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Defining Life Histories of Precocious Male Parr, Minijack, and Jack Chinook Salmon Using Scale Patterns

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Abstract
Male Chinook salmon *Oncorhynchus tshawytscha* have multiple life history strategies tied to smolting, age, and size at maturation. Precocious strategies include mature parr, minijacks, and jacks; however, there are conflicting definitions of what constitutes a minijack. We describe the variety of growth and life history patterns in precocious spring–summer Chinook salmon in the Snake River basin as inferred from scale patterns. We found six repeatable patterns on the scales collected that differed in average number of freshwater and saltwater circuli and average spacing of circuli during the period of fastest growth. This represented four life histories with two variations. These life histories were differentiated by length distribution: mature headwater parr that never left their natal stream (8–15 cm fork length), mature river parr (17–24 cm), minijacks that spent 3–4 months in the estuary or ocean (24–37 cm), and jacks that spent one winter in the ocean (≥36 cm). Thus, male Chinook salmon have a continuum of life history strategies. Mature parr spend their entire life in freshwater, mature headwater parr have parr marks, and the mature river parr are more silver in appearance. Neither of these stages have scale resorption. Some parr stay in headwater streams while others make short-distance migrations to larger rivers. Minijacks make long-distance migrations to the estuary or ocean but only stay a few months before returning to the spawning grounds. Jacks spend 1 year in the ocean and have many saltwater circuli. Minijacks and jacks are spotted similar to full-size spawning adults and have scale resorption consistent with a long spawning migration. Finally, our data demonstrate that minijacks are capable of successfully traveling from Idaho to the Columbia River estuary and back (a minimum of 2,600 river kilometers from the Pahsimeroi River) within approximately 4 months.
attain sizes greater than that of both mature parr and minijacks, but they are typically smaller than males that spend two or more years at sea (Quinn 2005).

Minijacks have become a topic of interest in the past few years. However, in the literature there are several conflicting definitions for minijack using at least one of the following criteria: length, hormone levels, age, or saltwater residence. When viewed at the Columbia River dams during their upstream migration, minijacks are defined as Chinook salmon 15–30 cm in fork length (Fish Passage Center, www.fpc.org). Larsen and colleagues used hormone levels at release and subsequent migratory behavior, as derived from detections of passive integrated transponder (PIT) tags, to define minijacks in the Yakima River, Washington (Larsen et al. 2004, 2010; Beckman and Larsen 2005). Larsen et al. (2004) and Beckman and Larsen (2005) introduced the concept that not all minijacks complete their migration to saltwater, and Larsen et al. (2010) further distinguished between migratory and nonmigratory minijacks. These three studies examined juvenile Chinook salmon sampled during out-migration in the spring. Using otolith microchemistry, Zimmerman et al. (2003) found that minijacks from the Umatilla River, Oregon, had spent a brief period in saltwater before returning to their natal river to spawn, and were usually <30-cm fork length for spring Chinook salmon. Thomas et al. (1969) found evidence of saltwater residence using scale patterns. These two studies examined mature precocious Chinook salmon sampled during return migration in the fall. A manager’s definition of a minijack is an upstream migrating fish of a certain fork length. Thomas et al. (1969) and Zimmerman et al. (2003) added that the fork length was attained owing to the length of time the minijack spent in saltwater. This conflicts with Larsen et al.’s (2004) and Beckman and Larsen’s (2005) definition that a minijack can be a nonmigratory fish. Given the variability in the definition of minijacks among the studies, more information on life-cycle performance is necessary to identify and manage all precocial life history strategies.

Scale patterns are a useful tool in identifying different life histories. Biologists have used scales to describe age and growth of fishes since at least 1912 (Gilbert 1912; Koo and Isarankura 1967; Fisher and Pearcy 1990, 2005; Shearer 1992; Connor et al. 2005). Scale patterns can provide detailed life history information such as growth rates at specific times in specific macrohabitats.

We sought to understand precocious life histories by using scale patterns as an indication of growth performance and movements among macrohabitats. Fork length, migration history, tag recoveries, sample location, and physical characteristics were also used to corroborate the life histories inferred from scale patterns. Our objective was to compare and contrast life histories and length groups for mature parr, minijacks, and jacks in order to show how minijacks are distinct from other precocious life histories.

