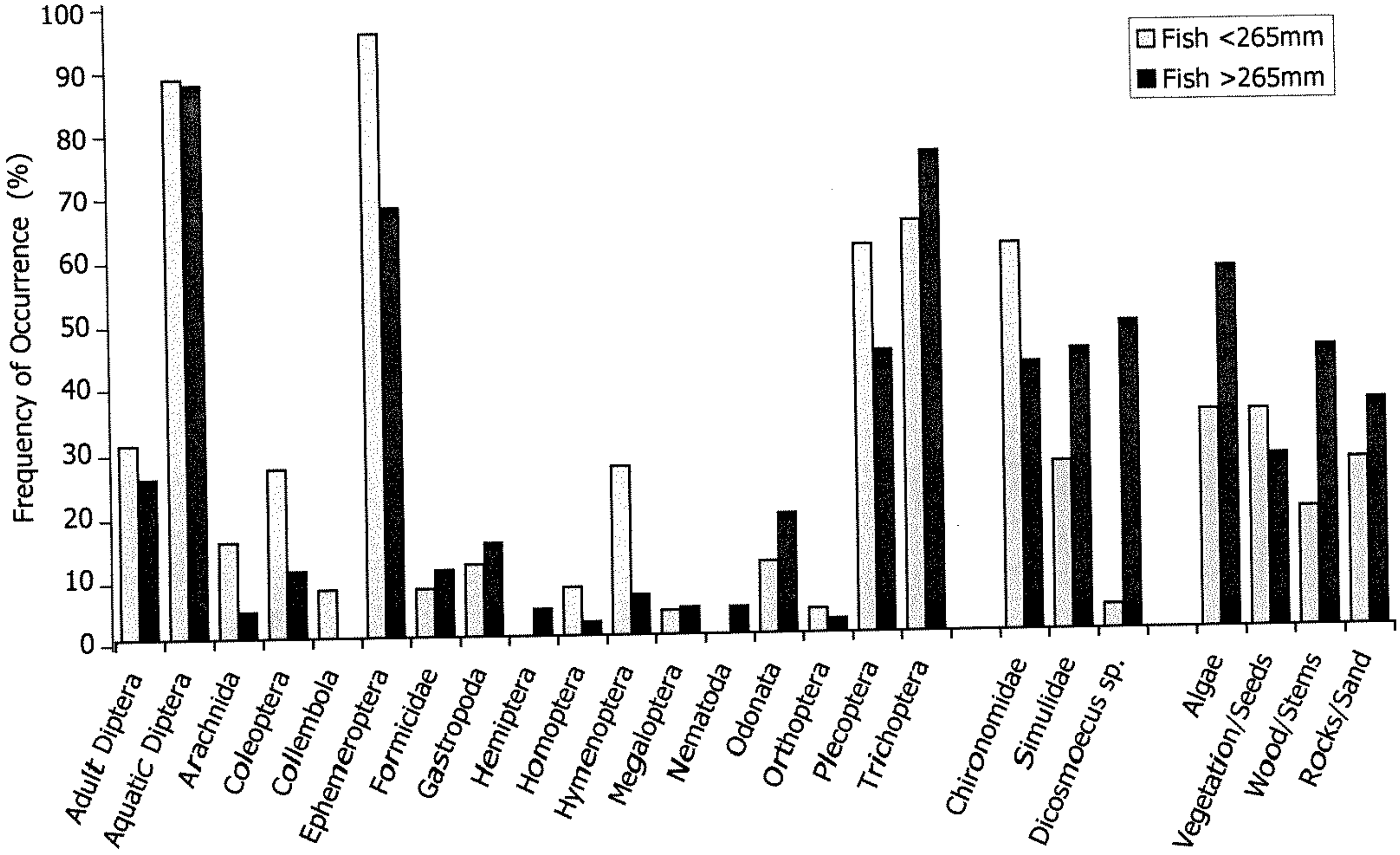


Figure 16. Frequency of occurrence of diet items found in stomachs of upper Sacramento River wild rainbow trout < 265mm (n = 31) and >265mm (n = 40). Fish were sampled between June and November 1998-2001.

trout consumed simulids at a greater frequency than smaller fish (Figure 16). Consumption of Ephemeroptera was highest in smaller trout (FO = 96%), but larger trout were still consuming them frequently, as they were found in almost 70% of the larger fish. Trichoptera were found in the stomachs of both size classes at a high frequency, but were more common in larger trout and were consumed with their protective cases. Plecoptera were found more frequently in smaller trout (FO = 62%), but were still fairly common in stomachs of larger trout (FO = 45%). Other invertebrate orders that were found in the trout stomachs occurred substantially less often than the four main groups mentioned previously. It is noteworthy that more terrestrial flying insects (Hymenoptera, Coleoptera, Adult Diptera) occurred in the smaller fish compared to larger fish, and that both size classes consumed snails (Gastropoda).

Larger fish had indigestible debris (algae, stems, rocks and sand) in their stomachs at a much greater frequency than did smaller fish (Figure 16). Substantial amounts of algae were found in stomachs of the larger trout sampled in September and October. Surprisingly, no sculpin, trout fry, or non-game fry were found in any of the rainbow trout sampled. Furthermore, there was no sign of any piscivory whatsoever, because there were no fish skeletal pieces, otoliths or other fish parts of any kind found in any of the 71 trout sampled.

The most striking difference in the gut contents of smaller fish compared to larger fish was consumption of *Dicosmoecus* sp., a large caddisfly common to the upper Sacramento River (Figure 16). *Dicosmoecus* sp. were found only in larger trout (>232mm), and were consumed whole with their protective cases. Apparently, only larger fish were able to consume them due to their large mean size (1 g wt., 50mm length, 7.5mm width). This caddisfly species had the highest FO for larger fish compared to other caddisflys, provided they were available as prey. *Dicosmoecus* sp. is plentiful for most of the year throughout the upper Sacramento River, however, they become unavailable to trout in early September, as they pupate and disappear beneath cobbles and boulders (personal observations from snorkeling). Figure 16 shows that nearly 50% of all trout over 265mm had *Dicosmoecus* sp. in their stomachs, but this value jumps to 92% for the same size class of trout sampled before September 5, when larval *Dicosmoecus* sp. were available as prey.

The separation and weighing of gut contents by invertebrate orders revealed no significant trends for the smaller size classes of trout, although mayflies and chironomids generally made up the larger percentage in terms of weight and number consumed. Gut contents of larger fish (>232mm), however, showed that *Dicosmoecus* sp. made up the highest proportion by weight in the gut contents. The average total weight of *Dicosmoecus* sp. in stomachs of larger fish was 8.54g. this is significantly greater ($P < 0.0005$) than the average weight of all other gut contents combined (0.79g). Furthermore, the proportional weight of *Dicosmoecus* sp. compared to other diet items increased substantially as trout size increased (Figure 17). That is, larger trout ate more *Dicosmoecus* sp. and less of other available prey. Many of the biggest trout had bloated stomachs that contained surprisingly large numbers of *Dicosmoecus* sp. and almost nothing else (e.g. one 483mm trout contained 40 *Dicosmoecus* sp. and nothing else in its stomach).

