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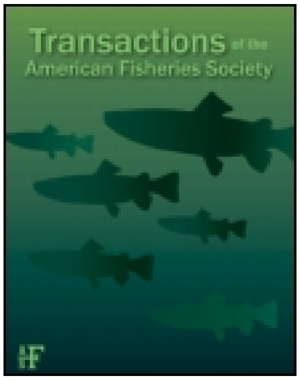

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Juvenile Anadromous Salmonid Production in Upper Columbia River Side Channels with Different Levels of Hydrological Connection

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ARTICLE

Juvenile Anadromous Salmonid Production in Upper Columbia River Side Channels with Different Levels of Hydrological Connection

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Abstract

We examined the contribution of three types of side channels based on their hydrologic connectivity (seasonally disconnected, partially connected, and connected) to production of juvenile anadromous salmonids. Juvenile steelhead *Oncorhynchus mykiss* and Chinook Salmon *O. tshawytscha* were found in all three of these side channel types and in each year of the study. Upon connection with the main stem at high flows, the seasonally disconnected side channels experienced an emptying out of the previous year's fish while filling with young-of-year fish during the 2- to 4-month period of hydrologic connection. There were no differences between the densities of juvenile steelhead and Chinook Salmon and the rate of smolts produced among the three types of side channels. Recently reintroduced Coho Salmon *O. kisutch* had sporadic presence and abundance in partially and connected side channels, but the smolt production rate was over two times that of steelhead and Chinook Salmon in seasonally disconnected side channels. Within seasonally disconnected side channels, young-of-year salmonids in deep pools (≥100 cm) had greater survival than those in shallow pools (<100 cm). Densities of juvenile steelhead in all side channel types were similar to those in tributaries and were higher than in main-stem lateral margins. Juvenile Chinook Salmon densities were higher in side channels than in both tributary and main-stem lateral margins. Our results suggest that improving quality of pool habitat within seasonally disconnected side channels can result in improved survival for juvenile anadromous salmonids during the period of disconnection. Habitat improvement in these seasonally disconnected side channels should be recognized as a worthy restoration strategy, especially when full connectivity of side channels may not be a feasible target (e.g., through lack of water availability) or when full connectivity may present too high a risk (e.g., flooding, stream capture, bank destabilization).

Floodplains play an important role in the diversity and health of ecosystems (Bayley 1995). The flood pulse concept of Junk et al. (1989) holds that annual high-water pulses are the principal force in determining existence, productivity, and interactions of major biota in river–floodplain systems. Junk et al. (1989) speculated that areas affected by flood pulses have higher productivity than areas that maintained continuous flow. This concept recognized the important contributions of off-channel habitat that were missing from the previously established river-continuum concept (Vannote et al. 1980). The river-continuum concept did not account for important zones of high production from floodplains (Johnson et al. 1995). These floodplains typically contain a diversity of off-channel habitats. Off-channel habitats include, but are not limited to, sloughs, beaver ponds, wetlands, alcoves, side channels, and other permanent or seasonally flooded lands. Floodplains can provide high spatial heterogeneity (differences in depth, substrate size, and velocity), a large supply of organic matter, and shallow habitat with few large-sized fish predators, which can make them productive habitat for small fish (Schlosser 1991).

The availability of off-channel habitat has been greatly reduced over the last century by human activities (Hicks et al. 1991; Slaney et al. 1996; Giannico and Hinch 2003). Historically, off-channel habitat made up 84% of potential habitat in

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the interior Columbia River basin (Hall et al. 2007). Stream modifications that reduce off-channel habitat, such as stream channelization (Sedell and Froggatt 1984), have contributed to widespread declines in anadromous fishes (Hall et al. 2007; Naiman et al. 2010). Off-channel habitats have the potential to improve growth and survival, reduce competition for food and space, and improve predator avoidance (Henning et al. 2006; Csoboth and Garvey 2008). In addition, off-channel habitats can serve as refugia from main-stem habitat during periods of high flows (Harvey et al. 1999; Bell et al. 2001). The benefits for juvenile salmonids are probably affected by connectivity, hydroperiod (the period of time the area is covered with water), distance to main-stem river channels, dissolved oxygen levels, and water temperatures (Henning et al. 2006).

