PRIMARY RESEARCH PAPER

Relationship of winter concealment habitat quality on pool use by juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Grande Ronde River Basin, Oregon USA

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Abstract Winter concealment habitat quality was assessed and its use by juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) quantified in three hatching areas of the Grande Ronde River Basin, Oregon USA. Fish densities were significantly higher in pools with a higher winter concealment habitat index than pools with a lower index. The mean fork length and mean growth rate of fish did not differ between pools with a higher or lower winter concealment habitat index, even though residual fish were significantly larger than fish that emigrated. Biomass–density was significantly higher in pools with a higher winter concealment habitat index than pools with a lower index in all three hatching areas. Biomass–density was positively associated with the amount of cobble substrate (10–24.9 cm/m^2) in all three hatching areas, and inversely associated with embeddedness in two of the hatching areas. Results of this study indicate that enhancing winter concealment habitat could improve habitat quality resulting in increased carrying capacity and winter usage by juvenile spring Chinook salmon.

Keywords Fish size · Fish density · Nocturnal activity · Winter habitat use · Water temperature · Biomass

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Introduction

Concealment cover is a critical aspect of winter habitat for juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) (Riehle & Griffith, 1993). The quality and quantity of winter concealment habitat has been shown to greatly influence carrying capacity of the stream for the species (Hillman et al., 1987). Juvenile salmon utilize a variety of cover types for overwintering habitat, including interstitial spaces amid the substrate (Hillman et al., 1987; Cunjak, 1988), large woody debris and rootwads (Bustard & Narver, 1975), submerged and overhanging banks, and vegetation (Hillman et al., 1987; Heggenes et al., 1993). Hillman et al. (1987) introduced cobble substrate to a highly sedimented Idaho stream and found that significantly more spring Chinook salmon subsequently used the habitat in

winter. Meyer & Griffith ([1997](#)) assessed use by steelhead (*Oncorhynchus mykiss*) of artificial habitats of varying winter concealment habitat quality and found that significantly more steelhead remained in wire-mesh enclosures when more concealment cover, in the form of cobbles, was available.

The influence of winter concealment habitat quality on overwinter survival and carrying capacity is mediated by behavioral interactions among individuals (Hartman, [1965](#); Quinn & Peterson, [1996](#)). As winter approaches, high densities of juveniles have been shown to elicit social interactions among fish in the forms of aggression, competition, and movement within and out of rearing areas (Chapman, [1962](#); Chapman & Bjornn, [1969](#); Everest & Chapman, [1972](#)). Differences in spawning and emergence timing have also played an important role in segregation among similar species (Lister & Genoe, [1970](#)). Mason & Chapman ([1965](#)) found that early emerging coho salmon (*Oncorhynchus kisutch*) were larger and tended to remain longer in an artificial stream channel than later emerging fish, but factors other than size, aggressive behavior, and food availability determined residency since some large fish emigrated from stream channels with small fish. Research by Keeley ([2001](#)) with artificial stream channels indicated that food and space were important factors shaping demographic changes in salmonid populations, but that neither exclusively limited abundance.

Combining juvenile spring Chinook salmon biomass and density could be useful in predicting when winter concealment habitat requirements are lacking and when density-dependent responses occur. Other researchers have used biomass–density to predict density-dependent response for intraspecific competition-driven populations of plants (Westoby, [1981](#); Weller, [1987](#)), sessile animals (Hughes and Griffiths, [1988](#)), and mobile animals (Elliott, [1993](#)) that lacked necessary spatial requirements. Unlike plants and sessile animals, self-thinning in mobile animals may be regulated by two unique but not mutually exclusive factors: space and metabolic rate (Fréchette & Lefaivre, [1995](#)). Elliott ([1993](#)) determined that this relationship reflected differences in carrying capacity of habitat used by juvenile anadromous brown trout (*Salmo trutta*). When spatial requirements are limited, density-dependent growth, mortality, and emigration have been shown to occur even though some fish do not actively compete for territories

(Grant & Kramer, [1990](#)). Territorial behavior was considered a mechanism for self-thinning in mobile fish competing for food and space (Steingrímsson & Grant, [1999](#)). Keeley & McPhail ([1998](#)) identified that determining density-dependent response in saturated habitats is most meaningful when applied to individual species or individual populations.

Restoration of spring Chinook salmon in the Grande Ronde River Basin and other Pacific Northwest River basins requires knowledge of factors limiting seasonal carrying capacity of their stream habitats including overwinter habitat. The objective of this study was to assess the relationships between winter concealment habitat quality, fish density and size of juvenile spring Chinook salmon in pools of the Grande Ronde River Basin. Although causality cannot be proven with our field observational approach, our data were evaluated as to their conformity with the following four hypotheses: (1) fish densities in pools with a higher winter concealment habitat index will be significantly greater than fish densities in pools with a lower winter concealment habitat index, (2) mean fork lengths and mean specific growth rates of fish that rear in pools with a higher winter concealment habitat index will be significantly greater than those that rear in pools with a lower winter concealment habitat index, (3) juvenile fish biomass–density will be significantly greater in pools with a higher winter concealment habitat index than in pools with a lower winter concealment habitat index, and (4) biomass–density will be significantly associated with each of nine winter concealment habitat attributes.

Materials and methods

Study area

The Grande Ronde River Basin (Fig. [1](#)) encompasses 10,697 km^2 of Oregon and Washington (Seaber et al., [1987](#)). Elevations within the basin range from 2,440 and 2,134 m above sea level (a.s.l.) in the Wallowa and Blue Mountains down to 705 m a.s.l. at the confluence of the Grande Ronde and Snake rivers. The basin contains three water-resource management areas (Fig. [1](#)), referred to as Watersheds, which were delineated using United States Geologic Survey fourth field hydrologic units (HUC4). The present investigation took place in primary hatching areas of

