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Growth, Smoltification, and Smolt-to-Adult Return of Spring Chinook Salmon from Hatcheries on the Deschutes River, Oregon

BRIAN R. BECKMAN,* WALTON W. DICKHOFF,[1] AND WALDO S. ZAUGG

Integrative Fish Biology Program, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

CAMERON SHARPE[2]

Oregon Cooperative Fishery Research Unit, Biological Resources Division, U.S. Geological Survey, Oregon State University, Corvallis, Oregon 97331, USA

STEVE HIRTZEL[3]

Integrative Fish Biology Program, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

ROBIN SCHROCK

Columbia River Research Station, Biological Resources Division, U.S. Geological Survey, Cook Underwood Road, Cook, Washington 98602, USA

DONALD A. LARSEN

Integrative Fish Biology Program, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

RICHARD D. EWING[4]

Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97330, USA

ALDO PALMISANO

Biological Resources Division, U.S. Geological Survey, 6505 65th Street, Seattle, Washington 98115, USA

CARL B. SCHRECK

Oregon Cooperative Fishery Research Unit, Biological Resources Division, U.S. Geological Survey, Oregon State University, Corvallis, Oregon 97331, USA

CONRAD V. W. MAHNKEN

Fisheries Enhancement Program, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Abstract.—The relationship between smoltification and smolt-to-adult return (SAR) of spring chinook salmon *Oncorhynchus tshawytscha* from the Deschutes River, Oregon, was examined for four release groups in each of three successive years. Fish were reared, marked with coded wire tags, and released from Round Butte Hatchery, Pelton Ladder rearing facility, and Warm Springs

* Corresponding author: brian.beckman@noaa.gov

[1] Also: School of Fisheries, University of Washington, Seattle, Washington 98195, USA.

[2] Present address: Washington Department of Fish and Wildlife, Kalama Research Station, 804 Allen Street #3, Kelso, Washington 98626, USA.

[3] Present address: U.S. Fish and Wildlife Service, 3310 El Camino Avenue, Suite 130, Sacramento, California 95821, USA.

[4] Present address: Biotech Research and Consulting, Inc., 2340 Southeast Ryan Street, Corvallis, Oregon 97333, USA.

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National Fish Hatchery. Smolt releases occurred in nearly the same place at similar times, allowing a direct comparison of SAR to several characters representing smolt quality. Return rates varied significantly among facilities, varying over an order of magnitude each year. The highest average SAR was from Pelton Ladder, the lowest was from Warm Springs. Each of the characters used as metrics of smoltification—fish size, spring growth rate (February–April), condition factor, plasma hormone concentration (thyroxine, cortisol, and insulin-like growth factor-I [IGF-I]), stress challenge, gill Na^+,K^+-ATPase activity, and liver glycogen concentration—varied significantly among facilities and seasonally within hatchery groups. However, only spring growth rate, gill ATPase activity, and plasma IGF-I concentration showed significant relationships to SAR. These characters and SAR itself were consistently lower for fish released from Warm Springs Hatchery than for fish from Round Butte Hatchery and Pelton Ladder. This demonstrates that differences in the quality of fish released by facilities may have profound effects on subsequent survival and suggests that manipulations of spring growth rate may be used to influence the quality of smolts released from facilities.

The role of hatchery-produced salmon *Oncorhynchus* spp. in ecosystems of the Pacific Coast of North America is currently being debated (Hilborn 1992; Meffe 1992). Some people have suggested that salmon produced by hatcheries are behaviorally dysfunctional, physiologically compromised, and disease prone—traits leading to poor postrelease survival and deleterious effects on wild fish (Steward and Bjornn 1990; Maynard et al. 1995; NRC 1996). These considerations, plus other concerns about hatchery practices and management, have led to a number of proposals for decreasing, altering, or eliminating hatchery production (NMFS 1995; NRC 1996). The controversy over the role of hatcheries so far has not acknowledged that hatcheries may differ in physical characteristics and rearing practices, that they may thus produce fish of differing quality, and that their ecological costs and benefits may therefore differ. Hatcheries that perform poorly might be closed. Alternatively, poorly performing hatcheries might be improved to mimic those that perform well. Both of these alternatives require accurate assessment of relative hatchery success.

Appraising the success of hatcheries is a task that has been attempted infrequently (Hilborn and Winton 1993; Winton and Hilborn 1994). It can be technically difficult and expensive, and the results may be inconclusive. The most widely used measure of hatchery success involves determining the percentage of fish released that return as adults or are caught in a fishery (the smolt-to-adult return, SAR). Although it may be the most accurate indicator of hatchery success, SAR is influenced by a variety of factors that may make direct comparison of rates between hatcheries difficult. This is especially true in the Columbia River basin, where hatcheries are distributed from near the estuary to tributaries such as the Salmon River, 1,200 km from the ocean. Fish that must travel from the Salmon River to the ocean, traversing eight mainstem dams and reservoirs with their resident predators, may suffer greater mortality than fish released close to the estuary (Raymond 1979, 1988). Upper-river hatcheries thus might have a lower SAR than a lower-river hatchery even if the hatcheries produce similar fish. Ideally, one needs an index at the time of release which is predictive of the ability of fish to perform in the natural environment.

Spring chinook salmon *O. tshawytscha* are typically released from hatcheries as yearling fish called smolts. Smolts are expected to migrate rapidly downriver, adapt to seawater, and then forage and grow in marine waters (Hoar 1976; Bern 1982). Several attempts have been made to quantify a ''smolt quality index'' based on smolt characters measured before release (Ewing and Birks 1982; Ewing et al. 1985; Zaugg 1989; Zaugg and Mahnken 1991; Farmer 1994). A general finding has been that fish released from a hatchery before they have begun smoltification (the parr stage) or while they are in early stages of smoltification have a lower likelihood of return than fish released further along in this physiological process (Wahle and Zaugg 1982; Zaugg 1989; Zaugg and Mahnken 1991). However, more rigorous attempts to compare smolt quality and SAR between hatcheries have been problematic, perhaps because smolt quality indices were inadequate. An accurate smolt quality index would allow direct comparisons between fish produced by different hatcheries or between fish reared under different conditions at the same hatchery. For the purposes of this paper, we define a smolt quality index as a variable measured on juvenile salmon during smoltification that shows a significant correlation with SAR. In contrast, a smolt character is simply some attribute that changes during smoltification.

Several biochemical methods have been used to

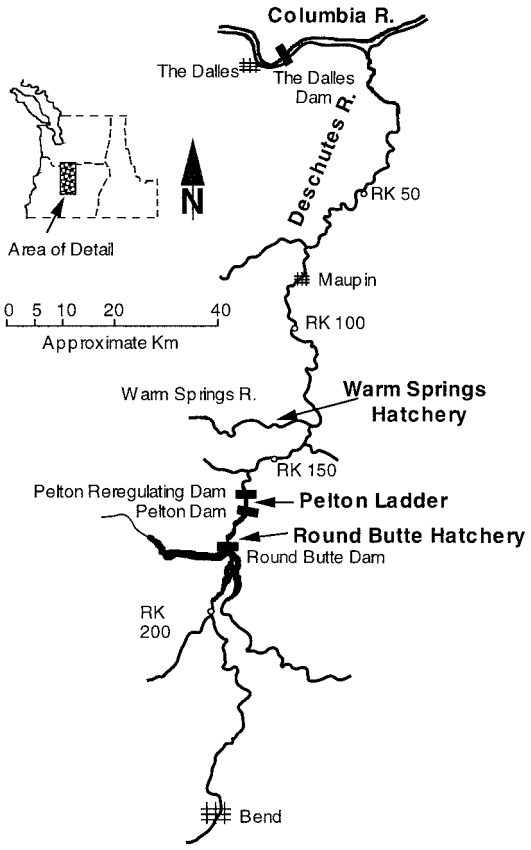

FIGURE 1.—Map of the Deschutes River, Oregon. Spring chinook salmon rearing facilities are designated with arrows. Distances upstream (in river kilometers, RK) from the Columbia River confluence are indicated.

measure smoltification (Folmar and Dickhoff 1980; Wedemeyer et al. 1980; McCormick and Saunders 1987), but they have been little tested for efficacy as smolt quality indices. Accordingly, we designed a study to relate smolt quality to adult returns covering 3 years of hatchery releases of spring chinook salmon. The facilities chosen were in close geographic proximity, on or near the Deschutes River, Oregon, a tributary of the Columbia River. These facilities released fish at nearly the same time in nearly the same place, and they reared genetically similar fish. The environmental challenges faced by fish released from these facilities were thus similar; any differences in SAR between fish released from these facilities should be due to the relative attributes of fish released from each facility. We tested for differences in smolt characters among facilities and whether these related to SAR. The study comprised a comparison of SAR, an evaluation of smoltification based on

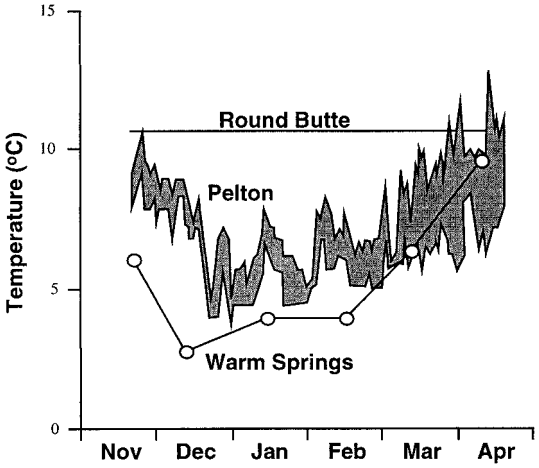

FIGURE 2.—Seasonal temperatures at Warm Springs Hatchery and temperature ranges at Round Butte Hatchery and Pelton Ladder, 1988–1989.

physiology and morphology, and an evaluation of the relation of smolt physiology and morphology to SAR.

Methods

Facilities and chinook salmon populations.—Chinook salmon were examined at Warm Springs National Fish Hatchery, Round Butte Hatchery (Oregon Department of Fish and Wildlife, ODFW), and Pelton Rearing Ladder (ODFW) (Figure 1). Deschutes River and Warm Springs fish are genetically similar and are closely related to a large group of Columbia River spring chinook salmon (Utter et al. 1989; Matthews and Waples 1991). Round Butte and Warm Springs hatchery histories, operations, and broodstock origins and collection were described by Howell et al. (1985), Lindsay et al. (1989), and Olson et al. (1995). Pelton Ladder is an abandoned fish passage facility that extends downstream from Pelton Dam to Pelton Reregulating Dam. The lower 0.5 km of the ladder is now used as a satellite rearing facility for Round Butte Hatchery.

At Warm Springs Hatchery, eggs were hatched in mid-November, fry were transferred to indoor fiberglass tanks in late December, and first feeding occurred in early January. Fry were transferred to outside concrete raceways in early March. Fish were reared in river water at temperatures typical of those shown in Figure 2. They were fed four to five times per day with a commercial feed (Biomoist diet). Fish were graded in late September; all fish longer than 140 mm were released (approximately 40% of the total) and those remaining

TABLE 1.—Summary of release information for spring chinook salmon smolts from Warm Springs, Round Butte, and Pelton Ladder facilities.