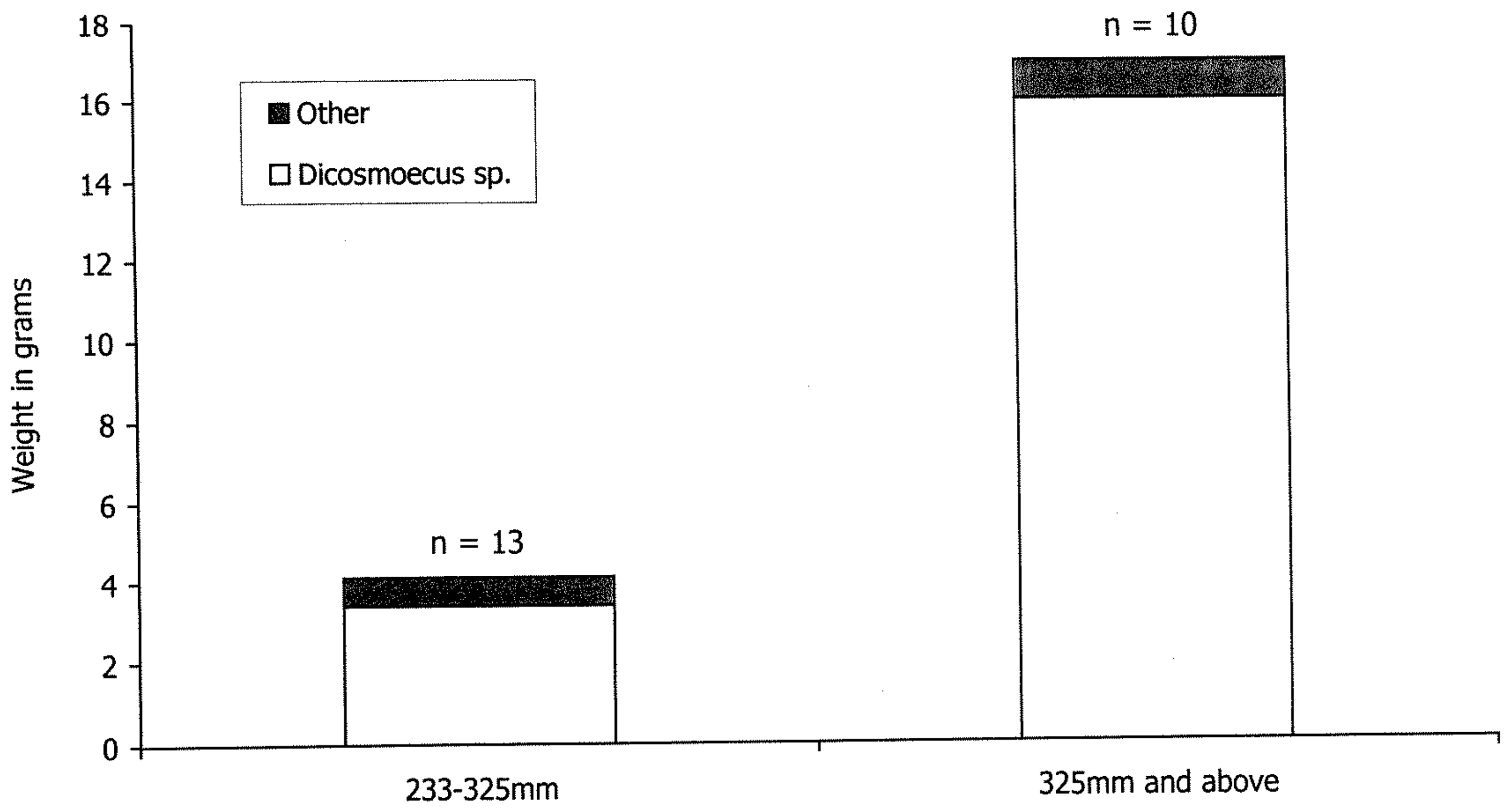


Figure 17. Average weights of total *Dicosmoecus* sp. caddisflys and all other diet items removed from stomachs of two size classes of wild rainbow trout sampled from the upper Sacramento River between June 1 and September 5, 2000-2001.

The results of weighing *Dicosmoecus* sp. with and without the protective cases revealed that on average the insect alone was 41% of the total insect weight with the case. Even after removing the protective cases, *Dicosmoecus* sp. weighed between 1-3 orders of magnitude more than other common prey and, in the river, were more plentiful compared to other prey that were similar in mass, like *Pteronarcys* sp. and megalopterans (personal observations from snorkeling). It seems clear that larger trout were getting the majority of their consumption energy from *Dicosmoecus* sp. when this prey was available. In autumn, when *Dicosmoecus* sp. larvae were no longer available to larger trout, the diet shifted to mostly mayfly and stonefly nymphs, and simulids.

Otolith Analysis

Out of the 24 otoliths that could be successfully aged, 23 out of 24 otolith age assignments matched the age designation of the corresponding scales. This resulted in 96% agreement between the age designations of scales and otoliths for sampled trout. For the otolith-scale pair that did not match, the scale had 4 annular marks, and the corresponding otolith had 3. If resorption of annuli on scales was occurring, there would be more annuli showing on the otolith when compared to corresponding scale. Based on this high percentage of agreement between scales and otoliths, there was no evidence of resorption of annular marks on scales for upper Sacramento River trout.

DISCUSSION

The results of this study show that there was a definite decrease in length at age and growth rates of the wild rainbow trout population in the upper Sacramento River following the 1991 Cantara Spill. This decrease in growth did not seem to occur immediately following the spill, however, as it was not evident in mean trout lengths and growth rates determined from the 1994 scale samples. Post-spill reductions in trout lengths and growth rates only became clearly evident in the growth determinations from the 1996 and 1997 scale samples, which showed that the growth decrease was most acute during the 3rd and 4th years of life. The growth rate decrease was most pronounced in 1995 and was seen in all age classes. The many possible reasons for these differences are considered later in this section.

The use of identical methodology for all scale sample analyses, and the comparison of several years of data prior to and following the spill, instead of data from only two years, revealed that the reservations about previous conclusions from preliminary studies were warranted. The results of the present study are not the same as a previous similar study by Turek (1995), whose back-calculations from the 1994 scale samples showed that there had been a drop in length at age for older rainbow trout (age 3 and 4) immediately after the spill, compared to CDFG back-calculations from scales collected in 1978 (Table 9). Results from my study showed that the mean trout length at age 3 from the 1994 samples was almost identical to the mean length calculated from

Table 9. Mean back-calculated lengths at ages 3 and 4 for rainbow trout from the upper Sacramento River based on scale samples from 1978 creel surveys and 1994 electrofishing surveys from two previous CDFG studies and the present study.

