Ecology of Winter Concealment Behavior of Juvenile Spring Chinook Salmon in the Grande Ronde River Basin, Oregon

Abstract

We characterized winter concealment behavior (WCB) for juvenile spring Chinook salmon (Oncorhynchus tshawytscha) from October through January in three study streams of the Grande Ronde River Basin, Oregon. The Nocturnal Index (NI), the frequency of fish using WCB, increased significantly as mean daily water temperature decreased. WCB was negatively associated with mean daily water temperature in all three streams, and positively associated with fish size in Catherine Creek and the Lostine River. WCB was not significantly associated with fish density in any of the three streams. Both the NI and detections of concealed fish indicated that fish were concealing amid interstitial spaces during the day and emerging at night as early as October–November, yet no population fully exhibited WCB during any month sampled. Although low water temperature influenced WCB in the Grande Ronde River Basin, other ecological factors affected the behavior because not all fish used WCB even when mean daily water temperatures were < 1 °C.

Introduction

Spring Chinook salmon (Oncorhynchus tshawytscha) in the Grande Ronde River Basin of Oregon and Washington have declined precipitously from historical levels. In 1995 the species was officially listed with other Snake River Basin populations as threatened under the Endangered Species Act (NMFS 1995). Poor overwinter survival as a result of a reduction in habitat complexity has been implicated as one cause of the decline. An estimated 80% of historical anadromous salmonid habitat in the upper Grande Ronde River has been degraded (USFS 1992); consequently, poor thermal buffering, sedimentation, reduction in riparian zone and loss of pool habitats have been identified as problems confronting recovery efforts (Bryson 1993).

Winter concealment behavior (WCB; Griffith and Smith 1993, Gregory and Griffith 1996a, Meyer and Gregory 2000) is one way that stream-dwelling resident and anadromous salmonids enhance survival during winter. Species exhibiting WCB typically shift from actively feeding during the day and night to concealing themselves amid interstitial spaces during the day and emerging at night (Hartman 1963, Rimmer et al. 1983, Riehle and Griffith 1993). The reason for the behavior change is still unclear. Two common theories are that fish are responding to predation or ice formation (Webb 1978, Fraser and Metcalfe 1997, Valdimarsson and Metcalfe 1998), or that they are seeking to minimize energy expenditures in the face of extreme environmental conditions (Taylor 1988, Meyer and Griffith 1997, Whalen et al. 1999). In addition, the timing of the onset of WCB has varied widely among species and locations. Atlantic salmon (Salmo salar) in the Little Sevogle River, New Brunswick moved from their unsheltered summer positions directly into winter concealment habitat (WCH) in the streambed in late September (Rimmer et al. 1983). Bradford and Higgins (2001) found juvenile spring Chinook salmon and steelhead (O. mykiss) in the Bridge River, British Columbia exhibiting WCB throughout the year. Although both studies found that fish demonstrated WCB in winter, Taylor (1988) found that juvenile Chinook salmon of the Fraser River, British Columbia remained in open water during winter even when water temperatures were between 0 °C – 2 °C.

Ecological factors implicated as possible causal mechanisms for the onset of WCB in salmonids during the day and emerging at night (Hartman 1963, Rimmer et al. 1983, Riehle and Griffith 1993).
include water temperature, size of fish, and fish density. Several studies have indicated that water temperature directly and indirectly influences the shift to WCB in salmonids (Bustard and Narver 1975, Rimmer et al. 1983, Chisholm et al. 1987, Jakober et al. 1998). Water temperature < 10 °C has been associated with the onset of WCB in spring Chinook salmon, while temperatures < 4 °C have been associated with most fish using daytime concealment (Hillman et al. 1987, Taylor 1988).

Fish size has also been shown to be related to the onset of WCB. Smaller juvenile steelhead were less likely to initiate encounters and were more likely to be displaced from simulated WCH than larger fish (Gregory and Griffith 1996b). Brown trout (S. trutta) and Atlantic salmon of similar size did not consistently out-compete one another for available WCH (Harwood et al. 2002).

