# GROWTH AND THERMAL BIOLOGY OF FEATHER RIVER STEELHEAD UNDER CONSTANT AND CYCLICAL TEMPERATURES

## ABSTRACT

## INTRODUCTION

The lower Feather River, tributary to the Sacramento River in California's Central Valley, supports a small (< 1000 adults) run of winter steelhead (*Oncorhynchus mykiss*), an anadromous strain of rainbow trout) (McEwan and Jackson 1996). Despite its small size, the Feather R. steelhead run is still one of the largest remaining runs of Central Valley steelhead. Similar to steelhead throughout coastal California, Oregon and Washington, Feather River steelhead population size has declined drastically due to migration barriers, changes in the hydrologic and thermal regime, and increased interspecific competition and predation by exotic species. These winter steelhead are recognized and protected as members of the Central Valley steelhead subunit (USFWS 1998). There are still some wild steelhead in the Feather River, but the population and fishery are primarily supported by hatchery production from the Feather River State Fish Hatchery (McEwan and Jackson 1996).

The listing of all wild California steelhead stocks as either threatened or endangered by the U.S. Fish and Wildlife Service in 1998 (USFWS 1998) led to increased interest by the California Department of Water Resources (CDWR) in improving Feather River conditions for steelhead. During surveys of juvenile steelhead distribution and abundance, CDWR biologists noted that wild parr were dramatically restricting their use of theoretically available habitat to more upstream areas. Possible explanations for this distribution include: different thermal preferences and tolerance for wild vs. hatchery steelhead, bioenergetic causes, and predation–related causes.

Our objective was to test two hypotheses to explain the observed distributions. 1. Hatchery reared Feather R. steelhead have a significantly different thermal preference and tolerance than wild–reared steelhead. 2. Different ration levels and thermal (diel cycling vs. constant) regimes significantly affect growth and thermal biology of Feather R. steelhead.

## MATERIALS AND METHODS

Three hundred juvenile Feather R. steelhead (mean weight: 2.4 g; mean standard length [SL]: 54 mm) were transported from the Feather R. State Fish Hatchery in Oroville, CA on June 16, 1999, to the University of California Davis (UCD) where they were acclimated from 12°C to 16°C at 1°C $d^{-1}$. Steelhead were weighed (to nearest 0.1 g), measured (standard, fork, and total length to nearest mm), and stocked (12 fish per tank) into 24 circular fiberglass tanks (110-L) receiving 4 L $min^{-1}$ of air-saturated well water through angled spray bars that produced a current of 1 body length (BL) per second. Four tanks were assigned to each of the six temperature (16 ± 0.1°C or 16 ± 2.0°C on a diel cycle) × ration level (100, 50, and 25% satiation) treatments. Water temperatures were monitored and maintained by microprocessor–controlled mixing valves. Figure 1 shows the diel temperature cycle. Fish were reared indoors with both natural and artificial lighting on a natural photoperiod (latitude 38.55°N, June – August). Food consumption, growth, and survival experiments were completed before thermal preference and thermal tolerance experiments were conducted.

Wild Feather R. steelhead (n: 22, mean weight: 15.1 g, mean SL: 84 mm) seined from Moe's Ditch, a side channel of the Feather R., on September 23, 1999 were transported to UCD. The wild steelhead were fed live dragonfly larvae (*Gomphus* spp.) every 2 days. Because of the restricted numbers of wild steelhead, each fish was used once in both thermal preference and thermal tolerance experiments.

Food consumption, growth, and survival experiments were conducted over 50 d. Steelhead were weighed and measured (SL, FL, TL) on day 0 and again on day 50. Steelhead were fed either 100% satiation rations (Silvercup floating steelhead pellets) or restricted 50% or 25% ration twice daily. Restricted rations were calculated from the previous day's full ration food consumption on a gram food per gram fish basis. Food remaining in each tank 5 minutes after feeding was siphoned to allow quantification of food consumption rates. Mean food consumption rates (% body weight $d^{-1}$), growth rates (% body weight $d^{-1}$), and gross conversion efficiencies were calculated following Myrick and Cech (in press). Survival was measured as the reciprocal of mortality over the 50–experiment. Mean initial and final weights for each treatment were compared using Student t-tests and food consumption rates, growth rates, and gross conversion efficiencies were compared using two-way analysis of variance with ration level and temperature treatment as factors. The Student-Newman-Keuls method was used for multiple pairwise comparisons.