Hatchery	Fish density	Brood year	Rearing density at release (kg/m^3)	Release date	Number of tagged fish released (1,000s)
Warm Springs[a]	High	1988	25.6	11 Apr 1990	46
		1989	27.2	17 Apr 1991	50
		1990	28.8	22 Apr 1992	45
	Low	1988	16.0	11 Apr 1990	24
		1989	14.4	17 Apr 1991	24
		1990	9.6	22 Apr 1992	13
Round Butte[b]		1988	17.6	19 Apr 1990	28
		1989	17.6	22–23 April 1991	29
		1990	14.4	20–21 April 1992	28
Pelton Ladder[c]		1988	1.6	23–26 April 1990	21
		1989	1.6	22–24 April 1991	20
		1990	1.6	20–22 April 1992	21

[a] Fish were released directly from raceways into Warm Springs River.
[b] Fish were trucked and released at a point directly below Pelton Reregulating Dam.
[c] The screen was removed from end of the ladder and fish moved volitionally into the Deschutes River directly below Pelton Reregulating Dam.

were reared through their second winter and released in mid- to latter April (Table 1). All of our samples came from fish retained after grading.

At Round Butte Hatchery, eggs were hatched in early December. Fry remained in Heath trays until late January or early February, when they were transferred to tanks and fed for the first time. They were transferred outside to a raceway in mid-March, reared in constant 10°C groundwater, and fed three to five times per day according to a projected growth schedule. In mid-April of their second spring, smolts were trucked from the hatchery to a release site just below Pelton Reregulating Dam (Table 1).

Pelton Ladder received approximately 60% of the nearly 1-year-old fish from Round Butte Hatchery in late November. The fish were placed in three 100-m sections separated by drum screens. The ladder is 3.3 m wide and water is 2.4 m deep, so the system is much larger than conventional hatchery raceways. Fish in the ladder were fed once per day, 5 d/week, at a lower rate than hatchery fish. However, a considerable amount of natural invertebrate production in the ladder also provided food. Daily temperature ranges were measured at Pelton Regulating Dam (Bill Nyra, Round Butte Hatchery, personal communication; Figure 2). Fish were allowed to leave the ladder volitionally during latter April (Table 1).

Fish sampling.—Fish from three brood years were sampled: brood year 1988 (BY88), spawned in September 1988 and sampled from September 1989 to April 1990; brood year 1989 (BY89), spawned in September 1989 and sampled from October 1990 to April 1991), and brood year 1990 (BY90), spawned in September 1990 and sampled from October 1991 to April 1992. Production fish, marked with coded wire tags (CWT), were sampled monthly at all facilities through their first fall and second winter until February; thereafter, they were sampled every 2 weeks through release in mid- to late April. At Warm Springs, we sampled a high-density raceway (Warm Springs-H, about 50,000 fish) and a low-density raceway (Warm Springs-L, about 25,000 fish BY88 and BY89 and about 13,000 fish BY90). Two raceways were sampled at Round Butte until fish were transferred to Pelton Ladder, after which fish in one raceway at the hatchery and in the lowest section of Pelton Ladder were sampled (each of the three fish rearing sections of the ladder contained fish with a different tag code). Fish from the tag group destined for release from Pelton Ladder are referred to as Pelton Ladder fish throughout the paper. Rearing densities at release are shown in Table 1.

Three samples of 15 fish were taken from each raceway on each sampling date. Fork length (mm), weight (g), and sex (after dissection) of each fish were noted. The first 15 fish obtained from a raceway were used to determine baseline plasma cortisol. Fish were dipnetted and immediately placed in a lethal concentration of tricaine methanesulfonate (MS-222). Fish were measured and then the caudal peduncle was severed; blood was collected

in a heparinized glass tube, placed on ice until all baseline cortisol samples were collected, and then centrifuged; plasma was removed and stored on dry ice. Sampling occurred after normal daily hatchery operations had begun, so although cortisol measurements were baseline with reference to stress challenge fish (below), they do not necessarily represent values for unstressed fish.

Fifteen stress challenge fish were dipnetted and immediately placed in a perforated bucket suspended in a raceway such that water barely covered their backs. After 1 h, fish were placed into a lethal concentration of MS-222 and plasma was collected as described above.

The third sample was dipnetted and placed live into a bucket of water. Fish were killed one at a time in MS-222. Plasma was collected as described above; then about 0.1 g of liver tissue was removed, flash frozen with liquid nitrogen, and stored on dry ice. Finally, gill tissue was collected as described by Zaugg (1982a) and stored on dry ice.

Fish could not be obtained with a dip net at Pelton Ladder. Instead, a 1.3-m-long × 1.3-m-wide × 10-cm-deep net was used to capture fish attracted to feed thrown on the water. All samples were collected from one haul of fish. Fifteen fish were immediately killed in MS-222 for baseline cortisol samples; another 15 fish were placed into the stress bucket and the stress challenge was begun immediately. A final 15 fish were placed live into a bucket and held until the other fish were processed; then tissues sampled as described above.

Laboratory methods.—Gill Na^+,K^+-ATPase (hereafter, ATPase) activities were measured as described by Zaugg (1982a). Plasma thyroxine (T_4) values were determined according to Dickhoff et al. (1982). Plasma cortisol was measured by the method of Redding et al. (1984). Plasma insulin-like growth factor-I (IGF-I) was quantified as described by Moriyama et al. (1994). Liver glycogen was measured as described by Wedemeyer and Yasutake (1977).

Calculations and statistics.—The smolt-to-adult return ratio for each tag group was obtained from the Pacific States Marine Fisheries Commission's (PSMFC) Regional Mark Information System in Gladstone, Oregon. Smolt-to-adult return was calculated as SAR = 100(number of tags collected from the hatchery and fisheries)/(number of tagged juveniles released). We examined SARs in relation to measured smolt characters. In addition to measures already mentioned, we calculated condition factor as $K = 10^5$(weight, g)/(length, mm)^3 and specific growth rates from February through April (spring) as SGR = 100. $\text{Log}_e (L_2 - L_1)/(d_2 - d_1)$, where L_2 = mean length on day (d) 2 and L_1 = mean length on day 1, and $(d_2 - d_1)$ is the number of days between measurements. Spring specific growth was measured over the periods 21 February–3 April 1990 (43 d) for BY88, 6 February–16 April 1991 (67 d) for BY89, and 5 February–7 April 1992 (73 d) for BY90.

We had two overall goals in analyzing the data collected: to describe differences in smolt characters among rearing facilities and among years; and to evaluate smolt characters as smolt quality indices. Analysis of smolt characters began with a two-way analysis of variance (ANOVA) with hatchery release group and date as the main effects. If significant differences were found ($P \leq 0.05$), the results were further examined by one-way ANOVA in which seasonal differences within a group or differences between hatchery groups on a given date were examined. Fisher's protected least significant difference (PLSD) multiple-range test was used to examine differences between individual means if one-way ANOVA indicated a significant difference. Significant seasonal changes within a given group are simply discussed in the text of the results, and differences between groups on a given date are indicated in the figures.

Many of the biochemical measures proposed for use as smolt indices show a cyclic pattern of change during the spring smolting season. Fish may be released from a hatchery either before or after the ''peak'' in a smolting cycle; thus a simple evaluation of the value of a character at release may not give an accurate indication of the progression of fish through the smoltification process. We used two analyses of each smolt character to fairly evaluate each character for whatever useful signal it may contain and to obtain some consensus on which method might prove most useful in extracting information from smolt indices. Specifically, we chose to evaluate either maximal or minimal values for each character, in each group of fish, found during the spring or the change (Δ) in character value (spring maximum − spring minimum, February through April). Spring Δ was calculated for each character, for each group, and for each year, then averaged over all 3 years fish were sampled. A one-way ANOVA was used to determine if Δ values differed significantly between groups over the years, indicating whether groups showed consistent changes in a character over all years. Differences in SAR, for all years combined,

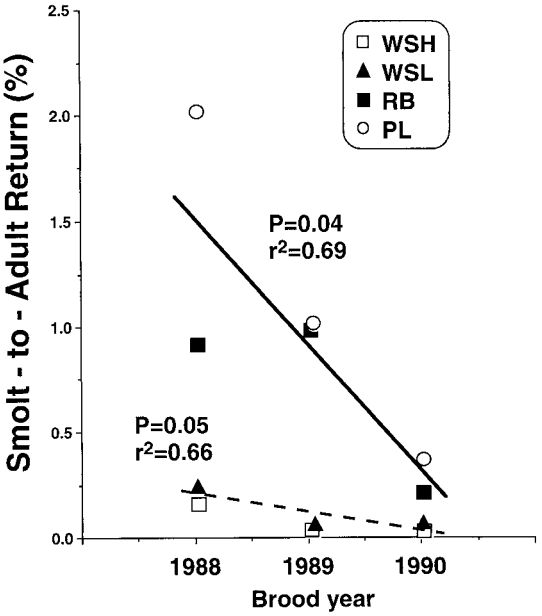

FIGURE 3.—Smolt-to-adult returns (SAR) of tagged chinook salmon released from Round Butte (RB), Pelton Ladder (PL), or Warm Springs facilities (WSH, high-density raceway; WSL, low-density raceway) for brood years 1988, 1989, and 1990. The solid regression line is for pooled Round Butte–Pelton Ladder data; the broken regression line is for combined Warm Springs data.

were determined with a Kruskal–Wallis nonparametric ranks test (Zar 1984). In addition, the relation between year of release and SAR was determined with linear regression. The regression lines for Deschutes River (Round Butte and Pelton Ladder) and Warm Springs fish were compared with a *t*-test (Zar 1984). A Spearman rank correlation test was used to assess the relation of each smolt character to SAR over all 3 years (both peak and Δ character). Simple linear regression was used to compare release length and spring growth rate to SAR within single brood years and was used to relate spring growth rate to average IGF-I or ATPase (values found for dates February through April). All statistics were calculated with Statview II software (Abacus Concepts Inc., Cupertino, California).

Results

Smolt-to-Adult Returns

Smolt-to-adult return varied by an order of magnitude among groups in each year (Figure 3). For example, returns for BY88 ranged from 2.0 (Pelton Ladder) to 0.14% (Warm Springs-H), whereas BY90 returns ranged from 0.35 (Pelton Ladder) to 0.01% (Warm Springs-H). The SAR was consistently greater for Pelton Ladder and Round Butte fish than for Warm Springs-L and H fish; overall, average SAR differed significantly among groups ($P = 0.04$). Significant decreases in SAR from BY88 to BY90 were revealed for Deschutes River and Warm Springs River fish by regression analysis (Figure 3). The two regression lines (Deschutes versus Warm Springs) were significantly different ($t = 2.55$, $P < 0.05$). These data suggest that there were consistent, significant differences in smolt performance associated with fish released from Round Butte and Pelton Ladder relative to Warm Springs (L and H) fish.

