Examining the Conflict between Smolting and Precocious Male Maturation in Spring (Stream-Type) Chinook Salmon

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Examining the Conflict between Smolting and Precocious Male Maturation in Spring (Stream-Type) Chinook Salmon

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Abstract.—Precocious male maturation is a natural life history strategy for spring Chinook salmon Oncorhynchus tshawytscha. During spawning, precocious males employ a “sneaker” strategy to fertilize eggs in competition with full-size anadromous adults. Hatchery rearing practices may increase the incidence of this phenotype beyond its natural levels. Previous research reported high rates (>40%) of precocious male maturation at age 2 (minijacks) in the Yakima River spring Chinook salmon supplementation program in Washington State. Minijack rates in wild populations are believed to be less than 5%. We compiled seasonal profiles for size, condition factor (K), gill Na⁺,K⁺-ATPase activity, whole-body lipid levels, plasma 11-ketotestosterone (11-KT), insulin-like growth factor-I (IGF-I), and thyroxine (T4) in minijacks and immature smolts in the hatchery and during out-migration. In the hatchery, minijacks were larger and had higher K, whole-body lipid, plasma 11-KT, and IGF-I levels than smolts. Plasma T4 and gill Na⁺,K⁺-ATPase activity increased in minijacks in spring, but the levels were slightly lower than those of smolts. Most minijacks are thought to remain resident in headwater streams throughout the summer in preparation for autumn spawning. A subset of these minijacks migrate hundreds of kilometers toward the ocean in the spring, only to reverse course later in the summer in an effort to return to their natal spawning grounds. These migrating minijacks had elevated plasma 11-KT, IGF-I, and T4 levels and gill Na⁺,K⁺-ATPase activity. It is generally thought that smoltification and reproductive maturation are mutually exclusive life history events in salmonid fishes. This investigation examined the physiology of a unique phenotype in which smoltification and downstream migration appear to occur in fish that have already initiated the maturation process. These results suggest that hatchery programs with high minijack rates may produce significant numbers of fish that are maladapted for either smoltification or competing on the spawning grounds, and it is likely that they die in the freshwater environment before contributing to subsequent generations.

Smoltification and reproductive maturation are two major developmental events in the life of anadromous salmonid fishes. Smolting is characterized by a suite of physiological, morphological and behavioral changes that prepare the freshwater dwelling parr for life as a seawater-adapted smolt (see Hoar 1988 for review). Physiological changes include increased activity of the thyroid, interrenal, and growth endocrine axes, and elevations in metabolism, lipolysis, and gill Na⁺,K⁺-ATPase (enzyme number 3.6.1.36; IUBMB 1992) activity. Morphological changes include decreased condition factor (K), increased body silvering, and darkening of the fin margins. Behavioral changes include schooling and downstream migration. By contrast, reproductive maturation involves gonad growth and maturation (see Nagahama 1983 for review), movement into freshwater, upstream migration, development of secondary sexual characteristics (nuptial coloration and changes in body morphology), courtship, and nest guarding (see Groot and Margolis 1991; Quinn 2005).

In Columbia River spring (or stream-type) Chinook salmon Oncorhynchus tshawytscha, male maturation can occur at ages 1 (precocious parr), 2 (minijacks), 3 (jacks), 4, or 5 years postfertilization, the age being influenced by both genetic (Silverstein and Hershberger 1992; Hankin et al. 1993; Heath et al. 1994; Unwin et al. 1999) and environmental factors, including body size, growth rate, and body lipid level (Silverstein et al. 1997, 1998; Shearer and Swanson 2000; Campbell et al. 2003; Larsen et al. 2004a, 2006; Shearer et al. 2006). Several studies in spring Chinook salmon have demonstrated that the male maturation process for any given age-class is physiologically initiated approximately 1 year prior to spermiation in autumn (Silverstein et al. 1997, 1998; Shearer and Swanson 2000; Campbell et al. 2003; Larsen et al. 2004a, 2006; Shearer et al. 2006).

