

Effects of High Water Temperature on Growth, Smoltification, and Predator Avoidance in Juvenile Sacramento River Chinook Salmon

KEITH R. MARINE*¹ AND JOSEPH J. CECH, JR.

Department of Wildlife, Fish, and Conservation Biology, University of California–Davis,
1 Shields Avenue, Davis, California 95616-8751, USA

Abstract.—Intensive water management and frequent drought cycles can increase water temperatures, thereby decreasing habitat quality for Chinook salmon *Oncorhynchus tshawytscha* inhabiting streams of California’s Central Valley. We studied the incremental effects of chronic exposure (>60 d; effects measured bimonthly) to three temperature regimes typical of the range of conditions experienced by Sacramento River fall-run Chinook salmon during juvenile rearing and smoltification (13–16°C, 17–20°C, and 21–24°C; diel fluctuations of 0.5–3°C were allowed within these limits). Our laboratory experiments demonstrated that Chinook salmon can readily survive and grow at temperatures up to 24°C. However, juveniles reared at 21–24°C experienced significantly decreased growth rates, impaired smoltification indices, and increased predation vulnerability compared with juveniles reared at 13–16°C. Fish reared at 17–20°C experienced similar growth, variable smoltification impairment, and higher predation vulnerability compared with fish reared at 13–16°C. These results improve our understanding of the range of juvenile Chinook salmon responses to elevated temperatures and should assist biologists and resource decision makers in coordinating water management and salmon conservation decisions.

Chinook salmon *Oncorhynchus tshawytscha* inhabiting California’s Central Valley streams have developed some of the most diverse life histories known for this species (Healey 1991; Moyle 2002). Anadromous salmonids in California’s streams regularly encounter some of the most severe streamflow and water temperature conditions found throughout the species’ geographic range (Scott and Crossman 1973; Healey 1991; Moyle 2002). Habitat degradation, water development, and overharvest have impacted all Central Valley salmon runs (California Advisory Committee on Salmon and Steelhead Trout 1988; USFWS 1995). Water management and climatic conditions frequently produce elevated water temperatures during spawning and rearing seasons. Because many Central Valley Chinook salmon runs have severely declined and are now protected under state and federal endangered species acts (Nehlsen et al. 1991; Fisher 1994; Yoshiyama et al. 1998), a better understanding of the physiological and ecological consequences of elevated water temperature on juvenile salmon is needed to specify the appropriate water temperature control and regulation measures for conserving and restoring these runs.

Effects of elevated water temperatures have been studied for several anadromous salmonids. Brett (1952) identified Chinook salmon as the most tolerant of five Pacific salmon species from Canadian streams, with a 24–25°C upper incipient lethal temperature. Brett et al. (1982) further determined that the optimal growth temperature for young Chinook salmon decreased from 19°C with maximal rations to 14.8°C when only 60% of the maximal ration was available. Coutant (1973) found that warm-temperature-shocked Chinook salmon were more susceptible to predation by larger rainbow trout *O. mykiss*. Elevated stream temperatures during rearing or downstream smolt migration appear to inhibit adaptation to salt water and cause smolt-to-parr reversion in steelhead *O. mykiss* (Zaugg and McLain 1972; Adams et al. 1975) and hatchery- and stream-reared Atlantic salmon *Salmo salar* (Duston et al. 1991; McCormick 1994). Although water temperature may influence smoltification and development of emigration behavior in some Pacific salmon species (Zaugg et al. 1972; Zaugg and McLain 1972, 1976; Adams et al. 1973, 1975; Ewing et al. 1979), it is not clear whether elevated temperatures impair smoltification in juvenile Chinook salmon.

Most of the prior investigations have focused on more northerly salmon stocks. Application of these results to southerly distributed salmon stocks is probably not appropriate because differences among anadromous fish stocks in their physiolog-

* Corresponding author: marine@modoc.c-zone.net

¹ Present address: North State Resources, Inc., 5000 Bechelli Lane, Suite 203, Redding, California 96002, USA.

Received August 26, 2002; accepted May 5, 2003

ical responses to temperature have been reported (Myrick and Cech 2000, 2002). What little is known of the effects of temperature on Central Valley salmon runs is primarily based on indirect evidence from tagging studies, which suggests that the survival of fall Chinook salmon smolts decreases with increasing water temperatures between 15°C and 24°C in the Sacramento–San Joaquin Delta (Kjelson and Brandes 1989). However, the mechanisms underlying the observed mortality are uncertain, since it occurred at temperatures well below those determined to be lethal in laboratory studies (Brett 1952; Orsi 1971). Indirect effects of elevated water temperature are hypothesized to affect mortality of migrating smolts (Kjelson and Brandes 1989). Sublethal water temperatures may influence growth, development, metabolism, and ecological interactions such as predation, competition, or disease, which ultimately affect survival and population levels (Sylvester 1972; Coutant 1973; Wurtsbaugh and Davis 1977b; Coutant et al. 1979; Fagerlund et al. 1995; Myrick and Cech 2002). Our objective was to examine the effects of elevated water temperatures on Chinook salmon growth, smolt development, and predation vulnerability. We evaluated the null hypothesis that no differences in these factors would occur over the temperature ranges and exposure durations commonly experienced in Central Valley streams and the Sacramento–San Joaquin estuary.

Methods

Rearing and temperature treatments.—Sacramento River fall-run Chinook salmon fry from nine mated pairs at Coleman National Fish Hatchery, Anderson, California, were selected in equal numbers, mixed together, and transported in oxygenated hatchery water to the University of California–Davis. Fish were gently crowded, randomly (blindly) netted, and transferred in groups of 550 fish to each of six, 400-L (1 m in diameter \times 0.5 m deep), circular rearing tanks. Rearing tanks had continuous aeration and a continuous, non-chlorinated, flow-through water supply (10–15 L/min in each tank) from Putah Creek; the water was filtered through a sand bed filter and ultraviolet water sterilizer (Aquanetics Systems, Inc., San Diego, California). Treatment temperatures were controlled by mixing ambient water with heated water or partially recirculated, chilled water. Heated water was passed through a packed column aerator and stripping column to eliminate supersaturated gases before entering the water-

mixing system. Twice-weekly measurements of total gas saturation did not exceed 100.5% (Weiss satrometer). Three temperature treatments were used for this experiment (two tanks per treatment): 13–16°C (mean = 14.4°C, simulating cool to intermediate-temperature rearing habitat), 17–20°C (mean = 18.7°C, simulating intermediate to warm rearing habitat), and 21–24°C (mean = 22.3°C, simulating very warm rearing habitat). Treatment temperatures were allowed to vary within the 3°C limits during the study, and therefore represent the maximum range of diel temperature variation for each treatment. However, daily temperatures generally fluctuated only by about 1.5–2°C.