Fig. 1 Map of the Grande Ronde River Basin including Hydrologic Units (HUC4) of Lower Grande Ronde, Wallowa and Upper Grande Ronde River Watersheds. The river kilometer (rkm) location of the rotary screw traps, the extent of area used by spring Chinook salmon for spawning, and the primary hatching areas are marked for each study stream
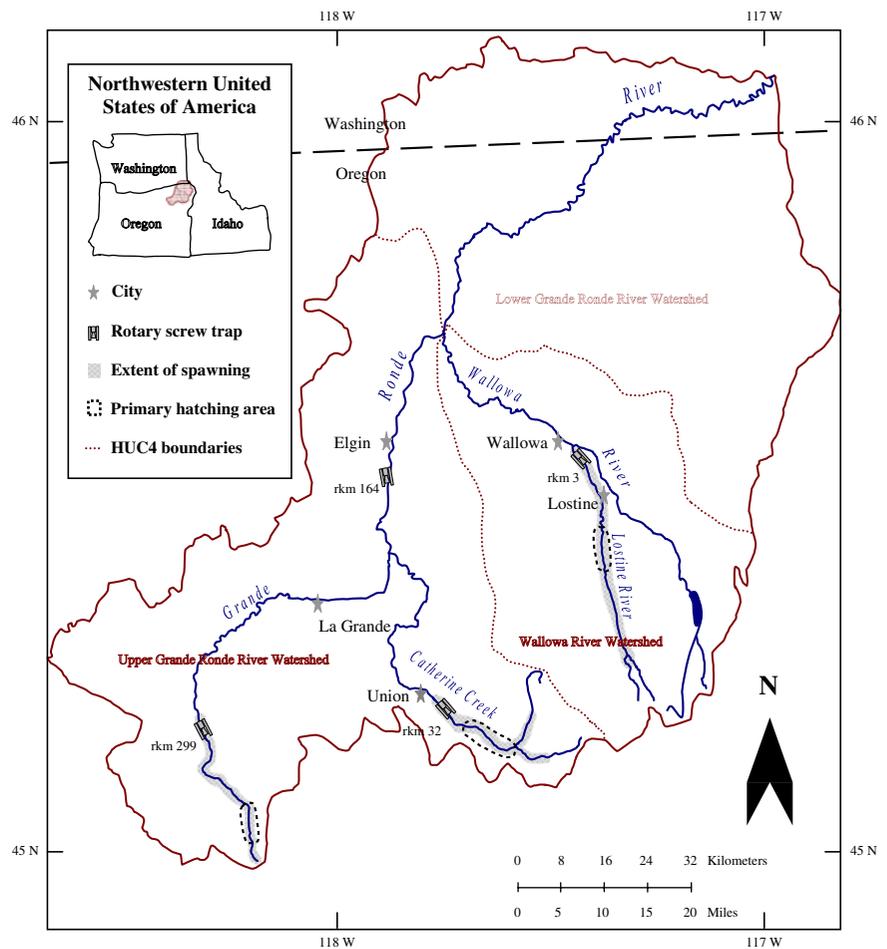
two study streams in the upper Grande Ronde Watershed, Catherine Creek and upper Grande Ronde River, and one study stream in the Wallowa River Watershed, the Lostine River. Frost-free conditions persist in the basin for 130–160 days annually. Winter conditions bring cold temperatures and precipitation, mostly snow, that averages more than 152 cm per year in high elevations. Annual increases in river flow occur during April–June and October–November (Nowak, 2004). Daily mean water temperatures range from 0 to 24°C annually. The river and tributaries are generally characterized by icing conditions from November to April.

Although population abundance in the basin remained lower than historic levels, Catherine Creek and Lostine populations were increasing in number while the upper Grande Ronde population was static during the study period. Based on redd counts collected by the Oregon Department of Fish and

Wildlife, a total of 131 redds produced the juveniles present in Catherine Creek in 2002 while 156, 182, and 14 redds produced the juveniles present in 2003 in Catherine Creek, Lostine, and upper Grande Ronde rivers, respectively. Spring Chinook salmon utilize approximately 32 km of stream to spawn in Catherine Creek, of which over half of the redds counted occurred in a 12 km section in the middle of the area (Fig. 1). Spring Chinook salmon utilize approximately 33 km of stream to spawn in the Lostine River, of which over half of the redds occurred in a 5 km section in the middle of the area (Fig. 1). Spring Chinook salmon utilize approximate 23 km of stream to spawn in the upper Grande Ronde River, of which over half of the redds occurred in a 5 km section in the headwater area (Fig. 1). For the purpose of this study, the areas with greater than half of the redds were designated as the primary hatching area (Fig. 1).

Winter concealment habitat

During June and July of 2002 and 2003 the number of pool habitats was counted in the primary hatching areas of Catherine Creek, Lostine River, and the upper Grande Ronde River, Oregon. The primary hatching area was identified as a continuous section of stream that contained more than half of the previous year's redds and was based on total redd counts in established spawning ground reaches (unpublished data, ODFW Fish Research La Grande, Oregon, USA). These reaches encompassed all available spawning habitat in each of the three study streams. If a single reach did not contain more than half the redds, the adjacent reach with the highest number of redds was included until the designated hatching area contained over half the year's redds. From each primary hatching area, six pools were randomly selected where winter concealment habitat, fish density, and fish size were to be determined.

During daylight hours in August or September, habitat attributes in each randomly selected pool were quantified using a 2×2 m grid made of lead-core line that encompassed the entire pool. The wetted surface area (m^2) of each pool was measured. Stream depth (cm) and water velocity (m/s) were measured in the upstream right corner of each 2×2 m cell. Substrate pieces with diameter between 10 and 24.9 cm were counted using a template that represented the largest particle size of the modified Wentworth classification, and overall embeddedness of those pieces was visually estimated (Platts et al., 1983) within each 2×2 m cell. The percent of fine sediments in each 2×2 m cell was visually estimated. The wetted area within the 2×2 m cell occupied by woody debris greater than 10 cm in diameter, rootwads, terrestrial and aquatic vegetation, and undercut banks was recorded.

Markers were put at the upstream and downstream end of each pool to help consistently locate the pool from month to month. Wetted pool surface area was measured each time a pool was sampled. Habitat inventory measurements were not repeated each month, however, because no major hydrologic events occurred over the sampling periods, and major physical habitat features that provided interstitial spaces for concealment (e.g., woody debris, substrate composition) did not change noticeably.

Habitat attributes were used to rank pools in terms of winter concealment habitat. Nine attributes were included in the total ranking system, and were based on criteria from the literature that were found to be important winter concealment habitat for fish (Table 1). Ranking was based on a scale from 1 to 5 where the highest score (5) represented values found to be strongly associated with winter rearing behavior and beneficial to overwinter survival, and the lowest score (1) represented values found to be poorly associated with winter rearing behavior and detrimental to overwinter survival. The direction of the relationship was used to identify the appropriate increase or decrease in the measured attribute, and was set using biologically and statistically meaningful ranges (Table 1). The nine rank scores were summed (45 points possible) and the highest overall score indicated the best winter concealment habitat quality. For each of the three study streams, the top three ranked pools were designated as pools with higher quality winter concealment habitat, and the three lowest ranked pools were designated as pools with lower quality winter concealment habitat. These groupings of three pools each were used to test hypotheses. The overall winter concealment habitat index represented a combination of quantity and quality of winter concealment habitat. In 2002, only Catherine Creek was ranked for winter concealment habitat quality and analyzed to test hypotheses; in 2003 all three study streams were evaluated.