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It is generally thought that precociously mature males (parr and minijacks) remain resident in headwater streams throughout life, employing a “sneaker” mating strategy with anadromous pairs. But recent studies have described a novel phenotype among minijacks that migrate large distances downstream, in a smolt-like manner, after initiating reproductive maturation and consequently migrating back upstream within the same year (Zimmerman et al. 2003; Larsen et al. 2004a; Beckman and Larsen 2005). These studies suggest that these animals are initiating reproductive maturation and then smolting, an occurrence that has been suggested to be physiologically untenable in Atlantic salmon Salmo salar (see Thorpe 1987, 1994; Thorpe and Metcalfe 1998) and Chinook salmon (Foote et al. 1991). However, studies in sockeye salmon O. nerka (Foote et al. 1994; Urawa and Kaeriyama 1999) have provided evidence of a lack of inhibitory effect of maturation on smoltification.

The Yakima River spring Chinook salmon supplementation program in Washington State (see Fast and Berg 2001; Knudsen et al. 2006) has been the site of a series of investigations aimed at characterizing the physiological development and life history of hatchery and wild spring Chinook salmon (Beckman et al. 1998, 2000; Larsen et al. 2004a, 2006; Beckman and Larsen 2005). Previously, we reported that in the first few years of operation of this facility, approximately 37–49% of the male hatchery-reared fish produced by this program matured as minijacks rather than the more typical age 3 to 5 for spring Chinook salmon stocks (Larsen et al. 2004a). By comparison, the incidence of precocious male maturation (age 1 or 2) in wild spring Chinook salmon is poorly characterized but reportedly constitutes less than 5% of males (Gebhards 1960; Mullan et al. 1992). From a fisheries management perspective, unnaturally high rates of precocious male maturation may result in the loss of returning anadromous adults, skewed female : male gender ratios on the spawning grounds, and ecological and genetic impacts to wild populations. In the current investigation, the relatively high proportion of minijacks in this population afforded us the opportunity to take a closer look at the underlying physiology of the minijack phenotype and to answer the following question: do minijacks, including those that migrate during spring, exhibit any of the physiological characteristics of smolts? To that end, we present comparative physiological profiles for length, weight, condition factor (K), whole-body lipid levels, gill Na+,K+-ATPase activity, and plasma levels of 11-ketotestosterone (11-KT), insulin-like growth factor-I (IGF-I), and thyroxine (T4) throughout development of smolts and minijacks in the hatchery and during downstream migration. The intent of this comparison is twofold: (1) at the applied level, this information helps one interpret the physiology underlying the previously documented differential migration patterns of some minijacks (Zimmerman et al. 2003; Larsen et al. 2004a; Beckman and Larsen 2005); and (2) at the basic level, we hope to provide physiological evidence that under some circumstances salmonid smoltification and reproductive maturation are not always mutually exclusive developmental events.

Methods

Study area and fish.—This research was conducted using fish from three consecutive brood years (BYs; 1997–1999) at the Yakima Supplementation and Research Facility on the Yakima River near the town of Cle Elum, Washington (river kilometer [rkm] 291; Figure 1). Brood year refers to the year adults returned to the Yakima River and spawned, producing each year-class of progeny studied. Salmon production at this facility is described in Fast and Berg (2001) and Knudsen et al. (2006). Briefly, each year wild adult spring Chinook salmon are randomly collected throughout the duration of their spawning migration at the Adult Collection and Monitoring Facility located at Roza Dam on the Yakima River (rkm 208). Adults are artificially spawned at the Cle Elum Hatchery in September; fry are ponded the following April and reared in concrete raceways (30-m length × 3-m width × 1-m depth) at a density of 45,000 fish per raceway, and broadcast fed by hand or by automatic belt feeder. The water source comes from a combination of Yakima River water and subsurface well water in seasonally varying proportions (temperature range = 2–15°C). All fish are coded wire tagged and approximately 5–10% are passive integrated transponder (PIT) tagged in October of year 2. In early February of year 2, fish are transported by tanker truck from the Cle Elum Hatchery to each of three remote acclimation sites (total of six raceways per site) at Easton upstream of the Cle Elum Hatchery (rkm 311), Jack Creek on the North Fork Teanaway River tributary (confluence with the Yakima River at rkm 286), and Clark Flat downstream of the Cle Elum Hatchery (rkm 272). The rearing conditions and configuration at each of the remote acclimation sites are essentially identical to that of the Cle Elum Hatchery with the exceptions of water flow (lower at the acclimation sites) and the seasonal thermograph that varies with acclimation site location (water temperature range = 2–7°C). At all acclimation sites, surface river water is used. In mid-March, volitional migration of the smolts is allowed from the acclimation sites. At the end of May, all remaining fish are flushed into the river.

