Title
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Authors
Cech, Joseph J, Jr.
Myrick, Christopher A

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By

Joseph J. Cech, Jr. and Christopher A. Myrick.

Department of Wildlife, Fish, and Conservation Biology

University of California, Davis

Davis, CA 95616

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ABSTRACT

The bioenergetics of two anadromous native salmonid fishes in California were investigated, concentrating on effects of water temperature and ration size on juvenile Nimbus Hatchery strain steelhead (*Oncorhynchus mykiss irideus*) and juvenile Nimbus strain chinook salmon (*Oncorhynchus tshawytscha*). Nimbus strain steelhead reared at water temperatures of 11, 15, and 19°C and ration levels of 100 and ca. 87% satiation showed increases in growth rates, food consumption rates, and upper acute thermal tolerance at increased temperatures. Temperature generally did not affect steelhead oxygen consumption rates, swimming performance, or thermal preference. Ration level affected oxygen consumption rates. Juvenile Nimbus strain steelhead differ from some other anadromous and resident rainbow trout strains. Nimbus strain chinook salmon reared at water temperatures of 11, 15, and 19°C and ration levels of 100 and 25% satiation showed increases in growth rates and food consumption rates with temperature. Salmon recieving the 100% ration grew faster than those on the restricted ration at all temperatures. Salmon fed the unrestricted ration at 19°C had higher swimming performances than those fed the restricted ration; no ration dependent–differences in upper acute thermal tolerance or oxygen consumption were observed.

Keywords:

Anadromous fish and fisheries, bioenergetics, American River, species variation, temperature, ration level, chinook salmon, steelhead, *Oncorhynchus mykiss*, *Oncorhynchus tshawytscha*.

STATEMENT OF PROBLEM AND RESEARCH OBJECTIVES

California's limited supply of fresh water is shared among three major user groups: urban, agricultural, and wildlife/fisheries (Miller 1993; SWRBC 1993). Because the current demand for water exceeds the supply compromises on the allocation of this resource must be made. Historically, water allocations have favored agricultural and urban users, with the wildlife and fisheries getting what little water remains (Miller 1993; SWRBC 1993). This situation has severely affected the state's aquatic resources (Moyle 1976; Moyle and Williams 1990; Moyle and others 1995).

Most of California's water is located in the northern half of the state, while most of the users are in the southern half. An extensive system of impoundments, pumps, and aqueducts has been constructed to make timely deliveries of water to the areas of greatest demand. Components of this water distribution system have had severe impacts on the aquatic biota (Herbold and others 1992; Moyle 1976; Moyle and Williams 1990; Moyle and others 1995). The adverse effects of these structures can be placed in one of two classes:

1. Loss of habitat because of physical barriers to migration in the form of dams, diversions and pumps (Clay 1995; Fletcher 1985; Moyle and others 1995).

2. Alterations in environmental conditions; both abiotic ones such as temperature profiles, flow regimes, and substrate; and biotic ones such as food availability and species composition (Moyle and Williams 1990; Moyle and others 1995).

Steelhead trout (*Oncorhynchus mykiss*) and chinook salmon (*O. tshawytscha*) have been severely impacted by these impoundments and diversions (Chatters and others 1991; Moyle and others 1995; Taylor 1988). Researchers have recognized that studying the effects of temperature and ration size on the physiological responses are critical for establishing management criteria for these "at risk" species (Heming and McInerney 1982; Kope and Botsford 1990; Kreiberg 1989; Neilson and Geen 1985). The previous citations represent just a few studies of a substantial, yet inadequate body of literature in reference to steelhead and chinook salmon populations in California.

It has been conclusively shown that *Oncorhynchus* species in a different drainages have genetic differences (Beacham 1990; Beacham and Evelyn 1992; Beacham and Withler 1991; Gall and others 1992) that result in differences in physiological performance (Cheng and others 1987; Kreiberg and others 1988), behavior (Taylor 1990b; Taylor and Foote 1991; Taylor and McPhail 1985) and life-history strategies (Clarke and others 1992; Healey 1994; Taylor 1990a). Because the California populations of steelhead and chinook salmon reside at the southernmost limit of these species' distributions (Moyle 1976), one can expect the fish to show significantly different responses to environmental conditions compared with their more northern conspecifics, thereby creating the need for research on California strains.

There have been limited studies on the physiological responses of California strains of steelhead and chinook salmon to different environmental conditions, especially temperature and ration size (Castleberry and Cech 1993; Castleberry and others 1991; Mulchaey 1994; Rich 1987). Mulchaey (1994) showed that hatchery-reared steelhead fed maximal rations are

significantly better swimmers than resident rainbow trout. Rich (1987) measured the growth and survival of juvenile American River chinook salmon fed maximal rations at a variety of temperatures to determine the temperature optima. The optimal range Rich [Rich, 1987 #960 reported for the laboratory-reared fish was 12.2 - 15.5°C. Castleberry et al. (1993; 1991) evaluated the relations among river conditions and growth rate, condition, and physiological performance of wild-caught chinook salmon and steelhead from the American River. The feeding and thermal history of these fish was not well known, but they appeared to be growing well in water of 15 - 17°C. This study identified a need for: 1) laboratory experiments that could establish cause and effect relations among various conditions, including temperature, on the performance of American River salmonids and; 2) laboratory experiments that would assess and validate their in *situ* measurements of growth.

The objective of this study was to evaluate the effects of temperature, ration size and genetics on the growth, survival, and bioenergetics of California strains of chinook salmon and steelhead. The parameters measured included food (energy) consumption rates (C consumption rate, % body weight per day), growth rates (G: growth rate, % body weight per day), active and resting routine respiratory metabolic (oxygen consumption) rates and mortality rates (from temperature exposure, poor condition, susceptibility to being swept downstream).

The primary goal of this study was to collect a baseline data set that would provide water and fisheries resource managers with critical data on California strains for application to current management decisions involving steelhead and salmon populations. Examples would

include helping set water quality criteria for the American, Sacramento-San Joaquin Rivers and Delta, and helping set suitable approach velocities for water diversions to minimize the entrainment and impingement losses of juvenile salmonids at pump and water diversion intakes, currently a major source of out-migrant mortality (Fletcher 1985; Herbold and others 1992; Miller 1993; Moyle and Williams 1990; Moyle and others 1995). The data set will also determine the suitability of using published data on non-California steelhead and chinook salmon strains for management decisions within California.

Additionally, results of the proposed study will be useful for modeling exercises and to delineate future research efforts. The collected data are suitable for use in individual-based bioenergetic models that would allow resource managers to explore different management strategies through computer simulation (Hewett and Johnson 1992). the results could also be used for baseline comparisons with future studies of 1) family differences to assess natural variability within spawning runs (e.g., fall-run) of chinook salmon, 2) other runs (e.g., winter-run, spring-run) of chinook salmon, and 3) other anadromous species (e.g. coastal coho salmon and cutthroat trout).

REVIEW OF METHODOLOGY

Facilities Description

All experiments were conducted at the Center for Aquatic Biology and Aquaculture facility on the University of California, Davis, campus. Both steelhead and chinook salmon were held indoors in a facility that received both natural light through translucent roof panels and artificial lighting set to the natural photoperiod (July to September for steelhead; May to July for chinook salmon). The 100–L round fiberglass tanks received a constant flow (4 L min^{-1}) of air-equilibrated well water at temperatures of either 11, 15, or 19°C (± 0.5 °C). Water temperatures were maintained by a computer–controlled mixing valve and were constantly monitored by microcomputer. In–tank water velocities were adjusted using angled spray bars to 1 body length per second (BL s^{-1}). Flow direction was reversed every 5 days to uniformly exercise the fish. Mean well water characteristics during the experiments were: total dissolved solids 390 mg L^{-1}, total suspended solids < 5.0 mg L^{-1}, total alkalinity 300 mg L^{-1}, pH 7.8 and hardness 320 mg L^{-1}. Dissolved oxygen levels in the flow-through experimental tanks, which also incorporated continuous aeration, were never below 90% air–saturation; weekly tests for dissolved ammonia detected none (0.1 mg L^{-1} detection limit).

Source and Care of Steelhead

Age–0 winter–run steelhead hatched from Nimbus strain eggs collected from the American R. at the Nimbus State Fish Hatchery in the winter of 1996 – 1997 were reared at the Mokelumne River State Fish Hatchery (tributary to the Sacramento-San Joaquin R. system).

Steelhead (mean weight: 2.7 g, mean standard length [SL]: 59.2 mm) were taken to the University of California, Davis, and acclimated to air–equilibrated well water at 11, 15 and 19°C at 1°C d^{-1}. Steelhead were stocked in 110–L round fiberglass tanks (4 replicate tanks per temperature/strain treatment) at a density of 25 fish per tank. Steelhead were fed Silvercup floating steelhead pellets.

Source and Care of Chinook Salmon

Age–0 fall–run chinook salmon from Nimbus strain eggs collected from the American R. at the Nimbus State Fish Hatchery in the fall of 1997 were hatched and reared at the Nimbus State Fish Hatchery. Chinook salmon (n = 720; mean weight: 1.65 g, mean total length [TL]: 60.4 mm) were taken to the University of California, Davis, in late April, 1998 and acclimated to air–equilibrated well water at 11, 15 and 19°C at 1°C d^{-1}. Salmon were stocked in 110–L round fiberglass tanks (4 replicate tanks per temperature/ration treatment) at a density of 30 fish per tank. Chinook salmon were fed Rangen semi-moist salmon pellets.

Food Consumption and Growth

All steelhead and chinook salmon were first used in 30–d food consumption and growth experiments. At the conclusion of these experiments, the rearing conditions (ration levels and temperature regimes) were continued while the individual fish were used in oxygen consumption, swimming performance, thermal tolerance, and thermal preference experiments. Fish were fed a satiation ration (100%) or a reduced ration (ca. 87% for steelhead, ca. 25% for chinook salmon). The reduced rations were calculated using:

$$\text{Reduced ration} = \frac{\sum FC_{d-1}}{\sum W_f} \times W_r \times k \qquad (1)$$

where ΣFC_{d-1} is the total amount of food consumed (g) by all the 100% satiation tanks at temperature T the previous day, W_f is the sum of the biomass (g) of the 4 full ration tanks at temperature T from the previous weighing, W_r is the biomass (g) of the particular reduced ration tank from the previous weighing, and k is the reduction coefficient (ca. 0.87 for steelhead and 0.25 for chinook salmon). The amount of food consumed was quantified after each feeding by subtracting the weight of the uneaten pellets from the weight of the food given. Mean consumption rate (C) in percent body weight of food consumed per day was calculated for each tank (Wurtsbaugh and Davis 1977b) using:

$$\text{consumption rate (\% body weight d}^{-1}) = \frac{C}{0.5\,(W_1 + W_2)t} \times 100 \qquad (2)$$

where W_1 is the initial estimated dry weight of a group of fish, W_2 is the final dry weight of the group of fish, t is the duration of the experiment in days (30 days), C = estimated dry weight of food consumed. Dry weights were estimated by multiplying the total wet weight of the fish in each tank by the mean dry weights determined by oven–drying a subsample of 5 fish per treatment per sampling date at 60°C until no reduction in weight was detected (approximately 4 days).

Growth rates were calculated for each tank. All fish were weighed and measured on day 0, 10, 20, and 30. Fish were fasted for 24 h prior to weighing, anesthetized (50 mg L^{-1} MS-222; 3 g L^{-1} NaCl ; 0.1 g L^{-1} $NaHCO_3$), weighed to the nearest 0.1 g on a calibrated electronic

balance and standard length (SL), fork length (FL), and total length (TL) measured to the nearest mm. Initial (W_1) and final (W_2) dry weights (g) for each time interval (t) were used to calculate the mean growth rate (G, % body weight per day) for each tank (Wurtsbaugh and Davis 1977b) using:

$$\text{growth rate (\% body weight d}^{-1}) = \frac{W_2 - W_1}{0.5(W_1 + W_2)t} \times 100 \quad (3)$$

Mean specific growth rates (SGR, % body weight per day) were also calculated for each steelhead tank using:

$$\text{SGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \times 100\%; \quad (4)$$

where $t_2 - t_1$ is the duration of the growth experiment in days (Busacker and others 1990) and W_1 and W_2 are as above.