High fish density can influence behavior in juvenile spring Chinook salmon by inducing aggression, competition and movement within and out of rearing areas (Bjornn 1971, Everest and Chapman 1972, Hillman et al. 1987). Density-dependent factors lead to aggressive competition for available WCH and may have an effect on carrying capacity in winter (Gregory and Griffith 1996b). A better understanding of the relationships between WCB and water temperature, fish size and fish densities would aid managers in their efforts to increase Chinook salmon carrying capacity and aid recovery of depressed populations.

Our objectives were to determine when juvenile spring Chinook salmon of Catherine Creek, Lostine River and upper Grande Ronde River shift to WCB, and to identify how water temperature, fish size and fish density influenced the onset of WCB. Two research hypotheses were tested: 1) the nocturnal index (NI), the frequency of fish using WCB, will increase as mean daily water temperature decreases; and 2) the number of fish detected using WCB will be inversely correlated with mean daily water temperature, and positively correlated to fish size and fish density.

Study Area

The Grande Ronde River Basin (Figure 1) encompasses 10,697 km² of Oregon and Washington, USA (Seaber et al. 1987). Elevations within the basin range from 2440 m and 2134 m in the Wallowa and Blue Mountains (respectively) to 705 m at the confluence of the Grande Ronde and Snake rivers. This investigation took place in the primary spring Chinook salmon hatching areas of three streams, Catherine Creek, the Lostine River, and the upper Grande Ronde River. Frost-free conditions persist in the basin for 130–160 days annually. Winter conditions bring cold temperatures, and precipitation that averages >152 cm per year in high elevations, mostly as snow. Annual increases in river flow occur in April–June from snowmelt, and October–November from autumn rain (Nowak 2004). Mean daily water temperatures range from 0 °C to 24 °C annually. The upper river and tributaries generally are iced over from November to April.

Although population abundance in the basin remained lower than historical 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. Primary spawning areas were identified as those in which over half of the redds occurred. In Catherine Creek over half of the redds were in a 12 km section in the middle of the 32-km spawning area, whereas in the Lostine and upper Grande Ronde rivers over half of the redds occurred in 5 km sections of the 33-km and 23-km areas, respectively (Figure 1).

Because juvenile spring Chinook salmon primarily rear in pool habitats in summer through winter (Lister and Genoe 1970, Everest and Chapman 1972, Scarnecchia and Roper 2000), the number of pools > 40 m² and > 80 cm depth were counted in the primary hatching area. Initial inventories identified 47, 51, and 73 pools within the designated hatching areas of Catherine Creek, Lostine River, and upper Grande Ronde River, respectively. Median pool surface areas at base-flow were 139, 287, and 119 m² in each of the aforementioned sub-basins, respectively. We used a random number generator to select six pools in each stream to study WCB.

Methods

Winter Concealment Behavior (WCB)

We assessed the frequency of WCB from October through January in 2002 and 2003 in Catherine
Creek, and from October through January in 2003 in the Lostine and upper Grande Ronde rivers. Snorkel surveys were conducted each month to count the number of juvenile spring Chinook salmon in the water column of each pool during the day, and repeated again that night. Counts from each period each month were used to identify the Nocturnal Index (NI; Fraser et al. 1995). The NI was expressed as:

\[
NI = \frac{E_n}{E_n + E_d} \times 100
\]

where \(E_n\) is the number of fish counted at night, and \(E_d\) is the number of fish counted in the day. An NI > 50% indicated the fish population had shifted primarily to WCB.

Ecological Factors Related to WCB

We collected juvenile spring Chinook salmon from pools at night with seines or dip nets. Captured fish were measured to the nearest 1 mm fork length, weighed to the nearest 0.1 g, and tagged with passive integrated transponder (PIT) tags before

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release back into the same pool. The number of PIT tagged fish that were concealed during the day was identified using a Destron-Fearing 2001F PIT tag reader and watertight antenna. Concealed fish were located by scanning over all substrate types and physical structures following daytime snorkel counts. The locations of concealed fish were verified by peering through the interstitial space or gently moving cover. In addition, we used the Destron-Fearing 2001F tag reader to identify if fish tagged at night were also active during day by scanning fish that were found swimming in the water column the day before and day after tagging each month. A snorkel surveyor approached fish from an upstream direction, slowly maneuvering the watertight antenna near the fish, and waiting for it to swim near or by the antenna.