Thermal preferences of individual steelhead were determined using a circular horizontal gradient apparatus (Figure 2) in which a 20°C thermal gradient (10 to 30°C) was established. Ten hatchery steelhead were used per treatment, and 14 24-h fasted wild steelhead and 8 fed wild steelhead were used. Hatchery steelhead were fed < 24 h before being used, because 24-h fasted 25% satiation fish used in pilot thermal preference experiments had > 25% mortality during the fasting period. Steelhead were transferred to the gradient apparatus at their rearing (i.e., acclimation) temperature and allowed 1 h handling recovery before the gradient was established.

The fish's location and water temperature at that location (2-mm-diameter thermistor probes) were recorded just after the gradient was established and subsequently every 15 minutes for 1 h. The final ($T_{60}$) preferred temperature (at t = 60 min) and mean preferred temperature $\left(T_{mean} = \frac{T_i + T_{15} + T_{30} + T_{45} + T_{60}}{5}\right)$ were determined and were compared using T-tests. Two–way analyses of variance were used to detect differences among the treatments' initial, final, and mean preferred temperatures. Multiple pairwise comparisons were made using the Student–Newman–Keuls method.

Acute upper thermal tolerance was evaluated on individual steelhead (10 hatchery fish per treatment) and wild steelhead (14 fed fish, 8 fasted fish) using Young and Cech's (1996) modified critical thermal maxima (CTM) procedure. Starting from rearing (i.e., acclimation) temperatures, we increased the water temperature by 0.3°C $min^{-1}$, using a loss of equilibrium endpoint. Two way analyses of variance were used to detect differences among mean treatment critical thermal maxima, and the Student–Newman–Keuls methods was used for multiple pairwise comparisons.

## RESULTS

Survival during the 50 d growth and food consumption experiment exceeded 85% in all treatments and no ration level, thermal regime, or interaction effects were present (Table 1). Food consumption rates showed the expected ration–related trend, with 100% satiation > 50% satiation > 25% satiation (Table 2). The cyclical temperature treatments tended to have lower consumption rates than the constant temperature treatments receiving the same ration, but the trend was not significant. There was no interaction effect (Table 2).

The 50% satiation fish had higher initial weights than the 100% or 25% satiation fish (Table 1), and the 50% cyclic fish were longer than the 100 or 25% cyclic fish, but no other differences in initial morphometrics were present. All treatments' mean wet weights and standard lengths increased significantly after 50 days (Table 1), indicating positive growth in mass and length under all treatment conditions. A significant ration effect was observed with the 100% > 50% > 25% in order of decreasing weight and length gain. We observed a trend ($p = 0.065$) where the fish in the cyclical temperature treatments were lighter than their constant temperature counterparts (Table 1). The 100% constant fish were significantly longer than the 100% cyclical fish, but no other differences in final standard length were observed. No interaction effects were detected. Water contents of the 100% satiation treatments decreased slightly, those of the 50% satiation treatments remained about the same, and those of the 25% satiation treatment increased slightly from the initial water content (Table 1), although none of these differences were statistically distinguishable.

Feather River steelhead growth rates were significantly affected by ration level, but not by thermal regime, and no interaction effect was observed. Steelhead receiving the satiation ration grew faster than those receiving a 50% or 25% satiation ration (Table 2). Fish receiving the 25% satiation ration had a negative growth rate in part due to their higher water content (Table 2). Although not constituting a statistically significant difference, steelhead reared under the cycling thermal regime tended to grow at consistently slower rates than steelhead fed the same ration but reared under constant temperature conditions (Table 2).