Gross food conversion efficiencies (GCE, %) were calculated for each tank using:

$$\text{gross conversion efficiency } (GCE, \%) = \frac{W_2 - W_1}{\sum_{30}^{1} C_i} \times 100 \quad (5)$$

where W_2 and W_1 are as above, and C_i is the daily amount of food consumed. Steelhead and chinook salmon results were analyzed separately. The mean initial and final weights for each treatment were compared using Student t-tests. Differences among treatment mean C, G, GCE, and SGR were tested for using ANOVA. Multiple pairwise comparisons were made using the Student–Newman–Keuls method.

Immediately following the conclusion of the 30–d growth and food consumption experiment, the chiller supplying our system with cold water failed and began leaking refrigerant and oil into the 11 and 15°C treatment tanks. Because of the unknown, but potentially toxic effects of these compounds, and because of the loss of the cold water supply, we did not conduct oxygen consumption, thermal tolerance, or swimming velocity experiments on the 11 and 15°C salmon. Also, the loss of the cold water prevented us from conducting thermal preference experiments on any chinook salmon.

Resting Routine Oxygen Consumption

Resting routine oxygen consumption (MO_2) was measured in 900–ml cylindrical glass static respirometers. Oxygen consumption experiments were conducted on 24-h fasted fish in temperature–controlled water baths set to the fish's rearing temperature. Individual fish (8 to 10 replicates per steelhead treatment; 19 replicates per chinook salmon treatment) were placed in covered respirometers and allowed $\geq$ 4 h to reach a quiescent state. Water in the respirometers was exchanged at 100 ml min^{-1} during this period. After 4 h, an initial water sample was taken using a 1 ml glass syringe, and the respirometer was sealed. The partial pressure of oxygen (PO_2) in the water sample was measured using a Radiometer PHM71/D616/E5046 thermostatted O_2 analyzer system. PO_2 values were converted to O_2 contents (mg O_2 L^{-1}) using a solubility nomogram. After enough time elapsed for a 20 – 30 mm Hg drop in PO_2 (25 – 45 min, depending on temperature) the final water sample was taken for analysis and the respirometer unsealed. The volume of the respirometer was

determined, and the fish removed, over-anesthetized (500 mg L^{-1} MS-222), weighed, and measured. $\dot{M}O_2$ was calculated using:

$$\dot{M}O_2 = \frac{(\text{initial } O_2 \text{ content} - \text{final } O_2 \text{ content})}{\text{elapsed time of experiment}} \times \text{volume of respirometer} \quad (6)$$

We tested for differences between steelhead treatments' mean oxygen consumption rates and morphometrics using ANOVA; differences between chinook salmon treatments were tested for using Student T-tests.

Critical Thermal Tolerance

Acute upper thermal tolerance was evaluated on individual 24–h–fasted fish (8 to 10 replicates per steelhead treatment; 20 replicates per chinook salmon treatment) using Becker and Genoway's (1979) critical thermal maxima (CTM) procedure as modified by Young and Cech (1996). Fish were acclimated to their rearing temperature (11, 15, or 19°C) for at least 30 d. We increased the water temperature from the acclimation temperature by 0.3°C min^{-1} using loss of equilibrium as our primary endpoint. Differences among steelhead treatment CTM and morphometric values were tested for using ANOVA procedures. Student T-tests were used to detect differences among mean chinook salmon treatment morphometric and CTM values.

Swimming Performance

Steelhead and chinook salmon aerobic swimming performance was assessed by measuring the critical swimming velocity (U_{crit}) (Brett 1964) of individual 24–h–fasted fish (7 to 10

replicates per steelhead treatment; 11 to 15 replicates per chinook salmon treatment) in a 152–L Brett–type swimming flume (modified from Bell and Terhune's 1970 design). Fatigue was taken as the point where the fish would not move off the rear screen of the swimming flume, even after reductions in current velocity and gentle prodding with a nylon rod. We used a short 10–min interval and a 1 BL s^{-1} velocity increment because we were solely concerned with a comparative measure of swimming performance (Hammer 1995). We accounted for fish size differences by dividing the U_{crit} by the TL, giving the length–specific U_{crit} in BL s^{-1}. Differences among steelhead critical swimming velocities and morphometrics (fish length and weight) were detected using ANOVA. Student's t-tests were used to detect differences among chinook salmon mean treatment U_{crit} and morphometric values.

Thermal Preference

The 1-h thermal preferences of individual, 24–h–fasted steelhead were determined using 1.5–m–long thermal gradient tanks in which a 20°C thermal gradient (10 to 30°C) was established. Individual steelhead (10 replicates per treatment) were carefully transferred to the tank at their acclimation temperature. Fish were allowed 1 h to recover from handling before the gradient was established by introducing 10 and 30° water at opposite ends of the tank. The fish's location and water temperature at that location were recorded every 15 minutes for 1 h. The initial (control, T_0), final preferred temperature (temperature at t = 60 min) and mean preferred temperature:

$$\left(T_{avg} = \frac{T_0 + T_{15} + T_{30} + T_{45} + T_{60}}{5}\right) \quad (7)$$

for each fish were determined. T-tests were used to compare each treatments mean and final preferred temperatures. 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.

DISCUSSION OF RESULTS AND THEIR SIGNIFICANCE

Results

Food Consumption, and Growth All steelhead were treated for a *Costia* infection a week before the experiments started, but there was some residual mortality during the first week of the food consumption and growth study. Survival rates varied greatly within and among treatments (by up to 22%), but there were no significant differences among treatments' survival rates (Table 1). Reduced ration food consumption rates were 82, 92, and 88% of satiation rations at 11, 15, and 19°C, respectively. We observed a trend of increasing consumption rates at 19°C, comapred with those at the two lower temperatures, but this was only statistically significant between the 19°–reduced ration steelhead and their reduced ration counterparts at 11 and 15°C (Table 1). The overall food consumption rate Q_{10} (11 – 19°C) for the full and reduced ration steelhead were 1.30 and 1.63, respectively.

Mean steelhead size increased significantly (postive growth) in all treatments (Table 1). Full ration steelhead had consistently higher final wet weights than reduced ration steelhead but this pattern was not reflected in the G or SGR values (Table 1). Morphometrics (body proportions) were not sensitive to these temperature/ration treatments (slopes of the log length–weight relationships were not significantly different, Table 2). The 19°C full–ration steelhead grew significantly faster than the 11 or 15°C full ration steelhead and the 19°C reduced ration steelhead (Table 1). No other significant differences among growth rates were observed. Gross food conversion efficiencies were temperature and ration level–independent (Table 1).

Food consumption and growth rates for chinook salmon fed to satiation increased significantly with temperature (Table 3). We did not detect a significant temperature effect on full ration salmon gross conversion efficiencies, although an increasing trend with increasing temperature was seen. Reduced ration chinook salmon growth rates were similar, and negative, at all temperatures tested (Table 3). Reduced ration food consumption rates increased with temperature because of their dependence on the corresponding full ration treatment's food consumption rate (Table 3). Reduced ration gross conversion efficiencies were also similar, and negative, at all temperatures tested (Table 3). Full ration tanks had significantly higher chinook salmon growth rates and conversion efficiencies than the corresponding reduced ration tanks at the same temperature (Table 3).

Resting Routine Oxygen Consumption Mean steelhead weights among treatments were not significantly different. The 19°C reduced–ration fish had significantly lower mean oxygen consumption rates than the 19°C, full–ration steelhead (Figure 1). A similar trend was observed within the 11 and 15°C treatments, but the differences were not statistically significant (Figure 1). No temperature effect was detected among either reduced or full–ration treatments. The mean weight of the 19°C full–ration salmon was not significantly different from that of the 19°C reduced–ration salmon. Although the 19°C reduced–ration oxygen consumption rate was 1.5 times higher than that of the full ration fish, the difference is not statistically significant due to substantial individual variability(Figure 2).

Critical Thermal Tolerance Juvenile steelhead critical thermal maxima increased significantly with rearing/acclimation temperature (Table 4). Ration did not have a significant effect within an acclimation temperature, with the exception of the 3.4% higher CTM of the 15°C reduced–ration treatment (Table 4).

Despite a significant difference between the weights of 19°C full–ration salmon and the 19°C reduced–ration salmon (14.7 ± 1.2 g and 3.2 ± 0.4 g, respectively), their critical thermal maxima were not significantly different (Figure 3).

Swimming Performance The larger 15 and 19°C full–ration steelhead swam significantly faster than the 11°C full ration steelhead (Table 4). Additionally, the 15°C full–ration steelhead swam significantly faster than the smaller 15°C reduced–ration steelhead (Table 5). No other ration or temperature–related differences were observed (Table 5).

The larger 19°C full–ration chinook salmon swam faster than the 19°C reduced–ration salmon (Table 6).

Thermal Preference Steelhead in all but the 19°C treatments selected significantly higher final and mean temperatures than their initial temperature (rearing/acclimation temperature) (Figure 4). There were no significant differences between the mean or final preferred temperatures of any treatment (Figure 4). No significant ration or thermal acclimation effects were observed.

PRINCIPAL FINDINGS, CONCLUSIONS, AND RECOMMENDATIONS

Steelhead

Juvenile Nimbus strain steelhead show a higher level of temperature–independence of growth, oxygen consumption, food consumption, and thermal preference than has been previously reported for other steelhead strains over the 11 to 19°C range. Nimbus steelhead swimming performance and thermal tolerance generally increased with increasing temperatures. Reduced ration levels of 82 to 92% reduced growth rates, swimming performance, and oxygen consumption rates.

Food Consumption, and Growth A fish's ingested energy (C) (Warren and Davis 1967) is allocated to somatic and reproductive growth (G_s and G_r, respectively), maintenance and activity metabolism (M_r and M_a, respectively), specific dynamic action (SDA), and losses in fecal (F) and urinary wastes (U) according to:

$$C = (M_r + M_a + SDA) + (F + U) + (G_s + G_r). \quad (8)$$

Nimbus steelhead food consumption rates increased with temperature increases to 19°C. The Q_{10} (temperature–dependent rate constants) of 1.30 and 1.63 for the reduced and full–ration fish, respectively, are lower than the Q_{10} values of 2 to 3 more typically observed (Schmidt-Nielsen 1990). Elevated consumption rates may result from an increased ability to eat or in response to elevated energy demands at higher temperatures, as has been reported for other fishes (Jobling 1997). Temperature–related increases in some right side variables (energy use) in equation 8 must balance decreases in other right side variables or increases on the left

(energy ingestion) side. Because reproductive growth in juvenile fish is negligible, and losses due to egestion and energy used for SDA are functions of the food consumption rate (Beyer and others 1988; From and Rasmussen 1984), the surplus energy must have been partitioned into growth, activity, and maintenance metabolism. Steelhead growth rates showed an increasing trend with temperature increases to 19°C.. Resting routine oxygen consumption rates were temperature–independent; possible reasons for this are discussed below. Steelhead activity levels may have increased at the warmer temperatures, but these were not quantified. Increased activity rates as temperatures approach the upper incipient lethal limit have been documented in rainbow trout (Briggs and Post 1997).

Our steelhead had lower consumption rates than resident Eagle Lake or Mt. Shasta strain rainbow trout used in a similar study (Myrick and Cech in press) (Table 7). The two studies were similar, differing primarily in the type of feed used and the stocking density (25 fish/tank vs. 30 fish/tank). Some size differences were also apparent. Our full ration steelhead consumed less food than Oregon steelhead (Table 7), but consumed more food than 4 – 8 g rainbow trout used by Alsop and Wood (1997). The differences between the values reported in these studies and our study may have resulted from differences in fish size, feed type or experimental protocol. Rainbow trout and sockeye salmon (*O. nerka*), consumption rates are generally inversely related to fish size (Brett and others 1969; Wurtsbaugh and Davis 1977a).

Given the similarity of the two ration levels, the statistically indistinguishable growth rates between ration treatments (Table 1) was not surprising. The ability of the reduced ration fish

to match the growth rates of the full ration fish suggests differences may have been due to activity. Reductions in conversion efficiency at ration levels approaching C_{max} have been noted in brown trout (Elliott 1976), but we observed no temperature or ration–related differences in conversion efficiency (Table 1). This result is important because it suggests that juvenile Central Valley steelhead do not require maximal rations to achieve high growth rates. However, the two ration levels were too close to conclusively demonstrate this.