Water temperature loggers were placed in each study unit of the three study streams during September to measure changes in temperature throughout the study period. Mean daily water temperature (°C) was selected as the variable to be measured against the onset of WCB.

Changes in fish size were evaluated monthly by collecting juvenile spring Chinook salmon from each pool at night using seines or dip nets. Each fish was measured to the nearest 1 mm fork length, weighed to the nearest 0.1 gram, and interrogated for a PIT tag. Fish size was calculated using the log of fork length times the log of fish weight to account for the exponential relationship between the two measured attributes, and to better account for differential growth among periods.

Changes in fish density per 100 m^2 were evaluated using the collection methods described for fish size. The numbers of tagged and untagged fish were recorded for each pool monthly. All untagged fish were tagged prior to release. Population estimates were determined using the Schnabel population expression (Seber 1982):

\[
\hat{N} = \frac{\sum C_i M_i}{\sum R_i}
\]

(2)

where \( \hat{N} \) is the estimated population size, \( M \) is the number of fish initially tagged and released, \( C \) is the number of fish collected and examined for tags in the second period, and \( R \) is the number of recaptures found in \( C \). 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 the hatching area using the equation (Jonasson et al. 1999):

\[
\hat{L} = \frac{T}{E}
\]

(3)

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 \( E \) is the estimated trap efficiency.

Data Analysis

We tested the hypothesis that the frequency of fish using WCB increased as mean daily water temperature decreased using the Kruskal-Wallis test (\( P < 0.05 \)). Given that this study was not conducted in laboratory setting, we used a nonparametric analysis of variance to address issues such as unequal sample sizes at each temperature range measured. To test the hypothesis that the number of fish detected exhibiting WCB was inversely related with mean daily water temperature, fish size and fish density, we used Pearson’s correlation coefficients. Because the asymptotic standard error (\( \chi^2 \)) may not be valid when sample sizes are small (< 500), the Exact test was used to test the null hypothesis of no association (\( H_0: |r| = 0; \alpha < 0.05 \)).

Results

Winter Concealment Behavior (WCB)

The NI increased significantly in every stream as mean daily water temperature decreased. The NI increased significantly as mean daily water temperature decreased during both years in Catherine Creek (Kruskal-Wallis test; 2002 \( H = 14.65 \), df = 4, \( P < 0.01 \), and 2003 \( H = 12.80 \), df = 3, \( P < 0.01 \)), and in 2003 in both the Lostine River (Kruskal-Wallis test; \( H = 13.29 \), df = 3, \( P < 0.01 \)) and the upper Grande Ronde River (Kruskal-Wallis test; \( H = 8.26 \), df = 3, \( P = 0.04 \)). In Catherine Creek during 2002, an NI > 50 was found in at least one pool during every month sampled (October to January), and every pool had an NI > 50 by December (Figure 2). All fish were concealed during the day (NI = 100) in two of ten pools in December, and five of ten pools in January. In Catherine Creek
During 2003, an NI > 50 was found in at least one pool during every month sampled, and every pool had an NI > 50 by November (Figure 2). All fish were concealed during the day (NI = 100) in one of six pools in December, and four of six pools in January. In the Lostine River during 2003,
only one pool had an NI < 50 during any month sampled (October to January), and all pools had an NI > 50 by the last week in November (Figure 2). All fish were concealed during the day (NI = 100) in three of the six pools in November, five of six pools in December, and four of six pools in January. In the upper Grande Ronde River during 2003, only one pool had an NI < 50 during any month sampled, and all but one pool had an NI > 50 in October (Figure 2). All fish were concealed during the day (NI = 100) in two of six pools in November, and three of six pools in December.