Fish density

Juvenile spring Chinook salmon were sampled at night from pool habitats using either a passive seining technique in which snorkelers located and herded the fish into a stationary seine, or by dip netting individual fish. Although the intent was to collect every fish present in each pool, capture activities generally did not exceed 30 person-min. Aerated 3.8 l containers were used to hold captured fish at streamside. Data were collected from each fish immediately following the completion of each sampling period. Prior to handling, fish were anesthetized in an aerated bath containing 40–50 mg/l of tricaine methanesulfonate (MS 222). Fish were then measured for fork length to the nearest mm and weighed to the nearest 0.1 g. Each fish was interrogated for a PIT tag

Table 1 Attributes used to rank winter concealment habitat in Catherine Creek, Lostine River, and upper Grande Ronde River. Habitat attributes were set according to criteria adopted from the literature listed at bottom of table

Score	Number of cobble substrate 10–24.9 cm/m^2 [a]	Mean embeddedness rating [b]	Percent of pool cells with embeddedness rating >4 [c]	Percent of pool with velocity <0.25 m/s [d]	Percent of pool with velocity < 0.5 m/s & depth <51 cm [e]	Mean depth (cm) [f]	Mean velocity (m/s) [g]	Percent instream cover in pool [h]	Percent of substrate <6.3 cm [i]
5	>15	>4	>50	>50	>50	>50	<0.25	>25	<30
4	14.9–12	3.9–3.5	49–40	49–40	49–40	50–41	0.26–0.35	25–20	30–40
3	11.9–9	3.4–3	39–30	39–30	39–30	40–31	0.36–0.45	19–15	41–50
2	8.9–6	2.9–2.5	29–20	29–10	29–10	30–21	0.46–0.55	14–5	51–60
1	<6	<2.5	<20	<10	<10	<20	>0.55	<5	>60
j	+	+	+	+	+	+	−	+	−

[a] Criteria based on findings of Bjornn (1971), Bustard and Narver (1975), Hillman et al. (1987), Griffith and Smith (1993), Meyer and Griffith (1997), Bain and Stevenson (1999)

[b] Criteria based on findings of Platts et al. (1983), Hillman et al. (1987), Bain and Stevenson (1999)

[c] Criteria based on findings of Bjornn (1971), Hillman et al. (1987), Griffith and Smith (1993)

[d] Criteria based on findings of Bustard and Narver (1975), Chandler and Bjornn (1988), Taylor (1988), Hillman et al. (1987)

[e] Criteria based on findings of Everest and Chapman (1972), Edmundson et al. (1968), Cunjak (1988)

[f] Criteria based on findings of Edmundson et al. (1968), Lister and Genoe (1970), Everest and Chapman (1972), Bustard and Narver (1975), Hillman et al. (1987)

[g] Criteria based on findings of Lister and Genoe (1970), Everest and Chapman (1972), Bustard and Narver (1975), Hillman et al. (1987), Chandler and Bjornn (1988), Taylor (1988)

[h] Criteria based on findings of Taylor (1988), McIntosh et al. (1994), Quinn and Peterson (1996)

[i] Criteria based on findings of Bjornn (1971), Platts et al. (1983), Hillman et al. (1987), McIntosh et al. (1994), Bain and Stevenson (1999)

[j] Expected direction of the relationship

using a Destron-Ferring 2001F PIT tag detector and the numbers of tagged and untagged fish were recorded. All untagged fish were tagged prior to release using modified hypodermic syringes (Prentice et al., 1990). All fish were released in the pool of their capture on the same day they were handled.

Initial fish densities were determined using a mark-recapture method of population estimation. Recapture was conducted at night in each pool approximately 24 h after release. Initial abundance with variance was estimated using the Peterson index (Van Den Avyle & Hayward, 1999). Bailey's modification of the Peterson index was used when the number of recoveries was less than seven (Van Den Avyle & Hayward, 1999).

Changes in the number of PIT-tagged fish over time were used to estimate changes in total fish densities within each pool from September to January. Population estimates with variance were determined using the Schnabel population expression (Seber, 1982). The number of fish initially tagged and released (M) in a pool each month was reduced to account for tagged fish that migrated out of the hatching area prior to

resampling, and was based on estimates generated from monthly detections at rotary screw traps using the equation (Jonasson et al., 1999):

$$\hat{L} = \frac{T}{\hat{E}} \qquad (1)$$

where $\hat{L}$ is the estimated number of tagged fish that migrated out of the hatching area, T is the number of fish initially tagged and released in the hatching area that were detected in rotary screw trap catch, and $\hat{E}$ is the estimated trap efficiency.

Fish size and growth

Descriptive statistics were used to describe the size and growth rate of juvenile spring Chinook salmon captured in pools in the hatching areas of each stream (see Electronic Supplementary Material). Fork length and weight was measured for every fish captured in each hatching area each month. Specific growth rate (G) was determined for PIT-tagged fish only, and was calculated as:

$$G = \frac{\ln W_t - \ln W_O}{t} \qquad (2)$$

where W_t is the last observed weight, W_O is the initial weight, and t is the growth period (days) between observations (Fausch & White, 1986).

The number of PIT-tagged fish that emigrated from hatching areas was monitored from tagged fish captured in rotary screw traps that were located downstream of the hatching area in each study stream. From each emigrant the pool of origin, month of emigration, fork length, and weight were determined for use in identifying possible ecological mechanisms related to size and growth of emigrants.

Fish biomass–density

Fish biomass and density were combined to identify the relationship between carrying capacity and winter concealment habitat quality within indexed pools through time using the equation:

$$BD = \ln (\hat{N} \cdot \bar{W}) \cdot \ln \hat{D} \qquad (3)$$

where BD is fish biomass–density in a pool, $\hat{N}$ is the estimated number of fish, $\bar{W}$ is the mean weight (g), and $\hat{D}$ is the fish density/100 m^2. Westoby (1981) and Elliott (1993) among others have argued that this relationship is an indicator of carrying capacity.

Analysis

Fish density, mean fork length, mean specific growth rate, and biomass–density were ranked for each pool September through January and their relationships with winter concealment habitat rankings for six pools in each study stream evaluated using Spearman's rank correlation coefficient. Using the asymptotic standard error (χ^2) may not be valid when sample sizes are small (<500; SAS, 1999), so the Exact test was used to test the null hypothesis of no correlation (Ho: $r = 0$; $P < 0.05$). In addition, fish density, fork length, mean specific growth rate, and biomass–density were evaluated among hatching area pools by grouping five monthly means for pools with the three higher and three lower winter concealment habitat scores, and analyzing the differences using single factor analysis of variance (ANOVA; $P < 0.05$). Similarly, mean fork lengths and mean

specific growth rates of tagged fish that emigrated each month from October to January were compared to tagged fish that remained in the hatching areas during the same month using ANOVA ($P < 0.05$). All analyses utilized Tukey's Studentized Range test to confirm significant difference when the null hypothesis of no difference was rejected ($P < 0.05$).

Associations among biomass–density and the nine habitat attributes used to rank winter concealment habitat quality were compared using Spearman's rank correlation coefficient. Since sample sizes were <500 (SAS, 1999), an Exact test was used to test the null hypothesis of no association (Ho: |r| = 0; $P < 0.05$).