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Fish were sampled once or twice a month from September (1 year postfertilization) to February at the Cle Elum Hatchery. Following transfer to the remote acclimation sites, fish were sampled twice a month from March to May at the Clark Flat acclimation site. Volitionally migrating fish were collected by dip net around dusk (a time period when salmonids prefer to migrate; see Beckman et al. 1998) from the exit pipes connecting the raceways with the Yakima River from March to May (BY 1997 only). Out-migrating fish were sampled from the smolt bypass trap located at Roza Dam (rkm 208) from April to May (water temperature range = 6–8°C) and at Prosser Dam (rkm 27) from April to May (water temperature range = 11–15°C) on the Yakima River. Finally, in May PIT-tagged Cle Elum hatchery spring Chinook salmon, migrating from the Yakima River, were collected at the code separator facility (operated by the Pacific States Marine Fisheries Commission; http://www.psmfc.org/) at John Day Dam (rkm 348) on the Columbia River.

**Figure 1.**—Map of the Yakima River system. Juvenile spring Chinook salmon are reared at Cle Elum Hatchery and transferred to the Easton, Jack Creek, and Clark Flat acclimation sites in the spring. During volitional out-migration, fish are captured as they exit the raceways at Clark Flat and at smolt trap facilities at Roza, Prosser, and John Day dams.
Table 1.—Mean ± SE measurements of physiological factors in immature Chinook salmon smolts and minijacks sampled at the Clark Flat acclimation site prior to release, at the Clark Flat acclimation site during volitional migration, at Roza and Prosser dams on the Yakima River, and at John Day Dam on the Columbia River during smolt migration. Asterisks indicate significant differences (P ≤ 0.05) between smolts and minijacks with respect to the factor in question.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Developmental stage</th>
<th>Brood year</th>
<th>Collection site</th>
</tr>
</thead>
<tbody>
<tr>
<td>11-KT (ng/mL)</td>
<td>Male smolt</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>48</td>
<td>0.2 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>50</td>
<td>0.3 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>45</td>
<td>0.2 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>99</td>
<td>60</td>
<td>8.4 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>109</td>
<td>5.0 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>107</td>
<td>5.3 ± 0.3</td>
</tr>
<tr>
<td>Weight (g) Smolt</td>
<td>1997</td>
<td>323</td>
<td>21.5 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>147</td>
<td>17.7 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>117</td>
<td>20.7 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>99</td>
<td>61</td>
<td>30.2 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>109</td>
<td>27.9 ± 1.0</td>
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<tr>
<td></td>
<td>1999</td>
<td>107</td>
<td>23.0 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>99</td>
<td>323</td>
<td>125.0 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>147</td>
<td>116.6 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>117</td>
<td>123.4 ± 0.8</td>
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<tr>
<td></td>
<td>99</td>
<td>61</td>
<td>137.7 ± 1.6</td>
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<td></td>
<td>1998</td>
<td>109</td>
<td>132.6 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>107</td>
<td>133.2 ± 1.1</td>
</tr>
<tr>
<td>IGF-I (ng/mL)</td>
<td>Smolt</td>
<td>1997</td>
<td>13.0 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>147</td>
<td>14.2 ± 0.4</td>
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<tr>
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<td>1999</td>
<td>116</td>
<td>12.8 ± 0.4</td>
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<td>20.0 ± 0.8</td>
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<td>1998</td>
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<td>107</td>
<td>16.4 ± 0.7</td>
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<td>99</td>
<td>323</td>
<td>1.08 ± 0.01</td>
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<td>1.07 ± 0.01</td>
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<td>1998</td>
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<td>1.14 ± 0.01</td>
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<td>117</td>
<td>1.12 ± 0.01</td>
</tr>
<tr>
<td>Gill ATPase</td>
<td>Smolt</td>
<td>1997</td>
<td>2.8 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>146</td>
<td>2.7 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>117</td>
<td>1.7 ± 0.1</td>
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<td>99</td>
<td>61</td>
<td>2.2 ± 0.1</td>
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<tr>
<td></td>
<td>1998</td>
<td>109</td>
<td>2.2 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>107</td>
<td>1.5 ± 0.03</td>
</tr>
<tr>
<td>T4 (ng/mL)</td>
<td>Smolt</td>
<td>1997</td>
<td>6.5 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>41</td>
<td>3.5 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>214</td>
<td>5.3 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>99</td>
<td>47</td>
<td>5.4 ± 0.2</td>
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<tr>
<td></td>
<td>1997</td>
<td>47</td>
<td>6.1 ± 0.2</td>
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<tr>
<td></td>
<td>1998</td>
<td>109</td>
<td>6.4 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>107</td>
<td>6.8 ± 0.2</td>
</tr>
</tbody>
</table>