Nimbus steelhead growth rates increased with temperature to a maximum at 19°C. Similar temperature effects have been reported for other fish, including Eagle Lake rainbow trout (*O. m. aquilarum*), Mt. Shasta rainbow trout (Myrick and Cech in press), and Oregon steelhead (Wurtsbaugh and Davis 1977b). It is premature to conclude that the optimal temperature for Central Valley steelhead growth is 19°C until further growth data are collected at temperatures just below (e.g., 17°C) and above 19°C. We can, however, conclude that the observed maximum growth rates correlate with mean preferred temperatures (Figure 4). This increase in growth rate would allow the steelhead to take advantage of the higher water temperatures of the primary rearing areas and maximize their growth, thereby reducing the effects of size–dependent predation (Brown and Moyle 1981) and enhancing ocean survival following emigration (Johnsson and others 1997; Mathews and Ishida 1989; Unwin 1997), providing sufficient food is available.

Nimbus steelhead had lower growth rates than those reported for other strains of resident rainbow trout (Myrick and Cech in press) and Oregon steelhead (Wurtsbaugh and Davis 1977b) (Table 7). Differences in fish size can account for the differences between our results

and those for the Oregon steelhead. The differences in growth rate between our fish and the Eagle Lake and Mt. Shasta rainbow trout probably result from those strains' higher food consumption rates.

Resting Routine Oxygen Consumption Mean steelhead weights among treatments were not significantly different. The 19°C reduced–ration fish had significantly lower mean oxygen consumption rates than the 19°C, full–ration steelhead (Figure 1). A similar trend was observed within the 11 and 15°C treatments, but the differences were not statistically significant (Figure 1). No temperature effect was detected among either reduced or full–ration treatments.

Nimbus steelhead used in our oxygen consumption experiments showed an interesting ration–related response. Although only significant at 19°C, full ration fish generally had higher oxygen consumption rates than reduced ration fish (Figure 1). It appears that the full ration treatment MO_2 included both the resting routine metabolism component and some SDA component. The factors that determine the duration of the SDA effect have not been exhaustively investigated, but are known to include temperature, meal size and type, fish size, and interval between meals. Jobling and Spencer–Davies (1980) reported that the duration of the SDA effect in plaice (*Pleuronectes decurrens*) decreased with increasing temperature and increased with the percentage of protein in the meal. Du Preez (1987) noted differences in the magnitude of the SDA effect in leervis (*Lichia amia*) that were related to the length of the interval between meals and Armstrong et al (1992) and Furnell (1987) reported that the SDA effect could be detected two or more days after feeding in northern pike (*Esox*

lucius) and sablefish (*Anoplopoma fimbria*), respectively. Although all of our steelhead were fasted for ≥ 24 h, this may have been insufficient time for complete gastric evacuation. Boyce and Clarke (1997) reported that larger Antarctic plunderfish (*Harpagifer antarcticus*) showed detectable SDA effects over a longer interval than smaller fish, but that neither the duration nor magnitude of the SDA effect was affected by ration size. If this observation holds true for juvenile steelhead, then the larger size of the full ration steelhead (1.2 to 1.6 times larger than the reduced ration steelhead) could have resulted in SDA effects with longer durations and therefore explain the observed MO_2 differences.

Nimbus steelhead used in our experiments had temperature–independent oxygen consumption rates over the narrow (8°C) range tested. The temperature–independent MO_2 appear surprising at first, as one normally expects a poikilothermic vertebrate's MO_2 to increase with increasing temperature (Schmidt-Nielsen 1990) but temperate fish are known to show reduced metabolic sensitivity to temperatures approaching their thermal optima (Taylor and others 1997). The preferred thermal range for Nimbus steelhead is 17 – 20°C (Figure 4), so their metabolic rates near that temperature range are likely to show thermal–independence (Taylor and others 1997). An ecological advantage of this temperature–insensitivity in respiration is that Central Valley steelhead can move to warmer water to take advantage of the higher growth and, possibly, activity rates without incurring a significant maintenance metabolic cost, providing sufficient food is available.

Full ration treatment oxygen consumption rates are comparable to those of resident Eagle Lake and Mt. Shasta strain rainbow trout (Myrick and Cech in press) and Little Kern River

golden trout (Myrick and Cech, unpublished data). The similarities among these four California *O. mykiss* strains oxygen consumption rates suggests that the thermal independence may be an adaptation to California's variable conditions. Although MO_2 measurements techniques are not as variable as those used for measuring growth or food consumption rates, differences due to fish size, respirometer design, and experimental procedures may influence comparison between studies. For example, our steelhead and resident rainbow trout (Myrick and Cech, unpublished data) MO_2 were 20 to 25% lower than those reported by Cech et al.(1990) for California rainbow trout.

Thermal Preference Nimbus steelhead used in this study preferred temperatures between 17 and 20°C, irrespective of ration level or rearing temperature (Figure 2). The lack of any kind of ration effect is interesting, as other studies have reported that fish may behaviorally thermoregulate and seek lower temperatures when rations were restricted to decrease their maintenance metabolic costs (Hughes 1998; Konecki and others 1995; Reynolds and Casterlin 1978). It is likely that the difference between the two ration levels was not sufficient to elicit such a response in our steelhead. Much variation in thermal preference was observed within each treatment. Konecki et al. (1995) investigated the potential for population–level variation in the related coho salmon (*O. kisutch*). They found that the large degree of variation at the individual level may have been masking any population–level differences.

Nimbus steelhead reared at 11°C have higher mean preferred temperatures than those reported by for anadromous Great Lakes rainbow trout acclimated to 10 to 11°C water but

show similar thermal preferenda at acclimation temperatures in the 15 to 19°C range (Cherry and others 1975; Cherry and others 1977). Our Nimbus steelhead preferred higher temperatures than the 7 to 15.6°C range reported as optimal for California steelhead (McEwan and Jackson 1996; McEwan and Nelson 1991; Zedonis and Newcomb 1997). Care should be taken before applying our thermal preference results because the interactive effects of factors like predation, inter– and intraspecific resource competition, disease, and instream hydraulics may influence temperature selection in the American River.

Thermal Tolerance Nimbus steelhead critical thermal maxima were significantly affected by acclimation (rearing) temperature, but not by ration level. However, steelhead receiving reduced rations tolerated slightly (but not significantly) higher temperatures than full–ration steelhead. This difference is interesting, because some studies have documented size–related differences in thermal tolerance (Baker and Heidinger 1996; Becker and Genoway 1979) while others reported that no size effect (Bidgood 1980; Bidgood and Berst 1969). If size did have an effect, one would expect the larger full–ration fish to display greater thermal inertia and hence a slightly greater thermal tolerance. We detected no size–related differences. One possible explanation for the observed trend involves the observed aerobic metabolic rate differences. In order to meet their elevated oxygen demand, the full–ration fish must extract more oxygen from the water by increasing gas exchange rate either by increasing gill ventilation volume, increasing gill perfusion and/or adjusting other efficiency variables (Campagna and Cech 1981; Randall 1982). The higher exchange efficiency of gill tissue may

translate into higher heat exchange, especially from convective ventilation and perfusion increases (Graham 1983), leading to a slightly faster submission to the acute thermal stress.

Past reports on salmonid acute thermal tolerance generally report a positive thermal acclimation effect (Bidgood 1980; Elliott 1991; Kowalski and others 1978). Our steelhead also displayed this positive thermal acclimation effect, showing that they have a limited ability to increase their tolerance when reared under elevated temperatures. Even though the magnitude of the acclimation effect is only 2°C, this could represent a significant difference under natural conditions. High summer and fall water temperature is the environmental factor that limits the survival of juvenile steelhead in the American River and adversely affects the production of yearling steelhead at Nimbus Fish Hatchery (McEwan and Nelson 1991). Our data indicate that Nimbus steelhead can tolerate higher temperatures, provided that dissolved oxygen levels remain near saturation and disease outbreaks are controlled.

The CTM values we reported for Nimbus steelhead were similar to those reported for other rainbow trout (both resident and anadromous). With the possible exception of lake trout (*Salvelinus namaycush*), Arctic charr (*S. alpinus*) (Lyytikäinen and others 1997) and other cold–adapted salmonid species restricted to high latitudes, salmonids appear to have very similar thermal tolerances, irrespective of origin (Grande and Andersen 1991; Lee and Rinne 1980).

Swimming Performance Nimbus steelhead critical swimming velocities were affected by fish size and to a lesser degree by temperature and ration level. The larger 15 and 19°C full–ration steelhead swam significantly faster than the 11°C full-ration steelhead. Although little

difference existed between steelhead length–specific swimming performances at 11 and 19°C, there is an increase in swimming performance between 11 and 15°C ($P = 0.07$) and a decrease in swimming ability between 15 and 19°C. This result suggests that the steelheads' locomotory muscular system (e.g., muscle fibers, enzymes) has an optimum operating temperature (Johnston and others 1990; Rome 1995; Rome and others 1990) between 15 and 19°C.

Although not statistically significant, full ration treatments had consistently higher relative U_{crit} than their reduced–ration counterparts. Nimbus steelhead fed full rations may have had larger endogenous energy stores that allowed them to maintain aerobic swimming performance longer than steelhead fed reduced rations. However, Alsop and Wood (1997) reported that rainbow trout fed to satiation at 15°C were 9 and 15% slower than fish fed a maintenance ration and fasted fish, respectively. They attributed the difference in aerobic swimming performance to a reduction in the maximum aerobic capacity because of the increased SDA associated with feeding to satiation. Because of the small difference between ration levels, and the 24-fasting period prior to the swimming trials, we suspect that the difference in performance may be related to size. A number of authors have reported that size influences swimming performance, with larger fish having lower relative swimming velocities than small fish (Brett 1965; Webb and others 1984). Full ration treatment steelhead were 1.1 to 1.4 times longer (TL) than reduced ration fish, yet they still showed higher U_{crit}. Taylor (1991; 1985) documented strain related differences in the swimming performances of the related sockeye and coho salmon, while Plaut and Gordon (1994) found that while individual wild–

type zebrafish (*Brachydanio rerio*) had highly variable swimming performances, those of cloned zebrafish were nearly identical. Our steelhead all came from the same strain, so the presence of population–related variation can be discounted, but it is almost certain that there is a high degree of individual variability, even among closely related hatchery steelhead. However, individual variability still does not provide an explanation for the observed trend. A final possibility is that steelhead fed full rations were able to draw on larger endogenous energy stores and thus maintain aerobic swimming performance longer than the reduced ration fish.

Nimbus steelhead aerobic swimming performances are intermediate compared with those reported for other resident and anadromous rainbow trout (Table 8). Resident Eagle Lake and Mt. Shasta rainbow trout (Myrick and Cech in press) were faster than the steelhead at all temperatures, as were Aberdeen strain steelhead swimming at 10°C (Hawkins and Quinn 1996). Nimbus steelhead swam at roughly the same velocity as Mad River hatchery steelhead (4.74 BL s^{-1}) (Mulchaey 1994) and were faster than the rainbow trout used by Alsop and Wood (1997). Variation among studies can be introduced by differences in fish size, conditioning (Bainbridge 1962; Hammond and Hickman 1966), experimental protocol (Peake and others 1997a), and apparatus design (Webb 1993). As a result of this, and because of the known performance differences between wild and hatchery fish (Brauner and others 1994; Duthie 1987; Peake and others 1997b) swimming performance data should be interpreted carefully.

Chinook Salmon

Water temperatures in the 11 – 19°C range significantly affected the food consumption and growth rates of juvenile Nimbus strain chinook salmon (Table 3). Chinook salmon fed a restricted (25% satiation) ration had reduced growth rates, swimming performance, and oxygen consumption rates, when compared to salmon receiving a satiation ration.

Food Consumption, and Growth As expected, increases in water temperature led to increases in chinook salmon food consumption rates, with a corresponding increase in growth rates. These results shows that temperature–related increases in the costs of maintenance are offset by the increased conversion efficiency, leading to higher growth rates at the warmer temperatures. Surprisingly, our chinook salmon reached a growth maximum at 19°C, where others have reported the growth maximum for chinook salmon occurs at or around 16°C (Rich 1987). The growth and conversion efficiency values we report in this study are consistently higher than those reported by Rich (1987) 2.6 – 3.0 g Nimbus strain chinook (Table 9). Unlike our study, Rich used filtered water from the American R. and encountered problems with disease and reduced dissolved oxygen levels. It is important to qualify our findings by stating that these were fish held under saturated dissolved oxygen conditions in pathogen–free well water, so some of the common problems associated with higher temperatures were controlled for.