Results

Fish densities and winter concealment habitat indices

Ranks of monthly juvenile spring Chinook salmon densities in each of the three streams were significantly correlated with ranks of winter concealment habitat scores every month in every year (Exact test; one sided $P = 0.04$). For two of the three streams, fish densities were significantly higher in pools with higher winter concealment habitat scores. Fish densities in pools with higher winter concealment habitat scores were significantly greater than in pools with lower winter concealment habitat scores in Catherine Creek during 2002 and 2003 (ANOVA; $P = 0.001$ and 0.005; Tukey's Studentized Range; $P < 0.05$) and the Lostine River ($P = 0.04$), but not in the upper Grande Ronde River ($P = 0.06$) during 2003. In Catherine Creek and the Lostine River, juvenile fish densities in pools were generally less than 200 fish/100 m^2, but were less than 75 fish/100 m^2 in the upper Grande Ronde River (Table 2). In Catherine Creek, monthly mean fish densities typically increased through either October or November and decreased thereafter for both pools with higher and lower winter concealment habitat scores (Fig. 2). In the Lostine River, monthly mean fish densities in pools with higher winter concealment habitat scores typically increased through January, while fish densities in pools with lower winter concealment habitat scores increased from September to October, decreased in November, and remained nearly constant through January. In the upper Grande Ronde

Table 2 Winter concealment habitat scores with rank in parentheses, and monthly density estimate of juvenile spring Chinook salmon/100 m^2 with rank in parentheses for pools of Catherine Creek, Lostine River, and upper Grande Ronde River

Stream (rkm), Year	Winter concealment habitat score (rank)	Number of fish/100 m^2 (rank)				
		September	October	November	December	January
Catherine Creek (42–45)						
2002	36 (1)	180 (1)	204 (2)	241 (2)	198 (1)	218 (1)
	34 (2)	100 (4)	114 (4)	125 (4)	100 (4)	99 (4)
	32 (3)	167 (2)	211 (1)	248 (1)	181 (2)	182 (2)
	27 (4)	81 (5)	84 (5)	96 (5)	90 (5)	89 (5)
	23 (5)	63 (6)	81 (6)	91 (6)	74 (6)	67 (6)
	21 (6)	135 (3)	174 (3)	204 (3)	140 (3)	142 (3)
2003	36 (1)	60 (6)	65 (6)	90 (4)	85 (4)	80 (4)
	32 (2)	134 (2)	119 (3)	129 (2)	129 (2)	105 (2)
	32 (3)	148 (1)	208 (1)	235 (1)	217 (1)	224 (1)
	30 (4)	72 (5)	70 (5)	70 (5)	71 (5)	64 (5)
	27 (5)	73 (4)	82 (4)	64 (6)	51 (6)	52 (6)
	23 (6)	113 (3)	124 (2)	127 (3)	124 (3)	100 (3)
Lostine River (20–21)						
2003	35 (1)	142 (1)	172 (3)	239 (1)	186 (2)	310 (1)
	35 (2)	114 (5)	173 (2)	186 (2)	196 (1)	216 (2)
	34 (3)	141 (2)	133 (5)	112 (5)	119 (5)	103 (5)
	32 (4)	124 (4)	150 (4)	140 (4)	125 (4)	143 (3)
	31 (5)	43 (6)	45 (6)	41 (6)	39 (6)	49 (6)
	27 (6)	127 (3)	245 (1)	143 (3)	142 (3)	133 (4)
Upper Grande Ronde River (321–324)						
2003	31 (1)	24 (5)	49 (3)	39 (5)	45 (5)	–
	28 (2)	43 (3)	49 (3)	51 (3)	53 (3)	–
	27 (3)	51 (1)	72 (1)	71 (1)	72 (1)	–
	26 (4)	46 (2)	59 (2)	61 (2)	65 (2)	–
	25 (5)	5 (6)	8 (6)	12 (6)	12 (6)	–
	23 (6)	41 (4)	46 (5)	50 (4)	50 (4)	–

River, monthly mean fish density generally increased each month regardless of the winter concealment habitat score (Fig. 2).

Growth and winter concealment habitat indices

Ranks of monthly mean fork lengths in each of the three streams (Table 3) were significantly correlated with ranks of winter concealment habitat scores every month in all years (Exact test; one sided $P = 0.04$). However, mean fork lengths of fish that reared in pools with higher winter concealment habitat scores were not significantly different from fork lengths of fish that reared in pools with lower scores in

Catherine Creek either year (ANOVA; $P = 0.78$ and 0.34) or the upper Grande Ronde River in 2003 ($P = 0.45$), while mean fork lengths of fish that reared in pools with higher winter concealment habitat scores were significantly larger than fork lengths of fish that reared in pools with lower scores in the Lostine River in 2003 ($P = 0.01$, Tukey's; $P < 0.05$). In addition, Catherine Creek fish that remained in the pools (residuals) were significantly longer (Table 4; Fig. 3) than fish that emigrated during both years (ANOVA; $P = 0.0004$ and 0.02, Tukey's; $P < 0.05$). No comparison in fork length between resident and migrant fish was possible for the other two streams because only one fish was
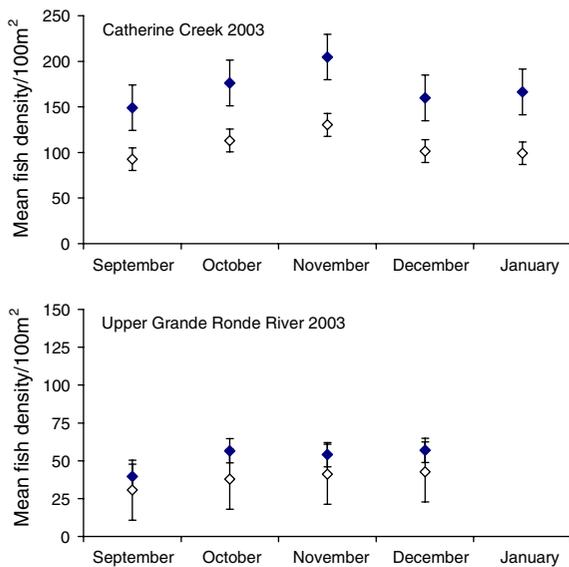
Fig. 2 Mean juvenile spring Chinook salmon densities and standard error in pools with the higher (◆) and lower (◇) winter concealment habitat scores

detected migrating out of the hatching areas of the upper Grande Ronde River and the trap was not operated on the Lostine River during 2003.

Ranks of monthly mean specific growth rates (Table 5) were also significantly correlated with ranks of winter concealment habitat scores every month in all years and streams (Exact test; one sided $P = 0.04$). However, only fish that reared in pools with higher scores in Catherine Creek during 2003 grew significantly faster than fish that reared in pools with lower scores (ANOVA; $P = 0.04$, Tukey's $P < 0.05$). Specific growth rate was significantly greater for tagged residual fish (Table 4; Fig. 4) than for emigrants in 2002 (ANOVA; $P = 0.001$, Tukey's; $P < 0.05$), but not in 2003 (ANOVA; $P = 0.26$). Again no comparison in mean specific growth rate between resident and migrant fish was possible for the other two streams.

Biomass–density and winter concealment habitat indices

Ranks of monthly biomass–density in each of the three streams (Table 6) were significantly correlated with ranks of winter concealment habitat scores every month in all years (Exact test; one sided $P = 0.04$).