When off-channel habitats become seasonally disconnected with the main-stem stream, fish such as juvenile salmonids may become trapped (Bradford 1997). Snodgrass et al. (1996) estimated that 21% of isolated wetlands contained fish and hypothesized that the frequency of drying and nearness to a source population would determine presence or absence of fish. When off-channel habitats lose connection to main-stem flow, water temperatures can exceed lethal limits (Limm and Marchetti 2009) and dissolved oxygen levels also can reach lethal limits (Henning et al. 2006, 2007), creating a net sink for salmonids. However, Brown and Hartman (1988) discovered that off-channel habitats that seasonally lost their connection to the main stem contributed from 15% to 23% of the watershed's production of Coho Salmon *Oncorhynchus kisutch* smolt over a 2-year period. Currently, it is unclear whether habitats that seasonally lose connection are a net source or sink for salmonid production, compared with habitat types that stay hydrologically connected (Brown 2002; restated by Sommer et al. 2005).

In efforts to restore Pacific salmonids listed as threatened or endangered species under the Endangered Species Act (ESA), managers have focused restoration actions towards habitat construction and improvement. These actions, while widely used, are rarely evaluated with respect to their effectiveness for fish recovery (Bernhardt et al. 2005; Kail et al. 2007; Roni et al. 2008; Nagayama and Nakamura 2010). To date, most design recommendations for habitat improvement have been focused on construction and engineering of structures rather than on fish habitat designs (Rosenfeld et al. 2008).

The middle Methow River, between the Chewuch River and Twisp River, has been largely channelized for flood control purposes and construction of roadways, changes that correspond with a large-scale loss in adult returns of anadromous salmonids (Methow Subbasin Plan 2004). Piety et al. (2009) found that side channels in the middle Methow River that maintain flow all year were limited to areas that are dredged or have a groundwater source. In 2012, managing agencies (Bureau of Reclamation, Yakama Nation, Bonneville Power Administration, Washington Department of Fish and Wildlife, U.S. Fish and Wildlife Service, Upper Columbia Salmon Recovery Board, Methow Salmon Recovery Foundation, and others) began implementing several planned restoration projects aimed at restoring floodplain connectivity in the middle Methow River by reconnecting and improving side channels and other off-channel habitats. The objectives of this study were to (1) document and compare the use, survival, and smolt production of juvenile steelhead *O. mykiss* (anadromous Rainbow Trout), Chinook Salmon *O. tshawytscha*, and Coho Salmon among three types of side channels (seasonally disconnected, partially connected, and connected); (2) compare fish densities in side channels with that in tributaries and main-stem lateral margins; and (3) provide recommendations for prioritizing potential stream restoration strategies.

STUDY AREA

The Methow River is a fifth-order stream in north-central Washington State that drains into the Columbia River at river kilometer (rkm) 843 in the upper Columbia River basin. The Methow River typically experiences peak flows during the spring into late summer, driven by snow melt-off from the Cascade Mountains. The watershed covers an area of 4,900 km^2 with average flow of 44 m^3/s, maximum flow of 816 m^3/s, and minimum flow of 4 m^3/s (USGS 2013). Elevation ranges from 244 m to 2,591 m. Annual precipitation varies from 25 cm at the valley bottom to 178 cm in headwaters (Methow Subbasin Plan 2004).