Smolt Characters

The average size of released fish differed consistently and significantly among facilities; Round Butte fish were 165–175 mm long at release, Pelton Ladder fish 150–160 mm, and Warm Springs-L and H fish 130–140 mm (Figure 4). Differences in body weight were similar to those of body length (Figure 5). Dip-net samples did not produce precise size estimates, because fish sometimes seemed to decrease in size between successive sampling dates. The samples did show overall size increases through time.

Spring growth rates (length) of Round Butte and Pelton Ladder fish were generally greater than 0.25%/d whereas those of Warm Springs-L and H fish were less than 0.15%/d (Figure 6). Over all 3 years combined, Round Butte and Pelton Ladder fish grew significantly faster than Warm Springs fish (Table 2). Growth rate did not differ significantly between the high- and low-density raceways at Warm Springs nor between Round Butte and Pelton Ladder. Overall, Round Butte and Pelton Ladder fish showed spring weight gains ranging from 15 to 30 g and Warm Springs-L and H fish showed weight gains ranging from 2 to 10 g (Figure 5).

Condition factors changed significantly through spring in all groups in all years (Figure 7). Spring condition factors were consistently highest for Round Butte fish, intermediate for Pelton Ladder fish, and lowest for Warm Springs fish. Condition factors decreased in all groups over the spring but ΔK did not differ significantly among groups over all years combined (Figure 8a; Table 2).

Gill ATPase activities increased strikingly and significantly from February through April at both Round Butte and Pelton Ladder in all years (Figure 9). Lesser but still significant ATPase increases also occurred in Warm Springs-L and H fish by

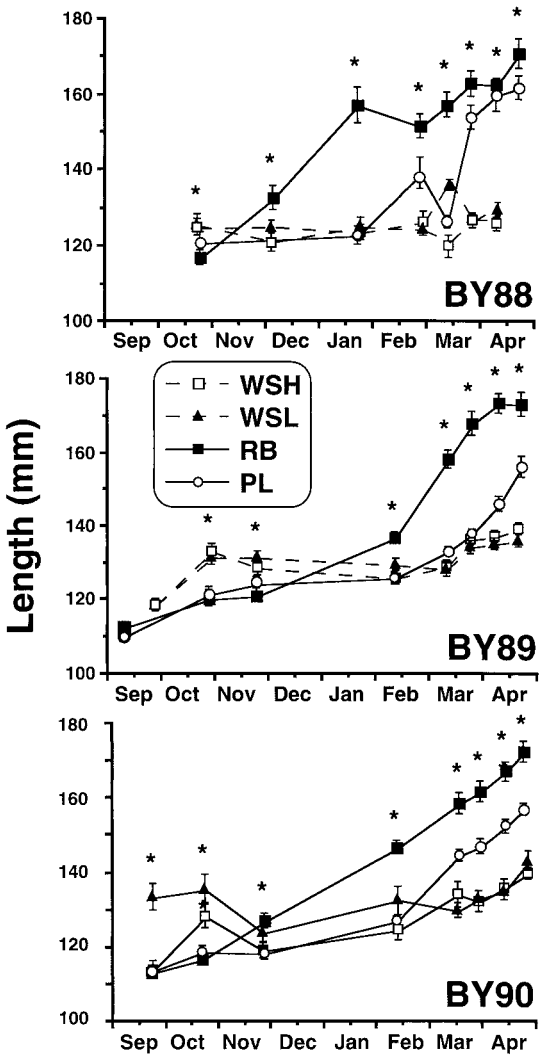

FIGURE 4.—Fork lengths (means ± SE) of juvenile chinook salmon through fall and second-winter rearing to their April release from Round Butte (RB), Pelton Ladder (PL), and Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

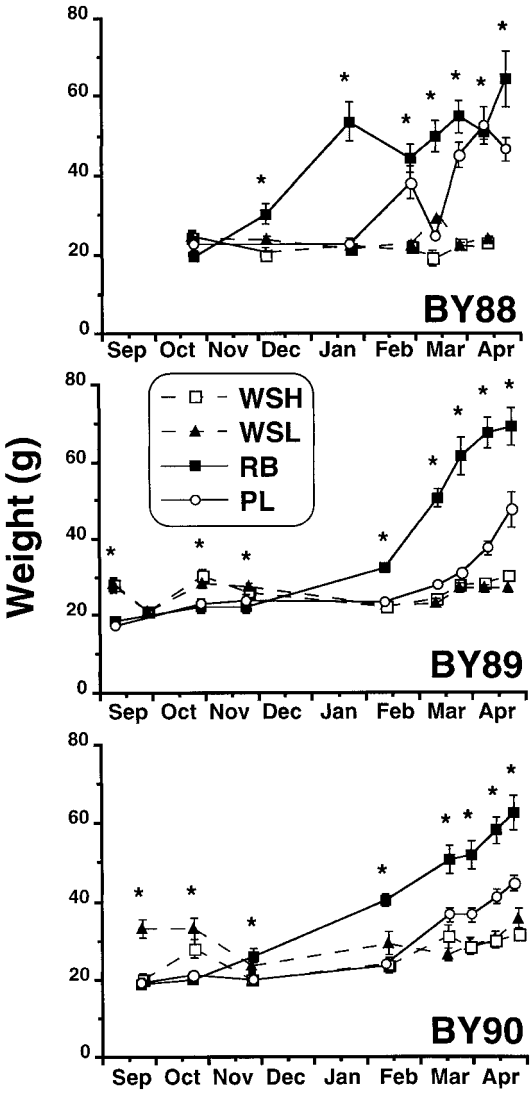

FIGURE 5.—Weights (means ± SE) of juvenile chinook salmon through fall and second-winter rearing to their April release from Round Butte (RB), Pelton Ladder (PL), and Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

April in all years (Figure 8b; Table 2). Thyroxine also increased significantly in all groups in the spring (Figure 10). Fish from Pelton Ladder tended to have higher T_4 values than did fish from other groups, most notably in BY90. Within groups, ΔT_4 ranged from 2.5 to 12 ng/mL but did not differ significantly among groups (Figure 8c; Table 2).

Plasma cortisol levels were significantly elevated in all groups in all years during the spring (Figure 11). Fish in Round Butte and Pelton Ladder consistently had large spring increases (>20 ng/mL). Fish in Warm Springs-L and H had variable responses (Figure 8d); spring elevations ranged from less than 10 to greater than 40 ng/mL. Overall, there was no significant difference in Δcortisol (Table 2).

There was a consistent seasonal increase in plas-

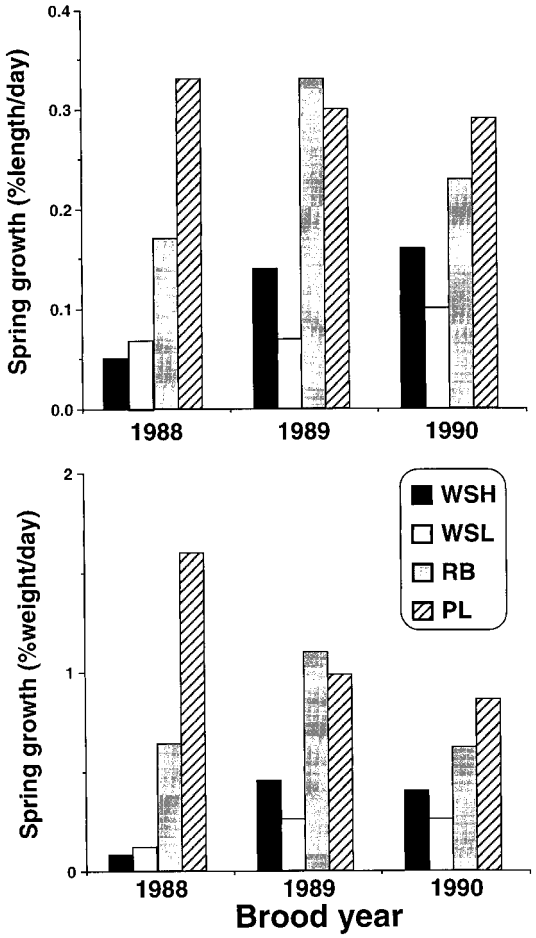

FIGURE 6.—Spring growth rates in length (above) and weight (below) of juvenile spring chinook salmon before they were released from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990.

ma cortisol response to stress challenge in all groups (Figure 12). Stress response was always greater in the spring than in the fall. There was no consistent difference between groups in spring stress cortisol level (SCL); differences were found among groups in March, but rarely in February or April (Figure 12). Spring changes in SCL (ΔSCL) were similar in all groups of BY88 and BY90 fish, though variable in BY89 (Figure 8e); no significant differences in stress cortisol between groups occurred overall (Table 2).

Insulin-like growth factor-I increased significantly during spring in Round Butte and Pelton Ladder fish of both BY 89 and 90 cohorts, and plasma IGF-I values were significantly higher in these fish than in both Warm Springs groups on most dates (Figure 13). Overall, ΔIGF-I was greater in Round Butte and Pelton Ladder fish than in Warm Springs-L and H fish (Figure 8f; Table 2).

Liver glycogen levels decreased consistently and significantly through the spring in all groups in all years (Figure 14). In BY88 groups, liver glycogen was appreciably greater in Round Butte fish than in Warm Springs-L and H fish through the spring; Pelton Ladder fish had intermediate levels. All BY88 and BY90 fish had Δliver glycogen values above 1.3 mg/g (Figure 8g). Among BY89 groups, Round Butte and Pelton Ladder fish had a similar Δliver glycogen levels, but Warm Springs-L and H fish had glycogen levels that were rather low in February and remained low through April. Overall, there was no significant difference in Δliver glycogen between groups (Table 2).

Hatchery Comparisons

The marked difference in smolt-to-adult survival between Round Butte–Pelton Ladder smolts and those from Warm Springs-L and H in each of the 3 years suggests that any character that would be an accurate smolt quality indicator should also show consistent differences between Deschutes and Warm Springs river fish over those 3 years. Spring growth rates and ΔATPase values for Round Butte and Pelton Ladder smolts were significantly greater than those for Warm Springs-L and H smolts for all 3 years combined (Table 2). The ΔIGF-I values for Round Butte fish were significantly greater than those for Warm Springs-L and H smolts over the 2 years IGF-I was measured. The ΔIGF-I values for Pelton Ladder smolts were greater than those of Warm Springs-H fish, though not significantly different from Warm Springs-L values. No other characters showed consistently significant differences in spring change when Round Butte and Pelton Ladder smolts were compared to Warm Springs-L and H smolts over the 3 years. When spring growth rates, ATPase activities, and IGF-I data are regressed against each other, strong and significant relations were found among them (Figure 15).

To determine whether any smolt characters were related to SAR, a Spearman rank correlation test was conducted between each character (represented by absolute maxima or minima and by spring changes, Δ) and SAR, including data from all 3 years (Table 3). Significant relations were only found with ATPase, IGF-I, spring growth rate, and ΔATPase. Release length was only marginally nonsignificant ($P = 0.06$). In addition, the relation

TABLE 2.—Mean changes (Δ, maximum − minimum, February–April) and standard errors (in parenthesis) in spring chinook salmon smolt characters over three brood years (1988, 1989, 1990) for Round Butte, Pelton Ladder, and Warm Springs facilities. Differences in mean spring change between facilities were assessed with 1-way ANOVA and Fisher's PLSD multiple-range test. For characters with significant ANOVAs, values along a row with no letter in common are significantly different ($P < 0.05$).