Monthly biomass–density was positively correlated with winter concealment habitat scores in all three streams during every month except September 2003 in Catherine Creek where a negative correlation was found. Mean biomass–density in pools with higher winter concealment habitat scores was significantly greater than in pools with lower scores in Catherine Creek (ANOVA; $P = 0.005$ and 0.004, Tukey's $P < 0.05$), the Lostine River ($P < 0.0001$), and the upper Grande Ronde River ($P = 0.04$). In Catherine Creek during 2002 and the upper Grande Ronde River during 2003, biomass–density differences appeared to be consistent over time between pools with higher and lower winter concealment habitat scores. Conversely, in Catherine Creek and the Lostine River during 2003 biomass–density between pools with higher winter concealment habitat scores and pools with lower scores interacted in November. In all three streams, biomass–density was consistently higher each month in pools with higher scores than in pools with lower scores (Fig. 5).

Biomass–density and winter concealment habitat attributes

The number of significant relationships between biomass–density and each of the nine attributes differed among streams (Table 7). In Catherine Creek, during both years there were significant relationships between biomass–density and each of the five attributes: number of cobble substrate 10–24.9 cm/m^2, mean embeddedness rating, percent of pool with embeddedness rating greater than 4, percent of pool with velocity less than 0.25 m/s, and pool depth (Exact Test; $P < 0.05$). There was a significant relationship between biomass–density and percent of pool with velocity less than 0.5 m/s and depths less than 51 cm in Catherine Creek during 2002 only (Exact Test; $P < 0.05$). Although correlation coefficients differed somewhat between 2002 and 2003 in Catherine Creek, most significant relationships between the biomass–density and the nine attributes used to rank winter concealment habitat were found in both years. However, the relationship between biomass–density and percent of pool with velocity less than 0.5 m/s and depths less than 51 cm changed from a positive in 2002 to negative in 2003. In the Lostine River there were significant relationships between biomass–density

Table 3 Winter concealment habitat scores with rank in parentheses, and monthly mean fork length of juvenile spring Chinook salmon with rank in parentheses in pools of Catherine Creek, Lostine River, and upper Grande Ronde River

| Stream, Year	Winter concealment habitat score (rank)	Monthly mean fork length (rank)				
		September	October	November	December	January
Catherine Creek						
2002	36 (1)	76.6 (5)	80.5 (2)	82.4 (2)	81.4 (4)	79.4 (6)
	34 (2)	78.8 (3)	78.3 (5)	82.1 (3)	81.8 (3)	82.4 (3)
	32 (3)	79.0 (1)	80.0 (3)	82.6 (1)	82.8 (2)	79.6 (5)
	27 (4)	78.0 (4)	79.0 (4)	81.9 (4)	83.2 (1)	84.6 (1)
	23 (5)	79.0 (1)	81.5 (1)	77.4 (6)	80.3 (5)	82.8 (2)
	21 (6)	75.5 (6)	75.3 (6)	78.1 (5)	77.3 (6)	82.0 (4)
2003	36 (1)	67.5 (5)	73.8 (3)	76.6 (3)	79.1 (1)	79.1 (1)
	32 (2)	68.7 (3)	73.4 (5)	76.0 (5)	78.4 (2)	76.5 (5)
	32 (3)	67.8 (4)	73.8 (3)	77.4 (2)	78.3 (3)	77.7 (2)
	30 (4)	70.3 (1)	75.9 (1)	76.4 (3)	76.1 (5)	77.2 (3)
	27 (5)	69.0 (2)	74.4 (2)	78.9 (1)	77.4 (4)	76.2 (6)
	23 (6)	66.1 (6)	70.3 (6)	67.3 (6)	69.5 (6)	77.0 (4)
Lostine River						
2003	35 (1)	66.7 (3)	75.3 (2)	75.8 (2)	78.1 (1)	77.0 (2)
	35 (2)	64.5 (5)	71.9 (4)	74.2 (3)	74.9 (3)	77.4 (1)
	34 (3)	70.0 (1)	77.3 (1)	76.6 (1)	76.2 (2)	76.6 (3)
	32 (4)	67.5 (2)	69.9 (5)	71.6 (4)	70.1 (6)	73.8 (5)
	31 (5)	63.9 (6)	73.8 (3)	70.2 (5)	74.2 (4)	76.6 (3)
	27 (6)	66.0 (4)	66.4 (6)	67.5 (6)	71.1 (5)	68.3 (6)
Upper Grande Ronde River						
2003	31 (1)	72.1 (3)	74.7 (3)	72.6 (4)	73.1 (5)	–
	28 (2)	68.6 (5)	71.8 (5)	72.2 (5)	74.5 (3)	–
	27 (3)	73.2 (2)	74.8 (2)	77.9 (1)	77.0 (2)	–
	26 (4)	69.8 (4)	72.6 (4)	74.4 (3)	74.4 (4)	–
	25 (5)	74.6 (1)	76.9 (1)	76.6 (2)	77.4 (1)	–
	23 (6)	66.6 (6)	69.7 (6)	68.3 (6)	69.4 (6)	–

and each of five attributes (Table 7): number of cobble substrate 10–24.9 cm/m^2, mean embeddedness rating, percent of pool with embeddedness rating greater than 4, pool depth, and mean velocity during 2003 (Exact Test; $P < 0.05$). Biomass–density was positively correlated with all of these attributes except pool depth. In the upper Grande Ronde River, there were significant relationships between biomass–density and each of four attributes (Table 7): number of cobble substrate 10–24.9 cm/m^2, percent of pool with velocity less than 0.25 m/s, percent of pool with velocity less than 0.5 m/s and depths less than 51 cm, and percent instream cover in pool (Exact Test; $P < 0.05$). Biomass–density was positively correlated with all four of these attributes.

Discussion

The higher densities of juvenile spring Chinook salmon in pools with higher winter concealment habitat scores than in pools with lower scores support the idea of the importance of winter concealment habitat in this system. In related studies, several other investigators have reported similar findings. Hillman et al. (1987) demonstrated that artificially increasing winter concealment habitat in a heavily sedimented stream increased use by juvenile spring Chinook salmon in winter. Griffith & Smith (1993) reported that winter concealment habitat that was embedded with fine sediment contained fewer trout than winter concealment habitat that was not embedded. Meyer &

Table 4 Monthly mean fork lengths and mean specific growth rates with standard error in parenthesis, of PIT-tagged spring Chinook salmon that residualized and emigrated in Catherine Creek, September 2002–January 2003, and September 2003–January 2004