Ecological Factors Related to WCB

The number of fish detected using WCB increased as mean daily water temperatures decreased in all three streams (Table 1). In Catherine Creek during 2002 and 2003, fish were first found concealed during the day when mean daily water temperatures were below 7 °C, and the number of concealed fish increased after water temperature fell below 3 °C. Cumulative detections of concealed fish increased from October through December (Figure 3). In the Lostine River during 2003, fish were first found concealing during the day when mean daily water temperatures were below 3 °C. Cumulative detections of concealed fish increased from October through January (Figure 3). In the upper Grande Ronde River during 2003, fish were first found concealing during the day when mean daily water temperatures were below 2 °C. Detections of concealed fish increased October through December (Figure 3). In all three streams fish were detected concealing within interstitial spaces created by substrate, wood or rootwad structure. Tagging fish at night did not show a bias toward night activity in that we detected many of the same tagged fish active in the water column both during the day and at night. In addition, tagged fish did not appear to move to other pools that we sampled the day before or day after tagging.

WCB was significantly associated with mean daily water temperature and fish size, but not with fish density. In Catherine Creek during 2002 and 2003, the number of concealed fish (i.e., using WCB) was negatively related to mean daily water temperature (Pearson’s correlation coefficient; Exact test; \( P = 0.05 \) and \( P = 0.02 \), respectively) and positively related to fish size \( (P = 0.04 \) and \( P = 0.04 \); Table 2). However, no relationship was found between the number of concealed fish and fish density in either year \( (P = 0.98 \) and \( P = 0.98 \). In the Lostine