For this study, we separated the Methow River into four sections: Chewuch River, upper Methow River (above Chewuch River), middle Methow River (Chewuch River to Twisp River), and lower Methow River (below Twisp River; Figure 1). Within these sections, side channels were selected in unconfined reaches that were similar to those in the middle Methow River. The Chewuch River and upper Methow River were in better condition with more natural conditions (especially on Forest Service land) than the disturbed sections of the middle and lower Methow River. Diking, water diversions, roads, and wood removal have led to a decrease in side channels in the middle and lower Methow River (Methow Subbasin Plan 2004; Piety et al. 2009). Side channels that remained in the middle and lower Methow River typically maintained connection to the main-stem river only during periods of peak flows. These seasonally disconnected side channels were connected in the spring and into summer, typically from mid-April through June. Side channels in the Chewuch River and upper Methow River were more diverse, ranging from seasonally disconnected, connected on either the upstream or downstream side, and connected on the upstream and downstream side.

Species found in the Methow River watershed include upper Columbia River steelhead, upper Columbia River spring Chinook Salmon, and Columbia River Bull Trout *Salvelinus confluentus*, all listed under the federal ESA. In addition to the ESA-listed species, the Methow River has anadromous populations of summer Chinook Salmon, Coho Salmon, and Pacific Lamprey *Lampetra tridentata*. Coho Salmon were largely extirpated from the Methow River in the 1920s (Mullan 1992), but

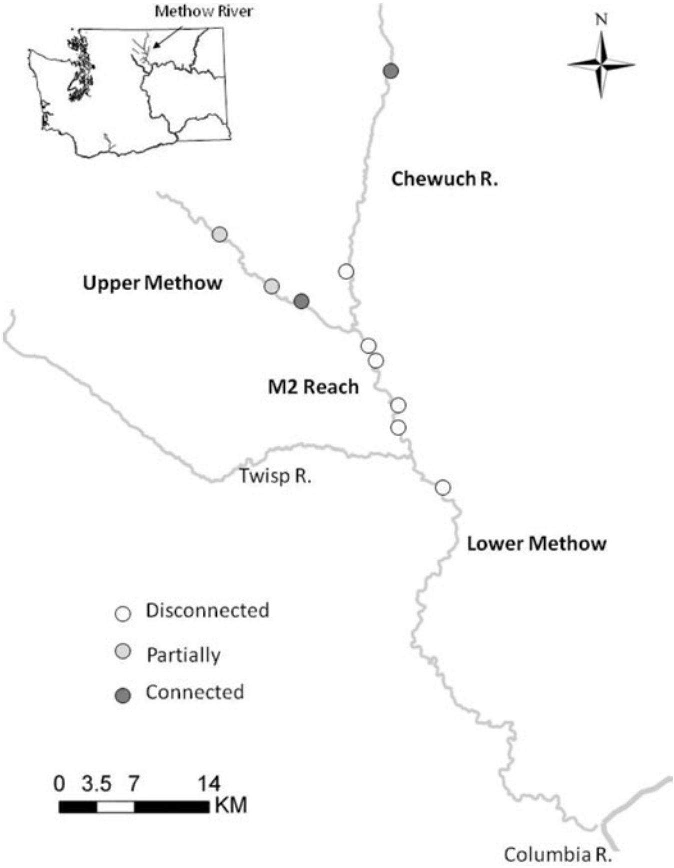

FIGURE 1. Map showing side channels sampled in the Methow River watershed (M2, middle Methow).

a recent aggressive reintroduction plan has led to their return to parts of the Methow River.