Restricting the ration level to 25% had the expected effect on the mean growth rates. Indeed, the 25% satiation ration did not provide enough energy for the fish to maintain their weight, and negative growth rates resulted. However, an interesting aspect of the restricted ration

treatments was the change in size distribution over the course of the experiment. As shown in Figures 5 through 7, the distribution of initial weights in the 25%–satiation treatments was normal, but at the end of the growth and food consumption experiment, there were a 1 to 2 very large fish in each tank, while the rest of the fish followed a regular weight distribution. The reason for the disparity in sizes and the change in the distribution is the establishment of dominance hierarchies within the tanks. The dominance of one individual in both laboratory and natural settings has been widely documented (Cutts and others 1998; Harvey and Nakamoto 1997; Johnsson and Åkerman 1998; McMichael and Pearsons 1998; Wagner and others 1996). The management implication of this result is that increasing the density of juvenile chinook salmon in the American River without increasing the available food base will probably reduce the growth rates of most of the juvenile salmon, though a small group of dominant individuals may experience high growth rates.

Resting Routine Oxygen Consumption Ration level had no significant effect on the oxygen consumption rates of juvenile chinook salmon held at 19°C. It is likely that the trend seen, with the reduced–ration fish having a higher oxygen consumption rate than the full–ration fish is due to differences in size. Size–related differences in oxygen consumption rate have been widely reported, though usually for sizes that differ by at least an order of magnitude (Cai and Summerfelt 1992; Maxime and others 1989). Although the difference was not statistically significant, the mean weight of the reduced–ration fish was 46% higher than that of the full–ration salmon. Because the differences in weight were not significant, we can compare the mass–specific oxygen consumption rates (mg O_2 consumed per hour per

gram of fish, or mg O_2 h^{-1} g^{-1}). As with the unadjusted oxygen consumption rates, there was no significant difference between the reduced ration salmon (0.28 mg O_2 h^{-1} g^{-1}) and the full–ration salmon (0.27 mg O_2 h^{-1} g^{-1}). This is an important result because it clearly demonstrates that in this case there was no SDA effect after the 24-h fast (unlike the steelhead mentioned above). Another important conclusion that can be drawn from this result is that the maintenance metabolic costs are independent of feeding history, at least for 24–h–fasted juvenile chinook salmon at 19°C.

Thermal Tolerance Juvenile Nimbus strain chinook salmon acclimated to 19°C showed no ration–related differences in upper critical thermal maxima. Despite a significant difference in mean weight between the reduced and full–ration salmon (3.2 g and 14.7 g, respectively; $P < 0.001$), we did not observe any size–related differences in critical thermal maxima. Juvenile Nimbus strain chinook salmon have a CTM that is approximately 1°C lower than that of juvenile Nimbus strain steelhead, but which is generally similar to those reported for other salmonids acclimated to 19°C. Because American R. temperatures are primarily managed for juvenile chinook salmon production, during the period the salmon are present (until early summer), conditions should be favorable for both juvenile salmon and steelhead (McEwan and Jackson 1996; McEwan and Nelson 1991). Following the out–migration of the majority of the salmon to the Sacramento River and Sacramento–San Joaquin Delta, the reduction in flows and subsequent increase in instream temperatures is deleterious for the remaining steelhead.

The critical thermal maxima protocol uses a very rapid rate of temperature increase. However, as Coutant (1973) demonstrated, even very short exposures to high temperatures affects the predator–avoidance response in chinook salmon. Coutant found that thermally shocked juvenile chinook salmon were selectively preyed upon by larger trout in the laboratory when exposure times to elevated temperatures exceeded a minimum duration. This duration was 10% (chinook) of the exposure duration that caused obvious loss of equilibrium (complete body inversion) of half a test population at that temperature (26 – 30°C). Longer exposures increased vulnerability to predation relative to controls almost exponentially. The thermal shock issue is of particular concern on the American River because of the temperature difference between the American River and the Sacramento River, into which it flows (up to 7°C difference). As juvenile salmonids move from the American to the Sacramento R., they may experience a period of enhanced vulnerability to predation because of the thermal shock. Better management of river temperatures (particularly Sacramento R. temperatures, e.g., through cold–water releases from the Feather R. impoundments) would help mitigate this problem.

Swimming Performance Juvenile chinook salmon aerobic swimming performance is affected by feeding history. Our study demonstrated that the larger (by 48%) full–ration 19°C salmon were 20% faster than the reduced–ration 19°C salmon. It is possible that the difference in critical swimming velocity is completely due to the greater size of the full–ration fish as larger salmonids are faster than small ones (Brett 1965; Brett and Glass 1973; Fry and Cox 1970; Taylor and Foote 1991). However, another possibility is that because the

larger full–ration salmon had greater endogenous energy stores, they were able to maintain a high level of aerobic activity for a longer interval than the reduced–ration salmon. In light of the resting routine oxygen consumption results reported above, this is an important finding. While there was no difference between the two ration levels' MO_2, the difference between their critical swimming velocities clearly indicates that the full–ration fish have a significant metabolic advantage over the reduced ration fish. Their greater aerobic swimming ability would allow them to exploit feeding lanes in areas with higher current for longer periods than the reduced–ration salmon, thereby increasing their feeding opportunities and their growth rates. Because larger juvenile salmon have a better chance of making the transition from freshwater–adapted parr to seawater–adapted smolt (Wallace and Collins 1997) and negotiating the Sacramento–San Joaquin Delta (Kope and Botsford 1990; Reisenbichler and others 1982), it is important that the system is managed to allow for maximum freshwater growth rates.

SUMMARY

Our study on the effects of temperature and ration level on Nimbus steelhead physiology demonstrated that this strain differs from other anadromous and resident rainbow trout strains in some respects. The presence of these strain–related differences recommend the use of strain–specific data, where they are available, in making management decisions or testing bioenergetic models. Although the steelhead population in the American River is primarily of hatchery origin, the population is still ecologically, economically, and aesthetically important (MacArthur and Wilson 1963; McEwan and Jackson 1996; McEwan and Nelson 1991). Nimbus steelhead, derived from Eel River (coastal steelhead) may be poorly adapted to the altered conditions in the American River.

Unlike the steelhead, the Nimbus strain chinook salmon appear well–adapted to conditions in the American River. They displayed temperature and ration–dependent growth rates, and ration–dependent critical swimming velocities. Our study demonstrated that temperatures up to 19°C are not a problem for these fish, provided that food and oxygen availability are not restricted and disease problems do not arise. The American River is managed for juvenile chinook salmon, and under current management practices should continue to produce acceptable returns of adult salmon to support the important adult salmon fishery (MacArthur and Wilson 1963; McEwan and Jackson 1996; McEwan and Nelson 1991).

If we truly want to make an effort at restoring the American River or any of the other Central Valley rivers, then temperature and flow conditions need to be jointly managed to avoid the

risk of creating thermal shock zones and/or conditions that are favorable for only one of the two anadromous salmonid species. Only by further studies of the different strains of anadromous salmonids present in the Sacramento–San Joaquin system will we collect the data needed to make sound management decisions. Because salmonids have highly variable life–history characteristics (Beacham and Evelyn 1992; Beacham and Withler 1991; Bradford and Taylor 1997; Healey 1994), it is important that future research efforts address this issue at the individual, run, and drainage level.

SOURCES CONSULTED

Alsop, D. H. and C. M. Wood. 1997. The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *Journal of Experimental Biology* 200:2337 - 2346.

Armstrong, J. D., I. G. Priede, and M. C. Lucas. 1992. The link between respiratory capacity and changing metabolic demands during growth of northern pike, *Esox lucius* L. *Journal of Fish Biology* 41(Supplement B):65 - 75.

Bainbridge, R. 1962. Training, speed and stamina in trout. *Journal of Experimental Biology* 39:537 - 555.

Baker, S. C. and R. C. Heidinger. 1996. Upper lethal temperature tolerance of fingerling black crappie. *Journal of Fish Biology* 48:1123 - 1129.

Beacham, T. D. 1990. A genetic analysis of meristic and morphometric variation in chum salmon (*Oncorhynchus keta*) at three different temperatures. *Canadian Journal of Zoology* 68(2):225-229.

Beacham, T. D. and T. P. T. Evelyn. 1992. Genetic variation in disease resistance and growth of chinook, coho and chum salmon with respect to vibriosis, furunculosis, and bacterial kidney disease. *Transactions of the American Fisheries Society* 121(4):456-485.

Beacham, T. D. and R. E. Withler. 1991. Genetic variation in mortality of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), challenged with high water temperatures. *Aquaculture and Fisheries Management* 22:125-133.

Becker, C. D. and R. G. Genoway. 1979. Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. *Environmental Biology of Fishes* 4(3):245 - 256.

Bell, W. H. and L. D. B. Terhune. 1970. *Water tunnel design for fisheries research.* Fisheries Research Board of Canada Technical Report. Water Resources Center, Project 195. Water Resources Center. University of California, Davis.

Beyer, J. M., G. Lucchetti, and G. Gerry. 1988. Digestive tract evacuation in northern squawfish (*Ptychocheilus oregonensis*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:548-553.

Bidgood, B. F. 1980. *Temperature tolerance of hatchery reared rainbow trout Salmo gairdneri, Richardson.* Fisheries Report. Water Resources Center, Project 14. Water Resources Center. University of California, Davis.

Bidgood, B. F. and A. H. Berst. 1969. Lethal temperatures for Great Lakes rainbow trout. *Journal of the Fisheries Research Board of Canada* 26(2):456 - 459.

Boyce, S. J. and A. Clarke. 1997. Effect of body size and ration on specific dynamic action in the Antarctic plunderfish, *Harpagifer antarcticus* Nybelin 1947. *Physiological Zoology* 70(6):679 - 690.

Bradford, M. J. and G. C. Taylor. 1997. Individual variation in dispersal behaviour of newly emerged chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1585 - 1592.

Brauner, C. J., G. K. Iwama, and D. J. Randall. 1994. The effect of short-duration seawater exposure on the swimming performance of wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. *Canadian Journal of Fisheries and Aquatic Sciences* 51:2188 - 2194.

Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* 21(5):1184-1226.

Brett, J. R. 1965. The relation of size to the rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* 22:1491 - 1501.

Brett, J. R. and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *Journal of the Fisheries Research Board of Canada* 30:379-387.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363-2394.

Briggs, C. T. and J. R. Post. 1997. *In situ* activity metabolism of rainbow trout (*Oncorhynchus mykiss*): estimates obtained from telemetry of axial muscle electromyograms. *Canadian Journal of Fisheries and Aquatic Sciences* 54:859 - 866.

Brown, L. R. and P. B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. *North American Journal of Fisheries Management* 1(2):104-111.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. Growth. pp. 363-388. In: C. B. Schreck and P. B. Moyle (ed.). *Methods for Fish Biology.* American Fisheries Society. Bethesda, Maryland

Cai, Y. and R. C. Summerfelt. 1992. Effects of temperature and size on oxygen consumption and ammonia excretion by walleye. *Aquaculture* 104:127-138.

Campagna, C. G. and J. J. Cech, Jr. 1981. Gill ventilation and respiratory efficiency of Sacramento blackfish, *Orthodon microlepidotus* in hypoxic environments. *Journal of Fish Biology* 19:581 - 591.

Castleberry, D. T. and J. J. Cech, Jr. 1993. Critical thermal maxima and oxygen minima of five fishes from the upper Klamath basin. *California Fish and Game* 78(4):145 - 152.

Castleberry, D. T. et al. 1991. *Growth, condition, and physiological performance of juvenile salmonids from the lower American River: February through June, 1991.* Report to the East Bay Municipal Utilities District. Water Resources Center, Project Water Resources Center. University of California, Davis.

Cech, J. J., Jr. et al. 1990. Distribution of California stream fishes: influence of environmental temperature and hypoxia. *Environmental Biology of Fishes* 29:95 - 105.