Mean Length (mm) at Age 3

Study	1978	1994
CDFG 1981	300	-
Turek 1995	-	246
Glowacki 2001	279	282

Mean Length (mm) at Age 4

Study	1978	1994
CDFG 1981	373	-
Turek 1995	-	320
Glowacki 2001	371	355

the 1978 samples. Although there was a small decline in mean back-calculated length of age 4 trout between 1978 and 1994, the decline was not statistically significant (Tables 8-9).

Back-calculated lengths for age 3 and 4 trout calculated by Turek (1995) were substantially smaller than the lengths calculated in this study and CDFG data from 1978, which led Turek to conclude that there was a decrease in trout length at age immediately following the spill. A possible reason for the differences in back-calculated fish lengths between this study and the one by Turek is differences in back-calculation methods. The present study used the log transformed Fraser-Lee equation for back-calculations, whereas Turek applied the "regression method" (Carlander 1981). There is evidence that the two methods can produce different lengths at age for the same fish because the regression method does not correct for differences in size of scales within a scale sample from a particular fish or among fish of the same length in a fish population, whereas the Fraser–Lee equation does (Carlander 1981). Fisheries biologists and statisticians have cautioned against the use of the regression method (Carlander 1981, Francis 1990), but have generally found little fault with the Fraser-Lee method (Carlander 1981, Francis 1990, Pierce et al. 1996, Klumb et al 2001).

Another factor contributing to the differing results could have been log transformation of the data in the present study but not in the one by Turek. Natural log transformation of the L on S regressions and the Fraser-Lee equation has been used in many other studies (Bartlett et al. 1984, Hooton et al. 1987, Ward et al. 1989, Brown and Moyle 1997), but overall, has seen relatively little use, even when there is clear evidence that the *L* on *S* relationship is not linear (Turek 1995, DeVries and Frie 1996, Pierce et al 1996). Using a linear back-calculation model when the body-scale relation is not linear can significantly reduce the accuracy of back-calculated lengths (Bartlett et al. 1984, Quinn and Deriso 1999).

An unanticipated benefit of log transformation of body-scale data in this study was that log transformation reduced y-intercept values that were inflated when small trout were not present in the samples. (as in 1978 and 1986). Capturing all age classes of fish is difficult when sampling fish populations. The completeness of the sample affects the intercept value of the *L on S* regression, and the accuracy of back-calculated lengths (Carlander 1982, Smale and Taylor 1987, Ricker 1992). My analysis supported these earlier studies, and confirmed that the y-intercept used in the Fraser-Lee equation has a profound effect on back-calculated lengths. After log transformation and pooling of pre-spill body-scale data, it was evident that inflation of the y- intercept value for the pre-spill regressions, and thus positive bias of the back-calculated lengths, was reduced substantially.

Use of the Fraser-Lee equation with its scale size correction factor was crucial in this study, especially because scales were collected from both creel surveys and electrofishing surveys, from a wide range of years, and by different people who likely did not take the scales from the same exact area on the fish. For example, scales of bigger fish from the creel survey samples were noticeably larger than scales from fish of similar length from the electrofishing samples. The Fraser-Lee equation has been shown to be effective in correcting for such poor scale collection (Carlander 1981). Furthermore, the Fraser-Lee equation has been validated in other studies of rainbow trout growth (Davies and Sloane 1986, Faragher 1992), thus fulfilling an important requirement for back-calculation methods, namely that the formula used accurately relates the scale radius and body size for each fish (Beamish and McFarlane 1983, Francis 1990). Moreover, many studies have shown that the Fraser-Lee model outperforms all other back-calculation models in terms of accuracy (Pierce et al. 1996, Klumb et al. 1999a, Klumb et al. 1999b, Klumb et al. 2001).

Since this study was carried out on archived scale samples from many years ago, direct validation of back-calculated lengths as stated by Beamish and McFarlane (1983) could not be done. Validation involves mark-recapture studies that were not undertaken either before or after the spill. A recognized alternative to direct validation was accomplished, however, through comparison of numbers of annuli on otoliths to those on scales (Beamish and McFarlane 1983). The results did show high percentage agreement (96%) between numbers of annuli on scales and corresponding otoliths, providing evidence that the annular marks on the scales were not being reabsorbed, and the age designations of scales were probably accurate. The comparison of scales to otoliths also provided evidence that annuli are formed only once per year, and that the supposed time of annulus formation is correct (Francis 1990). Annulus formation for upper Sacramento River rainbow trout appeared to occur at the start of the growing season in the late winter and early spring. This is the typical case for other temperate fishes (Sheri and Power 1969).

Because scale age designations and back-calculated lengths at age appear to be valid and accurate, the findings of no significant reduction in trout growth immediately after the spill, but then a reduction a few years later, are likely correct. It is surprising that there would not be a reduction in fish growth in the years right after the spill, given the severity of the disturbance. However, this has been observed in other studies of fish populations recovering from similar disturbances. In some cases there has been an increase in fish growth rates due to the lessening of competition for food resources (Schlosser 1982, Detenback et al. 1992, Crisp 1993). Fish densities were low for the first two years following the Cantara spill since fish were repopulating an essentially empty river (Allen 1999). Competition was probably low, and many studies have shown strong correlations between trout density, competition for food resources, and growth (Warren 1971, Huae and Parkinson 1987, Knapp and Dudley 1990, Hayes 1995).

Although the invertebrate food base for trout was eliminated by the spill, invertebrates were able to quickly recolonize the affected area of the river from tributaries and the 2.5-mile area of river above the spill site (Boles 1997). Invertebrate species which were seen in trout stomachs at high frequency (e.g., *Simulium* sp. and *Baetis* sp.) were reported to have recolonized rapidly, and developed large densities throughout the impacted areas of the river within months following the spill (Boles 1997). So there is evidence that there was invertebrate prey for rainbow trout after the spill, but not a diverse selection. Because rainbow trout consume a wide variety of prey, they apparently fed upon invertebrate species that had recovered, a pattern which has been documented for other fish populations recovering from large disturbances (Detenback et al. 1992). This is likely another part of the reason why there is not a decrease in lengths at age and growth rates exhibited in trout from 1994 scale samples.

If conditions for trout growth were not adverse in the years immediately following the Cantara Spill, then why was there a drop in length at age and growth rates shown in the 1996 and 1997 scale samples? The answer is probably related to several factors that occurred during the recovery period. The first possibility is that large increases in densities of trout, as seen by snorkel surveys (Figure 18), could have affected growth due to competition that was not a factor in the first few years after the spill. Growth of trout has been shown to be density dependent (Knapp and Dudley 1990, Crisp 1993, Chen and Harvey 1995, Hayes 1995). This could be why there is a significant decrease in growth rates shown in 1994 for trout in their 3rd year of growth (Figure 14), and simultaneously a substantial increase in densities of the 8-14" size class seen in the data from the 1994 snorkel surveys (Figure 18). Scale reading revealed that the majority of fish in their 3rd year of growth were in the 8-14" size range.