### TABLE 1

<table>
<thead>
<tr>
<th>Year, Stream, Month</th>
<th>Pools (n)</th>
<th>Total Fish</th>
<th>Mean Count Concealed</th>
<th>Mean Percent Nocturnal Index</th>
<th>Mean Daily Water Temperature (°C)</th>
<th>Mean Fish Size (log length x log weight)</th>
<th>Mean Fish Density (fish/100m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2002 Catherine Creek</strong></td>
<td>6</td>
<td>0</td>
<td>0.0 (0-0)</td>
<td>35 (31-38)</td>
<td>4.6 (4.4-4.7)</td>
<td>1.40 (1.26-1.49)</td>
<td>145 (81-211)</td>
</tr>
<tr>
<td>October</td>
<td>6</td>
<td>0</td>
<td>0.0 (0-0)</td>
<td>35 (31-38)</td>
<td>4.6 (4.4-4.7)</td>
<td>1.40 (1.26-1.49)</td>
<td>145 (81-211)</td>
</tr>
<tr>
<td>November</td>
<td>6</td>
<td>3</td>
<td>0.5 (0-2)</td>
<td>59 (43-79)</td>
<td>2.3 (1.9-3.5)</td>
<td>1.43 (1.34-1.49)</td>
<td>168 (91-248)</td>
</tr>
<tr>
<td>December</td>
<td>6</td>
<td>14</td>
<td>2.3 (0-6)</td>
<td>64 (55-79)</td>
<td>1.2 (0.5-1.6)</td>
<td>1.43 (1.29-1.50)</td>
<td>131 (74-198)</td>
</tr>
<tr>
<td>January</td>
<td>6</td>
<td>4</td>
<td>0.7 (0-1)</td>
<td>73 (48-100)</td>
<td>2.3 (0.5-3.4)</td>
<td>1.41 (1.30-1.47)</td>
<td>133 (67-218)</td>
</tr>
<tr>
<td><strong>2003 Catherine Creek</strong></td>
<td>6</td>
<td>2</td>
<td>0.3 (0-1)</td>
<td>48 (40-60)</td>
<td>7.0 (6.7-7.3)</td>
<td>1.18 (1.06-1.25)</td>
<td>111 (65-124)</td>
</tr>
<tr>
<td>October</td>
<td>6</td>
<td>2</td>
<td>0.3 (0-1)</td>
<td>48 (40-60)</td>
<td>7.0 (6.7-7.3)</td>
<td>1.18 (1.06-1.25)</td>
<td>111 (65-124)</td>
</tr>
<tr>
<td>November</td>
<td>6</td>
<td>10 (0-2)</td>
<td>78 (58-100)</td>
<td>0.7 (0.6-0.9)</td>
<td>1.22 (0.93-1.31)</td>
<td>119 (64-235)</td>
<td></td>
</tr>
<tr>
<td>December</td>
<td>6</td>
<td>7</td>
<td>1.2 (0-3)</td>
<td>82 (63-100)</td>
<td>1.4 (1.0-1.7)</td>
<td>1.25 (1.00-1.37)</td>
<td>113 (51-217)</td>
</tr>
<tr>
<td>January</td>
<td>6</td>
<td>5</td>
<td>0.8 (0-4)</td>
<td>93 (75-100)</td>
<td>0.8 (-0.1-0.5)</td>
<td>1.28 (1.26-1.31)</td>
<td>104 (52-228)</td>
</tr>
<tr>
<td><strong>Lostine River</strong></td>
<td>6</td>
<td>4</td>
<td>0.7 (0-4)</td>
<td>85 (42-100)</td>
<td>1.8 (0.0-3.7)</td>
<td>1.18 (0.98-1.35)</td>
<td>153 (45-245)</td>
</tr>
<tr>
<td>October</td>
<td>6</td>
<td>4</td>
<td>0.7 (0-4)</td>
<td>85 (42-100)</td>
<td>1.8 (0.0-3.7)</td>
<td>1.18 (0.98-1.35)</td>
<td>153 (45-245)</td>
</tr>
<tr>
<td>November</td>
<td>6</td>
<td>17</td>
<td>2.8 (0-6)</td>
<td>94 (72-100)</td>
<td>1.7 (0.0-3.6)</td>
<td>1.18 (1.00-1.32)</td>
<td>143 (41-239)</td>
</tr>
<tr>
<td>December</td>
<td>6</td>
<td>23</td>
<td>3.8 (0-9)</td>
<td>95 (71-100)</td>
<td>1.5 (0.1-3.0)</td>
<td>1.23 (1.10-1.36)</td>
<td>134 (39-196)</td>
</tr>
<tr>
<td>January</td>
<td>6</td>
<td>25</td>
<td>4.2 (0-12)</td>
<td>94 (69-100)</td>
<td>1.8 (0.3-3.2)</td>
<td>1.25 (1.03-1.33)</td>
<td>159 (49-310)</td>
</tr>
<tr>
<td><strong>Upper Grande Ronde River</strong></td>
<td>6</td>
<td>0</td>
<td>0.0 (0-0)</td>
<td>54 (44-80)</td>
<td>8.2 (7.8-8.9)</td>
<td>1.18 (1.07-1.30)</td>
<td>47 (8-72)</td>
</tr>
<tr>
<td>October</td>
<td>6</td>
<td>0</td>
<td>0.0 (0-0)</td>
<td>54 (44-80)</td>
<td>8.2 (7.8-8.9)</td>
<td>1.18 (1.07-1.30)</td>
<td>47 (8-72)</td>
</tr>
<tr>
<td>November</td>
<td>6</td>
<td>14</td>
<td>2.3 (0-6)</td>
<td>79 (54-100)</td>
<td>1.3 (0.9-1.6)</td>
<td>1.17 (0.96-1.31)</td>
<td>48 (12-71)</td>
</tr>
<tr>
<td>December</td>
<td>6</td>
<td>27</td>
<td>4.5 (1-14)</td>
<td>92 (69-100)</td>
<td>0.5 (-0.1-0.2)</td>
<td>1.19 (1.00-1.31)</td>
<td>50 (12-72)</td>
</tr>
</tbody>
</table>
Figure 3. PIT tagged juvenile spring Chinook salmon detected using winter concealment behavior (WCB) during the day in Catherine Creek, Lostine River and upper Grande Ronde River.