Feather River steelhead gross conversion efficiencies were significantly affected by ration level (100% satiation > 50% satiation > 25% satiation), but not by thermal regime, and no interaction effect was observed (Table 2). The negative conversion efficiencies of the 25% satiation treatments reflected their negative growth rates (Table 2).

Hatchery and wild Feather R. steelhead temperature preferences were not significantly affected by thermal regime or ration level (Figure 3). A non–statistically significant trend was observed where fish reared under the cycling thermal regime selected slightly higher temperatures than fish reared under constant temperature conditions (Figure 3). Each treatments' final and mean preferred temperatures were similar.

Hatchery Feather R. steelhead upper critical thermal maxima were remarkably similar, with no thermal regime, ration level, or interaction effects (Table 3). Wild Feather R. steelhead also showed no ration effects, but their critical thermal maxima were significantly higher than the hatchery steelheads' (Table 3).

## DISCUSSION

Juvenile Feather R. hatchery steelhead food consumption and growth rates responded more to ration level than to thermal regime. Ration level is more important than thermal regime for juvenile Feather R. hatchery steelhead. All treatments showed significant increases in mean wet weight and standard length (Table 1), but this was not reflected in the growth rates (Table 2) because of the differences in water content among treatments. Although the 25% satiation treatments' mean wet weights increased, the increases were primarily due to increases in water content, because both treatments experienced negative growth rates and food conversion efficiencies. Food consumption and growth rates of constant and cyclical thermal regime 100% ration Feather R. steelhead are 1.3 and 2.4 – 2.7 times higher, respectively, than those of Nimbus strain steelhead reared at 15°C under similar conditions (Myrick and Cech in review). The

Nimbus strain steelhead are coastal steelhead that were transplanted to the American River (Figure 4) in the Central Valley (McEwan and Nelson 1991), and it appears that the Feather R. steelhead are better adapted (e.g., in terms of faster growth, thereby reducing vulnerability to gape–limited predators, (Werner and Hall 1974)) to temperature conditions in Central Valley rivers than the coastal steelhead. The observed thermal regime trend reflects a widely reported phenomenon where fish reared in a cycling thermal regime that cycles around the growth optimum have lower growth rates than fish reared at the constant temperature (reviewed by Jobling 1997). A range of 7 to 15.6°C has been reported as optimal for juvenile steelhead (McEwan and Jackson 1996; Zedonis 1996) in California, though previous experiments conducted in our lab demonstrated that juvenile Nimbus strain steelhead grew faster at 19°C than at 15°C (Myrick and Cech in review).

Feather R. steelhead thermal preferences were independent of thermal regime or ration level, and surprisingly, there were no differences between wild and hatchery steelhead. If the preferred temperatures reflect those of the growth optimum, as has been reported (reviewed by Jobling 1997), then Feather R. steelhead optimal growth temperatures are higher than those reported for other non–California steelhead strains. In our previous study of Nimbus–strain steelhead thermal preference, we found that the thermal preferenda were independent of ration level and rearing temperature (11, 15, or 19°C) (Myrick and Cech in review). Interestingly, both the Nimbus strain steelhead from the previous study and the wild and hatchery Feather R. steelhead used in this study preferred temperatures between 17 and 20°C, suggesting that steelhead populations in California's Central Valley prefer higher temperatures than those from more northern latitudes. We did not observe any ration effect among hatchery steelhead treatments, possibly because we could not withhold food from the fish without consequent mortality for 24 h before the experiments.  Although not statistically significant, fed wild steelhead tended to select warmer temperatures than fasted wild steelhead (17.4°C vs. 17.0°C), suggesting that wild Feather R. steelhead, like freshwater rainbow trout, will select cooler temperatures when rations are withheld to decreases maintenance metabolic costs (Javaid and Anderson 1967).