Stream, Year, Month	Residuals				Migrants			
	Fish (n)	Mean fork length (mm)	Fish (n)	Mean specific growth rate	Fish (n)	Mean fork length (mm)	Fish (n)	Mean specific growth rate
Catherine Creek								
2002								
September	208	78.4 (1.1)	0	–	0	–	0	–
October	194	78.1 (1.1)	193	0.0015 (0.0003)	143	74.3 (1.1)	91	−0.0003 (0.0003)
November	91	79.0 (1.2)	87	0.0007 (0.0003)	84	75.8 (1.2)	82	0.0006 (0.0003)
December	129	80.0 (1.1)	117	0.0006 (0.0003)	37	78.0 (1.1)	28	−0.0002 (0.0003)
January	120	81.5 (1.6)	116	−0.0002 (0.0004)	8	76.9 (1.6)	8	0.0000 (0.0004)
2003								
September	98	68.2 (1.6)	0	–	28	66.9 (1.6)	0	–
October	69	73.1 (1.8)	69	0.0010 (0.0004)	25	69.7 (1.8)	21	0.0003 (0.0004)
November	56	75.7 (1.6)	56	0.0007 (0.0003)	40	69.3 (1.6)	24	0.0006 (0.0003)
December	57	75.5 (1.6)	57	0.0001 (0.0003)	29	73.3 (1.6)	24	−0.0001 (0.0003)
January	29	77.2 (1.6)	24	0.0003 (0.0003)	0	–	0	–
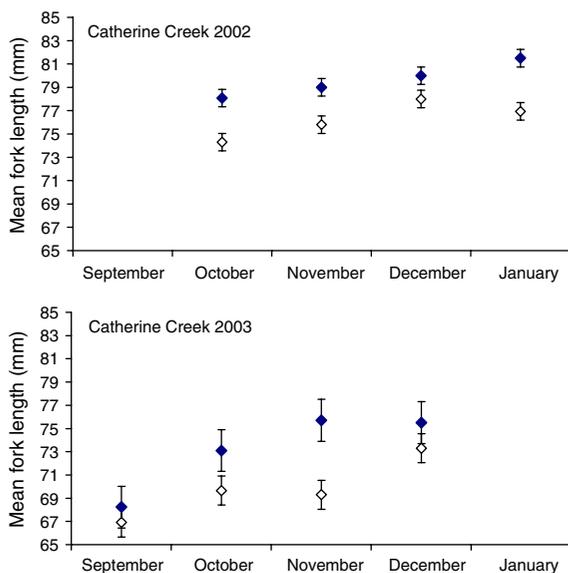
Fig. 3 Monthly mean fork lengths and standard error of PIT-tagged spring Chinook salmon residual fish (◆) and emigrants (◇) in Catherine Creek, September 2002–January 2003, and September 2003–January 2004

Griffith (1997) found that substrate enclosures with more concealment opportunities retained more rainbow trout following an increase in fish density than substrate that contained fewer concealment opportunities. Pools in Catherine Creek and the Lostine River with higher quality winter concealment habitat

provided more suitable overwintering habitat for more fish and sustained higher densities of fish. Although fish densities in the upper Grande Ronde River were also numerically higher in pools with higher winter concealment habitat scores than in pools with lower scores, the difference was just below that required for statistical significance ($P = 0.06$). Grant & Kramer (1990) found that they were unable to detect changes in fish density over time when fish densities were very low. Downstream dispersal by juvenile salmonids has been described as a density-dependent response (Elliott, 1986), and the lack of observed emigration in the upper Grande Ronde River may indicate that low fish density (less than one fish/m^2) found there was insufficient to induce density-dependent emigration. In this situation, no relationship would be expected between winter concealment habitat and fish density.

Fish that reared in pools with higher winter concealment habitat scores did not consistently attain significantly longer mean fork lengths or greater mean specific growth rates than those that reared in pools with lower winter concealment habitat scores. Since all of the pools selected in this study contained attributes preferred by juvenile spring Chinook salmon, the relationship between habitat availability and fish size may have contributed to the similarity of fish that residualized. Kruzic et al. (2001) found that coho salmon of hatchery origin that were stocked in

Table 5 Winter concealment habitat scores with rank in parentheses, and monthly specific growth rate with rank in parentheses in pools of Catherine Creek, Lostine River, and upper Grande Ronde River

Stream, Year	Winter concealment habitat score (rank)	Specific growth rate (rank)				
		September	October	November	December	January
Catherine Creek						
2002	36 (1)	–	0.0023 (5)	0.0007 (5)	0.0005 (5)	0.0002 (5)
	34 (2)	–	0.0019 (3)	0.0003 (3)	0.0013 (3)	0.0000 (3)
	32 (3)	–	0.0017 (1)	0.0003 (1)	0.0005 (1)	0.0000 (1)
	27 (4)	–	0.0014 (6)	0.0006 (6)	0.0003 (6)	−0.0004 (6)
	23 (5)	–	0.0016 (4)	0.0010 (4)	0.0003 (4)	0.0003 (4)
	21 (6)	–	0.0019 (2)	0.0014 (2)	0.0003 (2)	−0.0001 (2)
2003	36 (1)	–	0.0039 (1)	0.0009 (2)	−0.0001 (6)	−0.0003 (6)
	32 (2)	–	0.0021 (2)	0.0007 (3)	0.0005 (1)	0.0003 (2)
	32 (3)	–	0.0018 (3)	0.0015 (1)	0.0000 (4)	0.0006 (1)
	30 (4)	–	0.0007 (5)	0.0003 (5)	0.0001 (3)	0.0001 (4)
	27 (5)	–	0.0008 (4)	0.0002 (6)	0.0002 (2)	0.0002 (3)
	23 (6)	–	−0.0004 (6)	0.0005 (4)	0.0000 (4)	0.0000 (5)
Lostine River						
2003	35 (1)	–	0.0012 (4)	−0.0020 (6)	−0.0004 (6)	−0.0003 (6)
	35 (2)	–	0.0007 (6)	0.0008 (1)	−0.0001 (5)	0.0006 (1)
	34 (3)	–	0.0018 (2)	0.0003 (2)	0.0005 (1)	0.0006 (1)
	32 (4)	–	0.0017 (3)	−0.0001 (3)	0.0001 (4)	0.0003 (4)
	31 (5)	–	0.0028 (1)	−0.0005 (5)	0.0005 (1)	0.0006 (1)
	27 (6)	–	0.0012 (4)	−0.0001 (3)	0.0004 (3)	−0.0001 (5)
Upper Grande Ronde River						
2003	31 (1)	–	0.0028 (5)	0.0013 (1)	−0.0002 (6)	–
	28 (2)	–	0.0007 (3)	0.0003 (5)	0.0004 (1)	–
	27 (3)	–	0.0012 (1)	0.0004 (2)	0.0001 (4)	–
	26 (4)	–	0.0017 (6)	0.0004 (2)	0.0003 (2)	–
	25 (5)	–	0.0004 (4)	0.0004 (2)	0.0000 (5)	–
	23 (6)	–	0.0016 (2)	−0.0004 (6)	0.0003 (2)	–

block-netted areas of riffles did not grow at significantly different rates than those that were stocked in block-netted areas of pools, even though habitat conditions differed greatly between the riffles and pools. Chandler & Bjornn (1988) found that steelhead that emerged earlier had larger fork lengths than fish that emerged 28 days later, but did not differ in instantaneous growth rate or condition factor. They also found that in stream channels that contained only larger fish, the fish had similar fork lengths, instantaneous growth rates, and condition factors as in situations where both larger and smaller sized fish were present. In the present study, where suitable microhabitats existed in both pools with higher and lower winter concealment habitat scores, the growth