METHODS

We collected scale samples from Chinook salmon at multiple locations in Idaho in order to sample from the range of precocious life histories (Table 1; Figure 1). Sampling was opportunistic and intended to balance sample sizes among mature parr, minijacks, and jacks. Scales were collected from July through September during 2007 and 2008 at hatcheries and on the spawning grounds. Only a few mature parr carcasses were found on spawning grounds, so we also collected scales from live molt-producing males at rotary screw traps in August and September 2010. We collected scale samples from small Chinook salmon in the Hells Canyon Dam fish ladder on the Snake River in July. All other scale samples were collected in August and September during the spawning season. Scale samples were collected across a fork length range up to <46 cm that included all life stages from mature parr to jacks that were producing milt. The only exceptions were the Hells Canyon Dam fish, which had enlarged testes but were not producing milt at the time.

Scales and data from individual Chinook salmon were collected on-site or, in the case of some carcasses, the entire Chinook salmon was frozen and samples were taken later. Scale samples were removed from the preferred area immediately posterior to the dorsal fin and above the lateral line and placed in a scale envelope labeled with location, fork length, date, tag presence, and collector.

We used all hatchery and spawning ground samples and sub-sampled scales collected at screw traps (due to the high number of precocious males collected, \(n = 263\)). Samples were obtained from three different rotary screw traps and subsampled to assure that all sizes of parr were represented throughout the spawning period. Scales were cleaned and mounted between two glass slides.

Scale patterns were analyzed using methods similar to those described by Mosher (1968). Scales were read by two experienced technicians independently who had no knowledge of fish location, tag history, or length. Any discrepancies were resolved in a collaborative session with a third experienced technician. Scales were examined with a Leica DM 4000B microscope at 40× magnification. If they were too large to view in their entirety at 40× they were viewed at 25×. The scales in the best condition from each sample were digitally recorded with a Leica DC 500 camera mounted on the microscope.

Scale samples were grouped visually into distinct patterns based on circuli spacing characteristics and resorption. First, we looked at whether saltwater growth was absent, a few months, or a full year. Second, these groups were further differentiated by circuli spacing, growth disruption, and annuli presence or resorption, respectively. Resorption is a smooth erosion of the circuli pattern on the scale edge and occurs during the months spent in freshwater before spawning (Mosher 1968; Shearer
TABLE 1. Number of Chinook salmon used for analysis by collection site and scale pattern.

<table>
<thead>
<tr>
<th>Location</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Total collected</th>
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<tr>
<td><strong>Spawning grounds</strong></td>
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<td>1. Bear Valley Creek</td>
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<td>2. Cape Horn Creek</td>
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<td>3. Marsh Creek</td>
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<td>4. Red River</td>
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<td>5. Salmon River</td>
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<td>7. Hells Canyon Fish Ladder</td>
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<td>8. Pahsimeroi Hatchery</td>
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<td>26</td>
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<td>98</td>
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<td>9. Rapid River Hatchery</td>
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<td>51</td>
<td>18</td>
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<td>69</td>
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<td>10. Sawtooth Hatchery</td>
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<td>11</td>
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<td>12</td>
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<td>11. Dworshak Fish Ladder</td>
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<td>12. Kooskia Hatchery</td>
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<td><strong>Screw traps</strong></td>
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<td>13. Hayden Creek Trap</td>
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<td>14. Lemhi River Trap</td>
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<td>15. Marsh Creek Trap</td>
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<td>15</td>
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<td>16. Upper Salmon River Trap</td>
<td>7</td>
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<td>24</td>
<td>48</td>
<td>89</td>
<td>20</td>
<td>269</td>
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</table>

1992). In contrast, unresorbed scales are round and have unbroken circuli out to the margins.