Although growth rates for fish in their 3rd year of growth decreased significantly in 1994, they decreased even further in 1995. A significant decrease in trout growth was also seen in 1995 for the 2nd and 4th year cohorts. Among all years represented in scale

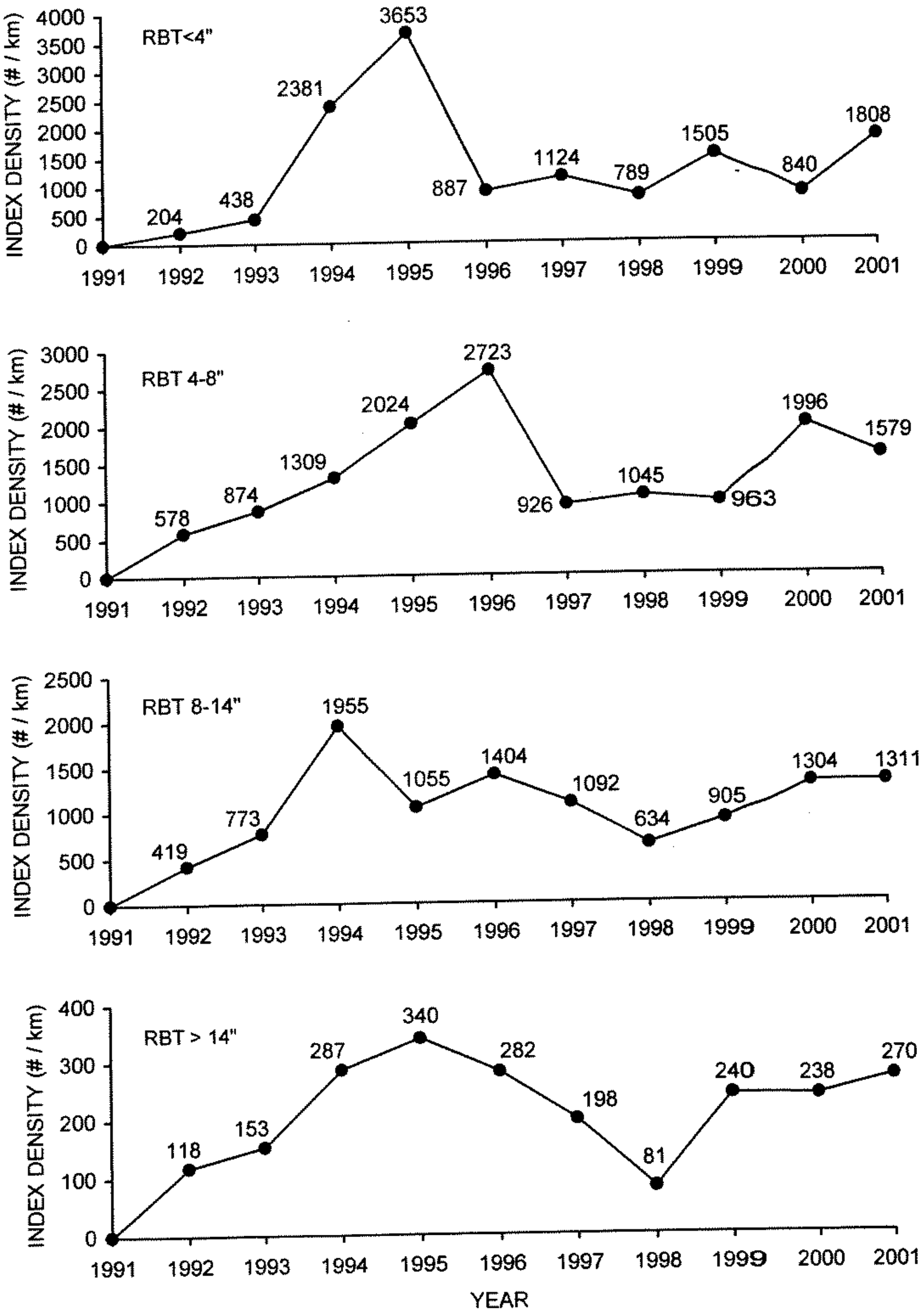


Figure 18. Index Densities (# / km) of rainbow trout in the upper Sacramento River, by size class through August 2001. Numbers are for the area of the river affected by the Cantara Spill. All estimates based on snorkel surveys in run, riffle and pool habitats combined. Data from Mark Allen, Thomas R. Payne and Associates.

samples for all fish in this study, 1995 clearly had the lowest growth rates (Figures 13-15). This significant decrease in rainbow trout growth rates for all cohorts suggests that a major environmental disturbance capable of affecting the entire rainbow trout population occurred between 1994 and 1996. Flow records show that 1995 was one of the highest water years on record for the upper Sacramento River (Figure 19), and 1995 had the highest flows during post-spill years in this study (Appendix A). The high flows lasted well into July, and there were two major peaks shown in the hydrograph of 1995 (Appendix A). This event could have had a negative effect on growth rates for the whole population of rainbow trout for several reasons.

Looking at the effects of a severe winter in terms of fish bioenergetics, fish would expend a great deal more energy during the high 1995 winter flows and the spring runoff period, swimming and foraging in faster than normal currents (Bachman 1984, Fausch 1984). Foraging during extra high flows requires more energy and affects trout growth rate (Cunjak and Power 1987, Jowett and Richardson 1989, Hayes et al. 2000). The extended high flows of 1995 also translated into cooler water temperatures through late spring and much of the summer when the bulk of fish growth would be taking place. Temperature data show that water temperatures for 1995 (a wet year) were substantially colder than 1994 (a dry year) for an extended period of time (Appendix B). Bioenergetics studies and computer modeling show that cooler temperatures for long periods of time can result in decreased growth rates for all size classes of fish (Hayes et al. 2000, Hagen and Quinn 1991). A severe or extended winter negatively affects trout