Hatchery Feather R. steelhead critical thermal maxima (CTM) were unaffected by either ration level or thermal regime.  Although the mean temperature for both thermal regimes was 16°C, we expected to see a greater thermal tolerance among the cyclical temperature treatments because of their repeated exposure to higher temperatures.  We observed thermal acclimation effects among Nimbus strain steelhead acclimated to constant temperatures of 11 to 19°C (Myrick and Cech in review) and resident California rainbow trout strains (Myrick and Cech in press) acclimated to 10, 14, 19, 22, and 25°C.  It appears that the thermal acclimation effect requires more than a 12-h daily exposure to cyclically elevated water temperatures.  The critical thermal maxima measured in this study for hatchery steelhead are comparable to those of Nimbus steelhead acclimated to 15 and 19°C (CTM range 28.4 – 29.9°C) (Myrick and Cech in review), and are also similar to those of resident Eagle Lake and Mt. Shasta rainbow trout reared at 14 and 19°C (CTM ranges: 28.6 – 29.6 and 28.4 – 29.3 for Eagle Lake and Mt. Shasta strain trout, respectively) (Myrick and Cech in press).

Wild Feather R. steelhead critical thermal maxima were significantly higher than those of hatchery steelhead. These results suggest that either these fish benefited from the thermal acclimation effect of being exposed to temperatures > 16°C, or that they possessed an intrinsically higher thermal tolerance than did hatchery fish reared under controlled, thermally homogenous conditions.  The former hypothesis is not supported by temperature data collected by a CDWR remote datalogger in Moe’s Ditch from June 23, 1999 to October 3, 1999 (Figure

5), but temperatures in the microhabitats used by these steelhead likely differed from those shown. Microhabitat studies on portions of the Sacramento–San Joaquin R. drainage have shown that juvenile rainbow trout (and presumably steelhead) select microhabitat on the basis of predation risk, thermal regime, interspecific competition, and food availability (Moyle and Baltz 1985; Brown and Moyle 1991).

Our study of the effects of ration level and thermal regime on hatchery Feather R. steelhead and our comparisons of wild and hatchery Feather R. steelhead thermal biology show that neither ration level or thermal regime are likely explanations for the distribution pattern observed in the Feather River. It is likely that the juvenile steelhead are selecting microhabitats to minimize direct predation risk (Brown and Moyle 1991), because of the Feather River's substantial populations of predatory Sacramento pikeminnows (*Ptychocheilus grandis*), smallmouth bass (*Micropterus dolomieu*), and striped bass (*Morone saxatilis*). A tethering study conducted by CDWR biologists during the summer of 1999 demonstrated that a predation gradient does exist, with the lowest predation rates in the areas where the juvenile steelhead are found (Jason Kindopp, CDWR, personal communication).

Our study is significant because it demonstrated that hatchery Feather R. steelhead derive no advantage from being reared under a diel cycling thermal regime with a mean temperature of 16°C. Also, we showed that while hatchery and wild steelhead have similar thermal preferences in the laboratory, their thermal tolerances are different. Finally, we demonstrated the value of both laboratory and field data for fisheries managers to address juvenile steelhead distribution and abundance questions.

## ACKNOWLEDGMENTS

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Table 1. Mean (± SE) hatchery steelhead morphometrics, water contents, and survival rates at 16 ± 0.1°C (constant) or 16 ± 2.0°C (cyclical). Superscript numbers indicate significant ration level effects, superscript letters indicate significant thermal regime effects. All treatments' final weights and lengths were significantly greater than their respective initial values.