METHODS

Sampling design.—Ten side channels were selected, based on type and availability. All side channels were low-gradient side channels, contained less than 25% of the water from the main channel during periods of low flow, and were in unconstrained reaches. Five side channels were sampled in 2009–2012; an additional five side channels were sampled in 2010–2012 to increase sample sizes of different types of side channels. Side channels were grouped by their level of connectivity, similar to the methods of Paillex et al. (2009). The three levels of connectivity are side channels that are connected only during high spring flows (seasonally disconnected), side channels that maintain a connection at either the top or bottom of the side channel year round (partially connected), and side channels connected to the main stem all year (connected). Six of the side channels were seasonally disconnected side channels, two were partially connected side channels, and two were connected side channels. The five side channels sampled in 2009–2012 (three seasonally disconnected, one partially connected, and one connected) included two in the upper Methow River (rkm 87 and 95) and three in the middle Methow River (rkm 66, 70, and 76). The additional five side channels sampled in 2010–2012 included one in the middle Methow River (rkm 75), one in the upper Methow River (rkm 89), two in the Chewuch River (rkm 6 and 22), and one in the lower Methow River (rkm 56).

For each year ($n = 4$) and each side channel, fish were sampled in three seasons: March–April (spring), July–September (summer), and October–November (fall). Spring sampling was done before high flows, when fish were still trapped in seasonally disconnected side channels. Summer sampling occurred after high flows and when seasonally disconnected side channels had lost their connection to the main stem, which resulted in some fish getting trapped in the side channels. Fall sampling occurred during low flows, when fish were still trapped in the seasonally disconnected side channels.

Habitat and fish sampling.—Within the side channels, we stratified the sampling effort based on habitat unit types (e.g., pools, glides, and riffles) and electrofished all habitat units. For every sampling occasion, each habitat unit was measured for length (m), average width (m), average depth (cm), and maximum depth (cm). For pools, a visual estimate of total cover was made, and further separated into types of instream cover (large woody debris, small woody debris, substrate, undercut bank, and other) and overhead cover (large woody debris, small woody debris, and other). Large woody debris was defined as any piece of wood larger than 10 cm in diameter and 1 m in length. Small woody debris was defined as any piece of wood smaller than large woody debris that acted as fish cover. Substrate was an estimate of any substrate that could be used as cover by target fish species (steelhead, Chinook Salmon, and Coho Salmon). When flow into or out of a habitat unit existed, the habitat unit was blocked off with nets during sampling to ensure no immigration or emigration of fish.

A backpack electrofisher was used to conduct two or more passes (a maximum of six) by using the removal-depletion methodology (White et al. 1982). The field guides of Connolly (1996) were used to determine the number of passes necessary to achieve the desired level of precision in the estimate of population abundance (CV [100 × SE/total population estimate] $<25\%$ for young-of-year salmonids and $<12.5\%$ for age-1 or older salmonids) of each sampling unit for each salmonid species (Bull Trout, Brook Trout *S. fontinalis*, Chinook Salmon, Westslope Cutthroat Trout *O. clarkii lewisi*, and steelhead) and age-group (young-of-year and age-1 or older). We considered all Rainbow Trout less than or equal to 300 mm FL as juvenile steelhead, which meant that some resident Rainbow Trout were likely included as juvenile steelhead in our analyses. If passes two and three did not meet the desired level of precision, fish counts from passes one and two were combined and compared with passes three and four, using the two-pass field guide of Connolly (1996) with the next lower CV (e.g., in place of the 25% column, the 12.5% column would be used) to determine the need for a fifth pass. On the rare occasion when fish counts continued to increase after the fifth pass, we would complete a sixth and final pass. As described in Bateman et al. (2005), we used Seber and Le Cren's (1967) estimator to gain a population estimate when we stopped at a two-pass depletion effort, we used Junge and Libosvarsky's (1965) explicit solution of Zippin's (1956) maximum likelihood estimator when we stopped at a three-pass depletion effort, and we used the removal estimator in the program Capture (Otis et al. 1978; White et al. 1982) when we conducted four or more passes. In habitat units that were too deep to effectively sample with removal techniques we used mark–recapture to determine population abundance. On the rare occasion that the mark–recapture estimator failed, or if a snorkel count was higher than the mark–recapture estimate, a direct snorkel count was substituted. Mark–recapture estimates of population abundance were calculated by using the Petersen estimator (Peterson and Cederholm 1984). Population estimates were then divided by stream area to derive fish density estimates. Smolts were identified as PIT-tagged fish detected by PIT tag interrogators at Columbia River dams. Smolt densities were calculated by the number of smolts divided by the length of the side channel and then multiplied by 100. Smolt densities were then divided by the number of tagged fish per 100 m to determine the smolt production rate.