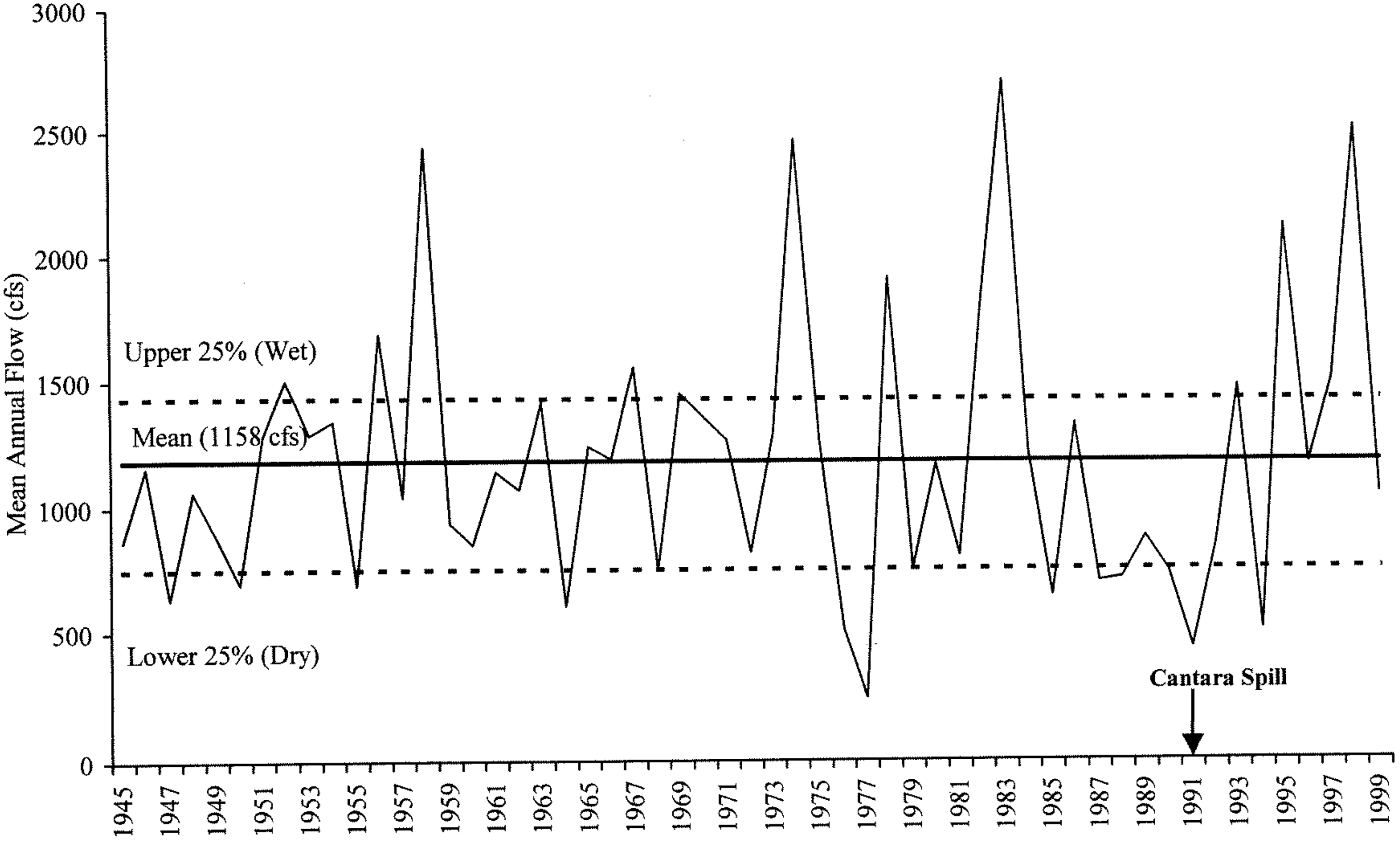


Figure 19. Mean annual streamflows (cfs) in the upper Sacramento River at the Delta from 1945 to 1998. The dotted lines show the upper 25% of means (wet years) and the lower 25% of means (dry years), the solid line is the overall mean.

in general, with consequences of extended winter and high flow conditions for trout being stunted growth, higher mortality, and a decrease in population numbers (Reimers 1963, Cunjak and Power 1987, Cunjak 1988, Jowett and Richardson 1989, Fausch and Bramblett 1991). Plotting trout growth rate data from this study against mean annual flows revealed a strong correlation between higher growth rates occurring during years with low mean annual flows, and lower growth rates occurring during years with high mean annual flows (Appendix C). This relationship is consistent for all age classes both before and after the spill, and becomes stronger with increasing age class. The effects of mean annual flow on trout growth are particularly significant for age 4 fish (Appendix C). Furthermore, the driest year of the study (1977) exhibited some of the highest growth rates for trout, while the wettest years (1983, 1995) exhibited some of the lowest growth rates (Figures 13-15, 19).

Another factor that likely contributed to the decrease in trout growth was that the invertebrate prey that the trout forage on were affected by severity of the flows in 1995. The Department of Water Resources (DWR) reported in 1996 that the aquatic macroinvertebrate communities still had not fully recovered from the spill. In addition, there was evidence from the 1996 invertebrate samples that suggested a recent disturbance had occurred, and had negatively affected invertebrate densities and diversity (Boles 1997). The aquatic macroinvertebrate communities in their incomplete state of recovery were likely more vulnerable to scouring flows from the severe winter of 1995. Flood events and extended high flows have a negative effect on the densities of aquatic macroinvertebrates (Jowett and Richardson 1989, Wright and Li 1998, Scrimgeour and Winterbourn, 1989, Bradt et al. 1999). Decreased prey availability would certainly have had a negative effect on rainbow trout growth rates for all age classes, given that the late-winter-through-spring period is crucial for trout in terms of regaining weight lost during the winter (Reimers 1963, Cunjak and Power 1987, Cunjak 1988).

Diet analysis revealed several important things about upper Sacramento River wild rainbow trout. First, the rainbow trout population consumes a wide variety of invertebrate prey. Both small and large trout are able to consume many of the same invertebrate prey in the river (see Figure 16). This allowed both small and larger trout to consume whatever was available after the spill. This dietary plasticity likely contributed to the ability of the trout population to recover quickly after the spill without a detectable reduction in growth.

Second, large trout did not seem to be consuming sculpin, which was contrary to what had been conjectured. It had been speculated that since sculpin were the most abundant fish in the system prior to the spill, the elimination of sculpin could affect growth of larger trout (Turek 1995). The results of my study suggest that larger trout do not consume sculpin with any frequency in the upper Sacramento River, although trout have been shown to prey on sculpin in other river systems (Dave Hankin, 2000, personal communication). It is noteworthy that the decrease in growth of larger trout occurred during the same time that there was a substantial increase in sculpin population numbers (Appendix D). The lack of sculpin predation by trout could be due to the upper

Sacramento River bottom morphology being predominantly cobbles and boulders, which provides excellent refuge for sculpin. Thus, they are quite unavailable to rainbow trout as prey (personal observations from snorkel surveys). Other research has shown that rainbow trout prefer invertebrate prey, and that they are not very efficient in catching prey fish. (Tippetts and Moyle 1978, Rand et al. 1993).