(water temperature range = 15–16°C). At the Cle Elum Hatchery and the Clark Flat acclimation site, eight fish from each of four raceways (32 fish total) were collected on each sampling date. The number of fish sampled at Roza, Prosser, and John Day dams varied according to the number of fish captured and the number of samples analyzed for a given parameter varied due to limitations in the volume of plasma available for some hormone analyses (see Table 1).

Fish were individually anesthetized in a buffered solution of 0.05% tricaine methanesulphonate (MS-222, Argent Chemical Laboratories, Redmond, Washington), weighed to the nearest 0.1 g, and measured for fork length to the nearest 1.0 mm. Blood samples were collected from the severed caudal vessel into heparinized Natelson tubes (VWR Scientific), centrifuged for 3 min at 3,000 × gravity, and stored frozen at −80°C. Plasma 11-KT levels were determined in selected BY
1997 male samples and most BY 1998 and BY 1999 male samples using an enzyme-linked immunosorbent assay (ELISA) according to the method of Cuisset et al. (1994). Total plasma IGF-I levels were measured in all samples (BY 1997–1999), following acid–ethanol extraction, with recombinant salmon IGF-I as standard and barramundi IGF-I antiserum obtained from Gro-Pep, Inc. (Adelaide, Australia) according to Shimizu et al. (2000). Plasma thyroxine levels were measured in select BY 1997 samples according to the method of Dickhoff et al. (1978, 1982). Gill tissue was sampled in all groups in all three BYs. Filaments from three gill arches were placed in a solution of sucrose, EDTA, and imidazole according to methods described by Zaugg (1982) and then frozen on dry ice and stored at −80°C. Gill Na+K+-ATPase activities were measured using the method of McCormick (1993; all values are reported with units of µmole PO4/[mg protein·h]). The remaining carcasses from sampled fish were collected approximately monthly in all groups in all three BYs and analyzed for whole-body lipid levels by the gravimetric method of AOAC (1975) using methylene chloride for lipid extraction. Condition factor (K) was calculated as

\[ K = \frac{w}{l^3} \times 100, \]

where w is weight in grams, l is fork length in centimeters.

Data analysis.—As previously noted, a principal goal of this study was to construct a physiological comparison between immature smolts and resident and migrating minijacks. For the fish sampled at the Cle Elum Hatchery and the Clark Flat acclimation site, we primarily present data from the BY 98 collections (except T4 levels that were only analyzed from BY 97). On each sampling date, all plasma samples from males were analyzed for 11-KT. Fish gender was determined for each brood year. Data were analyzed by a two-way analysis of variance (ANOVA) and after the start of volitional migration was determined for each brood year. Data were analyzed by logistic regression with the R statistical package version 2.8.1 (R Development Core Team 2008), using the glm function (family = binomial). Date of sampling was the independent variable and proportion of minijacks on each date the response variable.