Character	Round Butte	Pelton Ladder	Warm Springs		ANOVA	
			Low density	High density	*F*	*P*
Spring growth (% length/d)	0.24 (0.05) z	0.31 (0.01) z	0.12 (0.03) y	0.07 (0.02) y	14.0	0.002
Δ Condition (*K*)	0.07 (0.015)	0.10 (0.06)	0.03 (0.003)	0.05 (0.003)	0.9	0.47
Δ ATPase	15.9 (1.3) z	16.3 (2.4) z	6.3 (0.9) y	7.2 (0.8) y	12.9	0.002
Δ T_4	3.8 (1.1)	7.6 (2.1)	6.4 (0.5)	7.2 (0.8)	1.4	0.31
Δ Cortisol	33.9 (3.4)	33.3 (4.3)	20.9 (10.3)	14.3 (3.5)	2.5	0.13
Δ Stress cortisol	45.0 (5.2)	44.2 (6.9)	47.7 (8.1)	40.4 (13.9)	0.1	0.95
Δ IGF-I[a]	17.3 (4.3) z	15.1 (3.3) zy	7.5 (1.5) yx	4.7 (2.0) x	6.5	0.05
Δ Liver glycogen	1.8 (0.2)	2.3 (0.2)	1.3 (0.5)	1.3 (0.5)	1.5	0.3

[a] Brood years 1989 and 1990 only.

of spring growth rate to SAR was tested individually for each brood year (Figure 16a). Significant relations were found between spring growth rate and SAR for BY88 ($P = 0.006$, $r^2 = 0.998$) and BY89 ($P = 0.03$, $r^2 = 0.932$); the relation for BY90 was marginally nonsignificant ($P = 0.07$, $r^2 = 0.857$). A similar analysis was conducted to examine the relation between length at release and SAR (Figure 16b). In no year was there a significant relation (BY88: $P = 0.25$, $r^2 = 0.559$; BY89: $P = 0.09$, $r^2 = 0.82$; BY90: $P = 0.44$, $r^2 = 0.44$).

Discussion

This study documents dramatic differences in smoltification and SAR for chinook salmon raised at and released from facilities on or near the Deschutes River. A strong relationship was found between spring growth rate, smoltification, and SAR. These data suggest that success of hatchery releases may vary widely according to specific attributes of the released fish. In addition, this work emphasizes the importance of promoting smoltification of salmon juveniles in hatchery environments to increase postrelease survival. Finally, it suggests that the relative success of released fish may be predicted by measuring their growth rates during the spring smolting period.

We monitored four groups of fish in each year, two from Warm Springs Hatchery (raised at low and high densities), one from Pelton Ladder, and one from Round Butte hatchery. We did not perform an explicit overall analysis of differences between the two groups from Warm Springs; however, there was little qualitative or quantitative difference between the two groups, especially with regard to release size, spring growth rate, ATPase activity, or SAR. Therefore, for the rest of the discussion, we will simply refer to Warm Springs fish and not make a distinction between the low- and high-density groups.

Smolt-to-Adult Return

The SAR dropped dramatically from BY88 to BY90 at all facilities, suggesting either dramatic, correlated differences in the smolts released over the 3 years of this study or dramatic changes in environmental conditions over this period. Adult return rates decreased for many salmon runs (coho salmon *Oncorhynchus kisutch,* chinook salmon, sockeye salmon *O. nerka,* and steelhead *O. mykiss*) in the Columbia River from 1992 (4-year-old adult returns from BY88 releases) to 1994 (4-year-old adult returns from BY90 releases) (PSMFC 1996). These results indicate that environmental variation external to hatcheries caused the differences in SAR between years. Even though SARs decreased for each successive brood year of fish we examined, the rank order of SARs among release groups remained similar across years. Likewise, smolt characteristics differed consistently among groups across brood years. Together, these findings suggest that smolt quality makes an important contribution to determining relative SAR, but that smolt quality cannot override large-scale environmental changes.

The validity of our conclusions depends on the accuracy of the SAR values reported by the PSMFC. The PSMFC and cooperating agencies make extensive efforts to collect tags from ocean fisheries, but no ocean recovery of tags was reported for any of the groups we monitored. Ocean tag recoveries often require large numerical expansions when SARs are calculated, because ocean fisheries may not be thoroughly sampled. For our

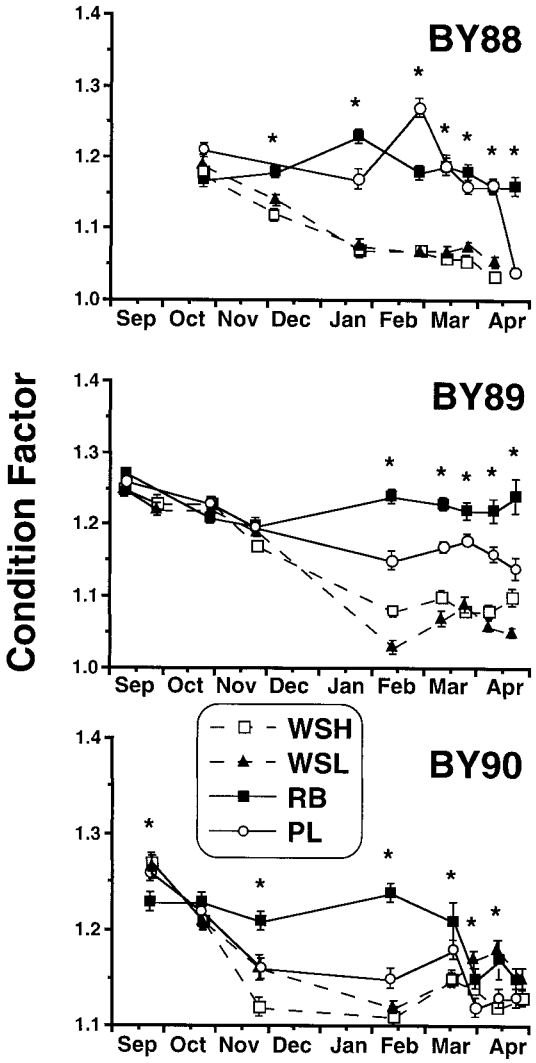

FIGURE 7.—Condition factors (mean ± SE) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

groups, most tags were recovered from fish returning to fish traps at Pelton Ladder and Warm Springs Hatchery; these numbers were not expanded. The rest of the tags were collected from Columbia River fisheries, where fisheries personnel collect snouts for tag analysis. In every case, more than 60% of the estimated recoveries for a tag group came from tags actually recovered from fish, which means that less than 40% of recovery was actually estimated. Thus the SARs calculated by PSMFC for groups we monitored are not likely to be unduly influenced by ''random'' tag recoveries that might be subjected to large expansions, producing erroneous SAR estimates. Additionally, adult chinook salmon from Warm Springs, Round Butte, and Pelton Ladder returned to nearly the same geographic part of one Columbia River tributary; they should have been subjected to quite similar fishing pressures and should have similar reporting rates for tags. Thus, there should be no bias towards recovery of tags from any one group.

The SARs for the groups we monitored were similar to those of other tag groups released from Warm Springs, Round Butte, and Pelton Ladder. In each year of the study, two tag groups were released from Round Butte (two different raceways), 3 tag groups were released from Pelton Ladder (three separate rearing sections in the ladder) and at least 12 tag groups were released from Warm Springs (different raceways). These groups may not be replicates of the groups we monitored, but comparing them will at least let us judge whether the SARs we report for the groups monitored are similar to those of other groups released from the same facility. For BY88, SARs of fish from Pelton Ladder ranged from 1.8 to 2.1%, SARs of Round Butte fish were 0.8 and 1.1%, and SARs of Warm Springs fish ranged from 0.04 to 0.4% (average, 0.17%). For BY89, SARs of fish from Pelton Ladder ranged from 0.8 to 1.0%, SARs of Round Butte fish were 0.5 and 0.8%, and SARs of Warm Springs fish ranged from 0.0 to 0.16% (average, 0.03%). For BY90, SARs of fish from Pelton Ladder ranged from 0.2 to 0.4%, SARs of Round Butte fish were 0.2 and 0.3%, and SARs of Warm Springs fish ranged from 0.00 to 0.024% (average, 0.015%). In all cases, SARs of our monitored groups were within the ranges and near the averages of SARs for other tagged groups. In each year, SARs of Warm Springs fish were an order of magnitude less than those of fish released from either Round Butte or Pelton Ladder. There was some overlap in SARs of fish from Round Butte and Pelton Ladder, but average return rates of Pelton Ladder fish were consistently greater than those for Round Butte fish. These data lend us confidence that the data reported in Figure 16 and Table 3 are representative.

Smolt Characters

We found significant spring changes in each smolt character for each group of fish in each year. In addition, there were consistent, sustained differences between Round Butte–Pelton Ladder and

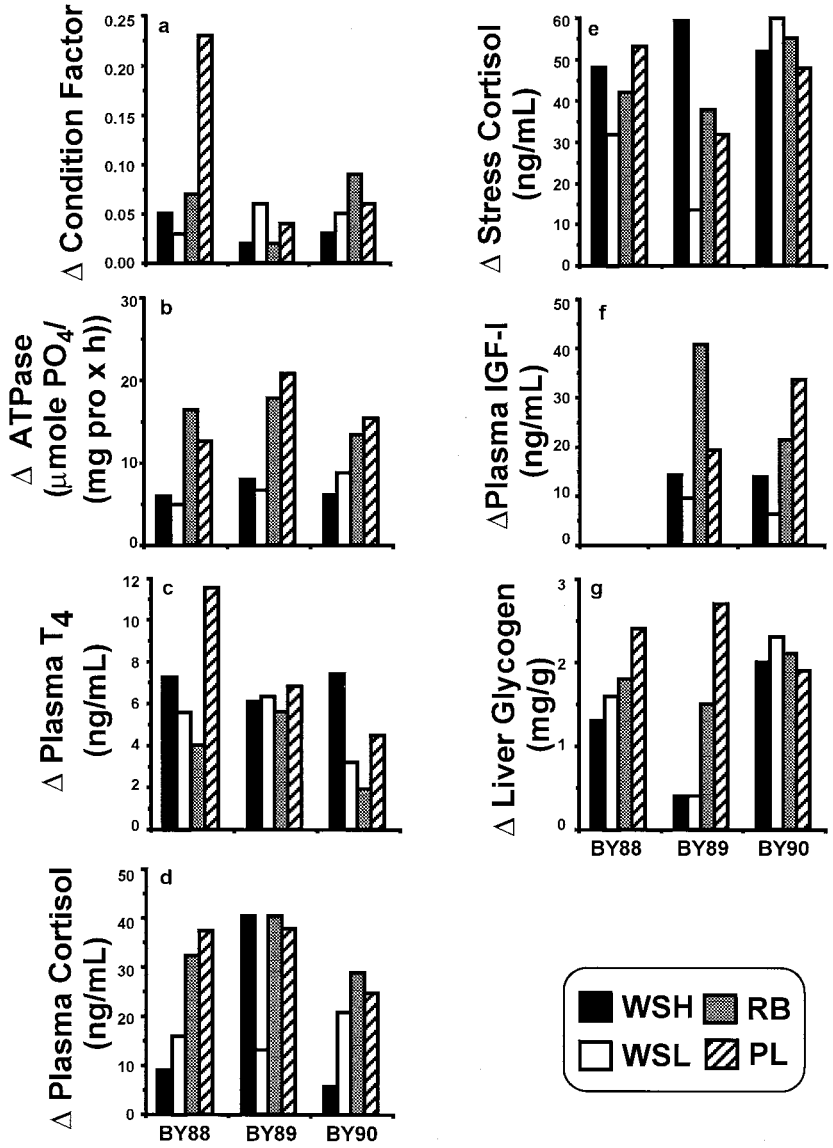

FIGURE 8.—Spring changes (Δ, maximum value − minimum value, February–April) in **(a)** condition factor, **(b)** gill Na^+,K^+-ATPase activity (pro = protein), **(c)** plasma thyroxine (T_4), **(d)** plasma cortisol, **(e)** plasma cortisol of fish subjected to a stress challenge, **(f)** plasma insulin-like growth factor-I (IGF-I), and **(g)** liver glycogen for juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990.