We quantified the patterns based on circuli spacing and number. Image-Pro Plus software was used to draw a line along the major axis perpendicular to the base of the scale, from the focus to the scale edge. We counted the number of circuli crossing that line within the freshwater and saltwater zones. The distance between five circuli from the period of fastest growth, indicated by the widest spacing between circuli, was measured on the longest axis of the scale. Minijack scales only had five circuli in the area of fastest growth; this was a limiting factor. Measuring the distance between the five circuli quantified the growth rate of each Chinook salmon in the most optimal conditions they experienced. On scales exhibiting saltwater growth, measurements started at least two circuli beyond the freshwater to saltwater transition to avoid circuli distortion. Measurements were recorded to the nearest 0.001 mm. Average circuli distances were calculated for a group of 10 Chinook salmon from each of the six distinct patterns. Ten Chinook salmon provided sufficient data to describe the pattern and balance sample sizes.

To contrast scale growth patterns, we compared fish length and growth rate. We plotted the length distribution of each pattern. We tested for differences among scale pattern types in the three variables quantified: number of freshwater circuli, number of saltwater circuli, and average width of five circuli from the period of fastest growth. We used an ANOVA model followed by Tukey’s test for pairwise comparisons adjusted to control experiment-wise error (Zar 1999). Only types with a saltwater transition were tested for the number of saltwater circuli. Model adequacy was checked by inspection of residual plots. Risk of type I errors was set at 0.10.

We used several types of ancillary information to corroborate inference of life history based on scale patterns. Annuuli were counted to determine age. We used the European aging nomenclature for salmon, in which two numerals (one representing winters in freshwater and the other representing winters in saltwater) are separated by a decimal point; total age is the sum of the two numerals plus the numeral 1 (Quinn 2005). For fish lacking saltwater growth, the letter “x” was used in place of the second numeral. Fish that spent time in saltwater but returned to freshwater before winter will have a 0 as the second numeral. Two of the Chinook salmon sampled had PIT tags, so we obtained detection histories from Lower Snake and Columbia River dams through the PIT Tag Information System (www.ptagis.org). These detection histories allowed us to examine migration timing past dams on the mainstem Snake and Columbia rivers. We also had scale samples from nine coded-wire-tagged hatchery Chinook salmon tags. Tag codes were used to verify origin and age. Lastly, we described the external appearance of the Chinook salmon: parr marks, a silvery appearance, or an olive appearance with black spots.
FIGURE 1. Locations of sampling sites in Idaho (and Bonneville Dam) where Chinook salmon were collected for scale samples. Location numbers are defined in Table 1.
RESULTS

We analyzed 269 spring–summer Chinook salmon scale samples. Of these, 14 samples were collected on the spawning grounds, 44 samples were subsampled from screw traps, and 211 samples were collected at hatchery facilities (Table 1; Figure 1). Fork lengths ranged from 19 to 45 cm at the hatcheries, from 8 to 15 cm from the screw traps, and from 11 to 40 cm on the spawning grounds.

Six distinct patterns were found on the scales we examined. Patterns 1 and 2 exhibited only freshwater growth (Figure 2). Scales exhibiting pattern 1 had narrow circuli spacing and scale size that was smaller than all other scale patterns. Pattern 2 scales were larger than pattern 1 scales and had accelerated freshwater growth after the first winter annulus. Nearly all of the pattern 1 and 2 scales had spent 1 year in freshwater after emergence (age 1.x). Patterns 3 and 4 exhibited a saltwater transition with a limited amount of saltwater growth (Figure 3). Patterns 3 and 4 were the same age as the pattern 1 and 2 scales (age 1.0). Both patterns 3 and 4 had wide spacing between circuli after their first freshwater winter annulus and exhibited resorption on the scale edge. Pattern 4 had a distinct disruption in freshwater growth. Patterns 5 and 6 exhibited a year of saltwater growth and resorption along the scale edge (Figure 4). Pattern 5 had completely resorbed its saltwater annulus, whereas pattern 6 showed a partial saltwater annulus (age 1.1).

The number of freshwater circuli differed among groups (Table 2; $F = 47.86, P < 0.001$). Pattern 1 had the fewest freshwater circuli, whereas patterns 2, 3, and 4 had the most. Patterns 5 and 6 were similar to each other and had an intermediate number of freshwater circuli. The number of saltwater circuli also differed among groups (Table 2; $F = 301.9, P < 0.001$). Patterns 5 and 6 had more saltwater circuli than patterns 3 and 4. Pattern 5 (resorbed saltwater annulus) had significantly fewer saltwater circuli than pattern 6, which had an intact saltwater annulus. Mean circulus spacing during fast growth also differed among groups (Table 2; $F = 56.3, P < 0.001$). Patterns 3 and 4 had the widest circulus spacing and were similar to each other. Pattern 1 had the narrowest spacing, and patterns 2, 5, and 6 had intermediate spacing. Circulus spacing was similar for patterns 5 and 6; spacing for pattern 2 was narrower than for patterns 5 and 6.