Results

Fish were sampled from three consecutive brood years (BY 1997–1999). As noted above, in the interest of conserving space, here we present only data from BY 1997 for samples collected at the Cle Elum Hatchery and the Clark Flat acclimation site. BY 1998 was selected for graphical presentation because collections in that year were the most comprehensive of the three BYs at these two collection sites. The only exception to this was the profile for plasma T4 that was from BY 1997 since that was the only brood year from...
which that hormone was measured. The number of minijacks sampled postrelease at Roza, Prosser, and John Day dams was often limited to just a few fish on any one date, but their presence and associated physiological trends were consistent between years. Mean ± SE data from fish collected before and after release are presented from each brood year in Table 1, but in the interest of space plotted graphically only for BY 97 since that was the only year in which thyroxine was measured and volitional out-migrant fish were collected.

**Prerelease Physiological Comparison between Smolts and Minijacks**

For collections at the Cle Elum Hatchery (September–January) and Clark Flat acclimation site (February–May), male fish with plasma 11-KT levels less than 0.8 ng/mL and all female fish were designated as immature smolts. All females were considered smolts since, unlike males that can mature as early as age 1 or 2, female spring Chinook salmon do not typically undergo maturation before at least age 3 due to the longer-term energetic requirements of ovarian development. As noted earlier, male fish with 11-KT levels in excess of 0.8 ng/mL were designated as minijacks. Plasma 11-KT levels in excess of 0.8 ng/mL were evident in some males as early as October at the Cle Elum Hatchery, and levels in this group of minijacks increased steadily from March to April before leveling off in May (Figure 2a).

Plasma IGF-I levels were higher in minijacks compared with immature smolts starting in November (Figure 2b). Levels increased steadily in both life history types starting in February, but declined in both groups in April and May after the initiation of volitional release. By contrast, plasma T4 levels increased steadily and were significantly higher in smolts compared with minijacks whose levels remained relatively unchanged throughout this same time period (Figure 2c).

Minijacks were significantly heavier and longer than smolts on all but one sampling date in January (Figure 3a, b). In both smolts and minijacks, $K$ decreased from autumn to winter, increased in early spring, then declined again from April to May. However, $K$ was significantly higher in minijacks than smolts in April and May (Figure 3c).

In both smolts and minijacks, gill Na$^+$,K$^+$-ATPase activity increased throughout early spring before declining in May, well after the initiation of volitional release. In May, levels were significantly lower in minijacks than smolts (Figure 4a). Similarly, whole-body lipid levels declined from 8% to 9% in the autumn to approximately 4% in smolts and 6–7% in minijacks by May of the following spring. Minijacks had significantly higher whole-body lipid levels than smolts in April–May (Figure 4b).

Logistic regression analysis revealed a significant increase in the proportion minijacks in the raceways over time for both BY 1998 ($Z = 2.48, P = 0.01$) and BY 1999 ($Z = 2.18, P = 0.03$), but not BY 1997 ($Z = 1.79, P = 0.07$; Figure 5a–c). In both BYs 1998 and 1999, over 60% of the males sampled in the raceways...
in May were minijacks, suggesting that a higher proportion of minijacks were remaining in the raceways while the smolts emigrated throughout spring.

**Postrelease Physiological Comparison between Smolts and Minijacks**

There was a significant amount of temporal overlap in collection periods at the postrelease sampling sites in all three BYs studied (Table 1). For graphical presentation, here we present BY 97 data averaged over all sampling dates for volitional outmigrants, and at Roza, Prosser and John Day dams (Figures 6–8). In addition, mean data from fish collected at the Clark Flat acclimation site before release are also presented for comparison.