Warm Springs fish for many smolt characters. This illustrates the difficulty in trying to relate physiological and biochemical changes during smoltification to SAR: everything changes and appears to give a relevant signal. However, further inspection showed that whereas all characters provided information about smoltification, not all were good predictors of SAR.

Spring growth rate, IGF-I, and ATPase activity all showed significant, positive relations with SAR. However, these characters were significantly correlated with each other, probably because of a common endocrine foundation. Pituitary growth hormone mediates somatic growth, directly stimulates production of IGF-I, and either directly or indirectly stimulates ATPase activities and (or)

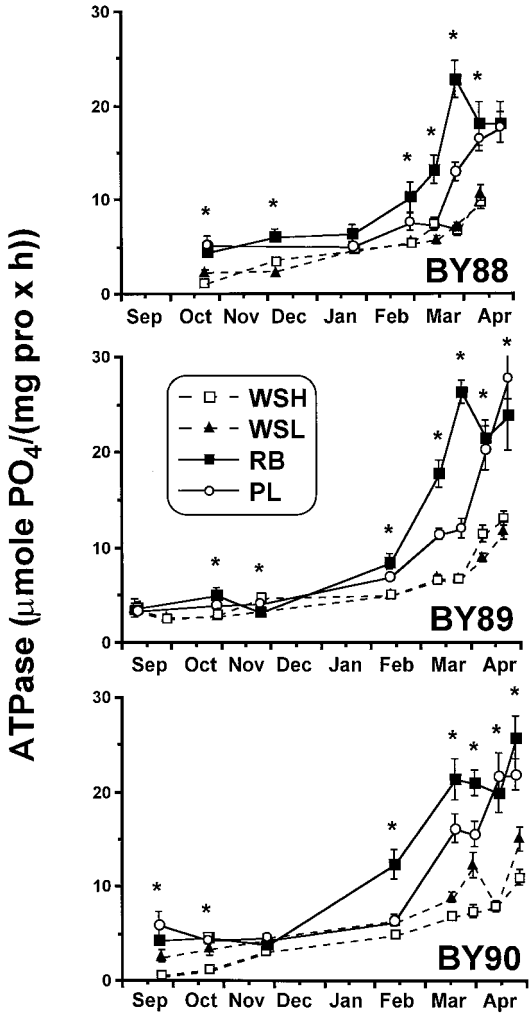

FIGURE 9.—Gill Na^+,K^+-ATPase activities (means ± SE; pro = protein) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

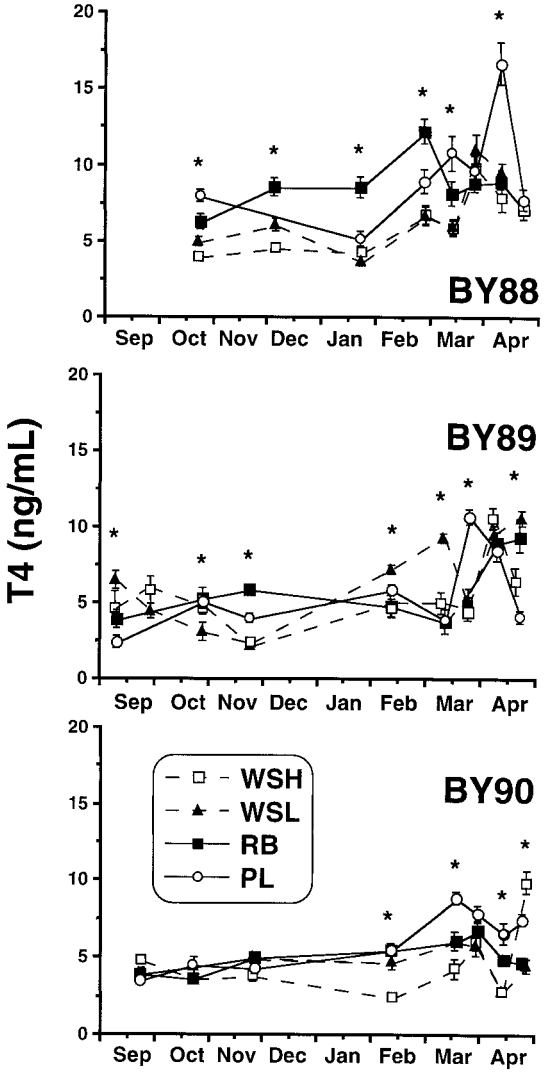

FIGURE 10.—Plasma thyroxine (T_4) levels (means ± SE) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway ; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

hypo-osmoregulatory ability in salmonids (Komourdjian et al. 1976a; Clarke et al. 1977; Bolton et al. 1987; Richman and Zaugg 1987; Madsen 1990; Duan et al. 1993; Sakamoto et al. 1993; Boeuf et al. 1994; Moriyama 1995; McCormick 1996). In addition, there appears to be a correlation between the environmental regulation of growth hormone (GH) and the environmental regulation of smoltification. The GH–IGF-I axis is influenced by photoperiod, water temperature, and nutritional state (Komourdjian et al. 1976b; Bjornsson et al. 1989; Stefansson et al. 1991; Duan and Plisetskaya 1993; Bjornsson et al. 1995; McCormick et al. 1995). Smoltification also is regulated by photoperiod and temperature (Saunders and Henderson 1970; Wagner 1974; Ewing et al. 1979; Clarke and Shelbourn 1985; Duston and Saunders 1990; Solbakken et al. 1994). In addition, plasma GH levels increase during smoltification (Sweeting et al.

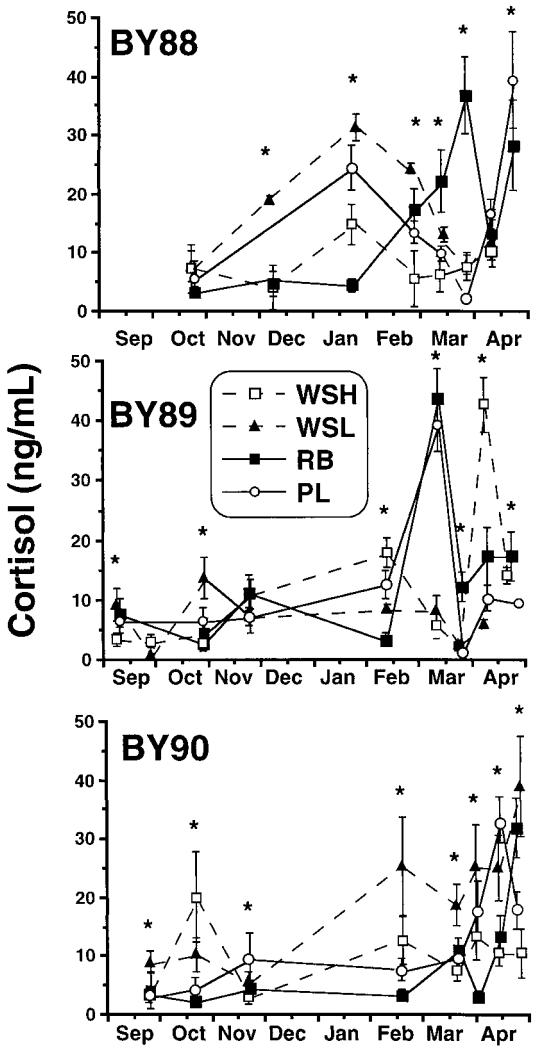

FIGURE 11.—Plasma cortisol levels (means ± SE) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

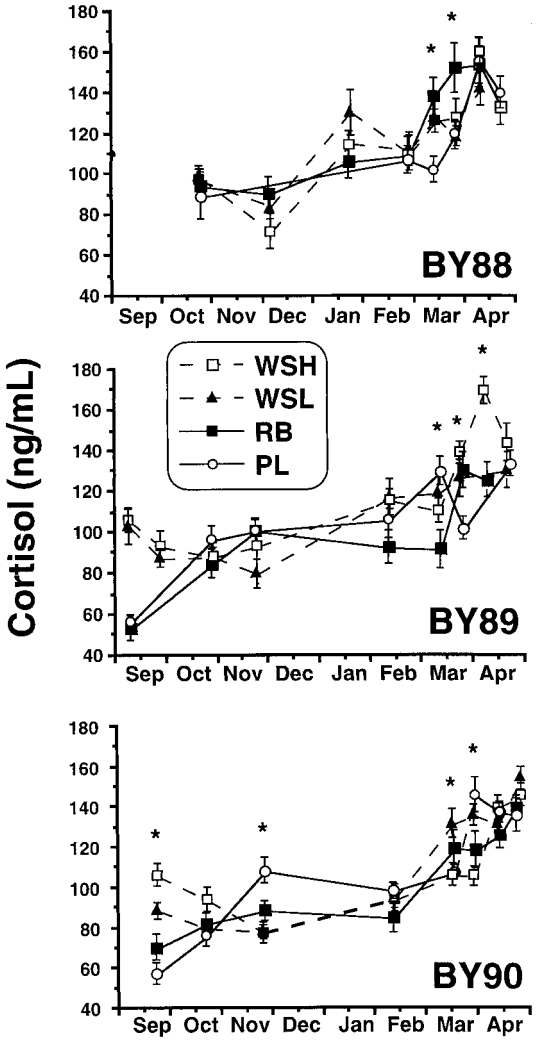

FIGURE 12.—Plasma cortisol levels (means ± SE) of juvenile chinook salmon subjected to a stress challenge before their release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

1985; Boeuf et al. 1989; Prunet et al. 1989; Young et al. 1989). Together, these data strongly support a primary role for GH in the regulation of smoltification (Dickhoff et al. 1997) Our results support that idea and in addition, suggest that characters associated with growth, IGF-I, and ATPase are good candidates for smolt quality indicators.