Fish were reared from February through June 1993. Ambient water temperatures (10–15°C) were used until mid-April, when temperatures were changed by 1°C per day to attain final treatment temperatures. Water temperatures for each treatment were continuously recorded by thermographs (Cole-Parmer; precision, $\pm 0.5^\circ\text{C}$), and the thermograph readings were verified twice daily with mercury thermometers. Water was of moderate hardness, and water quality was comparable to that found throughout the Chinook salmon rearing habitat in the Sacramento River, except that the conductivity and alkalinity of laboratory water were somewhat higher than those of the river (Table 1). Dissolved oxygen was monitored 2–3 d/week, and natural light and photoperiod (38°55'N latitude) were provided via skylights. Fish were fed rations of a moist, pelleted diet (Bioproducts, Inc., Warrenton, Oregon), ranging from 60% to 80% of a satiation ration based on reported feeding rates for juvenile Chinook salmon at different temperatures (Brett et al. 1982; Myrick and Cech 2002). Feed rations were dispensed throughout the day (5–8 times/d) by use of automatic feeders and were adjusted weekly to maintain similar growth rates among treatment groups (Wurtsbaugh and Davis 1977a; Piper et al. 1982). We chose the feeding levels to simulate those reported for juvenile anadromous salmonids feeding in the wild (Wurtsbaugh and Davis 1977b; Brett et al. 1982). Feed was withheld for 24 h prior to sampling and performance challenge tests. Mortalities were removed and recorded for each tank twice daily.

Growth and smoltification.—At 2-week intervals, during the weeks of the new and full moons between 13 February and 22 June, 10–15 fish per treatment were randomly sampled by gently crowding tanks and blindly netting fish, which were then euthanatized in a chilled (7–10°C), buff-

TABLE 1.—Water quality characteristics of the surface water supply at the University of California–Davis (UCD) Aquatic Center laboratories and those of the Sacramento River; TDS = total dissolved solids.

Location	pH	Conductivity ($\mu\text{mho/cm}$)	TDS (mg/L)	Total hardness (mg CaCO_3/L)	Na^+ (mg/L)	Cl^- (mg/L)	Ca^{++} (mg/L)	HCO_3^- (mg/L)
UCD Aquaculture laboratories ^a	8.1–8.3	330–380	214–278	186	2–12	14–24	14–26	134–213
Upper Sacramento River ^b	7.4–8.3	106–148	115	42–62	5–11	2–5	10–13	
Lower Sacramento River ^c	7.2–8.3	88–250		39–92	4–18	2–13	9–19	

^a Provided by University of California Agricultural Services; water samples were collected in 1988 and 1991 and analyzed by A&L Western Agricultural Laboratories, Modesto, California.

^b Provided by California Department of Water Resources, Northern Region. Samples were collected from the Sacramento River at Bend Bridge, 1992–1995.

^c Provided by California Department of Water Resources, Northern Region. Samples were collected from the Sacramento River at Knight's Landing and Verona, 1992–1995.

ered (sodium bicarbonate) solution of tricaine methanesulfonate (MS-222; 200 mg/L). Fish were measured for total length (TL, mm), fork length (FL, mm), and wet weight (g), and gills were excised for assays of sodium-potassium-activated adenosine triphosphatase (Na^+, K^+ -ATPase) activity. Gill tissue samples were excised from each fish within 5–10 min of euthanatization, immediately immersed in 1 mL of chilled sucrose–EDTA–imidazole (pH 7.2) solution, frozen on dry ice, and stored at -80°C . Carcasses were also immediately frozen on dry ice in individual polyethylene bags and stored at -20°C . Gill Na^+, K^+ -ATPase enzyme activities were measured within 6 weeks of sampling; we followed the method used by Zaugg (1982), except that 30-min reaction incubations were used to improve sensitivity and the phosphomolybdate complex was extracted into isobutanol and reduced with stannous chloride to produce a stable blue color (Richard Ewing, Biotech, Inc., personal communication). Carcasses were thawed, dried to a constant weight (60°C drying oven), and lipids were extracted by petroleum ether. Body composition percentages were calculated as percent moisture ($100 \times [\text{total wet weight} - \text{dry carcass weight}]/\text{total wet weight}$), and percent storage lipid ($100 \times [\text{dry carcass weight} - \text{lean dry weight}]/\text{total wet weight}$, where lean dry weight is the weight of the dried carcass after lipid extraction). Condition factor (C) was computed as $\text{weight}/\text{TL}^3$ for dry and wet weights.

Fish were subjected to 24-h seawater challenge tests (following Blackburn and Clark 1987) at the beginning of the experimental temperature regime and after 2 months' exposure. Fish from each rearing tank were randomly assigned to either a freshwater control ($n = 10$ –15) or seawater challenge ($n = 10$ –15) in 30-L aquaria. Fresh water of the same treatment temperatures and from the same water supplies as the rearing tanks was provided to both freshwater and seawater aquaria during a

12–18-h pre-experimental acclimation period. Actual seawater exposure challenges were initiated by a gradual displacement of fresh water with 30–35‰ seawater (artificial sea salts added to laboratory water) at the same treatment temperature, resulting in final salinities of 28–32‰. Dissolved oxygen and ammonia did not vary significantly during 24-h tests. After 24 h, fish were euthanatized and measured as described above, their caudal peduncles were severed, and blood from the caudal vasculature was immediately collected into ammonium-heparinized microhematocrit tubes (Houston 1990). Blood was centrifuged at $13,000 \times$ gravity (g) for 3 min, hematocrit levels were measured as percent packed erythrocytes, and the separated plasma was placed in 1.5-mL polyethylene vials, frozen on dry ice, and stored at -20°C for subsequent measurements of Na^+ and K^+ (Instrumentation Laboratories, model 343 flame photometer). Because of small fish size, plasma samples from two to three fish were pooled to provide sufficient sample volumes, yielding five plasma samples per seawater challenge aquarium.

Predation challenge.—Predation challenge tests, considered an ecologically relevant method of measuring physiological performance (Coutant 1973; Olla and Davis 1989; Mesa 1994), were conducted near the end of the rearing period to approximate the late portion of juvenile migration and entry into the estuary. Six hatchery-reared striped bass *Morone saxatilis* (range: 50–55 cm, 1.2–1.7 kg), an introduced predator in the Sacramento–San Joaquin estuary, were gradually converted to a diet of live and dead fish over a 2-month pre-experimental period and were used as predators in 1,000-L, circular, 1.2-m-diameter \times 1-m-deep tanks. Salmon were measured and freeze-branded (Everest and Edmundson 1967) at least 5 d before predation tests to identify each treatment group. Salmon were gradually acclimated ($\leq 2^\circ\text{C}$ per day) to predation tank temper-