Third, the large caddisly larvae *Dicosmoecus* sp. was the prey that large rainbow trout (> 25cm) were eating. This prey made up the most significant portion of the stomach contents by weight when this prey was available during spring and summer. High consumption of *Dicosmoecus* sp. by rainbow trout has also been recorded in the McCloud River, a watershed adjacent to the study area (Tippetts and Moyle 1978). Frequent consumption of *Dicosmoecus* sp. is probably due to the large size of the caddisfly, their abundance during spring and summer, and the ease with which they are captured (personal observations from snorkel surveys). It seems that smaller fish are not able to swallow them because of the limited size of their esophagus, or chew them up because of their protective case. Since *Dicosmoecus* sp. seems to be the prey most favored by large rainbow trout in the upper Sacramento River, then the significant decrease in length at age and growth rates seen in age 3 and 4 trout from the 1996 and 1997 scale samples could be related to decreased availability of *Dicosmoecus* sp. due to the severe winter of 1995. Although there are no data on *Dicosmoecus* sp. densities in the upper Sacramento River from 1995, the macroinvertebrate monitoring data from 1996 shows that abundance of *Dicosmoecus* sp. had decreased dramatically in 1996 compared to data prior to 1995 (Boles 1997). Thus, there is some evidence that *Dicosmoecus* sp. densities decreased at the same time the drop in large rainbow trout growth rates occurred in this study. Because of their non-streamlined shape and inability to attach firmly to the substrate, *Dicosmoecus* sp. has been found to be very vulnerable to floods (Power et al 1995, Wooton et al. 1996, Wright and Li 1998). Wright and Li (1998) found that a major flood event in an Oregon stream reduced *Dicosmoecus* sp. densities by 83%, and that recovery of the species took two years. Bioenergetics research also has shown that availability of large, easily attained prey is the key limiting factor for growth rates of large trout because foraging costs for smaller prey are higher while the net energy gain is lower (Hayes et al. 2000). Thus, it is probable that another principle reason growth rates of large trout decreased significantly in 1995, and remained low in 1996, was that high winter flows of 1995 significantly reduced densities of *Dicosmoecus* sp. and, thus, temporarily removed one of the most important diet items for large trout from the forage base.

This study provides some good news in that the 1991 Cantara spill does not appear to have had a lasting detrimental effect on growth and recovery of wild rainbow trout in the upper Sacramento River. However, the spill may have made the aquatic ecosystem more susceptible to natural disturbances (i.e. high flows, harsh winters) and less resilient over the short term. The trout population monitoring data shows a dramatic increase in trout numbers in the years immediately following the spill, which coincide with mild winters and below average flows. This trend contrasts with 1995 through 1998, a period of harsh winters and abnormally high flows (Figures 18, 19), which coincided with substantial decreases in numbers of rainbow trout. The trout population may have been more resilient to these natural disturbances had the spill not occurred, and if the ecosystem had not still been recovering from the Cantara spill.

The apparent recovery of the upper Sacramento River rainbow trout population took between 3-5 years based on peaks in densities of trout per river kilometer estimated from snorkel surveys (Figure 18). This was slower than what was seen in other studies of fish populations recovering from large disturbances (Olmstead and Cloutman 1974, Johnston and Cheverie 1980, Fausch and Bramblett 1991, Detenbeck et al. 1992), which reported re-population and rebound of fish numbers in about 1-2 years. However, the monitoring of fish populations following these other disturbances was short-lived, so it is not known if these other fish populations remained healthy after the initial rebound. If monitoring of the upper Sacramento River rainbow trout population would have ended after just a few years, then the results of this study would have been much different, and the effects of natural disturbances on the recovering trout population would have likely been missed. This finding stresses the importance of long term monitoring of fish populations after severe disturbances.

Although there was a reduction in rainbow trout numbers through 1995-1998, in which two of the highest water years on record occurred on the upper Sacramento River, the winters of 1999-2001 were mild and, fortunately, the trout population began to rebound again after the series of harsh winters (Figure 18). My observations of the river ecosystem during 1999-2001 rainbow trout abundance snorkel surveys were encouraging. Densities of rainbow trout, sculpin, aquatic invertebrates, and other aquatic species like turtles, crayfish and newts had noticeably increased over the three-year period in the absence of major floods and extended winter flows (Figure 18, Mark Allen, 2001, unpublished data, personal observations from snorkel surveys). By 2001 it was apparent that the ecosystem was reaching a state closer to full recovery (personal observations from snorkel surveys), although it may be impossible to determine if the upper Sacramento River will ever be the same as it was before the 1991 Cantara spill because of the lack of pre-spill fish population data. More research is needed to find out if rainbow trout growth rates rebounded with the increase in population numbers during 1999-2001.

To conclude, it should be noted that the significant decrease in mean length at age that was seen in the 1996 and 1997 scale samples was only around 2.5cm for large (3 to 4 year-old) trout, and less than 2.5cm for 1 to 2 year-old trout. This is in the neighborhood of 10%, and may not be very biologically significant for the fishery. Based on population monitoring and my observations from snorkel surveys of the affected reaches from 1997-2001 there are, once again, plenty of trophy-size wild rainbow trout in the upper Sacramento River, and it should still be regarded as a blue-ribbon wild trout fishery. This should not change any time in the near future unless there is another anthropogenic environmental disaster. The fact that the upper Sacramento River has recovered after such a devastating loss of natural resources should not be exploited to justify not taking steps that prevent damage to wild trout populations or the ecosystems in which they live. Nor should we in the scientific, environmental, and fishing communities become complacent with the belief that such an appalling catastrophic event could not happen again.