All fish were identified to species and measured for FL to the nearest millimeter, weighed to the nearest 0.1 g, and inspected for external signs of disease. In side channels of the middle Methow River, some fish were suspected to be Chinook Salmon and Coho Salmon hybrids, which was confirmed via genetic analysis (eight of eight suspected hybrids; USGS, unpublished data). In the field, fish identified as possible hybrids had a fin clip taken for genetic analysis and were noted in the data. Based on dominant characteristics, most of the suspected hybrids were labeled as either a Chinook Salmon or Coho Salmon in the data and analyzed as that species. During each sampling event, we tagged most target (steelhead, Chinook Salmon, and Coho Salmon) fish larger than 65 mm with a 12-mm PIT tag and fish 55–65 mm with a 9-mm PIT tag. The PIT-tagging procedures followed the guidelines outlined by Columbia Basin Fish and Wildlife Authority (1999).

Side channel use.—To further evaluate habitat and species interactions in side channels, we used Pearson correlations (Rodgers and Nicewander 1988) to compare species-specific density relationships with habitat parameters and fish density by species. Fish densities in pools from all types of side channels (seasonally disconnected, partially connected, and connected) sampled in the summer (just after hydrological connection) were combined for this analysis. This was done when fish were newly settled into their habitat units after connection and had not been affected by long periods of low survival that could influence the results. Significance was determined using $\alpha = 0.05$.

Side channel type comparisons.—Young-of-year densities of steelhead and Chinook Salmon were compared to determine whether either was present in higher densities in side channels of the lower (middle and lower Methow) sections than in the upper (upper Methow and Chewuch) sections of the Methow River. No differences between young-of-year densities (fish/m^2) of steelhead (*t*-test; $t = 0.297$, $P = 0.769$) and Chinook Salmon (*t*-test; $t = 0.240$, $P = 0.812$) were detected, which allowed us to test for differences between side channel types. Comparisons were made for average fish length, young-of-year densities, and smolt production rates between the three types of side channels by species. Because juvenile Coho Salmon were not fully colonized in the upper watershed, we did not compare Coho Salmon lengths or densities between side channel types. Fish density data, after failing a normality test, were log-transformed to normalize the data, and a one-way analysis of variance (ANOVA) tested for differences among the side channel types. After the smolt production data failed a normality test and did not normalize after log transformation, we ran Kruskal–Wallis one-way ANOVA on ranks test (Kruskal and Wallis 1952) and then used Dunn's method (Dunn 1961) to evaluate significant results. Fish length comparisons were done for young-of-year fish collected in the fall and spring, because they were the dominate age-class in the side channels. Since steelhead typically do not smolt after their first winter, length frequencies were used to remove steelhead from older age-classes from the analysis. An example of fish that were removed from the analysis is shown in Figure 2. Average young-of-year fish lengths were compared across side channel types by ANOVA tests. ANOVA tests that were found to be significant were evaluated using the Holm–Sidak multiple comparison method (Holm 1979). Significance for all tests was determined using $\alpha = 0.05$.