Chatters, J. C. et al. 1991. Potential impacts of global climate change on Pacific Northwest spring chinook salmon (*Oncorhynchus tshawytscha*): an exploratory case study. *The Northwest Environmental Journal* 7(1):71-92.

Cheng, K. M. et al. 1987. A comparison of survival and growth of two strains of chinook salmon (*Oncorhynchus tshawytscha*) and their crosses reared in confinement. *Aquaculture* 67:301-311.

Cherry, D. S., K. Dickson, L., and J. Carins Jr. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. *Journal of the Fisheries Research Board of Canada* 32:485 - 491.

Cherry, D. S., K. L. Dickson, and J. Cairns Jr. 1977. Preferred, avoided and lethal temperatures of fish during rising temperature conditions. *Journal of the Fisheries Research Board of Canada* 34:239 - 246.

Clarke, W. C., R. E. Withler, and J. E. Shelbourn. 1992. Genetic control of juvenile life history pattern in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Science* 49(11):2300-2306.

Clay, C. H. 1995. *Design of fishways and other fish facilities.* Lewis Publishers. Boca Raton.

Coutant, C. C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. *Journal of the Fisheries Research Board of Canada* 30:965 - 973.

Cutts, C. J., N. B. Metcalfe, and A. C. Taylor. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology* 52:1026 – 1037.

Du Preez, H. H. 1987. Laboratory studies on the oxygen consumption of the marine teleost, *Lichia amia* (Linnaeus, 1758). *Comparative Biochemistry and Physiology* 88A(3):523 - 532.

Duthie, G. G. 1987. Observations of poor swimming performance among hatchery-reared rainbow trout, *Salmo gairdneri*. *Environmental Biology of Fishes* 18(4):309 - 311.

Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *Journal of Animal Ecology* 45:923 - 948.

Elliott, J. M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* 25(1):61 - 70.

Fletcher, I. A. 1985. Risk analysis for fish diversion experiments: pumped intake systems. *Transactions of the American Fisheries Society* 114:652 - 694.

From, J. and G. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. *Dana* 3:61 - 139.

Fry, F. E. J. and E. T. Cox. 1970. A relation of size to swimming speed in rainbow trout. *Journal of the Fisheries Research Board of Canada* 27(5):976 - 978.

Furnell, D. J. 1987. Partitioning of locomotor and feeding metabolism in sablefish (*Anopoploma fimbria*). *Canadian Journal of Zoology* 65:486 - 489.

Gall, G. A. E. et al. 1992. Geographic variation in population genetic structure of chinook salmon from California and Oregon. *Fishery Bulletin* 90:77-100.

Graham, J. B. Heat transfer. pp. 248 - 279. In: P. W. Webb and D. Weihs (ed.). *Fish Biomechanics*. Praeger Publishers. New York, USA

Grande, M. and S. Andersen. 1991. Critical thermal maxima for young salmonids. *Journal of Freshwater Ecology* 6(3):275 - 279.

Hammer, C. 1995. Fatigue and exercise tests with fish. *Comparative Biochemistry and Physiology* 112A(1):1 – 20.

Hammond, B. R. and C. P. Hickman. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate, and glucose in rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 23(1):65 - 83.

Harvey, B. C. and R. J. Nakamoto. 1997. Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. *Canadian Journal of Fisheries and Aquatic Sciences* 54:27 - 31.

Hawkins, D. K. and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Science* 53:1487 - 1496.

Healey, M. C. 1994. Variation in the life history characteristics of chinook salmon and its relevance to conservation of the Sacramento winter run chinook salmon. *Conservation Biology* 8(3):876 - 877.

Heming, T. A. and J. E. McInerney. 1982. Effect of temperature on initial feeding in alevins of chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Science* 39(12):1554-1562.

Herbold, B., A. D. Jassby, and P. B. Moyle. 1992. *San Francisco estuary project: status and trends report on aquatic resources in the San Francisco estuary.* San Francisco Estuary Project. San Francisco.

Hewett, S. W. and B. L. Johnson. 1992. *Fish Bioenergetics Model 2: An Upgrade of a Generalized Bioenergetics Model of Fish Growth for Microcomputers.* University of Wisconsin Sea Grant Institute. Madison, Wisconsin.

Hughes, N. F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology* 79(1):281 - 294.

Jobling, M. Temperature and growth: modulation of growth rate via temperature change. pp. 225 - 254. In: C. M. Wood and D. G. McDonald (ed.). *Global Warming: Implications for Freshwater and Marine fish.* Cambridge University Press. Cambridge, UK

Jobling, M. and P. Spencer-Davies. 1980. Effects of feeding on metabolic rate, and the specific dynamic action in plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 16:629 - 638.

Johnsson, J. I. and A. Åkerman. 1998. Intersexual differences in aggression in juvenile rainbow trout. *Journal of Fish Biology* 52:1292 - 1294.

Johnsson, J. I. et al. 1997. Does presmolt growth rate in steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) predict growth rate in seawater? *Canadian Journal of Fisheries and Aquatic Sciences* 54:430 - 433.

Johnston, I. A., J. D. Fleming, and T. Crockford. 1990. Thermal acclimation and muscle contractile properties in cyprinid fish. *American Journal of Physiology* 259:R231 - R236.

Konecki, J. T., C. A. Woody, and T. P. Quinn. 1995. Temperature preference in two populations of juvenile coho salmon, *Oncorhynchus kisutch. Environmental Biology of Fishes* 44:417 - 421.

Kope, R. G. and L. W. Botsford. 1990. Determination of factors affecting recruitment of chinook salmon *Oncorhynchus tshawytscha* in Central California. *Fishery Bulletin* 88(2):257-269.

Kowalski, K. T. et al. 1978. Interspecific and seasonal differences in the temperature tolerances of stream fish. *Journal of Thermal Biology* 3:105-108.

Kreiberg, H. Year. Salmonid growth under different environmental conditions: toward a general growth model for chinook salmon. pp. 133-136. In: R. L. Saunders (ed.). *Canada-Norway Finfish Aquaculture Workshop*.

Kreiberg, H., R. E. Withler, and W. C. Clarke. 1988. Early seawater growth of chinook salmon strains at rearing sites in British Columbia. *Aquaculture Association of Canada Bulletin* 88(4):16-18.

Lee, R. M. and J. N. Rinne. 1980. Critical thermal maxima of five trout species in the southwestern United States. *Transactions of the American Fisheries Society* 109:632 - 635.

Lyytikäinen, T., J. Koskela, and I. Rissanen. 1997. Thermal resistance and upper lethal temperatures of underyearling Lake Inari Arctic charr. *Journal of Fish Biology* 51:515 - 525.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17(4):373-387.

Mathews, S. B. and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:1216 - 1226.

Maxime, V. et al. 1989. Comparative study of the energetic metabolism of Atlantic salmon (*Salmo salar*) parr and smolts. *Aquaculture* 82:163 - 171.

McEwan, D. and T. A. Jackson. 1996. *Steelhead Restoration and Management Plan for California.* California Department of Fish and Game. Sacramento, California.

McEwan, D. and J. Nelson. 1991. *Steelhead restoration plan for the American River.* California Department of Fish and Game. Sacramento.

McMichael, G. A. and T. N. Pearsons. 1998. Effects of wild juvenile chinook salmon on growth and abundance of wild rainbow trout. *Transactions of the American Fisheries Society* 127:261 - 274.

Miller, W. J. 1993. *The delta.* Water Resources Center, Project Water Resources Center. University of California, Davis.

Moyle, P. B. 1976. *Inland Fishes of California.* University of California Press. Berkeley, California.

Moyle, P. B. and J. E. Williams. 1990. Biodiversity loss in the temperate zone - decline of the native fish fauna of California. *Conservation Biology* 4(3):275 - 284.

Moyle, P. B. et al. 1995. *Fish species of special concern in California.* Final Report. Water Resources Center, Project 2128IF. Water Resources Center. University of California, Davis.

Mulchaey, B. W. 1994. *An evaluation of the swimming performance of two strains of hatchery-reared rainbow trout (Oncorhynchus mykiss).* Masters Thesis, Humboldt State University.

Myrick, C. A. and J. J. Cech, Jr. in press. Physiological performance of two California rainbow trout strains: life near the limit. *Fish Physiology and Biochemistry*

Neilson, J. D. and G. H. Geen. 1985. Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile chinook salmon, *Oncorhynchus tshawytscha. Fishery Bulletin* 83(1):91-101.

Peake, S., C. Barth, and R. S. McKinley. 1997a. Effect of recovery parameters on critical swimming speed of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Zoology* 75:1724 - 1727.

Peake, S. et al. 1997b. Influence of transmitter attachment procedures on swimming performance of wild and hatchery-reared Atlantic salmon smolts. *Transactions of the American Fisheries Society* 126:707 - 714.

Plaut, I. and M. S. Gordon. 1994. Swimming metabolism of wild-type and cloned zebrafish *Brachydanio rerio. Journal of Experimental Biology* 194:209 - 223.

Randall, D. J. 1982. The control of respiration and circulation in fish during exercise and hypoxia. *Journal of Experimental Biology* 100:275 – 288.

Reisenbichler, R. R., J. D. McIntire, and R. J. Hallock. 1982. Relation between size of chinook salmon released at hatcheries and returns to hatcheries and ocean fisheries. *California Fish and Game* 68(1):57–59.

Reynolds, W. W. and M. E. Casterlin. 1978. Thermoregulatory behavior of brown trout, *Salmo trutta*. *Hydrobiologia* 62(1):79-80.

Rich, A. A. 1987. *Report on studies conducted by Sacramento County to determine the temperatures which optimize growth and survival in juvenile chinook salmon (Oncorhynchus tshawytscha).* Water Resources Center, Project Water Resources Center. University of California, Davis.

Rome, L. C. Influence of temperature on muscle properties in relation to swimming performance. pp. 73 - 99. In: P. W. Hochachka and T. P. Mommsen (ed.). *Biochemistry and Molecular Biology of Fishes.* Elsevier Science B.V. Amsterdam

Rome, L. C., R. P. Funke, and R. M. Alexander. 1990. The influence of temperature on muscle velocity and sustained performance in swimming carp. *Journal of Experimental Biology* 154:163 - 178.

Schmidt-Nielsen, K. 1990. *Animal Physiology: Adaptation and Environment.* University of Cambridge Press. Cambridge.

SWRBC. 1993. *Draft Water Right Decision 1630.* State Water Resources Control Board. Sacramento.

Taylor, E. B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream channel. *Transactions of the American Fisheries Society* 117(1):22 - 28.

Taylor, E. B. 1990a. Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 37(1):1-17.

Taylor, E. B. 1990b. Variability in agonistic behavior and salinity tolerance between and within two populations of juvenile chinook salmon, *Oncorhynchus tshawytscha*, with contrasting life histories. *Canadian Journal of Fisheries and Aquatic Sciences* 47(11):2172-2180.

Taylor, E. B. and C. J. Foote. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* 38:407 - 419.

Taylor, E. B. and J. D. McPhail. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* 42:2029 - 2033.

Taylor, E. W. et al. Factors which may limit swimming performance at different temperatures. pp. 105 - 134. In: C. M. Wood and D. G. McDonald (ed.). *Global Warming: Implications for Freshwater and Marine Fish.* Cambridge University Press. Cambridge, UK

Unwin, M. J. 1997. Fry-to-adult survival of natural and hatchery-produced chinook salmon (*Oncorhynchus tshawytscha*) from a common origin. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1246 - 1254.

Wagner, E. J., S. S. Intelmann, and M. D. Routledge. 1996. The effects of fry rearing density on hatchery performance, fin condition, and agonistic behavior of rainbow trout *Oncorhynchus mykiss* fry. *Journal of the World Aquaculture Society* 27(3):264 - 274.

Wallace, M. and B. W. Collins. 1997. Variation in use of the Klamath River estuary by juvenile chinook salmon. *California Fish and Game* 83(4):132 – 143.

Warren, C. E. and G. E. Davis. Laboratory studies on the feeding, bioenergetics, and growth of fish. pp. 175 - 214. In: S. D. Gerkin (ed.). *The Biological Basis of Freshwater Fish Production.* Blackwell Scientific Publications. Oxford, England

Webb, P. W. 1993. The effect of solid and porous channel walls on steady swimming of steelhead trout *Oncorhynchus mykiss*. *Journal of Experimental Biology* 178:97 - 108.