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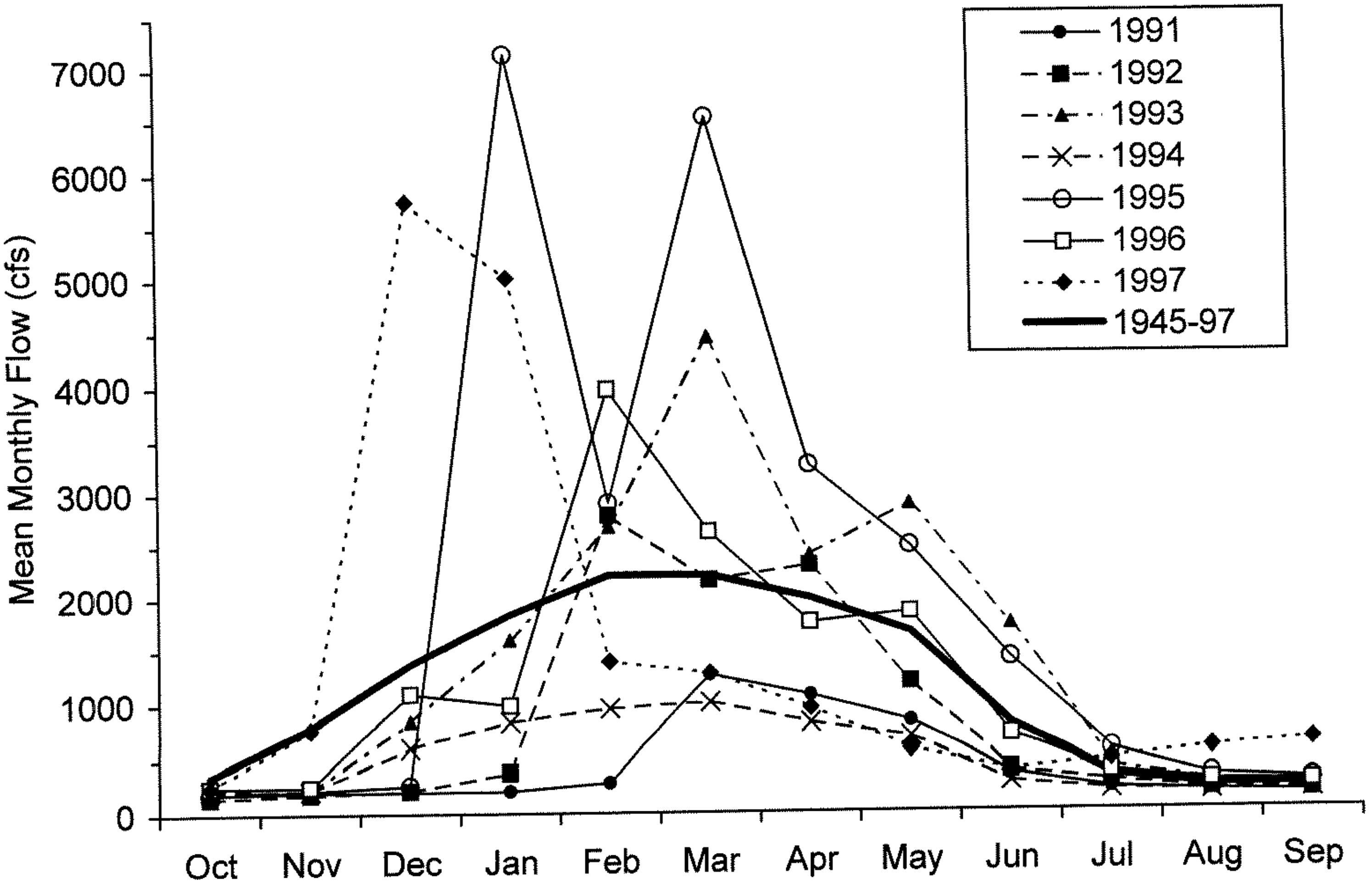
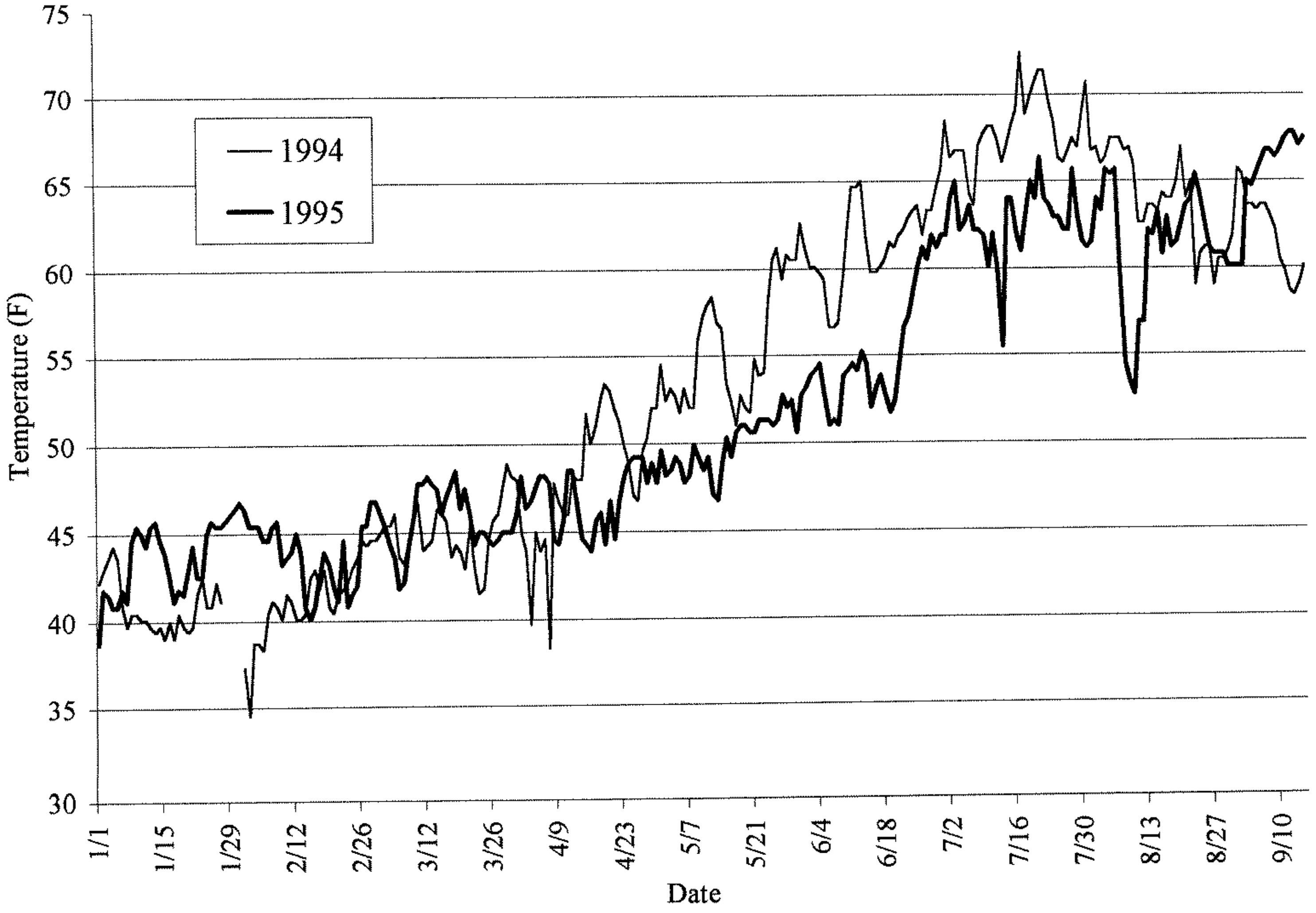
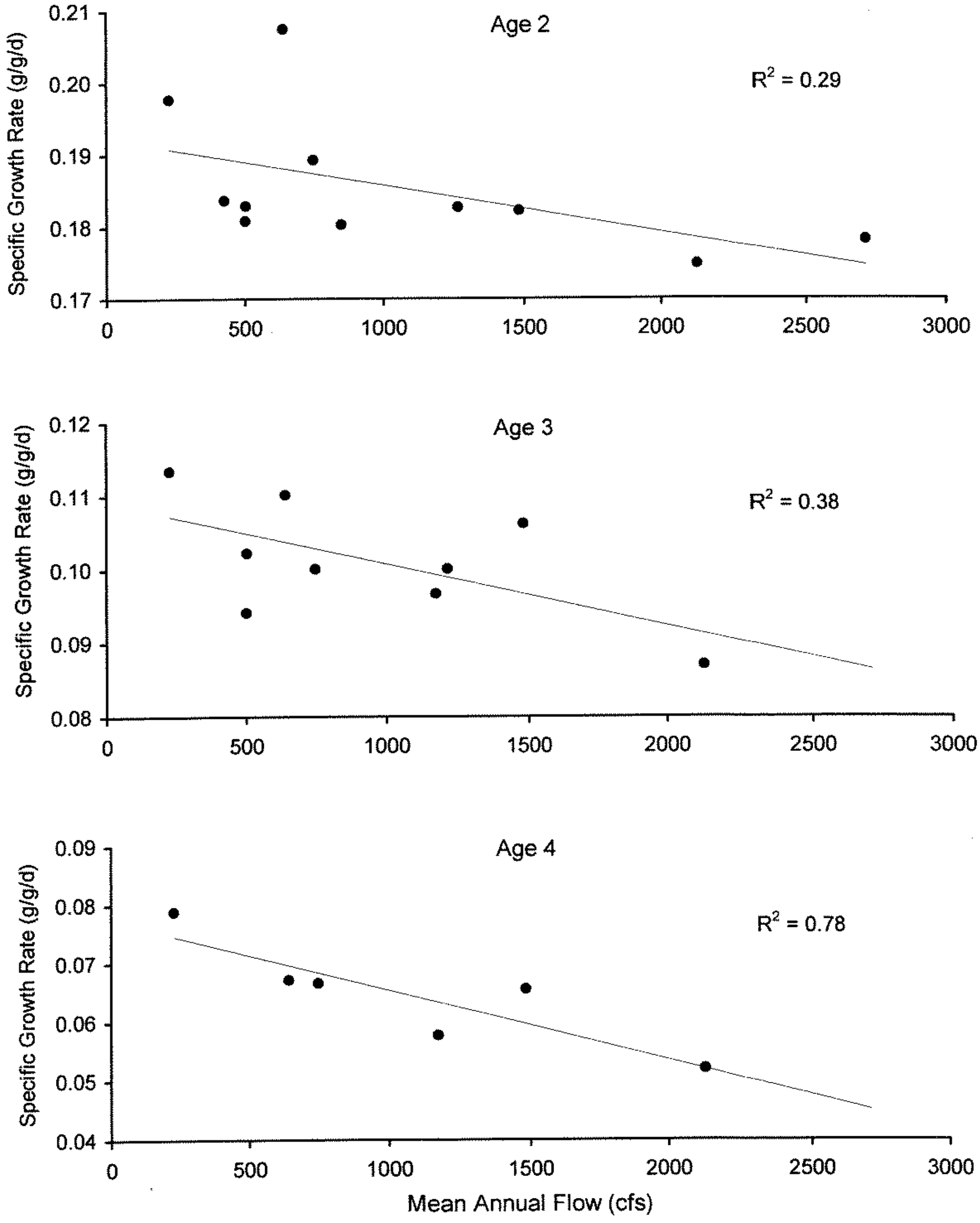