atures in separate, 115-L, aerated, flow-through tanks over the 4–5 d before the tests. Tests were conducted at 15–17°C ($n = 7$, simulating cool river/estuary conditions) and at 18–21°C ($n = 6$, simulating warm river/estuary conditions), reflecting two of the typical temperature regimes of the Sacramento–San Joaquin estuary, where predation is thought to be a principal mortality factor for rearing and emigrating juvenile salmon. Equal numbers ($n = 5$ or 10) of salmon were randomly sampled and measured from the three temperature treatments and placed into a perforated, 19-L, plastic container. Variable numbers of salmon used in these tests prevented habituation of striped bass to release-group sizes. The container was then suspended in the predator tank for 10–12 h before the salmon were released during the early evening, the time at which striped bass fed most readily in preliminary tests. Predation was allowed to proceed until no more than about 50% of the test salmon were eaten, as determined by observations through small viewing slits in a black polyethylene curtain surrounding the tanks. We assumed this threshold of consumption would allow for detection of predator preferences among the three treatment groups, following the methods of Bams (1967) and Coutant (1973). Test duration was noted, and all surviving salmon were netted, identified to treatment group, and measured. The proportion of each treatment group eaten was the variable used to determine predator preference. Because size selectivity of prey can be an important factor in predatory interactions (Parker 1971; Werner 1974; Coutant et al. 1979; Zaret 1980; Hargreaves and LeBrasseur 1985), and because salmon reared in the 21–24°C group were generally smaller than the other treatment groups (Tukey's test, $P = 0.03$ to <0.001) at the time of these tests, we compared the mean lengths of salmon surviving the predation challenges to those of their treatment release groups to evaluate the effect of predator size selectivity on the results.

Data analyses.—Data were analyzed by two-way analysis of variance (ANOVA) to determine the effects of water temperature and time of exposure on the size, growth, and smolt physiology of juvenile fall-run Chinook salmon. Seawater challenge tests were analyzed by use of one-way ANOVA. All data distributions were evaluated for independence of errors, normality, and homogeneity of variance. In a few cases, departures from the homogeneous variance assumption were addressed by pooling variances to adjust the statistical test for unequal variances. The ANOVA F -test is robust to moderate departures from this assumption (Steel and Torrie 1980; Sokal and Rohlf 1981; SYSTAT 1992). Sig-

nificant differences between factor effects were examined by post hoc, pairwise comparison procedures following Tukey's honestly significant difference tests (Steel and Torrie 1980; SYSTAT 1992). The two replicates per temperature treatment, small sample sizes, and low degrees of freedom limited statistical power (i.e., reduced the probability of correctly rejecting a false null hypothesis); therefore, we set α at 0.10 to reduce the probability of the more serious type II error (Steel and Torrie 1980). Chi-square goodness-of-fit tests (Sokal and Rohlf 1981) were used to evaluate whether predation was random among the three temperature treatment groups (i.e., a "null" predation ratio of 1:1:1). Student's t -tests of the differences between the mean lengths of surviving fish compared with the mean lengths of their release groups were used to detect whether prey size selection within treatments occurred in predation challenges.

Results

Survival

Overall survival was 97% or greater for all but one of the temperature treatments. One of the 13–16°C treatment units experienced 5% mortality, mostly during the last 4 weeks of the study, because of an outbreak of bacterial gill disease.

Growth

All fish grew similarly until 20 May. However, temperature had a significant effect on TL ($F = 20.6$, $P < 0.001$, $df = 2$) and weight ($F = 16.0$, $P < 0.001$, $df = 2$) during the last three sample dates (Figure 1). Growth of the 21–24°C-reared fish was significantly lower than that of the 13–16°C and 17–20°C groups by these latter dates (Tukey's test, $P = 0.03$ to <0.001). This decline in growth at the 21–24°C temperature regime coincided with an apparent rejection of food, evidenced by unconsumed food in these tanks. Both temperature and date had significant effects on body moisture (temperature: $F = 14.7$, $P < 0.001$, $df = 2$; date: $F = 124.9$, $P < 0.001$, $df = 7$) and lipid content (temperature: $F = 12.5$, $P < 0.001$, $df = 2$; date: $F = 28.9$, $P < 0.001$, $df = 7$). The 21–24°C treatment exhibited a significantly lower moisture content (Tukey's test, $P = 0.002$ to <0.001) and a significantly higher lipid content (Tukey's test, $P < 0.001$) than the other groups on the last two dates (Figure 2).

Smolt Indices

Gill Na^+ , K^+ -ATPase activity exhibited considerable variation among fish in all three temperature treatments (Figure 3). Though temperature treat-