Webb, P. W., P. T. Kostecki, and E. D. Stevens. 1984. The effect of size and swimming speed on locomotor kinematics of rainbow trout. *Journal of Experimental Biology* 109:77 - 95.

Wurtsbaugh, W. A. and G. E. Davis. 1977a. Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* 11:99 - 104.

Wurtsbaugh, W. A. and G. E. Davis. 1977b. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. *Journal of Fish Biology* 11:87 - 98.

Young, P. S. and J. J. Cech, Jr. 1996. Environmental tolerances and requirements of splittail. *Transactions of the American Fisheries Society* 125(5):664 - 678.

Zedonis, P. A. and T. J. Newcomb. 1997. *An evaluation of flow and water temperature during the spring for protection of salmon and steelhead smolts in the Trinity River, California.* U.S. Fish and Wildlife Service, Coastal California Fish and Wildlife Office. Arcata, CA.

TABLES

Table 1.

Effects of temperature and ration level on mean (± SE) food consumption rates, growth rates, and survival rates of juvenile Nimbus strain steelhead. Values that are significantly different from others at the same ration level are marked with 1; values that are significantly different from others at the same temperature are marked with 2, and; 3 denotes final weights that are significantly heavier than initial weights.

Treatment		Number of	Food consumption rate	Mean fish wet weights (g)		Growth rate	Specific growth rate	Gross conversion efficiency	Survival
Temp. (°C)	Ration level (% satiation)	replicates	(% body wt d^{-1})	Initial	Final	(% body wt d^{-1})	(% body wt d^{-1})	(%)	(%)
11	82	4	4.55 ± 0.36	3.06 ± 0.09	5.08 ± 0.16[3]	1.04 ± 0.14	1.48 ± 0.19	33 ± 11	85 ± 1.9
11	100	4	5.44 ± 0.60	3.08 ± 0.17	5.28 ± 0.31[3]	0.95 ± 0.13	1.34 ± 0.18	26 ± 8	88 ± 0.0
15	92	4	5.51 ± 0.25	2.15 ± 0.14[1]	4.70 ± 0.28[3]	0.85 ± 0.09	1.21 ± 0.12	22 ± 4	66 ± 4.2
15	100	4	5.25 ± 0.58	2.34 ± 0.11	4.72 ± 0.47[3]	0.82 ± 0.24	1.17 ± 0.34	21 ± 9	72 ± 2.8
19	88	4	7.40 ± 0.52[1]	2.59 ± 0.16	6.68 ± 0.16[1,3]	1.22 ± 0.29	1.70 ± 0.40	23 ± 11	66 ± 8.1
19	100	4	6.71 ± 0.08	2.96 ± 0.18	7.52 ± 0.28[1,3]	1.90 ± 0.10[1,2]	2.62 ± 0.14[1,2]	37 ± 3	86 ± 1.2

Table 2.

Summary of mean steelhead morphometrics and $\log_{10}$ length–weight relationships. Significant increases in length and weight over the 30–d experiment were observed in all treatments. There were no significant differences among the slopes of the log length–weight regression equations.

Treatment	Number of fish	Wet weight (g)	Total length (mm)	Intercept		Slope		r^2
				a	SE	*b*	SE	
Day 1								
11°C full ration	100	3.08	70.8	-4.83	0.203	2.86	0.11	0.87
11°C reduced ration	100	3.05	70.7	-5.12	0.194	3.02	0.11	0.89
15°C full ration	100	2.37	69.1	-5.49	0.140	3.17	0.08	0.95
15°C reduced ration	100	2.15	67.1	-5.20	0.218	3.01	0.12	0.87
19°C full ration	100	2.96	71.8	-5.67	0.121	3.30	0.07	0.96
19°C reduced ration	100	2.59	68.8	-5.72	0.113	3.33	0.06	0.97
Day 30								
11°C full ration	91	5.3	81.5	-6.38	0.212	3.69	0.11	0.93
11°C reduced ration	90	5.08	80.3	-6.23	0.165	3.61	0.09	0.95
15°C full ration	71	4.71	79.9	-6.53	0.219	3.75	0.12	0.94
15°C reduced ration	66	4.65	79.6	-6.85	0.265	3.92	0.14	0.92
19°C full ration	86	7.52	87.6	-6.15	0.175	3.58	0.09	0.95
19°C reduced ration	66	6.63	84.8	-6.07	0.250	3.55	0.13	0.92

Table 3.

Effects of temperature and ration level on mean (± SE) food consumption rates, growth rates, and gross conversion efficiency of juvenile Nimbus strain chinook salmon. Superscripted numbers denote statistically significant differences between ration levels at the same temperature. Superscripted letters denote statistically significant differences between temperatures at the same ration level. Asterisks denote significant differences between initial and final values.

Treatment Temperature (°C), ration level (%)	Number of replicates	Food consumption rate (% body wt./d)	Growth rate (% body wt./d)	Gross conversion efficiency (%)
11, 100	4	11.20 ± 0.26^{a1}	2.68 ± 0.16^{a1}	23.7 ± 4.4^{a1}
11, 25	4	3.72 ± 0.04^{b2}	-0.27 ± 0.08^{b2}	-7 ± 2.0^{b2}
15, 100	4	13.5 ± 0.26^{c3}	3.60 ± 0.06^{c3}	27 ± 0.4^{a3}
15, 25	4	5.49 ± 0.05^{d4}	-0.75 ± 0.14^{b4}	-13.5 ± 2.5^{b4}
19, 100	4	15.02 ± 0.53^{e5}	4.38 ± 0.06^{d5}	29.5 ± 1.2^{a5}
19, 25	4	5.64 ± 0.13^{d6}	-0.54 ± 0.18^{b6}	-9.7 ± 3.2^{b6}

Table 4.

Mean Nimbus strain steelhead critical thermal maxima. Superscript numbers indicate significant differences between temperatures and superscript letters indicate significant differences between ration levels.

Treatment	Number of replicates	Standard length (mm)	Weight (g)	Critical thermal maxima (°C)
11°C, reduced ration	10	76.5 ± 3.76	7.5 ± 1.15	27.8 ± 0.11^{1a}
11°C, full ration	8	78.3 ± 4.72	8.0 ± 1.60	27.5 ± 0.17^{1a}
15°C, reduced ration	10	76.0 ± 4.96	6.7 ± 1.39	29.4 ± 0.28^{2b}
15°C, full ration	9	82.6 ± 4.82	9.4 ± 1.81	28.4 ± 0.33^{3b}
19°C, reduced ration	10	72.7 ± 4.24	6.9 ± 1.53	29.9 ± 0.25^{4c}
19°C, full ration	10	89.1 ± 5.62	14.3 ± 2.91	29.6 ± 0.33^{4c}

Table 5.

Mean Nimbus strain steelhead critical swimming velocities. Superscript numbers indicate significant differences between temperatures and superscript letters indicate significant differences between ration levels.

Treatment	Number of replicates	Morphometrics			Critical swimming velocity	
		SL (mm)	TL (mm)	weight (g)	(m s^{-1})	(BL s^{-1})
11°C, reduced ration	10	100 ± 7.77	119 ± 8.55	17.9 ± 5.15	0.51 ± 0.04 ^{1a}	3.88 ± 0.30
11°C, full ration	10	118 ± 8.46	136 ± 9.48	29.3 ± 5.13	0.51 ± 0.02 ^{1b}	4.34 ± 0.22
15°C, reduced ration	7	84 ± 5.52	101 ± 6.29	9.6 ± 1.60	0.50 ± 0.05 ^{2a}	4.77 ± 0.25
15°C, full ration	10	124 ± 6.09	144 ± 6.76	31.7 ± 3.95	0.67 ± 0.02 ^{3c}	4.96 ± 0.38
19°C, reduced ration	10	101 ± 4.83	120 ± 5.75	16.4 ± 2.14	0.57 ± 0.04 ^{4a}	4.11 ± 0.28
19°C, full ration	9	141 ± 4.86	164 ± 5.52	48.7 ± 5.06	0.67 ± 0.04 ^{4c}	4.79 ± 0.31

Table 6.

Effects of ration size on the critical swimming velocity of juvenile Nimbus strain chinook salmon at 19°C. Asterisks indicate significant differences between treatment means.

Treatment	Number of replicates	Mean total length (mm)	Mean weight (g)	Critical swimming velocity (m/s)
19°C, 100% ration	15	111 ± 4.1*	15.7 ± 1.6*	0.61 ± 0.02*
19°C, 25% ration	11	75 ± 3.2*	3.8 ± 0.52*	0.51 ± 0.02*

Table 7.

Comparison of steelhead and rainbow trout food consumption and growth rates. Sources: 1. This study; 2. Myrick and Cech (in press); 3. Wurtsbaugh and Davis (1977).

Strain	Temperature (°C)	Size range (g)	Consumption rate (% body wt d-1)	Growth rate (% body wt d-1)	Source
Nimbus steelhead	11	3.1 – 5.3	5.4	0.95	1
Eagle Lake rainbow trout	10	2.3 – 5.2	8.7	2.56	2
Mt. Shasta rainbow trout	10	4.1 – 9.3	8	2.56	2
Nimbus steelhead	15	2.3 – 4.7	5.3	0.82	1
Eagle Lake rainbow trout	14	2.4 – 7.0	9.4	3.22	2
Mt. Shasta rainbow trout	14	2.7 – 8.3	9.7	3.31	2
Oregon steelhead (strain unspecified)	16.2	1 – 1.2	14.3	2.9	3
Nimbus steelhead	19	3.0 – 7.5	6.7	1.90	1
Eagle Lake rainbow trout	19	2.4 – 7.5	9.9	3.32	2
Mt. Shasta rainbow trout	19	2.3 – 7.6	10.8	3.56	2
Oregon steelhead (strain unspecified)	19.5	1 – 1.2	15.7	3.4	3

Table 8.

Comparison of steelhead and rainbow trout critical swimming velocities.

Species	Temperature	Total length (mm)	Critical swimming velocity (BL s^{-1})	Source
Nimbus steelhead	11	136	4.34	This study
Eagle Lake rainbow trout	10	102	5.20	Myrick and Cech (in press)
Mt. Shasta rainbow trout	10	120	5.27	Myrick and Cech (in press)
Aberdeen steelhead	10	100	7.69	Hawkins and Quinn (1996)
Nimbus steelhead	15	144	4.96	This study
Eagle Lake rainbow trout	14	107	5.72	Myrick and Cech (in press)
Mt. Shasta rainbow trout	14	114	5.47	Myrick and Cech (in press)
Great Lakes rainbow trout	15	90 - 120	3.85	Alsop and Wood (1997)
Nimbus steelhead	19	164	4.79	This study
Eagle Lake rainbow trout	19	113	5.66	Myrick and Cech (in press)
Mt. Shasta rainbow trout	19	109	5.24	Myrick and Cech (in press)

Table 9.

Comparison of chinook salmon growth rates and conversion efficiencies.