Mean plasma 11-KT levels were significantly higher in minijacks than smolts at all collection sites; however, levels in minijacks declined from over 8 ng/mL at Clark Flat to less than 2 ng/mL at John Day Dam (Figure 6a). Mean plasma IGF-I levels increased significantly in both smolts and minijacks throughout the out-migration period and with distance downstream (Figure 6b). Furthermore, plasma IGF-I levels were significantly higher in minijacks than smolts, and the difference between mean levels of the two phenotypes increased with distance downstream. Plasma T4 levels also increased significantly with time and distance downstream in both smolts and minijacks (Figure 6c). However, average T4 levels were significantly higher in smolts at two upstream collection sites (Clark Flat, volitional out-migrants) and generally higher in minijacks at the downstream collection sites (Prosser and John Day dams).

Similar to prerelease fish, postrelease minijacks were significantly longer and heavier than smolts at nearly all sample sites (Figure 7a, b). In smolts, $K$ decreased with distance downstream, but in minijacks...
remained relatively unchanged with distance downstream (Figure 7c).

In postrelease fish, gill Na\(^+\),K\(^+\)-ATPase activity increased in both smolts and minijacks with time and distance downstream. However, gill Na\(^+\),K\(^+\)-ATPase activity was consistently higher (significant in fish sampled at Clark Flat and Roza Dam, and in volitional outmigrants) in smolts compared with minijacks (Figure 8a). In postrelease smolts, average whole-body lipid levels decreased with distance downstream from greater than 5% at Clark Flat to less than 2% at John Day Dam. Whole-body lipid levels were equivalent to or higher than that of smolts at all sampling locations but did not show a consistent decrease with distance downstream (Figure 8b).

**Discussion**

Physiological evidence in support of the developmental conflict between smolting and maturation is
well established in several salmonid species. Treatment of parr with reproductive steroids has been shown to inhibit smolt development in immature amago salmon *O. rhodurus* (Miwa and Inui 1986), masu salmon *O. masou* (Ikuta et al. 1987), and Atlantic salmon (Lundqvist et al. 1989; Berglund et al. 1992), while castration of maturing masu salmon has been shown to essentially “permit” the smoltification process to progress (Aida et al. 1984). Seawater tolerance is poorer in previously mature (male parr) Atlantic salmon (Lundqvist and Eriksson 1985; Lundqvist et al. 1989), maturing brook trout *Salvelinus fontinalis* (McCormick and Naiman 1985), and precociously mature spring Chinook salmon compared with immature fish (Foote et al. 1991). Shrimpton and McCormick (2002) found that precocious male Atlantic salmon with higher plasma testosterone and 11-KT levels in the spring had lower gill Na\(^+\),K\(^+\)-ATPase activity than immature smolts, indicating inhibition of smolting. Finally, from a behavioral perspective, Berglund et al. (1994) found that treatment of immature Atlantic salmon with 11-KT implants resulted in a significant reduction in migratory activity as well as smolt development.

This study provided the opportunity to revisit this issue of “developmental conflict” from the perspective of both physiology and migratory behavior in spring Chinook salmon. In fish sampled at the Cle Elum Hatchery and Clark Flat acclimation site prior to release, smolt development of minijacks was suppressed relative to that of immature smolts. But, it should be noted that these samples contained a mixture of both putative migratory and nonmigratory minijacks. Plasma T4 and gill Na\(^+\),K\(^+\)-ATPase activity were
lower, and K and lipid levels were higher in minijacks compared with smolts. However, we have also shown that some male spring Chinook salmon possess characteristics of both sexual maturation and smoltification: elevated 11-KT, T4, and gill Na⁺,K⁺-ATPase activity. In addition, some of these fish were found hundreds of kilometers downstream from their release site, clearly demonstrating that they were migrating. From a developmental perspective, these fish provide a very unique physiological and endocrinological model as these data suggest that under some circumstances, early sexual maturation may not fully inhibit smolting and thus smoltification and maturation are not inherently exclusive.