The fork lengths exhibited by each pattern had a limited distribution (Figure 5). Fork lengths of pattern 1 fish ranged from 8 to 15 cm. Fork lengths for pattern 2 ranged from 17 to 24 cm. Patterns 1 and 2 did not overlap in fork length. Fork lengths for patterns 3 and 4 ranged from 24 to 37 cm and overlapped in fork length. Fork lengths of pattern 5 were as small as 36 cm and overlapped with pattern 6.

Outward physical appearance also differed among Chinook salmon with different scale patterns. During fieldwork, we observed that Chinook salmon with pattern 1 scales had parr marks, whereas those with pattern 2 scales had more of a silver appearance. Chinook salmon exhibiting patterns 3–6 displayed the typical spotting pattern and olive or yellowish skin pigmentation of adult Chinook salmon that spend 2–4 years in saltwater.

Tagged fish provided additional information to verify life history patterns in scales. There were two PIT tagged fish from Pahsimeroi Hatchery, Idaho, both of which exhibited pattern 4. Based on PIT tag detections, both migrated downstream of Bonneville Dam (the last dam before reaching the estuary and ocean) in May 2008 and migrated upstream in August 2008, returning to Pahsimeroi Hatchery. We also determined total age for nine coded-wire-tagged Chinook salmon from Pahsimeroi Hatchery. All were released in March and April 2008 and returned in August of 2008. Ages matched our scale analysis (1.0). Two fish exhibited pattern 3 and seven exhibited pattern 4. All tagged Chinook salmon matured the same year they were released from the hatchery.

DISCUSSION

We compared the scale patterns of the three precocious life histories: mature parr, minijacks, and jacks. This comparison provides clarification regarding the definitions of precocious male life histories in Chinook salmon. Male Chinook salmon have a continuum of life history strategies, which are evident in their scale patterns. In order to differentiate scale growth...
FIGURE 2. Examples of scale patterns of Chinook salmon with only freshwater growth. Top panel shows pattern 1, bottom panel shows pattern 2. The bar in each panel represents 1 mm on the microscope. See Table 2 for definitions of the patterns and key features.
FIGURE 3. Examples of scale patterns of Chinook salmon with limited saltwater growth. Top panel shows pattern 3, bottom panel shows pattern 4. The bar in each panel represents 1 mm on the microscope. See Table 2 for definitions of the patterns and key features.
FIGURE 4. Examples of scale patterns of Chinook salmon with extensive saltwater growth. Top panel shows pattern 5, bottom panel shows pattern 6. The bar in each panel represents 1 mm on the microscope. See Table 2 for definitions of the patterns and key features.
patterns, we examined several defining characteristics: the presence of saltwater growth, the number of circuli, and the presence of accelerated growth to assign a scale to a category. Circulus formation rate and spacing are related to growth and irregular spacing may indicate stress (Fisher and Pearcy 1990, 2005). We inferred life histories based on these criteria in addition to fork length, PIT tag information, and location collected. We believe these are more important than age, because salmon of the same age may exhibit very different strategies to mature, such as mature parr and minijacks. This makes age an inappropriate criterion to use to separate precocious life histories. In our discussion, we focus on size, growth, and macrohabitat occupied.

Inference of Life History Based on Scales

We determined that pattern 1 represented mature headwater parr. Of the fish we sampled, mature headwater parr had the least amount of growth (fork lengths from 8 to 15 cm); their scales were small and had the fewest circuli compared with the other patterns. Mature headwater parr tend to reside in or near the natal stream in which they were spawned (Gebhards 1960; Mullan et al. 1992). Most mature headwater parr scales showed 1 year of growth in freshwater after emergence from the gravel (age 1.x), tight concentric circuli, no accelerated growth, and no ocean growth, but there were two additional variations. One mature headwater parr sampled at the Marsh Creek screw trap spent 2 years in freshwater (age 2.x). Marsh Creek has a harsh environment with long winters and a short growing season. Conversely, five age-0.x mature headwater parr originated from Hayden Creek and the Lemhi River, which are warmer and more productive than Marsh Creek (Arthaud et al. 2010). All of the mature headwater parr from Marsh Creek, Hayden Creek, and Lemhi River had similar size scales and were within the length range of pattern 1 parr, regardless of their age.