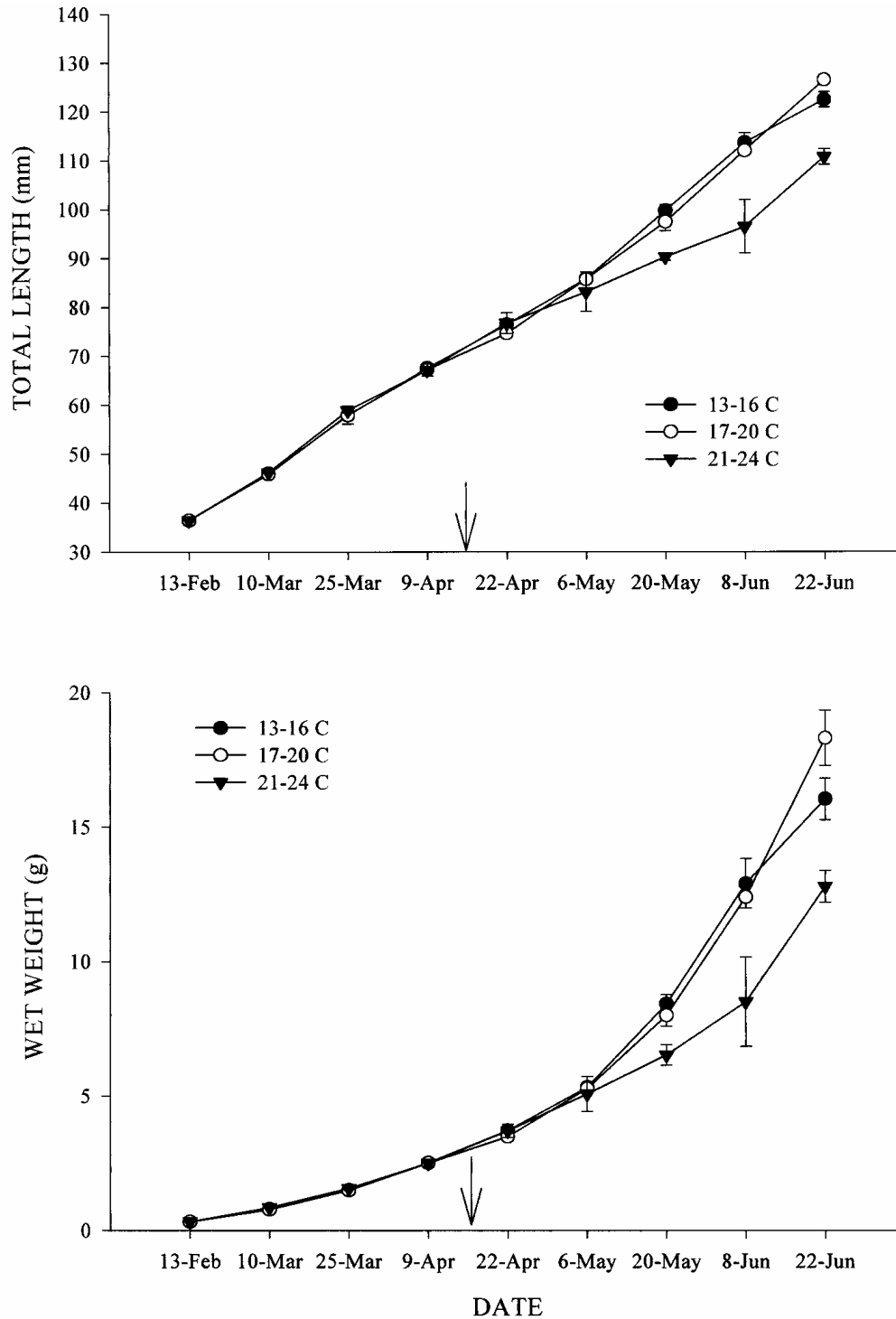


FIGURE 1.—Mean (\pm SE) total length (mm) and weight (g) of juvenile fall-run Chinook salmon reared at three water temperature regimes ($n = 10-15$ fish sampled per treatment per sample date). Arrows indicate the start of temperature treatments.

ment had a significant effect on gill Na^+, K^+ -ATPase activity ($F = 4.315$, $P = 0.03$, $df = 2$), as did date ($F = 2.3$, $P = 0.06$, $df = 7$), only on the last sample date was a significant difference

observed among treatment groups. On this date, the 21–24°C rearing group had a significantly lower gill Na^+, K^+ -ATPase activity than the 13–16°C group (Tukey's test, $P = 0.021$). The interaction

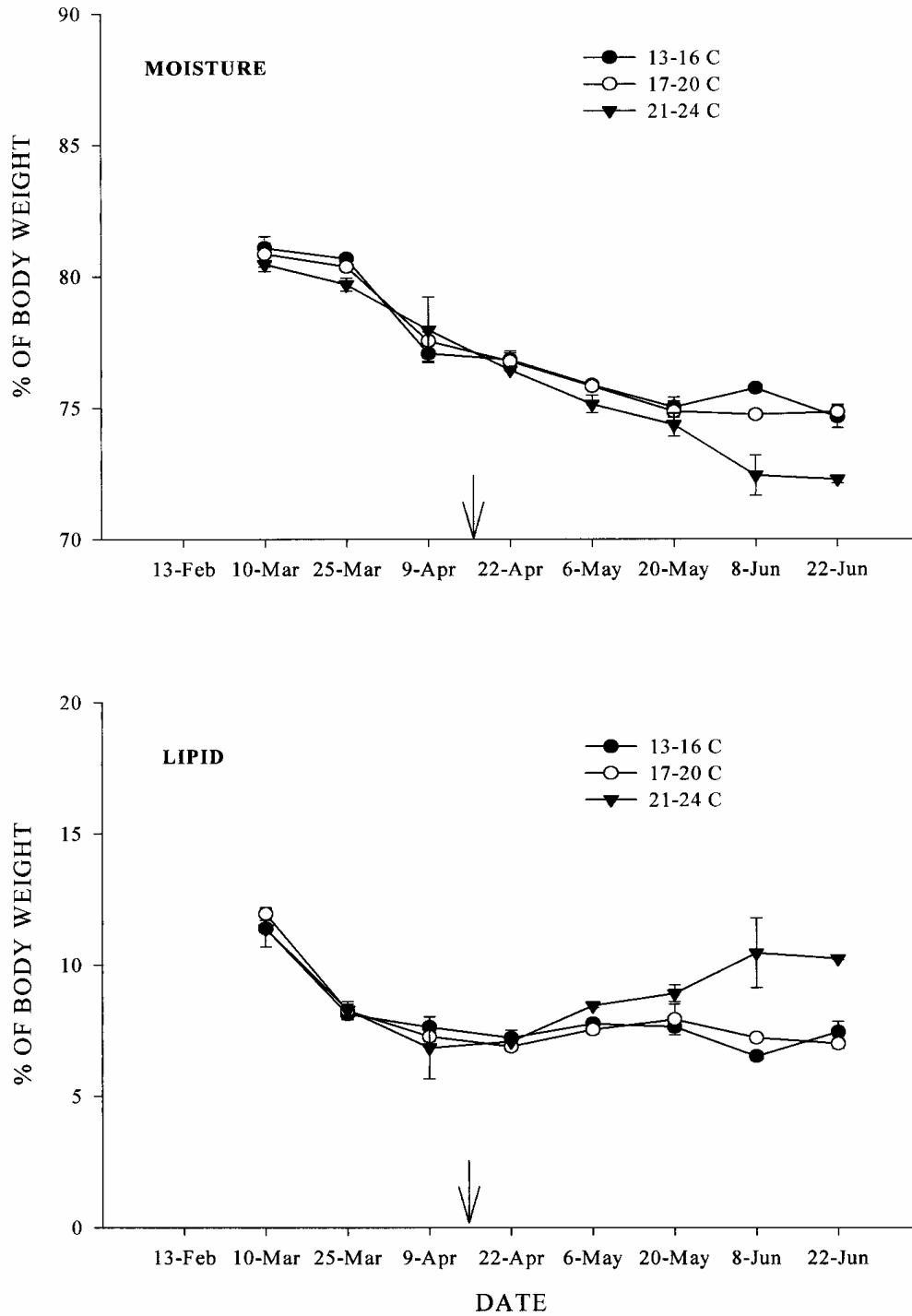


FIGURE 2.—Mean (\pm SE) moisture (upper panel) and lipid contents (lower panel) of juvenile fall-run Chinook salmon reared at three water temperature regimes ($n = 10-15$ fish sampled per treatment per sample date). Arrows indicate the start of temperature treatments.

between rearing temperature and date was not significant ($F = 0.23, P = 0.28$).