We cannot ascribe differences in SAR to a simple dichotomous difference in smolting; all groups of fish showed signs of smolting. Gill ATPase activity, T_4, cortisol, and SCL values all showed the expected increases in the spring, and condition factor and liver glycogen values showed the expected decreases. Rather, there was a quantitative difference in the degree to which endocrine and physiological factors associated with smoltification changed. This difference is most apparent in the ATPase data: smolts from both Round Butte and Pelton Ladder showed large, sustained increases in activity through the spring while smolts from

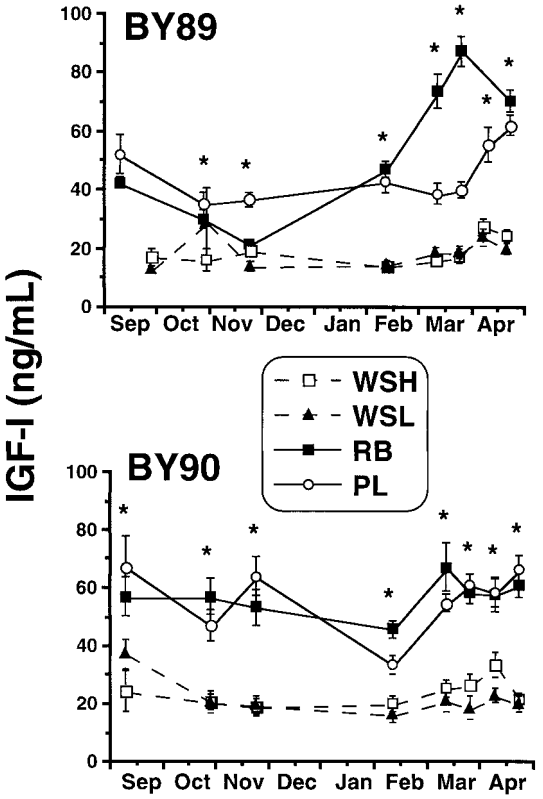

FIGURE 13.—Plasma insulin-like growth factor-I (IGF-I) levels (means ± SE) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1989 and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

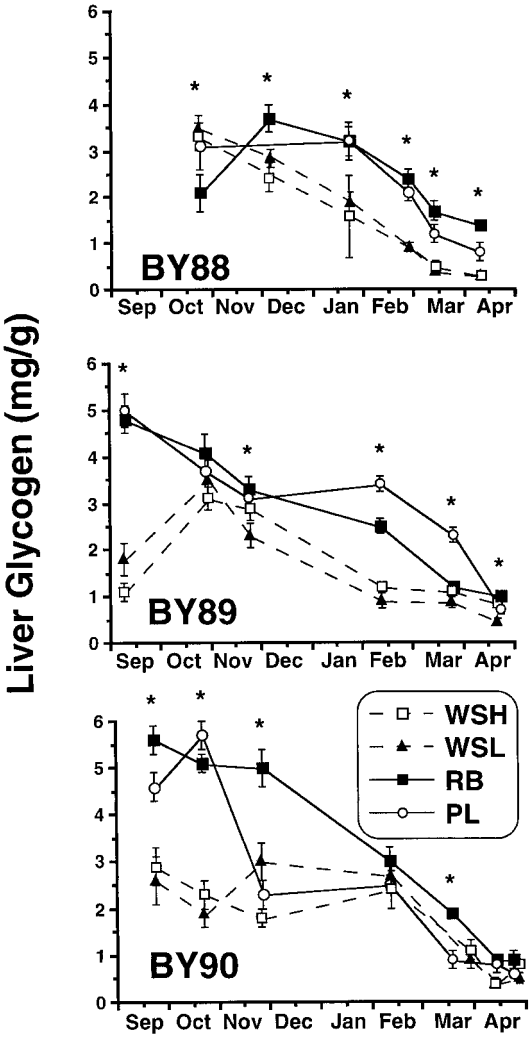

FIGURE 14.—Liver glycogen levels (means ± SE) of juvenile chinook salmon before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. An asterisk indicates a significant difference among groups on a given date (1-way ANOVA, $P < 0.05$).

Warm Springs showed lesser and later increases in ATPase activity. The simple quantitative differences in ATPase between these groups appear to accurately reflect differences in smolt quality as measured by SAR.

Analysis of maximum or minimum character values and analysis of the magnitude of change (Δ) in characters over the spring gave similar results except for condition factor and liver glycogen. The basic precept of smolt indicators is that one compares the level of a character over time in one group of fish to the level in another group. Fish with either the ''highest'' or ''lowest'' value are the ''best.'' In the data presented here, T_4, cortisol, SCL, and ATPase baseline levels (winter) were similar between all groups, so their peak levels and absolute changes gave equivalent information. Winter values for liver glycogen and condition factor differed considerably between groups, so their spring changes and minimum values yielded different results.

Differences in sample storage conditions and inter-assay variation will inevitably result in differences in baseline values of characters compared over several years. Thus Δ values of characters might best summarize smolt changes (Table 2). Our analysis showed that only spring growth rate, ΔATPase, and ΔIGF-I differed significantly between hatchery groups when years were combined.

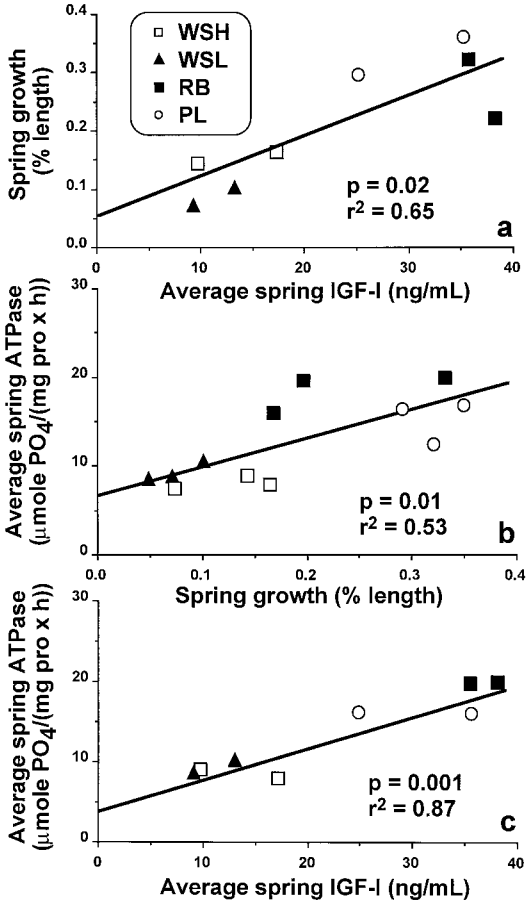

FIGURE 15.—February–April relationships (N = 5 each) between **(a)** average IGF-I and specific growth rate, **(b)** specific growth and average gill ATPase activity, and **(c)** average IGF-I and average ATPase activity for chinook salmon smolts before release from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years 1988, 1989, and 1990.

These are also the characters that showed significant relations to SAR, suggesting that spring Δ values provide useful tools for measuring relative differences in smoltification and assessing smolt quality.

The validity of our results for smolt characters depends on the accuracy with which we measured those characters. Some error was associated with measurement of fish size because unexpected decreases in length and weight were found on a few occasions. However, most of the ''fluctuation'' in size occurred in BY88; as the sampling crew improved its abilities, size estimates became more repeatable (BY 89 and 90). Several findings were clear: fish were consistently different in size between Warm Springs and other facilities; fish did not consistently differ in size between density treatments at Warm Springs; and different groups of fish showed distinct trends. Overall, assessment of neither size nor growth rate appears compromised, and we are skeptical that errors in size measurement seriously affect our conclusions.

TABLE 3.—Spearman correlations (ρ, with associated probabilities) of smolt-to-adult returns of chinook salmon with maximum or minimum spring value of smolt characters (February–April) or with spring changes (Δ) in those characters. Correlations are for brood years 1988, 1989, and 1990. Fish were released from Round Butte, Pelton Ladder, and Warm Springs facilities (N = 12 for all relations except N = 8 for IGF-I). Asterisks indicate $P < 0.05$.

Character	ρ	P
Spring maximum or minimum		
Fork length at release	0.57	0.06
Condition (K)	0.25	0.42
ATPase	0.64	0.03*
T_4	0.08	0.82
Cortisol	0.47	0.12
Stress cortisol	−0.07	0.83
IGF-I	0.80	0.03*
Liver glycogen	0.46	0.13
Spring change		
Spring growth rate	0.69	0.02*
Δ Condition (K)	0.35	0.25
Δ ATPase	0.68	0.03*
Δ T_4	0.08	0.81
Δ Cortisol	0.53	0.08
Δ Stress cortisol	−0.27	0.37
Δ IGF-I	0.64	0.09
Δ Liver glycogen	0.44	0.15

Sampling errors could have been associated with physiological characters as well, because only 15 fish were sampled from groups of up to 50,000 fish. However, raceways were sampled every 2 weeks throughout the spring, so our estimates of population status did not depend on single samples. Different characters showed different temporal trends and differing degrees of variability. It is unlikely that we would find distinct seasonal trends if our sampling was dominated by random error.

We might have reduced sampling error either by increasing sample size, by crowding fish in a raceway prior to taking samples, or by trying to eliminate variation in smolt characters due to hatchery practices (perhaps by sampling before morning hatchery operations began). However, our goal was to sample in a manner acceptable to hatchery managers and one that was logistically tractable

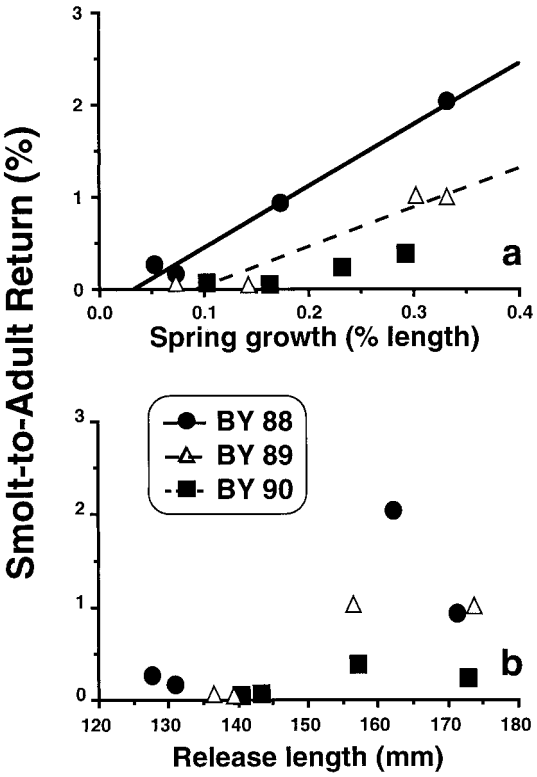

FIGURE 16.—Relationship between **(a)** growth rate and smolt-to-adult return (SAR) and **(b)** release length and SAR for individual brood years of chinook salmon smolts released from Round Butte (RB), Pelton Ladder (PL), or Warm Springs (WS) facilities (H = high-density raceway; L = low-density raceway) for brood years (BY) 1988, 1989, and 1990. Data for an individual brood year are connected with a line if there is a significant regression relation ($P < 0.05$).

in terms of numbers of samples. Our results suggest that some smolt characters, regardless of sampling error, were related to SAR. For characters showing no such relation, we cannot distinguish whether a relation was truly absent or obscured by sampling error. However, a character subject to large error under our sampling regime is unlikely to be a practical smolt quality index for use in routine hatchery assessments.