In prerelease samples, many of the profiles peaked in mid-April, followed by a leveling off or decrease. However, with the exception of 11-KT, levels for most parameters measured at the dams show a steady increase with distance downstream above and beyond the peak levels observed prior to release. This pattern may, in part, be a reflection of the fact that we were never serially sampling the same fish through time on successive sampling dates or at any site, and different individual fish may have been on slightly different developmental trajectories. Support for this is the observation that after the start of volitional migration, a larger proportion of the fish sampled were minijacks (Figure 5), and it is possible that the smolts that remained may have been less developed than those that already emigrated from the facility. So, the most accurate comparisons are between life history types on a given date rather than trends over time. Another explanation may be that migrating fish simply show more dynamic physiological changes than captive populations in tanks and raceways. Several studies have found that the act of migration enhances the expression of most smolt associated physiological indices (Zaugg et al. 1985; Beckman et al. 2000; Congleton et al. 2003).

Previous studies have compared 11-KT levels in immature and maturing salmonids and demonstrated that plasma levels of immature fish remain well below 1.0 ng/mL both before and during the period of spawning in the mature cohorts (Hunt et al. 1982; Mayer et al. 1990, 1992; Stead et al. 1999; Shrimpton and McCormick 2002; Campbell et al. 2003; Larsen et al. 2004a, 2006). Precocious males are typically larger and have higher K and whole-body lipid levels than immature fish (Flain 1970; Taylor 1989; Foote et al. 1991; Bernier et al. 1993; Shearer and Swanson 2000). Our results are in general agreement with these previous studies; however, it is worth noting that early detection using 11-KT revealed that minijacks were significantly heavier and longer than immature parr starting as much as 10 months prior to eventual spermiation. This trend continued in fish collected after release. Starting in spring, the Ks where significantly higher in minijacks than smolts as growth becomes reapportioned toward gonadal rather than somatic development, and they remained higher in the minijacks after release as well.

The growth hormone (GH)-IGF-I endocrine axis regulates cell growth and differentiation in vertebrate animals, and plasma IGF-I levels are strongly correlated with growth rate in salmonids (Pierce et al. 2001; Beckman et al. 2004b; Larsen et al. 2006). The role of GH in regulation of smolt associated hypoosmoregulatory capability through both direct effects on the gill and indirect effects mediated through IGF-I has been well documented (Young et al. 1989; Madsen and Bern 1993; Sakamoto et al. 1993; McCormick et al. 1995; McCormick 1996). During downstream migration, IGF-I levels increased modestly in the smolts but nearly doubled in minijacks. Previous studies have found higher IGF-I levels in maturing compared with immature spring Chinook salmon (Shearer and Swanson 2000; Campbell et al. 2003; Beckman et al. 2004; Larsen et al. 2006). In vivo treatment of Mozambique tilapia Oreochromis mossambicus with methyltestosterone (Riley et al. 2002) and coho salmon O. kisutch with testosterone or 11-KT (Larsen et al. 2004b) has been shown to increase plasma IGF-I levels. In this study, increases in 11-KT in October followed by increases in IGF-I levels in November in minijacks lend support to the close regulatory association between these key factors from the reproductive and growth endocrine axes.

Plasma T4 levels were only measured in the BY 1997 fish. Typical smoltification associated elevations in T4 were observed in the nonmaturing fish in the spring (Dickhoff et al. 1978, 1982). Since this was the first year of monitoring and the high rates of precocious male maturation were not fully appreciated at the time of collection, sufficient quantities of plasma were not collected in the early stages of the study to allow for measurement of both plasma 11-KT and T4. Minijacks had significantly lower levels of T4 in the spring compared with smolts. Interestingly, during downstream migration minijacks captured at the lower river collection sites of Prosse and John Day dams had T4 levels that were higher than or comparable to that of immature smolts. Numerous studies in salmonids have reported elevated T4 levels during early or later stages of sexual maturation (reviewed in Dickhoff et al. 1989). Whether the observed T4 elevations in migrating minijacks are a smolt or maturation-associated physiological event, or both, is unclear.