Pattern 2 fish show faster growth than pattern 1 fish. Most pattern 2 mature parr showed fork lengths and number of circuli that were nearly double that of mature headwater parr (fork lengths of 17–24 cm), even though they were the same age (1.x). Circuli spacing was 28% greater than in pattern 1. Pattern 2 parr were mostly hatchery Chinook salmon sampled in larger rivers. The period of greatest growth was after the first annulus. Adipose-fin-clipped and unmarked fish all showed the same pattern. Unlike pattern 1 parr, pattern 2 parr may have moved downriver to a more favorable growing environment. Most of the pattern 2 parr were collected below Hells Canyon Dam in the fish ladder on the Snake River. Connor et al. (2005) described the Snake River reach below Hells Canyon Dam as offering a relatively high level of opportunity for growth. Therefore, we infer that the other pattern 2 parr migrated to similarly productive environments downstream of their natal rearing area.

Patterns 3 and 4 were minijacks that migrated to the estuary or ocean and returned in the same year. We verified the presence of a saltwater transition based on PIT tag detections of fish migrating downstream from Bonneville Dam. These fish were collected only in the Pahsimeroi River, a migration of at least 2,600 river kilometers. Fish with both minijack patterns spent 1 year in freshwater and showed extremely fast growth once they reached the estuary or ocean (age 1.0). Pattern 3 fish showed consistent growth throughout development. Pattern 4 fish had a break in growth during the freshwater rearing phase corresponding to a disease outbreak and poor water quality in the rearing conditions.
ponds for a short period of time (T. Garlie, Pahsimeroi Hatchery manager, personal communication). Distance between circuli was larger in minijacks than all other Chinook salmon sampled, including jacks, making their life history easy to identify from scale patterns.

Identification of patterns 5 and 6 as jacks was based on the larger number of saltwater circuli (age 1.1). Pattern 6 exhibited a partial winter saltwater annulus; however, pattern 5 did not have a winter saltwater annulus because it was resorbed. Although the winter saltwater annulus was resorbed or partially resorbed, there was still much more saltwater growth (more circuli) compared with minijacks that spent only 3 months in saltwater.

Resorption on scales provided another clue to life history. The posterior scale edge and lateral edges of minijack and jack scales were not symmetrical, and therefore, they had been resorbed. Resorption of salmon scales occurs during migration from the ocean towards spawning streams (Mosher 1968) and was not found on mature parr; they spent their entire life in freshwater (patterns 1 and 2). We conclude that a minijack is an upstream migrating fish, and that is consistent with the working definition that the managers use.

Physical Characteristics

Fork length has been used to identify Chinook salmon ages and life histories but there are disparate definitions. Zimmerman et al. (2003) described returning spring Chinook salmon minijacks as <30 cm in length and fall Chinook salmon minijacks as <38 cm. The Fish Passage Center and Hooff et al. (1999) define minijacks as <30 cm, and both Thomas et al. (1969) and Torbeck et al. (2009) define them as <36 cm. One of our goals was to define length criteria for spring–summer minijacks; we were also able to define length groups for mature parr and jacks. The mature headwater parr ranged from 8 to 15 cm, the river mature parr ranged from 17 to 24 cm, minijacks ranged from 24 to 37 cm, and jacks were >36 cm. Note that our length range for minijacks is slightly larger than currently used at the counting windows at main-stem dams. This could lead managers to underestimate minijack abundance. To our knowledge, this study provides the most complete size criteria for Snake River spring–summer Chinook salmon minijacks. As more samples are collected from mature parr, minijacks, and jacks, it is likely that there will be some overlap in fork lengths. Length criteria will differ for fall Chinook salmon, which have a different life history than spring–summer Chinook salmon (ocean-type versus stream-type; see Quinn 2005).