Design of Smolt Quality Studies

Two distinctly different study designs have been used to relate smolt quality to SAR. In one, smolt characteristics are compared between groups released at the same time and place (Bilton et al. 1982; Martin and Wertheimer 1989; Virtanen et al. 1991; this study). In the other, fish are serially released and smolt characteristics are compared to SAR (Ewing et al. 1985; Zaugg 1989; Staurnes et al. 1993). The first design addresses the inherent performance characteristics of the fish released. The other addresses the environmental conditions into which fish are released. Several studies have shown that SAR is affected by the date fish are released (Bilton et al. 1982; Hansen and Jonsson 1989; Mathews and Ishida 1989; Lundqvist et al. 1994). Differences in SAR shown by time-of-release studies may have been due both to differences in the fish released and to changes in the environment. Divergent SARs, however, have often been ascribed to differences in either feeding conditions or predation in the ocean. Ocean conditions may differ (Johnson 1988), but smolt characteristics may also change month-to-month or year-to-year (Zaugg 1989), an additional potential source of differential survival. Simultaneous release of smolts of differing quality allows one to evaluate the importance of smoltification to SAR. Such a design also allows precise development and evaluation of smolt quality indicators. By focusing on time of release and ocean conditions only, one may miss the opportunity to maximize SAR by optimizing smolt quality.

Smolt Indices

A structured basis for discussing smolt indices is needed to sort out the many attributes previously nominated for use and to provide a logical basis for investigating why and how a potential index relates to smolt performance and SAR. We therefore divide potential indices (those measured in this study and others suggested in the literature) into five classes:

- *Performance indices* are measures of a smolt's ability to do a task essential for its survival (e.g., osmoregulatory capacity, migratory behavior). No performance indices are examined in this paper.
- *Directive indices* are factors (hormones) that stimulate the physiological, morphological, and behavioral traits that define a smolt. Our directive indices were T_4, cortisol, SCL, and IGF-I.
- *Functional indices* are attributes arising or changing during smoltification that directly relate, or have been hypothesized to relate, to performance characters. Our functional indices were size and ATPase.
- *Correlational indices* are attributes that change during the process of smoltification but are not directive, nor do they appear to relate to performance. Our correlational indices were con-

dition factor, liver glycogen, and spring growth rate.

- *Conditional indices* are attributes that relate to the overall health or physical robustness of juvenile salmon, but which may or may not change in relation to the smoltification process. We did not study conditional indices.

We discuss these classes in the following sections.

Performance indices.—We do not report any performance evaluations here; however, seawater challenge tests (Clarke and Blackburn 1977) were performed on our fish at release (Zaugg et al. 1991; Dickhoff et al. 1995). Reflection suggests that these tests were flawed. The fish were probably highly stressed, having been netted from raceways and immediately confined in 100-L plastic barrels of 35‰ seawater. Tests were conducted at ambient raceway temperatures, which makes comparisons of measurements between facilities of dubious value. In addition, these fish were released hundreds of kilometers from the ocean. Given well-documented physiological changes that occur during smolt migration (Zaugg et al. 1985; Rodgers et al. 1987; Muir et al. 1994a; Schrock et al. 1994; Haner et al. 1995), a single seawater challenge and subsequent estimate of osmoregulatory ability at the hatchery are unlikely to reflect the animal's ability to osmoregulate when it reaches the ocean.

Performance indices should have significant relations to SAR; the intention of these tests is to directly measure an attribute of smolt performance (such as osmoregulation). Several studies have shown good relationships between osmoregulatory ability and SAR (Virtanen et al. 1991; Staurnes et al. 1993); others have yielded little insight (e.g., Dickhoff et al. 1995). The seawater challenges we conducted did not give us a true measure of the animals' osmoregulatory competence, did not demonstrate seasonal changes in hypo-osmoregulatory ability, and did not allow us to make meaningful comparisons between fish from different facilities. However, other studies have clearly demonstrated that seawater challenge could be used to assess differences in hypo-osmoregulatory ability between groups of salmonids (Clarke and Shelbourne 1985; Johnsson et al. 1994). Thus we suggest care be taken in designing and conducting such tests and interpreting their results.

Directive indices.—Several hormones have been suggested as promoters of smoltification, including T_4, insulin, GH, and cortisol (Dickhoff 1993). Many studies have tried to relate endocrine measures to smolt performance and SAR (Specker and Schreck 1980; Folmar and Dickhoff 1981; Dickhoff et al. 1982; Ewing et al. 1985; Nishioka et al. 1989; Schreck et al. 1989; Virtanen et al. 1991). These results have varied with the species studied, the hormone measured, the performance tested (osmoregulatory capacity, SAR), and the analytical technique used. We found no relation of T_4, cortisol, or SCL to chinook salmon SAR.

It is paradoxical that hormone levels often are unrelated to smolt performance; smoltification is well established as an endocrine-mediated process. Differences in smolt performance should be related to differences in the endocrine factors responsible for promoting performance attributes. However, simple measurement of a given hormone need not provide a good indication of smolt quality. In particular, plasma hormone values show a great deal of variability on time scales of hours to days. Thus, selecting a temporal sampling regime that accurately reflects the biological activity of a hormone is difficult. In addition, the relations between plasma hormone concentrations and the biological activity of hormones are unclear. Hormones must bind to receptors to begin their action (Hadley 1992), and plasma hormone concentrations are functions of both production and clearance rates (Specker et al. 1984; Patino et al. 1985; Schreck et al. 1985; Sakamoto et al. 1991). Specker et al. (1992) showed that tissue triiodothyronine (T_3) concentrations (which might better reflect receptor binding rates) in yearling coho salmon showed poor relations to both plasma T_3 and T_4 concentrations.

It is not surprising that we found no correlation of T_4 with SAR because the full cycle of plasma T_4 should be measured in assessing seawater survival by coho salmon (Dickhoff et al. 1982). The full cycle could not be assessed in this study because all fish were released in April. Overall, we remain cautious about the utility of plasma hormone levels as smolt indices. However, the knowledge of how smoltification is controlled lies with an understanding of the endocrine mechanisms directing the process, so continued study is warranted.

We took advantage of a (then) new technique (described by Moriyama et al. 1994) to measure plasma levels of IGF-I in salmonids, and we report here the first significant relationship between IGF-I and SAR. Fish reared at Round Butte or Pelton Ladder had higher overall IGF-I levels than those at Warm Springs, and smolts from Round Butte or Pelton Ladder showed significantly greater spring elevations in IGF-I (ΔIGF-I). Beckman et al. (1998b) found that relatively fast-growing chinook

salmon smolts had significantly greater spring IGF-I elevations than slower-growing fish regardless of initial size. This suggests that the differences in IGF-I found between Round Butte–Pelton Ladder and Warm Springs smolts were related to differences in growth rate and not to differences in size. Together, these findings encourage further investigation of the significance of IGF-I to the smoltification process and indicate the value of plasma IGF-I levels as a smolt quality index.

Functional indices.—Functional traits should show a good relation to SAR; they are defined as attributes that directly relate to performance. Relatively large size may provide a functional advantage. Studies have shown differences in SAR between relatively large and small smolts for both experimental hatchery groups (Martin and Wertheimer 1989; Virtanen et al. 1991; Farmer 1994; Lundqvist et al. 1994) and wild populations (Ward and Slaney 1988; Ward et al. 1989; Henderson and Cass 1991). We found some evidence for a relation between release size and SAR over the three brood years we studied ($P = 0.06$). But although smolts from Round Butte and Pelton Ladder were consistently larger at release than those from Warm Springs, no significant relation was found between release length and SAR within any single release year. Smolts from Round Butte were always larger at release than those from Pelton Ladder, but SAR from Pelton Ladder was greater than from Round Butte in two (BY88 and BY90) of three years, which is why release size and SAR were not highly related in this study. Some factor in addition to size at release must be contributing to postrelease survival.

Our work does not suggest that smolt size is unimportant. This would contradict a large array of published studies. However, size is a nonspecific attribute that does not indicate whether a fish has begun the smoltification process. In addition, relative size has a functional advantage throughout a fish's life cycle; size benefits are not accrued only at the smolt stage. Finally, size does not always correlate well with smolt attributes (Wagner et al. 1969; Zaugg 1981a, 1982b) making us cautious about its applicability as an indicator of smolt quality.

We found ATPase activity to be a good indicator of smolt quality. Other studies have had mixed results. Zaugg (1989), Zaugg and Mahnken (1991), and Ewing and Birks (1982) showed positive relations between ATPase and SAR for some hatchery releases. In contrast, Ewing et al. (1985), Virtanen et al. (1991), and Staurnes et al. (1993) found no relation between ATPase and SAR. The latter studies compared SAR of smolts released either in different locations or on different dates, which compromises them as tests of ATPase as a smolt quality index. In addition, several studies showed an association between seasonally increasing ATPase and performance characters such as seawater tolerance (Saunders and Henderson 1978; Boeuf and Harache 1982) and migratory readiness (Hart et al. 1981; Zaugg 1981a; 1981b; 1989; Muir et al. 1994b). These studies, combined with our results, support the further use of ATPase as a smolt quality index.

Correlational indices.—Condition factor of juvenile salmon characteristically decreases during smoltification (Hoar 1976). Condition factor changes have been successfully used to discriminate differences in smoltification resulting from photoperiod and temperature manipulations (Saunders and Henderson 1970; Wagner 1974). However, *K* did not yield an important signal with regard to smolt quality in our study. Neither Virtanen et al. (1991) nor Staurnes et al. (1993) found a significant relationship between *K* and SAR for Atlantic salmon *Salmo salar*. In addition, changes in *K* are not specific to smoltification; for example, *K* decreases if fish are starved or otherwise perturbed. Overall, these results suggest that condition factor is a poor candidate for a smolt quality index.

Significant, sustained decreases in spring liver glycogen concentration accompany smoltification (Woo et al. 1978; Sheridan et al. 1985), but the functional advantage of this change is unknown. Further, the relation between liver glycogen and SAR is unclear (Soivio and Virtanen 1985; Virtanen et al. 1991). As with condition factor, changes in liver glycogen are not specific to smoltification; stress and food limitations may lower concentrations (Wedemeyer et al. 1984). We do not recommend liver glycogen level as a smolt quality indicator.

Spring growth rate was an excellent indicator of SAR in our study. Differences in growth rate do not cause differences in smoltification; rather, they reflect differences in the GH–IGF-I endocrine axis. Measuring growth rate over the spring may provide an integrative measure of GH and IGF-I production rates over the same period. In essence, growth rate may be a cumulative measure of directive factors, which may explain the good relationships we found between spring growth rate, ATPase, and SAR. However, growth is not specific to smoltification, so measuring growth rate in summer or winter is unlikely to provide useful infor-

mation about smolt quality for spring-smolting salmonids.