This investigation directly sampled immature smolts...
before and after release, and minijacks that were captured at downstream dams were considered migrating minijacks. Nonmigrating minijacks were not directly sampled from the river, but the physiological profile of these resident minijacks could be inferred from that of maturing males sampled in the raceways prior to and during volitional out-migration. Smolts, resident minijacks, and migrant minijacks are physiologically different. Hypothetical representations of profiles for each of the eight parameters examined in this study were constructed for the three phenotypes to facilitate a comparative summary of these differences (Figure 9).

**Figure 9.**—Hypothetical representations of seasonal profiles for (a) fork length, (b) weight, (c) gill Na⁺,K⁺-ATPase activity, (d) plasma IGF-I, (e) whole-body lipid, (f) K⁺, (g) plasma T4, and (h) plasma 11-KT in immature smolts, resident minijacks, and migrant minijacks, by month (September–May).
At the peak of development, smolts are characterized by high gill ATPase activity and plasma T4 levels; moderate size and plasma IGF-I levels; and low K, lipid, and plasma 11-KT levels. Resident minijacks are large; have high plasma IGF-I and 11-KT levels; moderate gill ATPase activity, K, and lipid levels; and low plasma T4 levels. By contrast, migrant minijacks are also large but have high gill ATPase activity, plasma IGF-I, and T4 levels; and moderate lipid, K, and 11-KT levels. Thus, migrant minijacks possess many of the physiological attributes of typical smolts, at least until the point where they presumably respond to the maturation process and cease downstream migration.

The developmental paradox presented by the presence of migrating minijacks begs the question: what is the ultimate fate of these fish? The PIT tag monitoring program in the Columbia River holds at least part of the answer to this question. In a previous study, we demonstrated that a significant number of PIT-tagged spring Chinook salmon, from the Cle Elum Hatchery and other hatcheries, migrating through hydroelectric bypass systems in the Columbia River, in fact turn around and migrate back upstream through adult ladders later in the summer (Beckman and Larsen 2005). These fish have not been sampled directly to confirm their state of reproductive development, but we feel relatively confident that these fish are minijacks migrating in a “smolt-like” manner toward the ocean in spring and returning upstream later in the summer of the same year as a maturing adult. This is a unique and previously underappreciated phenotype. Even age-3 jack males spend a minimum of one winter in the ocean prior to returning to spawn.

It is important to note that rates of early male maturation in the Yakima program approached 37–49% of all males at release (Larsen et al. 2004a). The proportion of minijacks increased in the raceways during out-migration (Figure 5), suggesting that many minijacks are not migrating downstream and smolting, and those that do migrate likely represent a smaller subset of the population. In this study, the percentage of males intercepted downstream that were considered migrating minijacks steadily declined with distance (Roza Dam = 14–40%; Prosser Dam = 3–8.1%; John Day Dam = 1.8–10.8%), suggesting that the majority of minijacks produced by this facility are not successfully migrating to even the middle reaches of the Columbia River at John Day Dam (rkm 348; Larsen et al. 2004a). This conclusion is mirrored by PIT tag interrogation records described in Beckman and Larsen (2005) as well. More recently, a long-term study aimed at monitoring minijack rates of wild and hatchery Yakima River spring Chinook salmon at Prosser Dam has been conducted each spring from 2003 to 2007 (Larsen et al. 2007). These surveys, involving 250–450 fish per group, have found minijack rates among migrating males ranging from 0% to 3.7% (average = 1.54%) and 9.7–20% (average = 16.1%) for wild and hatchery fish, respectively. Thus, by comparison, the percent of minijacks for wild fish are approximately 10-fold lower than that of hatchery fish. Finally, according to surveys conducted by the Washington Department of Fish and Wildlife, few minijacks are found on the spawning grounds the following autumn (Pearsoms et al. 2009). Taken together, whether the minijacks migrated downstream during smoltification or remain in the headwater streams, based on the small percentage of minijacks surviving to spawn from the Cle Elum Hatchery and others (Beckman and Larsen 2005) it appears that this is not a very ecologically viable phenotype. Further research of this phenomenon is warranted as high rates of early male maturation may lead to significant reductions, demographic alterations, or both in supplemented populations.

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