In seawater challenge tests, hematocrit levels in challenged groups decreased relative to freshwater control groups at all test temperatures (Table 2),

but with little notable difference among the temperature treatments. Hypoosmoregulatory capability in seawater was significantly affected by temperature ($F = 12.78, P < 0.001, df = 2$; Table 2). The 21–24°C-reared fish consistently exhibited

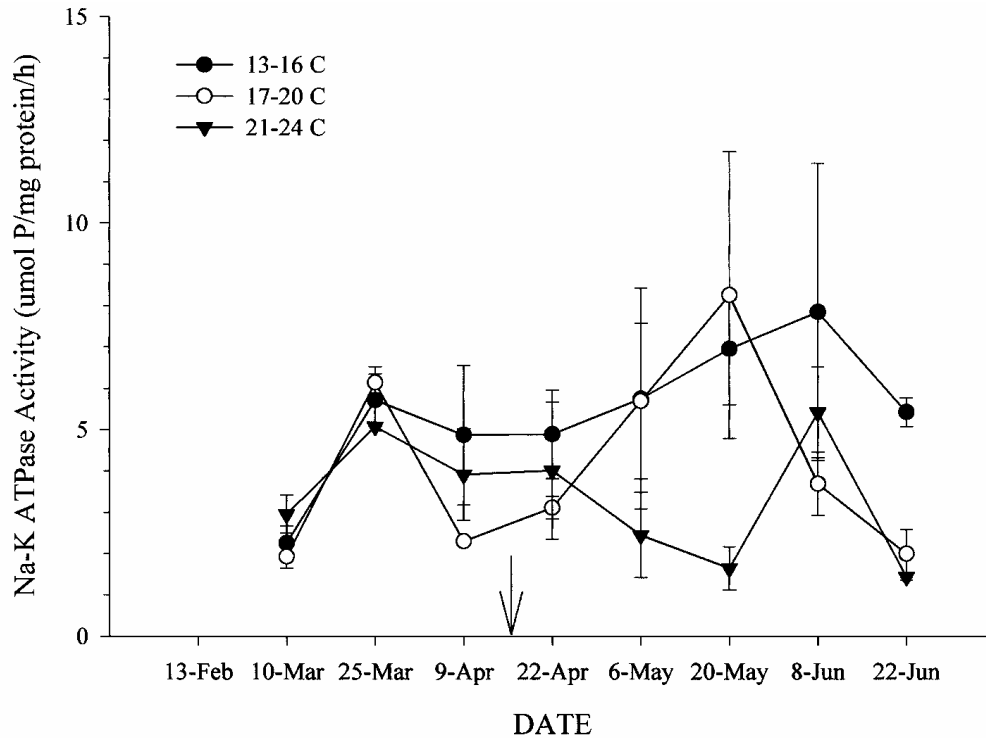


FIGURE 3.—Mean (\pm SE) gill Na^+ , K^+ -ATPase activity for juvenile fall-run Chinook salmon reared at three water temperature regimes ($n = 10$ – 15 fish sampled per treatment per sample date). The arrow indicates the start of temperature treatments.

greater osmoregulatory impairment ($\text{Na}^+ > 170$ mmol/L; Blackburn and Clark 1987) compared with the 13–16°C-reared group. The 21–24°C treatment exhibited greater mortality in the seawater challenges after 2 months, but not significantly so ($\chi^2 = 4.50$ – 5.34 , $P = 0.073$ – 0.113 , $df = 2$; Table 2). No freshwater (control) fish died in any of the seawater challenges.

Predation Challenge

Upon release from the acclimation containers, the juvenile salmon generally dispersed to all depths within the tank. As the predators began to attack (generally within 15 s), the salmon quickly aggregated into a tightly formed school and moved around the tank near the surface of the water. If predator attacks subsided for several minutes, the

TABLE 2.—Hematological indices and survival for seawater-challenged juvenile Sacramento River fall-run Chinook salmon reared at three temperature regimes (13–16°C, 17–20°C, and 21–24°C) during February–July, 1993 (RBC = red blood cells). Dissimilar letters indicate significant differences among treatment groups and between freshwater (FW) and seawater (SW) groups within a sample date. Values are means \pm SDs of paired replicate treatments ($n = 10$ – 15 fish per replicate).

Hematology and survival index	Temperature group	Apr 15	
		FW	SW
Hematocrit (% packed RBCs; $n = 20$ – 24)	13–16°C	43 \pm 1 z	41 \pm 1 z
	17–20°C	43 \pm 1 z	38 \pm 2 y
	21–24°C	43 \pm 1 z	39 \pm 1 y
Plasma sodium (mmol/L; $n = 6$ – 10)	13–16°C	139.5 \pm 9.7 z	147.1 \pm 7.2 z
	17–20°C	130.4 \pm 20.4 z	165.8 \pm 8.8 y
	21–24°C	124.4 \pm 6.3 z	184.6 \pm 7.0 y
Plasma potassium (mmol/L; $n = 6$ – 10)	13–16°C	2.24 \pm 0.53 z	2.44 \pm 0.50 z
	17–20°C	2.31 \pm 0.73 z	4.05 \pm 0.71 y
	21–24°C	3.45 \pm 0.61 zy	4.60 \pm 0.44 y
24-h survival (%)	13–16°C	100	100
	17–20°C	100	100
	21–24°C	100	100

salmon school would become less tightly aggregated. As predator attacks increased in intensity, which generally occurred within 2–3 min, the attacks would repeatedly break up the schooled salmon, with most successful attacks occurring on single fish disaggregated from the school and swimming along the tank wall perimeter. Tests performed at the 15–17°C predation tank temperature range indicated that salmon were not randomly eaten ($P < 0.0013$): fish from the 21–24°C rearing treatment were consumed more frequently than fish from the other two treatments (Table 3). In contrast, no significant differences ($P = 0.737$) in predator selectivity among the rearing temperature groups were detected in the tests performed at the 18–21°C predation tank temperature range (Table 3). No statistically significant differences were detected within treatments between the mean sizes of the surviving fish and those of their release groups (Student's *t*-tests, $P = 0.163$ – 0.927).

Discussion

Temperature Effects on Survival and Growth

We demonstrated that juvenile Sacramento River Chinook salmon can survive and grow at chronically elevated seasonal water temperatures of 17–24°C during the latter portion of the freshwater rearing period. However, protracted rearing within this elevated temperature range, especially at temperatures of 20°C or greater, decreased growth and appetite, altered smolt physiology, and increased predation vulnerability compared with juvenile salmon reared at a temperature range considered to be near optimal (13–16°C) for the species. Our results were consistent with those of Brett (1952), who reported that although juvenile Chinook salmon could be successfully reared at temperatures as high as 24°C without significant mortality, their

growth rate at this temperature was reduced compared with fish reared at 15°C. Armour (1991) derived a recommended upper limit of 15.6°C to provide optimal growth and survival conditions for spring Chinook salmon, above which sublethal detrimental effects on growth could be expected. Our results are not consistent with this recommendation because growth performance of juvenile Sacramento River Chinook salmon remained similar among the temperature regimes that included daily maximum temperatures up to 20°C, when fed rations similar to those reported for wild fish (Wurtsbaugh and Davis 1977b; Brett et al. 1982). The effect of diel temperature fluctuations on salmonid growth response differs from the results of experiments conducted under constant (less natural) temperature regimes (Hokanson et al. 1977), which may account for discrepancies between our results and those reported by other researchers. However, these differences may also suggest that juvenile Sacramento River Chinook salmon are able to maintain growth rates at slightly higher temperatures than more northerly stocks, which is consistent with results reported for at least one other Central Valley fall-run Chinook salmon population (Myrick and Cech 2002). Brett et al. (1982) reported that the peak growth responses of several British Columbia Chinook salmon stocks shifted from 18.9–20.5°C for fish fed maximal rations to 13.5–16°C for fish fed 60% of maximum ration. Castleberry et al. (1993) found that growth rates of juvenile anadromous fishes in the American River, California, changed little over the temperature range from 10.3°C to 18.4°C. Clarke and Shelbourn (1985) reported that growth rates of age-0 fall Chinook salmon increased as temperature increased from 7°C to 17°C, maximum growth occurring at about 17°C. Banks et al. (1971) also

TABLE 2.—Extended.