| Treatment | | Wet weight (g) | | Standard length (mm) | | Water content (% of wet weight) | | Survival (%) |
|---|---|---|---|---|---|---|---|---|
| Ration level (% satiation) | Thermal regime | Initial | Final | Initial | Final | Initial | Final | |
| 100 | constant | 2.4 ± 0.08 $^{1\,a}$ | 8.6 ± 0.49 $^{1\,a}$ | 54 ± 0.7 $^{1\,a}$ | 79 ± 1.8 $^{1\,a}$ | 76 ± 2 $^{1\,a}$ | 74 ± 1 $^{1\,a}$ | 96 ± 1 $^{1\,a}$ |
| 100 | cyclical | 2.3 ± 0.14 $^{2\,a}$ | 7.4 ± 0.08 $^{2\,a}$ | 53 ± 0.8 $^{2\,a}$ | 75 ± 1.7 $^{2\,b}$ | 76 ± 2 $^{2\,a}$ | 74 ± 4 $^{2\,a}$ | 94 ± 1 $^{2\,a}$ |
| 50 | constant | 2.6 ± 0.09 $^{3\,b}$ | 5.3 ± 0.22 $^{3\,b}$ | 55 ± 0.7 $^{1\,b}$ | 66 ± 2.0 $^{3\,c}$ | 76 ± 2 $^{1\,b}$ | 77 ± 3 $^{1\,b}$ | 92 ± 2 $^{1\,b}$ |
| 50 | cyclical | 2.7 ± 0.03 $^{4\,b}$ | 5.1 ± 0.36 $^{4\,b}$ | 56 ± 0.7 $^{3\,b}$ | 66 ± 2.3 $^{4\,c}$ | 76± 2 $^{2\,b}$ | 78 ± 7 $^{2,3\,b}$ | 85 ± 5 $^{2\,b}$ |
| 25 | constant | 2.4 ± 0.05 $^{1\,c}$ | 3.4 ± 0.36 $^{5\,c}$ | 54 ± 0.7 $^{1\,c}$ | 59 ± 1.8 $^{5\,d}$ | 76 ± 2 $^{1\,c}$ | 80 ± 6 $^{1\,c}$ | 92 ± 2 $^{1\,c}$ |
| 25 | cyclical | 2.3 ± 0.13 $^{2\,c}$ | 2.9 ± 0.16 $^{6\,c}$ | 52 ± 0.8 $^{2\,c}$ | 56 ± 1.3 $^{6\,d}$ | 76 ± 2 $^{2\,c}$ | 81 ± 6 $^{3\,c}$ | 94 ± 1 $^{2\,c}$ |

Table 2. Mean (± SE) hatchery steelhead food consumption rates, growth rates, and gross conversion efficiencies at 16 ± 0.1°C (constant) or 16 ± 2.0°C (cyclical). Superscript numbers indicate significant ration level effects, superscript letters indicate significant thermal regime effects.

| Treatment | | Food consumption rate (% body weight $d^{-1}$) | Growth rate (% body weight $d^{-1}$) | Gross conversion efficiency (%) |
|---|---|---|---|---|
| Ration level (% satiation) | Temperature regime | | | |
| 100 | constant | 7.33 ± 0.23 [1 a] | 2.31 ± 0.09 [1 a] | 34 ± 1 [1 a] |
| 100 | cyclical | 7.08 ± 0.38 [2 a] | 2.08 ± 0.10 [2 a] | 32 ± 1 [2 a] |
| 50 | constant | 4.76 ± 0.17 [3 b] | 0.86 ± 0.22 [3 b] | 19 ± 5 [3 b] |
| 50 | cyclical | 4.54 ± 0.19 [4 b] | 0.71 ± 0.14 [4 b] | 17 ± 3 [4 b] |
| 25 | constant | 2.73 ± 0.08 [5 c] | –0.14 ± 0.16 [5 c] | –5 ± 6 [5 c] |
| 25 | cyclical | 2.43 ± 0.02 [6 c] | –0.15 ± 0.08 [6 c] | –7 ± 3 [6 c] |

Table 3. Hatchery and wild Feather River steelhead mean (± SE) critical thermal maxima (CTM) at 16 ± 0.1°C (constant) or 16 ± 2.0°C (cyclical). Superscript numbers indicate significant ration level effects, superscript letters indicate significant thermal regime effects.

| Treatment | | Number of replicates | CTM (°C) |
|---|---|---|---|
| Ration level (% satiation) | Temperature regime | | |
| 100 | constant | 10 | 29.4 ± 0.46 [1 a] |
| 100 | cyclical | 10 | 29.4 ± 0.19 [2 a] |
| 50 | constant | 10 | 29.6 ± 0.14 [1 b] |
| 50 | cyclical | 10 | 29.5 ± 0.20 [2 b] |
| 25 | constant | 10 | 29.5 ± 0.19 [1 c] |
| 25 | cyclical | 10 | 29.8 ± 0.11 [2 c] |
| wild steelhead | | | |
| fasted | natural | 14 | 30.6 ± 0.77 [3 d] |
| fed | natural | 8 | 31.0 ± 0.14 [4 d] |

Figure 1. Typical 24-h record of temperatures in the 16 ± 2°C diel cycling regime (dashed line) and the 16 ± 0.1°C constant regime.