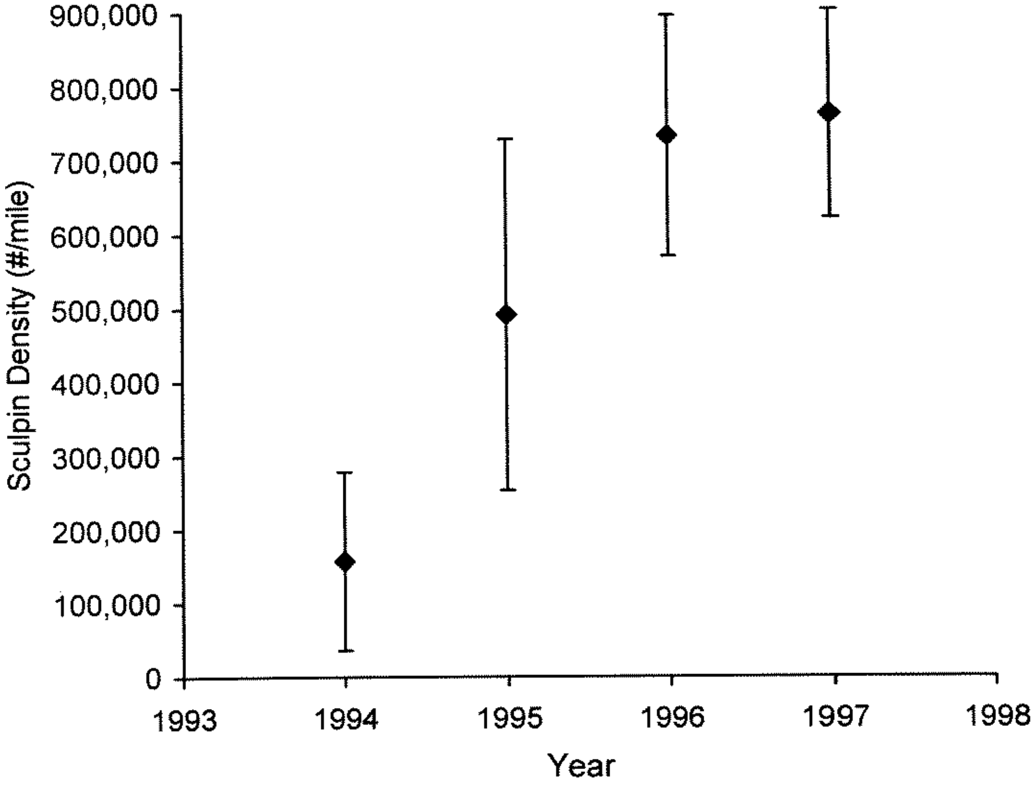
Appendix A. Mean monthly flow data for upper Sacramento River for post-spill years and overall average from 1945-1997. 1995 was the year with the highest flow and exhibits two peaks.



Appendix B. Average temperatures for a drought year (1994) and a flood year (1995) on the upper Sacramento River.



Appendix C. Adjusted specific growth rates of upper Sacramento River rainbow trout in relation to mean annual flow for the period 1975 through 1996. Growth rates based on back-calculated lengths from CDFG scale samples.



Appendix D. Sculpin abundances showing estimated index density (# / mile) of sculpin in upper Sacramento River run habitats following the Cantara Spill. Vertical bars are 95% confidence intervals. Data from Mark Allen, Thomas R. Payne and Associates.