Temperature (°C)	Number of replicates	Growth rate (% body wt./d)	Gross conversion efficiency (%)	Source
10.5	2	2.1	21.2	Rich (1987)
11	4	2.68	23.7	This study
15	4	3.6	27	This study
15.2	2	2.8	24.9	Rich (1987)
19	4	4.38	29.5	This study
19	2	2.4	22	Rich (1987)

FIGURES

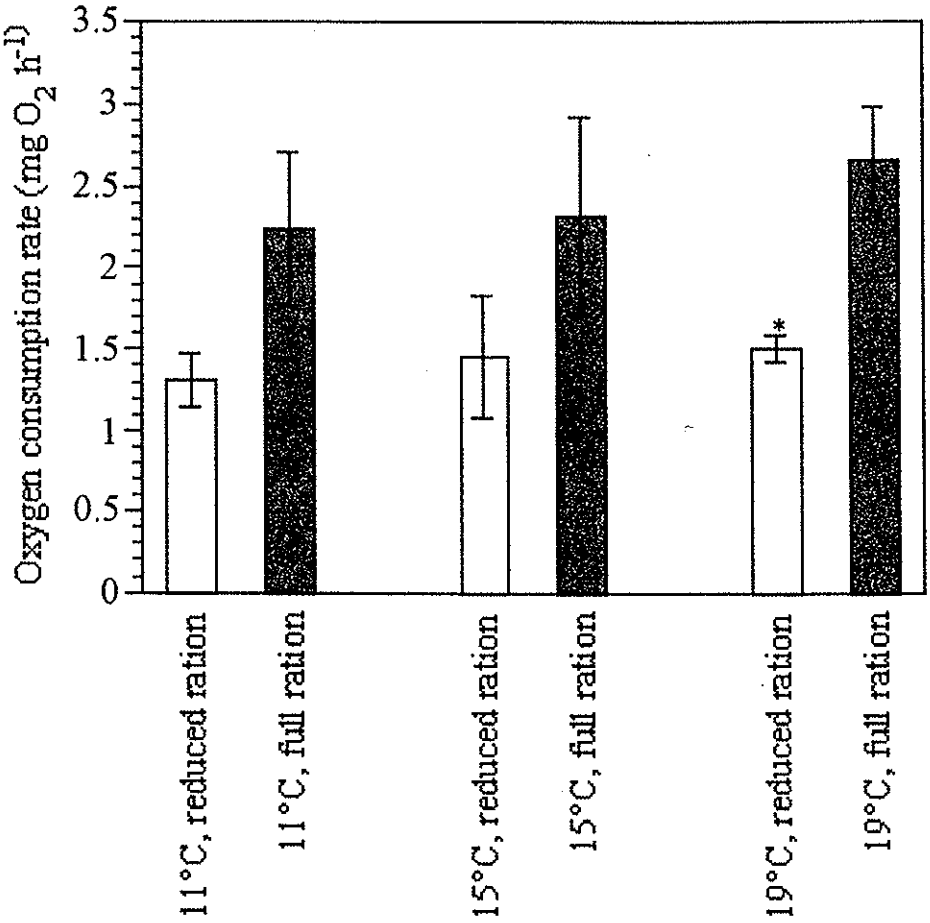


Figure 1. Effects of temperature and ration level on Nimbus strain steelhead resting routine oxygen consumption rates. Error bars are standard errors. The asterisk indicates a significant difference between ration levels at a particular temperature.

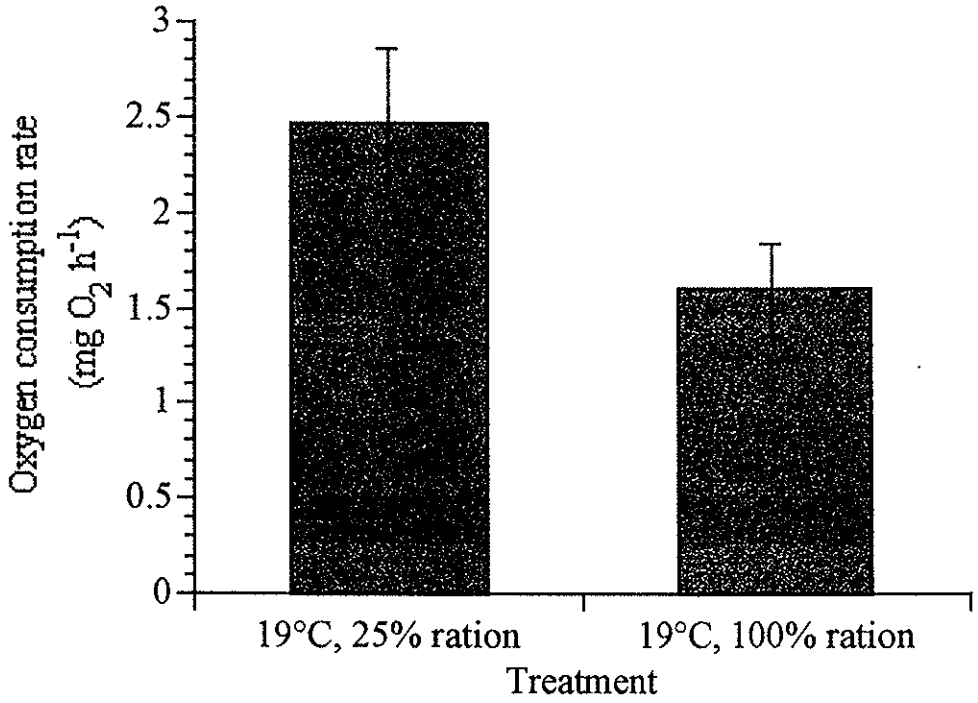


Figure 2. Effects of ration level on 19°C Nimbus strain chinook salmon resting routine oxygen consumption rates. Error bars are standard errors. There were no statistically significant differences between treatment means.

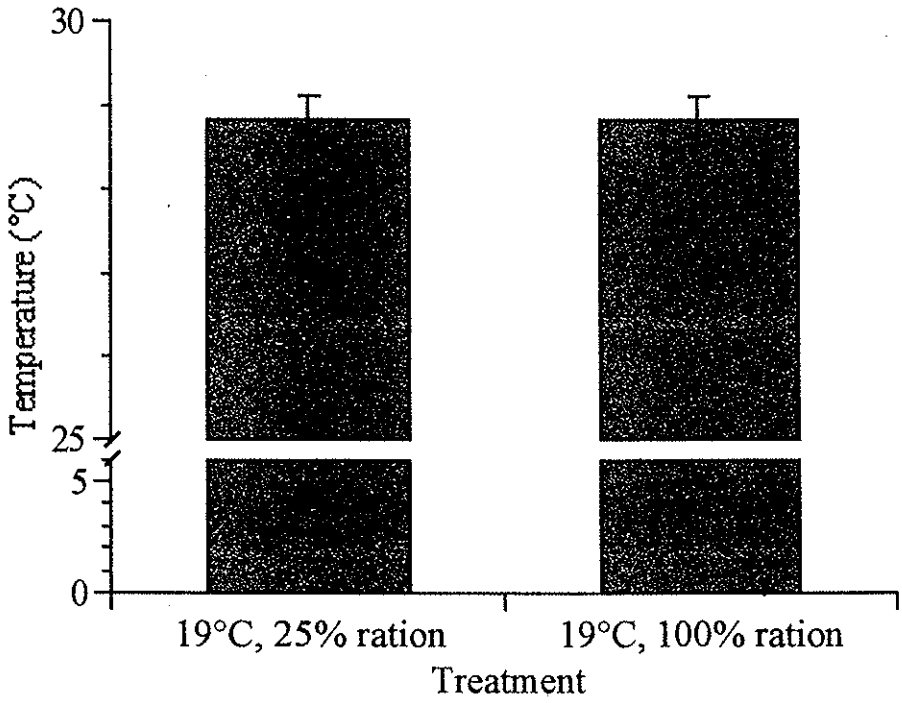


Figure 3. Effects of ration level on the critical thermal maxima of juvenile Nimbus strain chinook salmon acclimated to 19°C. There are no significant differences between treatment means. Error bars are standard errors.

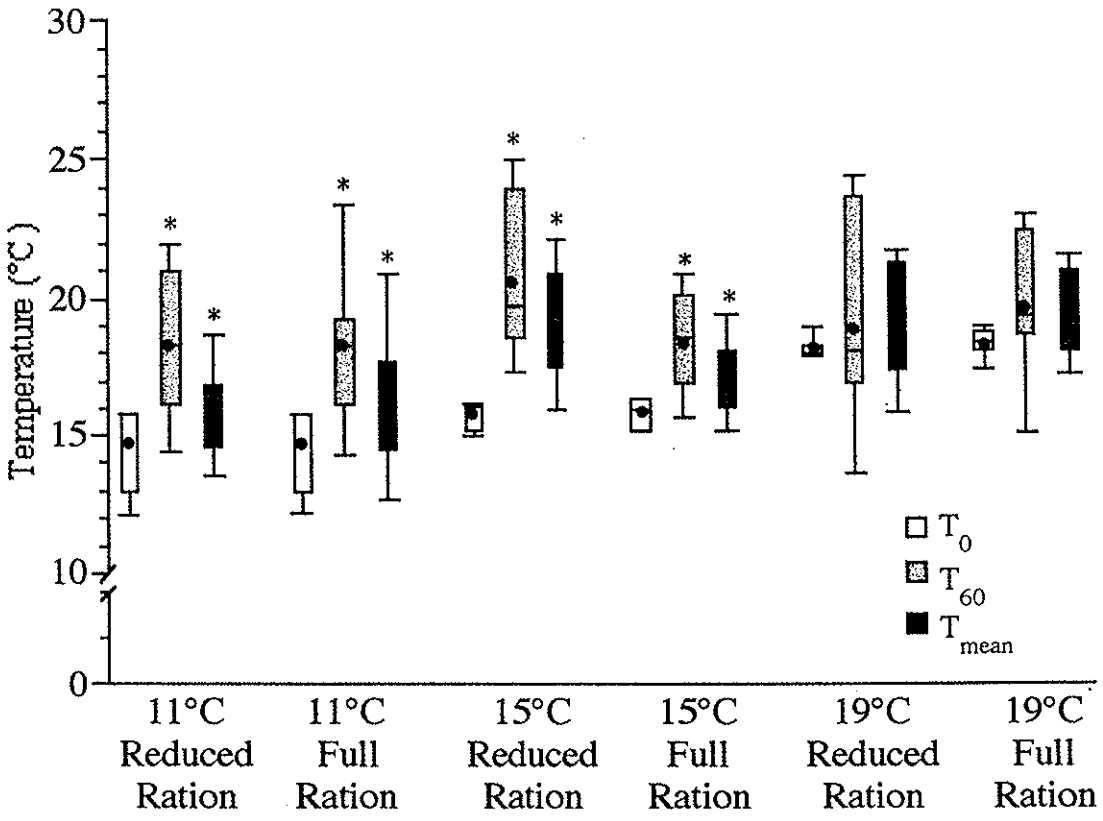


Figure 4. Box plots of initial (T_0), final (T_{60}), and mean (T_{mean}) preferred temperatures for Nimbus steelhead reared under different temperature and ration treatments. Dots represent treatment means; the top, bottom and line through the middle of the box correspond to the 75th, 25th, and 50th percentile, respectively, and; error bars represent the 10th and 90th percentile. Asterisks indicate final and mean preferred temperatures that are significantly higher than their respective initial temperature.

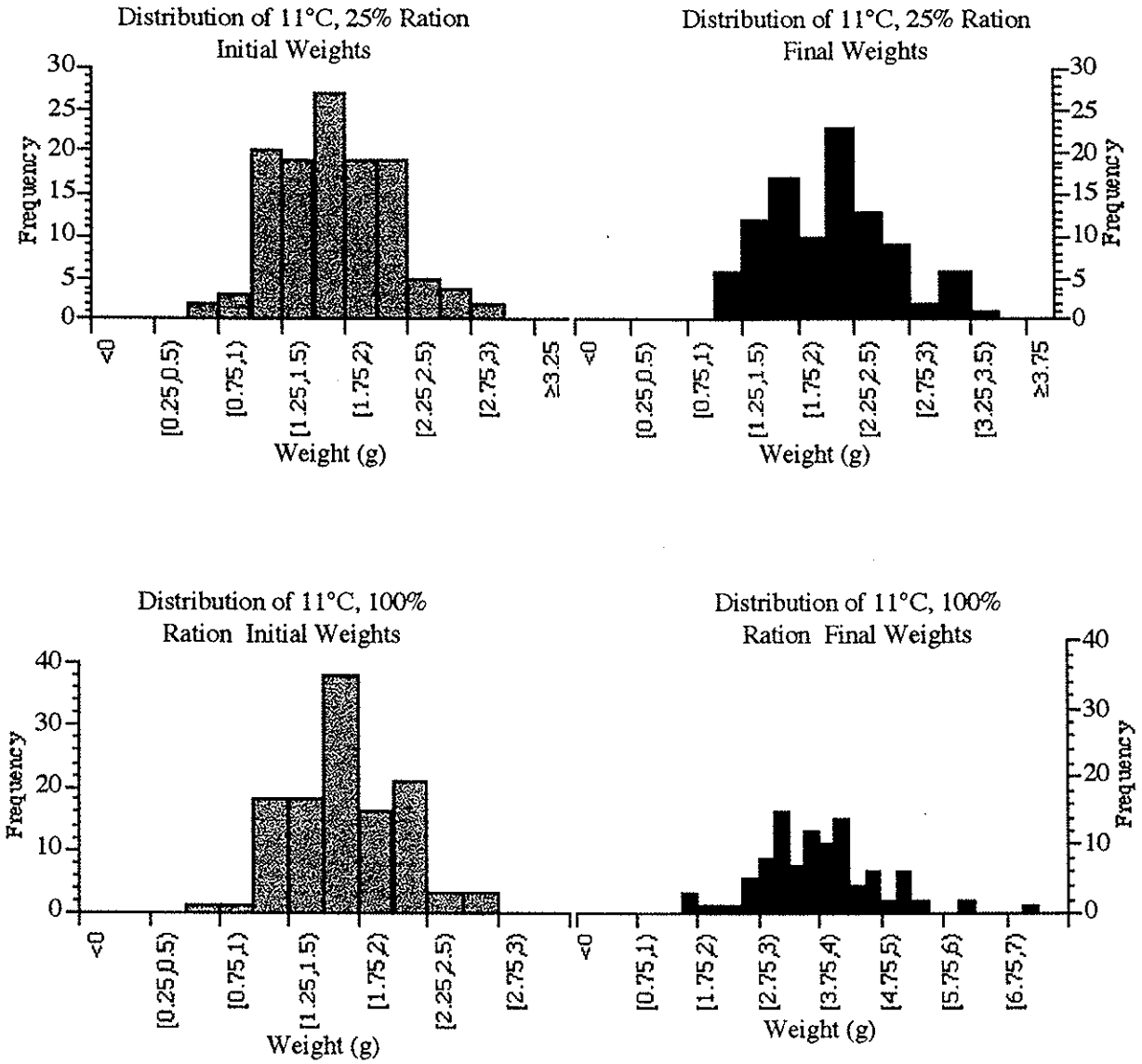


Figure 5. Histograms showing the change in distribution of 11°C chinook salmon initial and final weights.