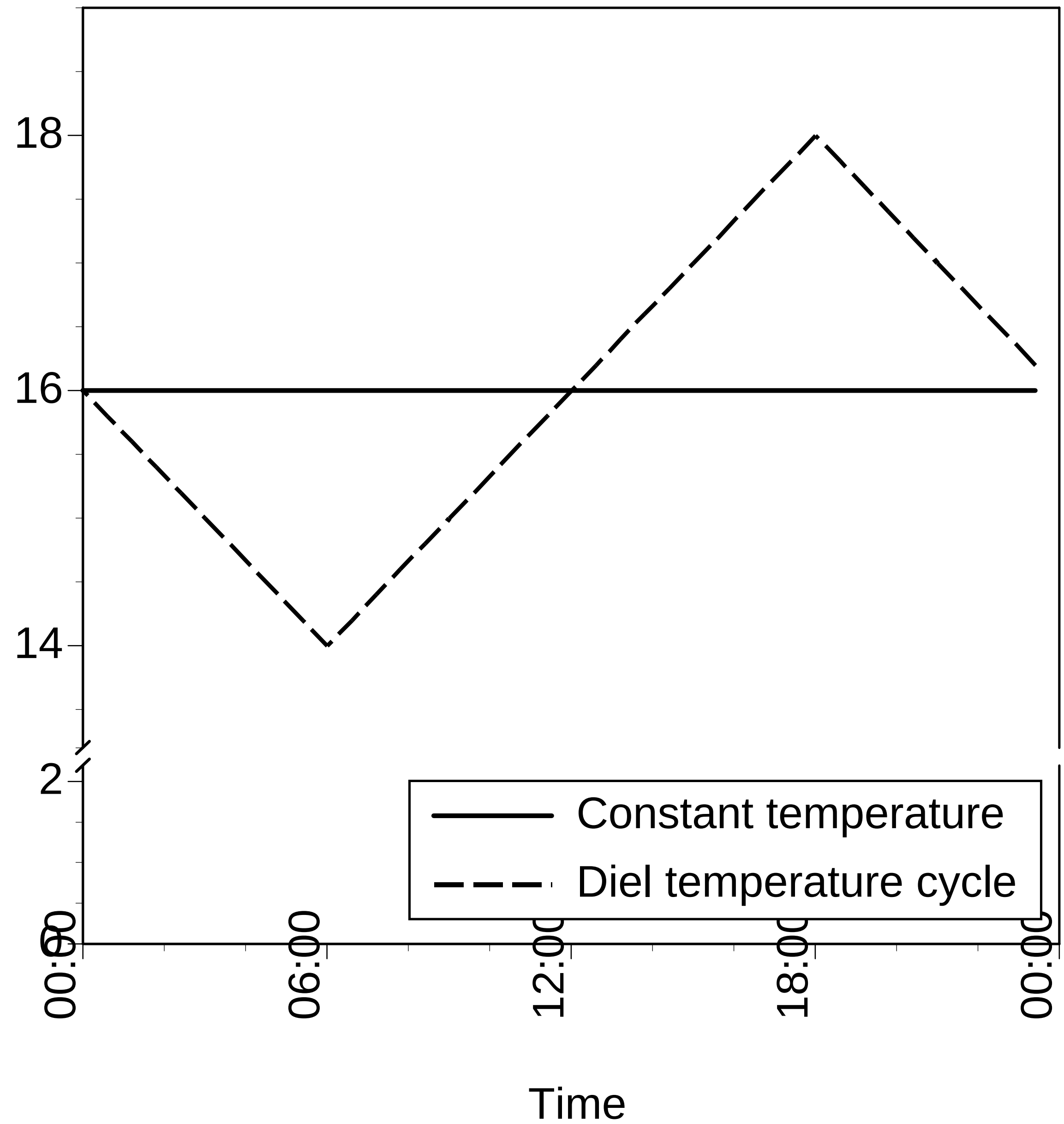

Figure 2. Schematic diagram of the circular, horizontal thermal gradient apparatus.