In addition to length, physical appearance also provides evidence of whether a precocious male went to the ocean. We observed that mature headwater parr have parr marks and large river parr have a silvery appearance indicative of developing smolts. By contrast, minijacks and jacks displayed the typical spotting pattern and olive or yellow skin pigmentation characteristic of spawning adult Chinook salmon. As the name implies, minijacks are smaller versions of jack Chinook salmon.

Implications for Further Research

Due to their small size and cryptic coloration, systematic studies of the incidence of precocious males on the spawning grounds are very limited (Gebhards 1960; Quinn 2005; Pearsons et al. 2009). The incidence of minijacks in the spawning population is also probably very low relative to other life history types (Beckman and Larsen 2005). A review of PIT tag histories through the eight major dams of the Columbia and Snake rivers leads us to conclude that many minijacks never make it back to the spawning grounds (Beckman and Larsen 2005; Stuart Rosenberger, Idaho Power Company, personal communication). Minijack movement upriver at Bonneville Dam lags behind that of older adults by about 2 months (Beckman and Larsen 2005). Most of the Idaho hatcheries have ceased collecting their broodstock before minijacks arrive. So, information on abundance and demographics of the minijack life history is relatively limited compared with all other life histories. We were able to collect minijacks at Pahsimeroi Hatchery, because that fish trap is operated later than other Idaho hatcheries.

Minijacks are noteworthy because they initiate reproductive maturation while apparently undergoing smoltification. The male maturation process for any given age-class is physiologically initiated approximately 1 year before spermiation in autumn (Silverstein et al. 1998; Larsen et al. 2004, 2006). While once thought to be exclusive processes (Thorpe 1987), reproductive maturation and smoltification may be able to operate simultaneously (Larsen et al. 2010). Based on the timing of their downstream and upstream migrations past Bonneville Dam, it is highly likely that minijacks are maturing and smolting simultaneously. It follows from the inhibition model of maturation (Thorpe 2007; Wright 2007), smoltification will cease if conditions restraining maturation relax. At this point, the minijacks return to freshwater to spawn.

We inferred that minijacks had high growth rates immediately after the saltwater transition based on the distance between scale circuli. Growth during early saltwater residence has been implicated as important to survival of young Snake River spring–summer Chinook salmon to adulthood (Scheuerell and Williams 2005). Currently, abundance of Chinook salmon in the Columbia River basin is forecasted using a sibling regression technique, i.e., the abundance of returning spawners at older ages can be predicted from abundance of the same cohort in previous years (e.g., Torbeck et al. 2009). If the incidence of minijacks is thus related to the same phenomena that produce good ocean survival of young Chinook salmon, then minijack abundance may be useful in improving forecasts of eventual abundance, which may provide additional insights for fisheries management.

Conclusions

We were motivated to write this paper, in part, by a desire to provide clarification in the literature regarding the definitions of precocious male life histories in Chinook salmon. By definition, a minijack should be a small jack. However, this definition
conflicts with some of the other definitions that discuss migratory and nonmigratory minijacks (Larsen et al. 2010). Since jacks migrate to the ocean, it follows that minijacks should also migrate to the ocean. Our data demonstrate that minijacks are capable of successfully traveling from Idaho to the Columbia River estuary and back (a minimum of 2,600 river kilometers from the Pahsimeroi River) within approximately 4 months. Therefore, our definition of a minijack is a small Chinook salmon that can migrate to the estuary or ocean and return at a very small size (24–37 cm fork length) due to a shortened stay in saltwater. Minijacks look like a small version of a jack and have scale resorption like a jack. Mature parr spend their entire life in freshwater, have parr marks or a silver appearance, and do not have scale resorption typical of salmon returning to spawn from the ocean. Some mature parr stay in headwater streams, while others may migrate to larger rivers to take advantage of more favorable growth macrohabitat. Jacks spend 1 year in the ocean, are typically longer than 36-cm fork length, and have many saltwater circuli. They may have saltwater anuli or the anuli could be entirely resorbed, depending on when the scales were collected. Minijacks and jacks are spotted like the adults that spend 2 to 4 years in the ocean. These definitions help clarify the terminology used in research of precocious salmon.

ACKNOWLEDGMENTS

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REFERENCES