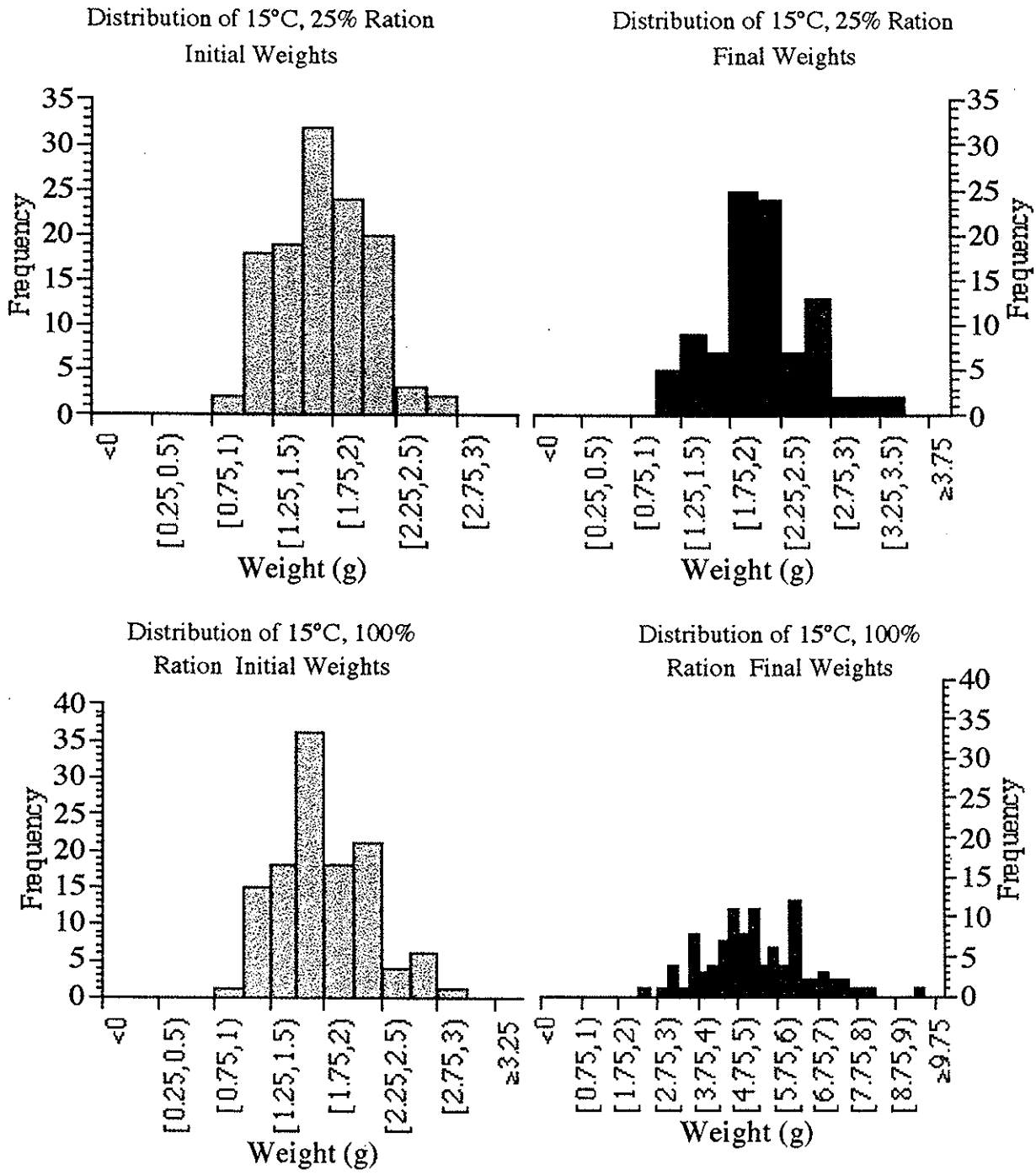
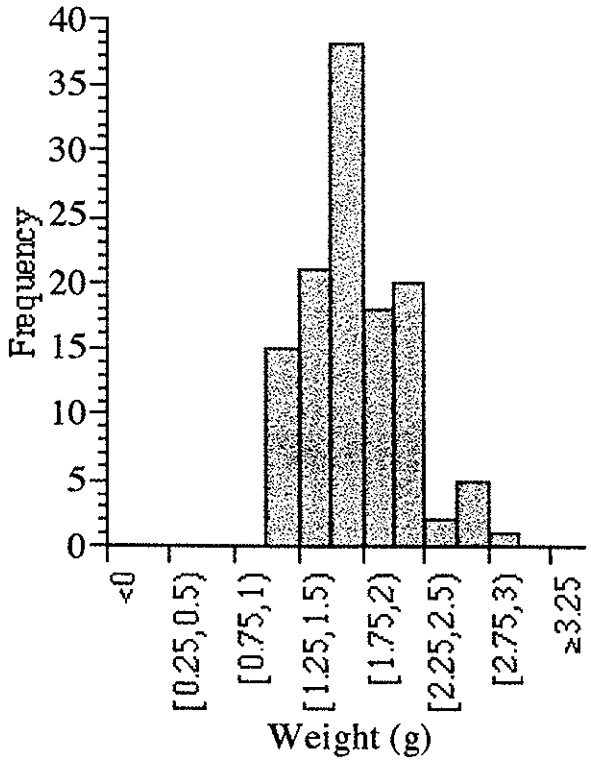
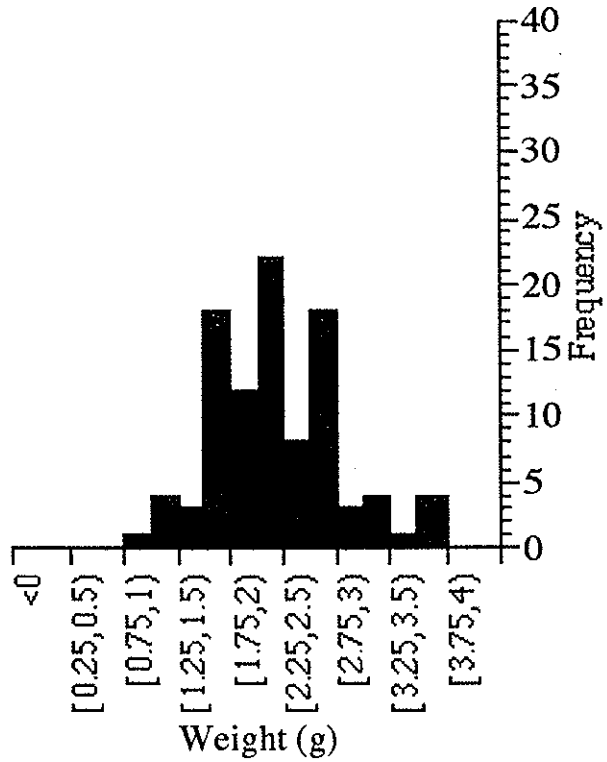


Figure 6. Histograms showing the change in distribution of 15°C chinook salmon initial and final weights.

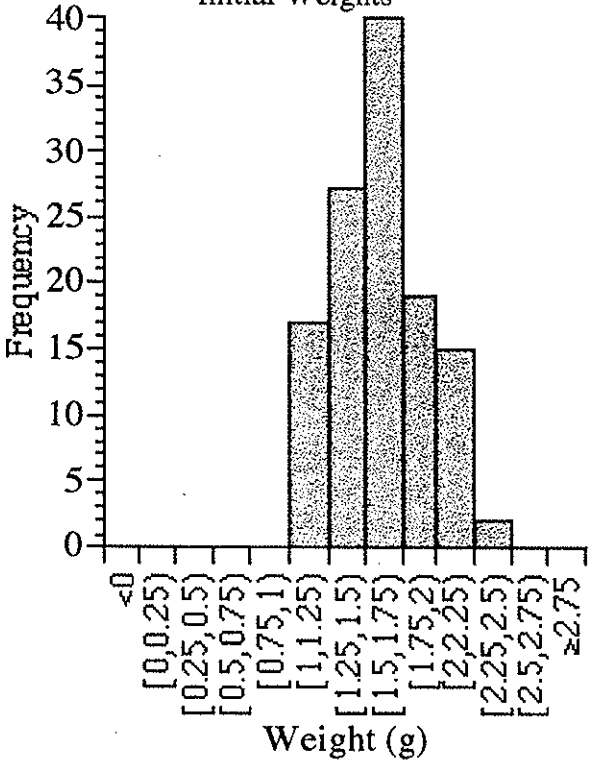
Distribution of 19°C, 25% Ration
Initial Weights



Distribution of 19°C, 25% Ration
Final Weights



Distribution of 11°C, 25% Ration
Initial Weights



Distribution of 11°C, 25% Ration
Final Weights

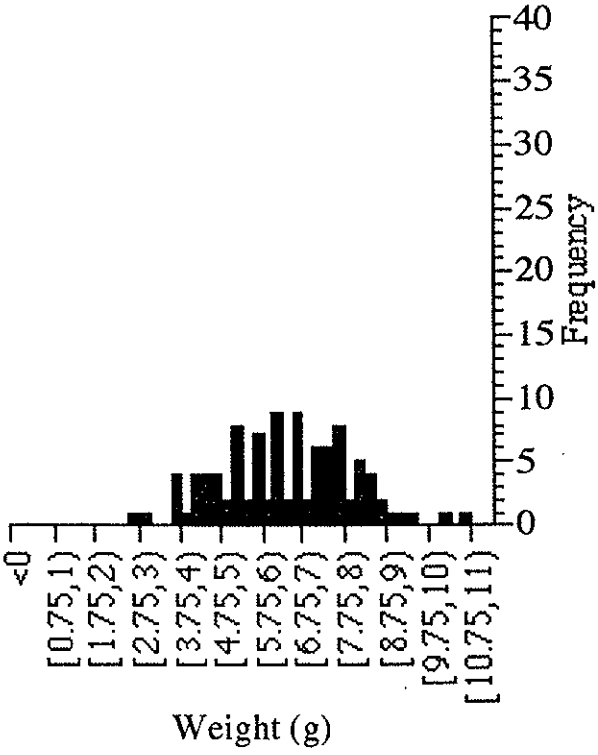


Figure 7. Histograms showing the change in distribution of 19°C chinook salmon initial and final weights.

PH.D. DISSERTATION

Myrick, C. A. 1998. Temperature, genetic, and ration effects on juvenile rainbow trout (*Oncorhynchus mykiss*) bioenergetics. Ph.D. Dissertation, University of California.