Figure 3.  Final (black bars) and mean (white bars) preferred temperatures (± SE) of hatchery and wild Feather River steelhead exposed to a 10°C to 30°C thermal gradient.  There were no significant ration or thermal regime effects, nor was there a significant interaction effect among any of the treatments.

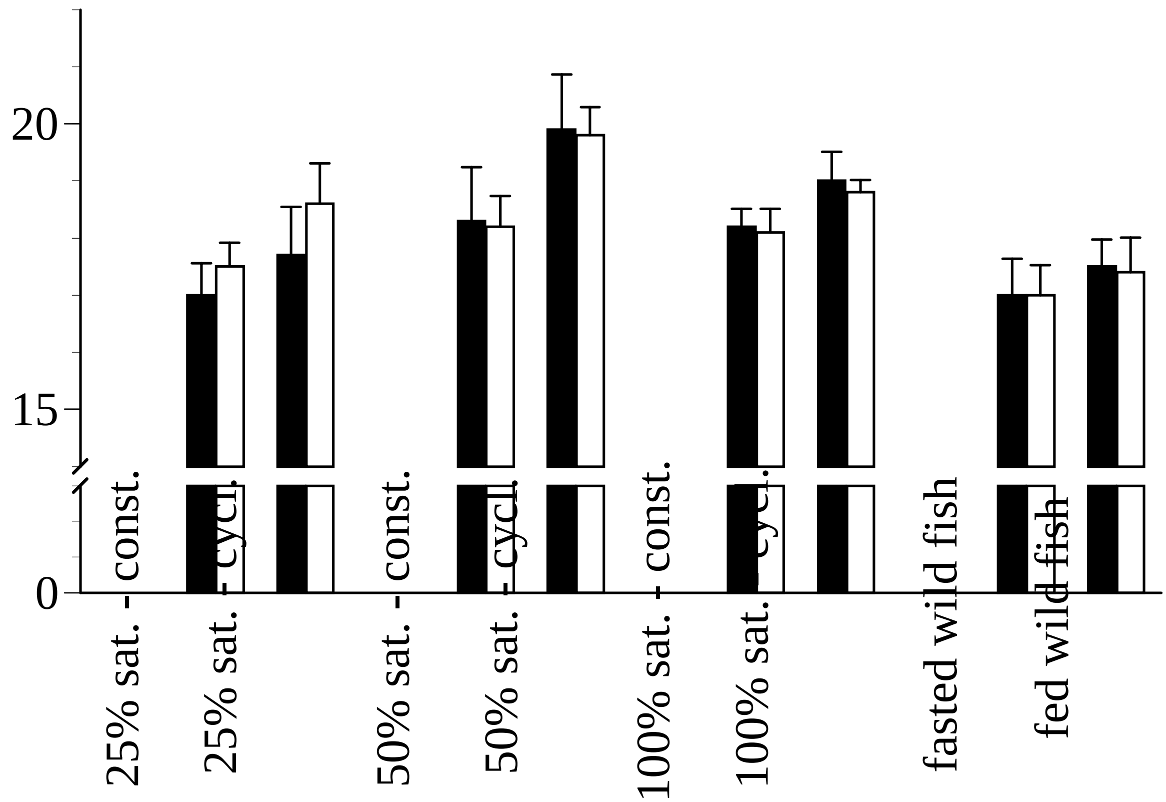

Figure 4. Map of California's Central Valley showing the location of the Feather and American Rivers (Figure 5 from McEwan and Jackson 1996).

Figure 5. Temperature record from Moe's ditch from June 23, 1999 to October 3, 1999. The dashed line shows the mean acclimation/rearing temperatures for the hatchery Feather R. steelhead treatments.