TABLE 2. Pearson correlation coefficients with significant relationships ($P < 0.05$) in bold for the number of juvenile spring Chinook salmon detected using winter concealment behavior (WCB) and mean daily water temperature, fish size, and fish density in the hatching areas of Catherine Creek, Lostine River and upper Grande Ronde River.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Catherine Creek</th>
<th>Lostine River</th>
<th>Upper Grande Ronde River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean daily water temperature (°C)</td>
<td>-0.992</td>
<td>-0.992</td>
<td>-0.993</td>
</tr>
<tr>
<td>Fish size (Log L*W)</td>
<td>0.996</td>
<td>0.997</td>
<td>0.988</td>
</tr>
<tr>
<td>Fish density (100m²)</td>
<td>-0.030</td>
<td>-0.006</td>
<td>0.048</td>
</tr>
</tbody>
</table>
River during 2003, the number of concealed fish was negatively related to mean daily water temperature (Pearson’s correlation coefficient; Exact test; \( P = 0.02 \)), and positively related to fish size \( (P = 0.04; \text{Table 2}) \). No relationship was found, however, between the number of concealed fish and fish density \( (P = 0.95) \). In the upper Grande Ronde River during 2003, the number of concealed fish was negatively related to mean daily water temperature (Pearson’s correlation coefficient; Exact test; \( P < 0.01; \text{Table 2} \)). No relationship was found between the number of concealed fish and fish size \( (P = 0.06) \) or the number of concealed fish and fish density \( (P = 0.49) \).

Discussion

The relationship we found of increasing WCB with decreasing mean daily water temperature is similar to what other investigators have reported. Fraser et al. (1995) demonstrated that the shift from daytime to nighttime activity by juvenile Atlantic salmon was linked to decreasing water temperature rather than to inherent annual rhythms or photoperiod, because fish suppressed activity during the day at cold water temperatures at all times of the year. They attributed this shift in behavior to an increase in WCB rather than more fish migrating into a site at night. Meyer and Gregory (2000) found that rainbow \( (O. mykiss) \) and brook trout \( (Salvelinus fontinalis) \) also increased in density at night as water temperatures decreased below 10 °C regardless of age or size. Results of this study support their claim in that higher NI ratios were found as water temperatures decreased below 7 °C.

Differences in capture probabilities between daytime and nighttime snorkel counts may have introduced an unknown level of bias into our NI analysis. Rodgers et al. (1992) were not able to effectively estimate abundance of coho salmon using daytime snorkel counts during winter in small Oregon coastal streams. Winter water temperatures in their investigation averaged 10 °C, which may have reduced the level of concealment behavior that coho salmon were exhibiting. Roni and Fayram (2000) also identified differences in relative efficiency among daytime snorkeling, nighttime snorkeling and multiple-pass electrofishing in estimating the abundance of coho salmon, steelhead and cutthroat trout \( (O. clarki) \) in 32 stream reaches of 4 different western Washington coastal streams. They also found that daytime snorkeling was the least efficient of the three methods at estimating true population size, but that nighttime snorkeling had a higher efficiency than electrofishing estimates. We hesitate to directly apply sampling efficiency findings between costal streams and the streams in our study area because of differences between spatial and temporal characteristics found in the two regions from October to January. For instance, the kinds of conditions that hamper visibility during winter sampling in western Oregon and Washington coastal streams (highly fluctuating flows and high particulate loads) do not parallel those found in high elevation interior streams (ice formation and freezing) of these states. We did not encounter fluctuating increases in flow or highly turbid conditions during the study period. Likewise, habitat types and complexity in our study area were specific to pools that did not contain much complex structure. Thurow et al. (2006) described these conditions as being the best conditions for readily observing fish using snorkeling techniques and generally had the most valid sampling efficiencies. A post hoc look at our snorkel data may provide additional insight into the level of bias between diel period counts, and possible trends associated with using these metrics to describe relationships within and among seasons.