Jun 8		Jun 22	
FW	SW	FW	SW
45 ± 1 z	40 ± 1 y	53 ± 1 z	45 ± 1 y
46 ± 1 z	40 ± 1 y	51 ± 1 z	43 ± 1 x
44 ± 1 z	42 ± 1 y	46 ± 1 y	42 ± 1 x
130.3 ± 1.9 z	173.1 ± 3.2 x	142.6 ± 1.0 z	176.2 ± 3.7 y
139.3 ± 1.1 y	197.5 ± 4.6 w	139.8 ± 2.2 z	169.4 ± 4.1 y
134.9 ± 3.1 z	188.7 ± 6.1 w	136.5 ± 1.0 z	196.2 ± 9.9 x
7.28 ± 1.18 z	7.13 ± 1.06 z	1.55 ± 0.18 z	3.01 ± 0.31 z
7.30 ± 0.96 z	8.49 ± 0.70 z	2.50 ± 0.26 y	4.27 ± 0.39 y
3.46 ± 0.81 y	6.78 ± 0.84 z	2.92 ± 0.16 y	6.43 ± 0.41 x
100	100	100	95
100	95	100	100
100	85	100	81

TABLE 3.—Results of predation tests conducted at 15–17°C (simulating cool river or estuary conditions and 18–21°C (simulating warm river or estuary conditions) for juvenile Chinook salmon reared at three temperature regimes (13–16°C, 17–20°C, and 21–24°C). Striped bass were used as predators. The chi-square goodness-of-fit statistic (Sokal and Rohlf 1981) indicated that predation rates among the temperature groups differed significantly ($P < 0.10$) from a hypothesized random ratio of 1:1:1.

Predation test temperature	Number eaten			Total presented	Percent eaten	df	χ^2	P	
	By rearing temperature (°C)								
	13–16	17–20	21–24	Total					
15–17°C	9	16	23	48	150	32	2	13.61	0.0013
18–21°C	10	9	12	31	90	34	2	0.689	0.7373

reported that maximum growth rates of fall Chinook salmon occurred at temperatures between 15.5°C and 18.3°C. In our study, we did not observe significant reductions in growth rates for juvenile salmon reared with adequate food to promote growth until daily temperatures (daily means or daily maxima) exceeded 20°C.

However, as other research has shown, increases in stream temperatures without adequate food availability would result in effects on growth and survival of juvenile salmonids (Bisson and Davis 1976; Wurtsbaugh and Davis 1977b; Brett et al. 1982; Myrick and Cech 2002).

Temperature Effects on Smoltification and Smolt Indices

Significant reductions in hypoosmoregulatory capability and slight (though not significant) decreases in survival during acute seawater exposure challenges during the latter part of freshwater rearing indicated some impairment of the seawater tolerance of salmon smolts reared at temperatures exceeding 17°C compared with those reared at 13–16°C. Gill Na^+, K^+ -ATPase activity was quite variable, especially in the 13–16°C and 17–20°C groups, and this variability appeared to increase with time and fish size. Such a result apparently reflects the natural variability of this enzyme's activity in Sacramento River Chinook salmon, because although our replication was limited, our sample sizes were adequate to characterize the enzyme ($n = 10$ –15 fish per treatment), and our sampling technique was consistent across all sampling dates. However, the significant depression of Na^+, K^+ -ATPase activity on 22 June in the 21–24°C group compared with ATPase activity in the 13–16°C group indicates a temperature-associated alteration of activity, which can impair smolt survival (Zaugg 1989). Water temperature has been found to play an important role in modulating the physiological response of smolting salmonids to primary environmental cues, such as photoperiod

(Wagner et al. 1969; Ewing et al. 1979; Clarke et al. 1981; Johnston and Saunders 1981; Pereira and Adelman 1985). Elevated rearing temperatures during smolt development and emigration have been associated with acceleration of smolting, hastening of smolt-to-parr reversion, and inhibition of parr-smolt metamorphosis in steelhead and Atlantic salmon (Zaugg et al. 1972; Adams et al. 1975; Zaugg and McLain 1976; Wedemeyer et al. 1980; Duston et al. 1991). Adams et al. (1975) reported inhibition of gill Na^+, K^+ -ATPase activity and a corresponding decrease in seawater survival for juvenile steelhead reared at temperatures above 12°C. Zaugg and McLain (1976) reported that coho salmon *O. kisutch* exposed to rearing temperatures up to 20°C experienced a precocious smolt development pattern, with an accelerated peak in gill Na^+, K^+ -ATPase activity of similar magnitude to the peak at more optimal rearing temperatures. The major consequence of this accelerated smolt development pattern is a foreshortened period of smolting, which may result in reversion to parr, asynchronous smoltification, premature emigration, and arrival at the estuary with suboptimal hypoosmoregulatory capability. Such juvenile salmonids may require additional time in fresh or brackish water to adapt to higher salinities, thus lengthening residency in the lower reaches of rivers or estuaries and increasing predation risk. Handeland et al. (1996) found that Atlantic salmon smolts were more vulnerable to predatory Atlantic cod *Gadus morhua* as a result of less effective antipredator behavior during their acclimation to seawater. However, it remains to be tested whether such migration delays occur for wild Chinook salmon inhabiting California's Central Valley streams or whether an altered migration schedule affects survival to subsequent life stages.

We noted that the gill Na^+, K^+ -ATPase activities measured in our experiments were lower than expected from the Zaugg (1982) assay adapted for

our study. Other researchers (Zaugg and McLain 1972; Johnson et al. 1977; Zaugg 1982) have noted gill $\text{Na}^+\text{-K}^+\text{-ATPase}$ activities ranging from 5 to 65 $\mu\text{mol P/mg protein/h}$ for parr and smolts, whereas we observed 0.5–17 $\mu\text{mol P/mg protein/h}$. Our results were consistent with the expected patterns of increase in gill $\text{Na}^+\text{-K}^+\text{-ATPase}$ activities during smoltification and the temporal patterns of enzyme activity during freshwater rearing of juvenile Chinook salmon (Zaugg and McLain 1972; Johnson et al. 1977), but the high variability of this enzyme in the Sacramento River Chinook salmon used in our experiments limited its utility compared with other studies.