potential of dominant individuals may have been similar regardless of winter concealment habitat scores. Larger individuals securing dominance over an available microhabitat coupled with subsequent mortality or emigration of smaller subordinate fish can result in equalized fish size among pool habitats. In support of this explanation, Keeley (2001) found that when juvenile steelhead were allowed to emigrate from stream channels final size distributions of residuals normalized and mean fish size increased, even when food availability was decreasing. Steingrímsson & Grant (1999) indicated that shallower sites coupled with ontogenetic habitat shifts influenced density-dependent growth. Ontogenetic changes in behavior favored larger fish in the present
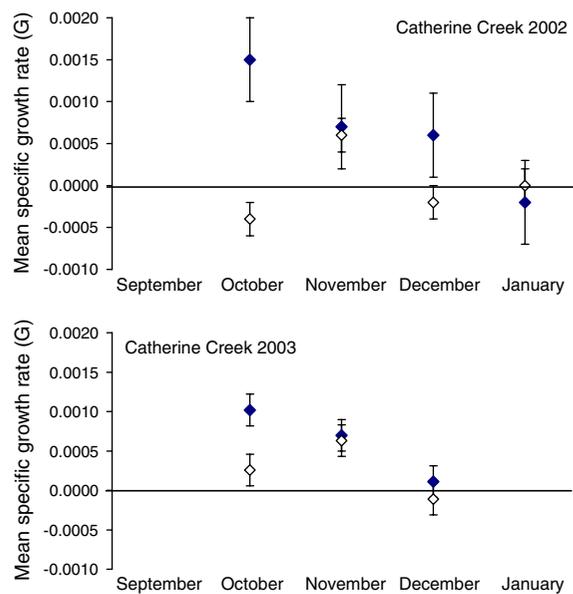
Fig. 4 Monthly mean specific growth rate and standard error of PIT-tagged spring Chinook salmon residual fish (◆) and emigrants (◇) in Catherine Creek, September 2002–January 2003, and September 2003–January 2004

study simply because unit selection was restricted to pools ≥90 cm deep. Westoby (1981) advised against using fork length or growth rate alone as indicators of habitat quality because the variables did not account equally for changes mediated by carrying capacity. In the present study, growth measurements were low, which may have limited the power to detect biologically meaningful differences. In addition, all the above cited studies occur during initial rearing (spring–summer) when growth potential is greater than those expected in fall–winter rearing, which could add bias when comparing patterns among seasons. For these reasons, quantifying fish size by biomass rather than length or weight may better characterize differences associated with different winter concealment habitat qualities.

The larger mean fork lengths and higher mean specific growth rates for residual spring Chinook salmon than for emigrants was not observed in each study stream. Mason & Chapman (1965) found that larger coho salmon that emerged first from simulated redds within artificial stream channels had an ecological advantage over fish that emerged later, which resulted in the larger fish tending to remain in stream channels and smaller fish tending to emigrate. A similar study conducted by Keeley (2001) found

that steelhead emigrants were not only smaller in length and weight than fish that residualized, but were also in poorer condition. This pattern of larger fish retaining the most suitable habitats while smaller fish are excluded has been attributed to competition (Elliott, 1993; Armstrong, 1997; Steingrímsson & Grant, 1999). Emigrants from hatching areas of Catherine Creek were smaller than residuals in both 2002 and 2003. In contrast, no emigration in the upper Grande Ronde River was found, suggesting that intraspecies interactions did not induce individual fish to emigrate out of the hatching area. Given these different observations, and that the growth measurements observed were low, interpreting whether fish behavior is influenced exclusively by winter concealment habitat quality must first consider how density-dependent and independent factors mediate rearing behavior.

The higher biomass–density found in pools with higher winter concealment habitat scores than in pools with lower scores in all three study streams implies that increasing the abundance of depressed populations could be achieved by enhancing winter concealment habitat quality in rearing areas. Steingrímsson & Grant (1999) found that juvenile Atlantic salmon density declined as habitat became less suitable, and indicated that changes in habitat preference played an important role in the response. Armstrong and Griffiths (2001) demonstrated that the proportion of juvenile Atlantic salmon that concealed in an indoor stream channel decreased as fish density increased. Harwood et al. (2002) found that Atlantic salmon and brown trout actively exhibited inter- and intraspecific competition for available winter concealment habitat and generally did not share a space. A reduction of suitable winter concealment habitat would result in an increase in competitive behavior and thus a reduction in overwinter carrying capacity. Carrying capacity in all three streams in the present study increased when winter concealment habitat quality increased. Density-dependent factors may influence competition more than differences in growth potential, in that space regulating factors may impact the results more than metabolic requirements.

Relationships between biomass–density and the nine attributes used to rank winter concealment habitat quality conformed to the hypotheses differently in each study stream. Biomass–density was significantly related to six winter concealment habitat

Table 6 Winter concealment habitat scores with rank in parentheses, and monthly biomass–density of juvenile spring Chinook salmon with rank in parentheses in pools of Catherine Creek, Lostine River, and upper Grande Ronde River

Stream, Year	Winter concealment habitat score (rank)	Monthly biomass–density (rank)				
		September	October	November	December	January
Catherine Creek						
2002	36 (1)	7.06 (1)	7.48 (1)	7.82 (1)	7.56 (1)	7.58 (1)
	34 (2)	5.79 (4)	6.03 (4)	6.28 (4)	6.00 (5)	5.97 (4)
	32 (3)	6.41 (2)	6.91 (2)	7.28 (2)	6.84 (2)	6.65 (2)
	27 (4)	5.65 (5)	5.74 (5)	6.07 (5)	6.02 (4)	5.97 (4)
	23 (5)	5.15 (6)	5.72 (6)	5.76 (6)	5.54 (6)	5.49 (6)
	21 (6)	6.03 (3)	6.49 (3)	6.91 (3)	6.33 (3)	6.40 (3)
2003	36 (1)	4.52 (6)	4.87 (6)	5.60 (4)	5.53 (4)	5.44 (4)
	32 (2)	5.92 (2)	5.82 (3)	5.99 (2)	6.08 (2)	5.73 (2)
	32 (3)	6.42 (1)	7.27 (1)	7.65 (1)	7.51 (1)	7.44 (1)
	30 (4)	4.96 (5)	5.13 (5)	5.17 (5)	5.15 (5)	5.03 (5)
	27 (5)	5.24 (4)	5.52 (4)	5.13 (6)	4.72 (6)	4.70 (6)
	23 (6)	5.68 (3)	5.83 (2)	5.66 (3)	5.66 (3)	5.66 (3)
Lostine River						
2003	35 (1)	6.10 (2)	7.12 (1)	7.98 (1)	7.66 (1)	8.29 (1)
	35 (2)	5.67 (4)	6.80 (4)	7.04 (2)	7.19 (2)	7.28 (2)
	34 (3)	6.79 (1)	7.02 (2)	6.64 (3)	6.75 (3)	6.51 (3)
	32 (4)	4.84 (5)	5.23 (5)	5.24 (5)	5.09 (5)	5.32 (5)
	31 (5)	4.39 (6)	4.70 (6)	4.42 (6)	4.41 (6)	4.89 (6)
	27 (6)	6.06 (3)	6.92 (3)	6.25 (4)	6.42 (4)	6.17 (4)
Upper Grande Ronde River						
2003	31 (1)	2.73 (5)	3.68 (5)	3.50 (5)	3.71 (5)	–
	28 (2)	4.39 (2)	4.69 (2)	4.74 (3)	4.90 (3)	–
	27 (3)	4.47 (1)	4.91 (1)	4.96 (1)	4.97 (1)	–
	26 (4)	4.08 (3)	4.65 (3)	4.77 (2)	4.94 (2)	–
	25 (5)	1.13 (6)	1.69 (6)	2.15 (6)	2.17 (6)	–
	23 (6)	3.61 (4)	3.85 (4)	3.85 (4)	3.90 (4)	–