The relation between spring growth rate and SAR has received little attention, though Wagner et al. (1969) suggested that growth rate may be more important than size in relation to smoltification. Release size may be an unreliable indicator of growth in the spring for yearling fish. However, when chinook salmon are released as underyearlings, size directly correlates with spring growth. Bilton (1984) found that larger underyearling chinook salmon survived to adulthood at a higher rate than smaller fish. Clarke and Shelbourne (1985) showed that larger underyearling chinook salmon have greater seawater tolerance than smaller fish. Several investigators have shown that growth rate of Atlantic salmon may play an important role in determining at what age smoltification occurs (Thorpe 1977; Metcalfe et al. 1988; Økland et al. 1993), faster-growing fish smolting at a younger age.

Conditional indices.—We do not report any conditional indices, but some studies have tried to relate SAR to smolt indices of a conditional nature (Virtanen et al. 1991; Farmer 1994). We do not dispute that diseased or acutely stressed fish are unlikely to perform well (Specker and Schreck 1980; Pascho et al. 1993) and probably will survive poorly (Banner et al. 1983; Schreck et al. 1989; Elliott et al. 1995). However, we prefer to keep conditional factors separate from other smolt indices. Various smolt performance attributes are not measurable by conditional measures; for instance, healthy, robust fish released in February, before they undergo any endocrine or physiological changes likely will show poor SAR, which would not be predicted by conditional factors. Conditional indices reflect the integrity of the fish, but they yield no insight into the degree of smolt development a fish has experienced and are thus unreliable predictors of smolt performance per se.

Connecting Physiology, Behavior, and SAR

The linkages between spring growth rate, IGF-I or ATPase, and SAR may not be intuitively obvious. We have shown differences in IGF-I between Round Butte, Pelton Ladder, and Warm Springs smolts. In addition, we have shown differences in spring growth rate and ATPase activity between these same fish, which we believe were directly due to hormonal differences related to the GH–IGF-I endocrine axis. In turn, we speculate that differences in hormone titer may be correlated with behavioral characteristics of smolts. This speculation is supported by work from other fields. Examples of strong relationships between hormones and specific behaviors are numerous (see Becker et al. 1992). Our speculation is strengthened by the well-established correlation between increased ATPase activities and directed downstream migration (Zaugg and Wagner 1973; Wagner 1974; Hart et al. 1981; Zaugg 1981a, 1981b; Muir et al. 1994b). These studies suggest that smolt migration rate is related to the degree of smolt development (endocrine condition) at the time of hatchery release.

The Columbia River migratory corridor is an area of intense predation by birds and other fishes on migrating smolts (Ruggerone 1986; Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Collis et al. 1995; Shively et al. 1996). Predation rates on groups of smolts could be directly proportional to the smolts' residence time in migrational corridors. From our ATPase values, we predict that Warm Springs fish display slower migration rates than Round Butte or Pelton Ladder fish. Thus, differences in SAR might be due to differential predation brought about by behavioral differences directly related to smolt quality. This is a very testable hypothesis. One could release tagged groups of smolts with varying smolt quality and observe migrational characteristics. We predict that higher-quality smolts would traverse migrational corridors faster and experience less predation than lower-quality smolts.

Growth Rate as a Smolt Quality Index

Our results suggest that smoltification and SAR may be enhanced by increasing the spring growth rate of hatchery chinook salmon. Several unknowns underlie a relationship between growth rate and smoltification, however. Moreover, our study was correlational; we did not demonstrate causation. Several investigators have shown that relatively warm temperatures impair smoltification (Zaugg et al. 1972; Zaugg and McLain 1976). Given that temperatures may stimulate growth, growth and smolting were not correlated under these warmwater conditions. Very large juvenile fish can be produced by replacing a seasonal photoperiod with continuous 24-h light, but the fish do not smolt (Saunders et al. 1985). These points emphasize the correlational relation of growth rate to smoltification. Growth does not cause smoltification; rather growth rate may be correlated with smoltification. Overall, we must develop a better understanding of the GH–IGF-I axis and its dual role in directing both growth and smoltification

before we can accurately predict the relation of growth to smoltification.

With our data, spring growth rate had strong linear relations to SAR (Figure 16). However, we had only four points to a line for a given year. Further, the inclusion of two points from Warm Springs provides a heavy statistical anchor to the results. Thus we do not place strong credence in the shape or the slope of the line produced. Rather, we suggest only a strong positive relation between spring growth rate and SAR; the actual shape (linear, curvilinear, sigmoid) or slope of the relation awaits further research and may vary with environmental conditions.

We have determined neither the magnitude nor the duration of differences in spring growth rate required to produce differences in smoltification. Differences in spring growth rate, reflecting the differences in smolt development documented here, were measured over at least 6 weeks (February to April). Beckman et al. (1998a) demonstrated differences in downstream migratory rate of experimental groups that were associated with differences in spring growth rate, growth being documented over at least 8 weeks. Smoltification is a broad developmental process embracing changes in various endocrine and physiological characters over weeks to months. Periods of growth stimulation lasting less than 4–6 weeks may not have significant effects on smolt quality.

It is important to understand relationships of size to growth, because hatchery rearing protocols often are based on attaining fish of a certain size at a certain date without regard to seasonal patterns of growth (Bonneville Power Administration 1994). Maintaining fish at a relatively small size initially, then inducing rapid growth in the final spring, may result in high-quality smolts, with a substantial savings in feed costs. Conversely, promoting rapid summer–fall growth in fish destined for yearling release, then just maintaining size in the spring, may result in large but poorly performing fish.

Several uncontrolled variables that differed between the Warm Springs, Round Butte, and Pelton Ladder environments could have influenced the growth, smoltification, behavior, or morphology of young chinook salmon, among them temperature, rearing density, raceway type, and nutrition (commercial feed or natural feed, feeding schedule, feeding rate). Thus, the positive relationships found between spring growth rate, smoltification, and SAR might be spurious. Fish-rearing conditions in Pelton Ladder (low density, natural food, cover provided by walls and baffles) appear similar to the seminatural rearing conditions recommended by Maynard et al. (1995). Differences in SAR between Round Butte, Pelton Ladder, and Warm Springs smolts could be due to behavioral and morphological factors that affect predator avoidance and foraging success. Yet, Round Butte and Warm Springs fish were both reared in hatchery raceways and SAR differed greatly between fish released from these two facilities. Banks (1994) showed that rearing density may have large effects on SAR, but although density at release was similar between Warm Springs-L and Round Butte fish, SARs differed dramatically. Fish from Pelton Ladder were released volitionally, whereas Round Butte and Warm Springs fish were forced from raceways; yet, again SAR differed dramatically between Warm Springs and Round Butte fish. Finally, several factors mentioned above (nutrition, density, and rearing environment) affect somatic growth (Nortvedt and Holm 1991; Mazur et al. 1993; Jorgensen et al. 1996), implying they would thereby influence the GH–IGF-I endocrine axis and smoltification. We do not wish to state that SAR was determined solely by spring growth rate and smoltification; behavioral and morphological differences between groups could have also contributed to differences in SAR. However, we have established strong correlations between spring growth rate, smoltification, and SAR that fit into a theoretical framework linking the GH–IGF-I endocrine axis to growth, smoltification, behavior, and SAR. This framework should be further investigated.

Hatchery Evaluation

The fish-rearing capabilities of individual hatcheries are constrained by their geographic settings. Among the hatcheries in our study, Round Butte has constant 10°C water, Pelton Ladder water shows a rapid temperature increase in the spring, and Warm Springs has quite low temperatures in winter and early spring and does not reach the higher temperatures of Round Butte and Pelton Ladder until April. Round Butte and Pelton Ladder waters support rapid growth of salmon juveniles in the spring when Warm Springs constrains fish growth to lower rates. To stimulate fish growth and smolt quality at Warm Springs, managers might consider releasing fish later in the spring after water temperature has warmed, artificially heating water (expensive), or perhaps diet manipulation to stimulate spring growth spring. Under the present rearing conditions, our data suggest that Warm

Springs fish are unlikely to match the SAR of Round Butte–Pelton fish.

This conclusion is subject to one uncertainty: the fall culling and release of relatively large fish at Warm Springs. Relatively large fish generally have higher SARs, so the release of large fish might have biased Warm Springs SARs downwards. Moreover, early release of large fish may have removed fish with the greatest growth potential, also biasing Warm Springs growth rates and smolt quality downwards. Finally, one might argue that the largest fish are the highest-quality fish and that their removal trivializes comparisons of Warm Springs with hatcheries that do not grade and release fish in the fall.

There is no evidence that retention of the larger fish at Warm Springs would have resulted in higher spring growth rates. This hatchery still would have had relatively lower water temperatures, and growth rates would have been constrained. The spring growth rate and size at release of Warm Springs fish is not atypical of Columbia River spring chinook salmon hatcheries (Dickhoff et al. 1995). Thus culling and releasing fish at Warm Springs did not result in an atypical pattern of spring growth or of release size. There is also little reason to believe that the smaller, retained fish did not have a good growth potential. Beckman et al. (1998a, 1998b) selected the smallest 25% of an experimental population of spring chinook salmon juveniles in the fall. Subsequently, these fish were capable of growing well, and displayed as good or greater smolt development and downstream migratory ability as a conspecific group of larger fish that grew at a relatively lower rate. Thus it is probable that the fish retained at Warm Springs through winter and spring had a potential for high growth rates and a potential to become high-quality smolts.

Finally, the purpose of our study was to evaluate fish released in the spring in terms of smoltification. The study clearly showed that smolts released from Pelton Ladder and Round Butte were of higher quality than those released from Warm Springs, regardless of the ultimate reason (culling at Warm Springs, water temperature differences at the different facilities) for the difference in quality. If the goal is to develop methods of assessing smolts at release, one must have groups of different quality so that a range of SARs can be related to smolt characters. This situation was provided by the fish released from Warm Springs, Round Butte, and Pelton Ladder.

The startling difference in performance of fish among these hatchery systems highlights the difficulties of making broad generalizations about the costs and benefits of hatchery releases. Round Butte–Pelton obtained an approximately 10 times greater SAR than Warm Springs over the course of our study. The ecological cost of Round Butte–Pelton smolts (negative impact on wild smolts) may be less than that of Warm Springs fish if they show the rapid downstream movement and estuarine-to-ocean transition suggested by their physiological status. Rapid movement from freshwater areas to the ocean would decrease competition between hatchery and wild smolts in rivers and the estuary and lessen the possibility of disease transfer from hatchery to wild fish. Thus one obtains a greater benefit from each Round Butte–Pelton fish released than from each Warm Springs fish, and this benefit may be obtained at less ecological cost (hatchery and wild smolt interactions). We urge that decisions on hatchery production rates and evaluations of the costs and benefits of hatchery releases be made case by case for individual hatcheries. This may optimize the societal benefits obtained by the hatchery production of salmon while minimizing the ecological costs associated with the release of hatchery juveniles.

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