In our study, the number of fish exhibiting WCB was inversely related to mean daily water temperatures. Taylor (1988) found a similar result where juvenile spring Chinook salmon and coho salmon \( (O. kisutch) \) became more closely associated with cover at 2 °C than at 12 °C. An affinity for physical structure as water temperatures decreased has also been observed by others (Bustard and Narver 1975, Cunjak 1988). However, the tendency for fish to exhibit WCB with a given decrease in temperature differed among the three streams studied. These differences may be because juvenile spring Chinook salmon are not as strongly associated with cover as other salmonids, instead having a tendency to remain active when temperatures are as low as 0 °C (Taylor 1988). Therefore, a threshold temperature for concealment may differ among species and in streams with different geomorphic characteristics.

The positive relationship between the number of fish using WCB and fish size in Catherine Creek and Lostine River indicates that larger fish were better able to secure and defend WCH. Gregory and Griffith (1996) found that larger subyearling
rainbow trout defended WCH more aggressively than smaller subyearling rainbow trout, and were less likely to be pushed out of WCH. They indicated that this behavior would cause some fish to be excluded from WCH when fish density was high and WCH was limited. Harwood et al. (2002) also identified aggressive behavior when two fish were provided with a single WCH opportunity. They found that residual fish had an advantage in retaining WCH, and that sharing of refuges was uncommon whether fish were competing for a single shelter or excess shelters were available. They suggested that competition for WCH would likely be intense in the wild when WCH was limited. In this study, it is also possible that the relationship between the number of fish detected using WCB and fish size was simply a result of fish being larger in December than they were in October, and the relationship has little to do with defense of WCH. This might be clarified with additional study that controlled for size at varying temperatures through time.

The number of fish detected using WCB was not consistently associated with fish density in the three study streams. In our study, not every fish exclusively exhibited WCB in any month (October to January) even when water temperatures were < 1 °C. Meyer and Gregory (2000) also found that not all adult rainbow trout exhibited WCB during winter, and attributed this behavior to individuals being out-competed for limited WCH. When WCH was limited, Gregory and Griffith (1996) and Harwood et al. (2002) found that salmonids aggressively competed for WCH and that they would not share the space with another fish. The availability of WCH in all of our study streams was limited because unembedded cobble substrate and complex instream cover was lacking. Competition for the limited WCH, therefore, may explain why the number of fish detected using WCB and fish density was not positively associated. Determining if WCB is associated with fish density may require additional research that introduces WCH in areas where fish did not exclusively exhibit WCB.

Because two of the key assumptions of the Schnabel method are that the population size remains the same throughout the study period (e.g., no immigration or emigration), and that there is no differential loss among study sites, using this method may have produced a positively biased estimate. Although we considered a post hoc change to a method that did not require closure assumptions, we feel that our approach reasonably approximated a closed system when we accounted for losses due to movement within and out of the hatching area. Overton (1965) used a similar approach to account for known losses of individuals from the population when using Schnabel method with closure assumptions. Seber (1982) found that Overton’s method produced a robust estimate of the population as long as removal was negligible, and the number of recaptures in each sample was not too small. Fish were rarely detected in other pools during the study. Although fish did exhibit dispersal behavior out of the hatching areas, they followed an anticipated decrease in November that remained relatively inactive until March (Van Dyke et al. 2008). None the less, an unknown level of bias may have influenced the robustness of fish density estimates.

Given that the extent to which fish exhibited WCB differed in each study stream, recovery efforts may be best served by characterizing population specific factors that limit overwinter success. Although water temperature was strongly associated with the onset of WCB, other unmeasured ecological factors may have been associated with the change in behavior. Additional research is needed to identify the extent to which individuals are competing for suitable habitat and how other factors related to carrying capacity regulate WCB.

Acknowledgements

We thank the staff of the Salmonid Early Life History Project for braving late nights in cold inclement conditions to acquire the information on WCB. This research was supported by the Oregon Department of Fish and Wildlife through funding from Bonneville Power Administration.
Literature Cited


Received 21 February 2008
Accepted for publication 26 February 2009