attributes in Catherine Creek, five winter concealment habitat attributes in the Lostine River, and four winter concealment habitat attributes in the upper Grande Ronde River. The different associations between biomass–density and eight of the nine winter concealment habitat attributes may indicate that density-dependent factors influence each population differently. Jaeger (1974) found that a competition-regulated response required that the demand for a resource exceeded its availability. It was evident that demand for available resources was exceeded in Catherine Creek because biomass–density decreased after November and smaller fish emigrated. Conversely, Westoby (1981) indicated that under-seeded habitats would be influenced by other random

variables not associated with competition-driven mortality and emigration. Changes in the population appeared to function independent of competition in the Lostine and upper Grande Ronde rivers because carrying capacity was not exceeded through January or few fish emigrated. Therefore, comparing results among the three study streams would be inappropriate because factors that regulated the response may be affected by varying levels of density-dependent and independent mortality and emigration.

Only one of the nine attributes, the amount of cobble substrates, was positively associated with biomass–density in each study stream. Larger amounts of cobble substrate appeared to conform to the notion that it is an important overwintering habitat for spring Chinook
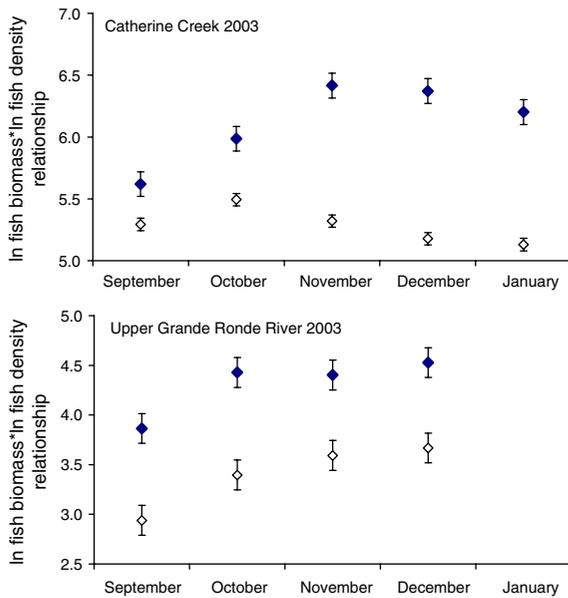
Fig. 5 Juvenile spring Chinook salmon biomass–density relationship among pools with the higher (◆) and lower (◇) winter concealment habitat scores. The biomass–density relationship utilizes natural logarithms to identify the relationship between carrying capacity and winter concealment habitat quality

salmon. Bjornn (1971) identified that carrying capacity was positively related with the quantity and quality of large substrates available to spring Chinook salmon for overwintering. Hillman et al. (1987) also identified that larger substrate piles increased the number of spring Chinook salmon that occupied the habitat. In

each study stream larger amounts of cobble substrate were related to more fish overwinter. Therefore, we recommend that habitat improvement projects that aim to increase overwinter survival and carrying capacity should include an assessment of the amount of available cobble substrate, and the natural processes that create and sustain cobble substrate.

Assessing factors associated with winter concealment habitat quality should be conducted separately for each stream and fish population. Although among stream comparisons are inappropriate for this study, associations did not conform categorically to all metrics, and thus may be less dependable for comparing among stream basins and populations. Fore (2003) described five safeguards used to reduce the probability of drawing unsubstantiated conclusions from metric data analysis: (1) randomize site selection across large geographic areas, (2) measures should be selected independently, (3) metrics tested in multiple years, (4) metrics tested across multiple gradients of condition, and (5) confounding factors that underlie patterns of condition and biology were explicitly tested. This study randomly selected sites across a large area using information from the literature, but we only repeated the assessment over 2 years in Catherine Creek, and we did not explicitly test the level of independence among metrics. Additional research may be needed to identify the level of bias associated with these factors.

Table 7 Spearman's correlation coefficients with significant relationships ($P < 0.05$) in bold for juvenile spring Chinook salmon biomass–density and nine habitat attributes used to rank winter concealment habitat in the hatching areas of Catherine Creek, Lostine River, and upper Grande Ronde River

Winter concealment habitat	Biomass–density			
	Catherine Creek		Lostine River	Upper Grande Ronde River
Variable	2002	2003	2003	2003
Cobble (m²)	**0.91**	**0.82**	**0.89**	**0.95**
Mean embeddedness rating	**0.76**	**0.77**	**0.90**	−0.24
Percent of cells with embeddedness > 4	**0.76**	**0.77**	**0.84**	−0.40
Percent of pool with velocity <0.25 m/s	**0.75**	**0.92**	−0.26	**0.76**
Percent of pool with velocity <0.5 m/s & depth <51 cm	**0.93**	−0.10	−0.09	**0.67**
Mean depth (cm)	**0.85**	**0.94**	**−0.79**[a]	−0.46
Mean velocity (m/s)	0.31	−0.22	**0.78**	−0.29
Percent instream cover in pool	−0.42	−0.25	−0.33	**0.96**
Percent of pool with fines	0.29	0.30	−0.17	−0.15

[a] Although the correlation coefficient was significant, the relationship was the opposite of what was hypothesized

Hatching areas in the Grande Ronde River Basin went through a reduction in physical habitat and an increased level of embeddedness between 1935 and 1992 (McIntosh et al., 1994). Although winter concealment habitat scores used in the present study cannot be compared directly with historic records, it appears that limited large woody debris, small substrate sizes and embeddedness continue to characterize habitat condition in the Grande Ronde River Basin. Loss of these habitat features has been shown to negatively impact survival (Quinn & Peterson, 1996) and use by fish (Hillman et al., 1987). In this investigation, fish favored pools with larger substrates that were not embedded. Therefore, achieving fish recovery goals in the basin should include management objectives that increase the ratio of pools that contain more unembedded cobble substrate piles in hatching areas.

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