Temperature Effects on Predation Vulnerability

Juvenile Chinook salmon reared at 21–24°C for 2.5 months exhibited an increased vulnerability to predation compared with fish reared at 13–16°C or 17–20°C. Our data did not allow us to fully separate the effect of temperature from that of fish size in the predation challenges, because fish reared at 21–24°C were significantly smaller than fish reared at 13–16°C and 17–20°C. While no predator size selection was detected within rearing temperature test groups, our data do not rule out size selectivity as a potential mechanism, because the 21–24°C group was significantly smaller than the other groups during these tests. If smaller prey size is preferred by predators, the reduced growth rates at the high test temperature may increase predation risk. However, it is likely that the combined effects of temperature on growth and on other performance traits, such as burst swimming to evade predators, ultimately determine vulnerability. Environmental stressors such as elevated water temperature may produce chronic, sublethal effects leading to incremental reductions in the performance capacity of fish and a reduced scope for coping with additional stressors (Wedemeyer et al. 1980; Barton et al. 1986; Sigismondi and Weber 1988; Mesa 1994; Mesa et al. 1994).

We also note that applicability of our results to fish in the wild is limited by the lack of refugial habitat for prey fish in the open tank experiments (Gregory and Levings 1996). Our test tanks represented a simple habitat with limited opportunity for successful antipredator behavior. Additionally, the prey were naive to predators, although Healey and Reinhardt (1995) found that predator avoidance in juvenile Chinook salmon did not change with prior predation experience.

Conclusions

Kjelson and Brandes' (1989) analysis of mark-recapture data of juvenile salmon migrating through the Sacramento–San Joaquin Delta indicated that survival declines steadily between about 16°C and 21°C, although they could not attribute this decline in survival to temperature alone. Baker et al. (1995) estimated an upper incipient lethal temperature of $23.01 \pm 1.08^\circ\text{C}$ for juvenile Chinook salmon emigrating through the Sacramento–San Joaquin estuary. They found this to be similar to results obtained from controlled experiments. Our laboratory results suggest that the temperature–survival associations detected by Kjelson and Brandes (1989) and Baker et al. (1995) may represent indirect effects as opposed to direct effects of elevated temperatures on survival, mediated potentially by increased predation vulnerability and reduced seawater adaptability of smolts migrating through the delta. While these results may help explain survival patterns of emigrating smolts, there are many other factors (e.g., upwelling strength in the coastal ocean) that determine survival to adulthood and the ultimate strength of returning salmon spawning runs (Ewing et al. 1985).

Acknowledgments

This study was funded by the Bay–Delta Interagency Ecological Program, Pacific Gas & Electric Company, Marin Rod and Gun Club and Stockton Sportsman's Club (for scholarships to KRM), and University of California Agricultural Experiment Station grant 3455-H to JJC. P. Lutes and B. Bentley assisted with facility design. L. Brink, A. Keasey, P. Moberg, J. Nolan, and C. Porter helped collect data. The U.S. Fish and Wildlife Service's Coleman National Fish Hatchery, California–Nevada Fish Health Laboratory, and Northern Central Valley Fish and Wildlife Office staffs and N. Villa with the California Department of Fish and Game assisted with logistics. J. Dykes consulted on statistical analyses, J. M. Roessig edited, and S. Doroshov, P. Moyle, M. Young, S. Riley, and three anonymous reviewers critically reviewed earlier drafts.

References

- Adams, B. L., W. S. Zaugg, and L. R. McLain. 1973. Temperature effect on parr–smolt transformation in steelhead trout (*Salmo gairdneri*) as measured by gill sodium–potassium stimulated adenosine triphosphate. *Comparative Biochemistry and Physiology* 44A:1333–1339.

- Adams, B. L., W. S. Zaugg, and L. R. McLain. 1975. Inhibition of salt water survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. *Transactions of the American Fisheries Society* 104:766–769.
- Armour, C. L. 1991. Guidance for evaluating and recommending temperature regimes to protect fish. U.S. Fish and Wildlife Service Biological Report 90.
- Baker, P. F., T. P. Speed, and F. K. Ligon. 1995. Estimating the influence of temperature on survival of Chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento–San Joaquin Delta of California. *Canadian Journal of Fisheries and Aquatic Sciences* 52:855–863.
- Bams, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. *Journal of the Fisheries Research Board of Canada* 24:1117–1153.
- Banks, J. L., L. G. Fowler, and J. W. Elliott. 1971. Effects of rearing temperature on growth, body form, and hematology of fall Chinook fingerlings. *Progressive Fish-Culturist* 33:20–26.
- Barton, B. A., C. B. Schreck, and L. A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. *Transactions of the American Fisheries Society* 115:245–251.
- Bisson, P. A., and G. E. Davis. 1976. Production of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream. U.S. National Marine Fisheries Service Fishery Bulletin 74:763–774.
- Blackburn, J., and W. C. Clark. 1987. Revised procedure for the 24-hour seawater challenge test to measure seawater adaptability of juvenile salmonids. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1515.
- Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Research Board of Canada* 9:265–325.
- Brett, J. R., W. C. Clarke, and J. E. Shelbourn. 1982. Experiments of thermal requirements for growth and food conversion efficiency of juvenile salmon, *Oncorhynchus tshawytscha*. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1127.
- California Advisory Committee on Salmon and Steelhead Trout. 1988. Restoring the balance. 1988 Annual Report submitted to the California State Senate, Sacramento.
- Castleberry, D. T., J. J. Cech, Jr., M. K. Saiki, and B. A. Martin. 1993. Growth, condition, and physiological performance of juvenile salmonids from the lower American River: February through July 1992. U.S. Fish and Wildlife Service, National Fisheries Contaminant Research Center and University of California, Final Report, Davis.
- Clarke, W. C., J. E. Shelbourn, and J. R. Brett. 1981. Effects of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. *Aquaculture* 22:105–116.
- Clarke, W. C., and J. E. Shelbourn. 1985. Growth and development of seawater adaptability by juvenile fall Chinook salmon (*Oncorhynchus tshawytscha*) in relation to temperature. *Aquaculture* 45:21–31.
- 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.
- Coutant, C. C., R. B. McLean, and D. L. DeAngelis. 1979. Influences of physical and chemical alterations on predator–prey interactions. Pages 57–68 in H. Clepper, editor. *Predator–prey systems in fisheries management*. Sport Fishing Institute, Washington, D.C.
- Duston, J., R. L. Saunders, and D. E. Knox. 1991. Effects of increases in freshwater temperature on loss of smolt characteristics in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:164–169.
- Everest, F. H., and E. H. Edmundson. 1967. Cold branding for field use in marking juvenile salmonids. *Progressive Fish-Culturist* 29:175–176.
- Ewing, R. D., A. R. Hemmingsen, M. D. Evenson, and R. L. Lindsay. 1985. Gill (Na⁺-K)-ATPase activity and plasma thyroxine concentrations do not predict time of release of hatchery coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) for maximum adult returns. *Aquaculture* 45:359–373.
- Ewing, R. D., S. L. Johnson, H. L. Pribble, and J. A. Lichatowich. 1979. Temperature and photoperiod effects on gill (Na and K) ATPase activity in Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of the Fisheries Research Board of Canada* 36:1347–1353.
- Fagerlund, U. H. M., J. R. McBride, and I. V. Williams. 1995. Stress and tolerance. Pages 459–503 in C. Groot, L. Margolis and W. C. Clarke, editors. *Physiological ecology of Pacific salmon*. University of British Columbia Press, Vancouver.
- Fisher, F. W. 1994. Past and present status of Central Valley Chinook salmon. *Conservation Biology* 8:870–873.
- Gregory, R. S., and C. D. Levings. 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus* spp., to predation by adult cutthroat trout, *O. clarkii*. *Environmental Biology of Fishes* 47(3):279–288.
- Handeland, S. O., T. Jārvi, A. Fermo, and S. O. Stefansson. 1996. Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2673–2680.
- Hargreaves, N. B., and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 42:659–668.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C.

- Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Healey, M. C., and U. Reinhardt. 1995. Predator avoidance in naive and experienced juvenile Chinook and coho salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 52:614–622.
- Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 34:639–648.
- Houston, A. H. 1990. Blood and circulation. Pages 273–334 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Johnson, S. L., R. D. Ewing, and J. A. Lichatowich. 1977. Characterization of gill (Na+K)-activated adenosine triphosphatase from Chinook salmon, *Oncorhynchus tshawytscha*. *Journal of Experimental Zoology* 199:345–354.
- Johnston, C. E., and R. L. Saunders. 1981. Parr–smolt transformation of yearling Atlantic salmon (*Salmo salar*) at several rearing temperatures. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1189–1198.
- Kjelson, M. A., and P. L. Brandes. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento–San Joaquin rivers, California. Pages 100–115 in C. D. Levings, L. B. Holtby, and M. A. Henderson, editors. *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks*. Canadian Special Publication of Fisheries and Aquatic Sciences 105.
- McCormick, S. D. 1994. Loss of smolt characteristics in hatchery- and stream-reared Atlantic salmon. Pages 51–56 in D. D. MacKinlay, editor. *High performance fish*. *Proceedings of an international fish physiology symposium held July 16–21, 1994*. Fish Physiology Association, Vancouver.
- Mesa, M. G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon. *Transactions of the American Fisheries Society* 123:786–793.
- Mesa, M. G., T. P. Poe, D. M. Gadomski, and J. H. Petersen. 1994. Are all prey created equal?: a review and synthesis of differential predation on prey in standard condition. *Journal of Fish Biology* 45(Supplement A):81–96.
- Moyle, P. B. 2002. *Inland fishes of California*. University of California Press, Berkeley.
- Myrick, C. A., and J. J. Cech, Jr. 2000. Temperature influences on California rainbow trout physiological performance. *Fish Physiology and Biochemistry* 22: 245–254.
- Myrick, C. A., and J. J. Cech, Jr. 2002. Growth of American River fall-run Chinook salmon in California's Central Valley: temperature and ration effects. *California Fish and Game* 88:35–44.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at a crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4–21.
- Olla, B. L., and M. W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture* 76:209–214.
- Orsi, J. J. 1971. Thermal shock and upper lethal temperature tolerances of young king salmon, *Oncorhynchus tshawytscha*, from the Sacramento–San Joaquin River system. California Department of Fish and Game, Anadromous Fisheries Branch, Administrative Report 71-11, Sacramento.
- Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *Journal of the Fisheries Research Board of Canada* 28:1503–1510.
- Pereira, D. L., and I. R. Adelman. 1985. Interactions of temperature, size, and photoperiod on growth and smoltification of Chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 46:85–192.
- Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. *Fish hatchery management*. U.S. Fish and Wildlife Service, Washington, D.C.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 184.
- Sigismondi, L. A., and L. J. Weber. 1988. Changes in avoidance response time of juvenile Chinook salmon exposed to multiple acute handling stresses. *Transactions of the American Fisheries Society* 117: 196–201.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*, 2nd edition. Freeman, San Francisco.
- Steel, R. G. D., and J. H. Torrie. 1980. *Principles and procedures of statistics: a biometrical approach*. McGraw-Hill, New York.
- Sylvester, J. R. 1972. Effects of thermal stress on predator avoidance in sockeye salmon. *Journal of the Fisheries Research Board of Canada* 29:601–603.
- SYSTAT. 1992. *SYSTAT for Windows: statistics, version 5*. SYSTAT, Evanston, Illinois.
- USFWS (U.S. Fish and Wildlife Service). 1995. *Working paper on restoration needs: habitat restoration actions to double natural production of anadromous fish in the Central Valley of California*. Prepared for the U.S. Fish and Wildlife Service under the direction of the Anadromous Fish Restoration Program Core Group, Stockton, California.
- Wagner, H. H., F. P. Conte, and J. L. Fessler. 1969. Development of osmotic and ionic regulation in two races of Chinook salmon *Oncorhynchus tshawytscha*. *Comparative Biochemistry and Physiology* 29: 325–341.
- Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Marine Fisheries Review* 42(6):1–14.
- Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some impli-

- cations. *Journal of the Fisheries Research Board of Canada* 31:1531–1536.
- 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.
- Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1998. Historical abundance and decline of Chinook salmon in the Central Valley region of California. *North American Journal of Fisheries Management* 18:487–521.
- Zaret, T. M. 1980. *Predation and freshwater communities*. Yale University Press, New Haven, Connecticut.
- Zaugg, W. S. 1982. A simplified preparation for adenosine triphosphate determination in gill tissue. *Canadian Journal of Fisheries and Aquatic Sciences* 39:215–217.
- Zaugg, W. S. 1989. Migratory behaviour of underyearling *Oncorhynchus tshawytscha* and survival to adulthood as related to prerelease gill (Na–K) ATPase development. *Aquaculture* 82:339–353.
- Zaugg, W. S., B. L. Adams, and L. R. McLain. 1972. Steelhead migration: potential temperature effects as indicated by gill adenosine triphosphate activities. *Science* 176:415–416.
- Zaugg, W. S., and L. R. McLain. 1972. Changes in gill adenosine triphosphate activity associated with parr–smolt transformation in steelhead trout, coho and spring Chinook salmon. *Journal of the Fisheries Research Board of Canada* 29:167–171.
- Zaugg, W. S., and L. R. McLain. 1976. Influence of water temperature on gill sodium, potassium stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). *Comparative Biochemistry and Physiology* 54A:419–421.