Young-of-year survival estimates were calculated from mark–recapture data between sampling seasons from the six seasonally disconnected side channels by using Cormack–Jolly–Seber estimates (Cooch and White 2012) from the program MARK (White and Burnham 1999). Separate models were evaluated for each species. Models of survival were then ranked

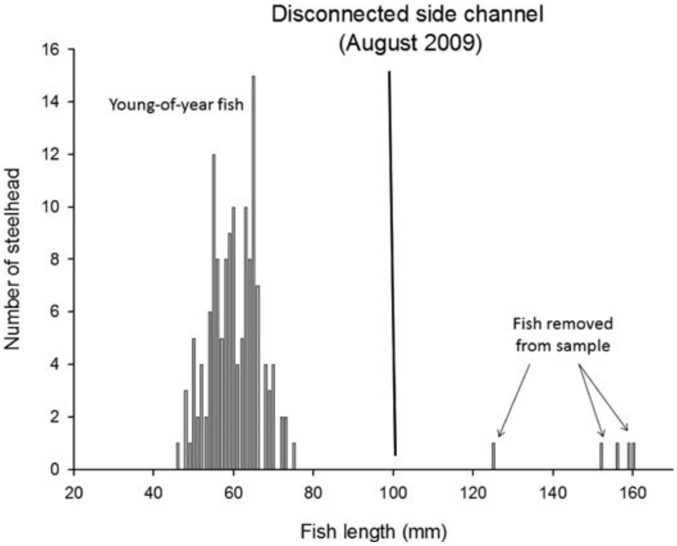

FIGURE 2. Typical length-frequency graph of steelhead from a seasonally disconnected side channel. All fish to the left of the solid vertical line were considered to be age-0.

using Akaike's Information Criterion corrected for small sample size (AICc), whereby smaller AICc values represented more realistic models (Burnham and Anderson 2002). Delta AICc models were selected for consideration depending on how they fell on Burnham and Anderson's three-level scale of support (0–2 substantial, 4–7 considerable, >10 essentially none). The Cormack–Jolly–Seber model provides estimates of detection probability and "apparent survival," where losses due to emigration are treated as additional mortalities. When the seasonally disconnected side channels lost their connection to the main stem, these estimates were of true survival, since emigration was not possible. Fish were separated into two groups of habitat source at time of tagging: deep pools ($\geq$100 cm) and shallow pools (<100 cm). Typically, riffle and glide habitat units would go dry and only pool habitat units would remain in the seasonally disconnected side channels after disconnection, with shallow pools accounting for 88% of the habitat units. Timing of sampling occasion was also evaluated (e.g., to test if there was there a difference between season and years). Four models were evaluated for survival: group and time, time only, group only, and with no groups and survival probabilities constant over time. Because of hybridization, we had a few cases where a fish identified as a Coho Salmon or Chinook Salmon was subsequently recaptured and identified as the other; when this occurred, we used the initial capture identification for survival analysis.

Side channel, tributary, and main-stem lateral margin comparisons.—Young-of-year density estimates in side channels were compared with estimates from tributary and main-stem lateral margins from Martens et al. (2014). Side channel and tributary fish density estimates were sampled with similar methods, while main-stem lateral margin density estimates were sampled by using the methods described in Connolly and Brenkman (2008). The tributary and main-stem lateral margin and fish density estimates were from work done simultaneously by the USGS as part of a separate study. Main-stem lateral margins consisted of sections of stream that extended 4.5 m from the stream bank into the main-stem channel. For this comparison, all three types of side channels were combined. Juvenile Coho Salmon were not fully colonized in tributaries and main-stem lateral margins, so we did not compare Coho Salmon densities. After fish density data failed the normality test and did not become normalized after log transformation, we ran Kruskal–Wallis one-way ANOVA on ranks test, using Dunn's method to evaluate significant results.

RESULTS

Side Channel Use

Juvenile steelhead, juvenile Chinook Salmon, and Sculpin *Cottus* spp. were the only species found in all 10 of the side channels. Coho Salmon were commonly found in seasonally disconnected side channels but were either absent or present only in low numbers in the connected and partially connected side channels. Other species found in the side channels during the study included Bridgelip Sucker *Catostomus columbianus*, Brook Trout, Brown Bullhead *Ameiurus nebulosus*, juvenile Bull Trout (<200 mm FL), Longnose Dace *Rhinichthys cataractae*, juvenile Mountain Whitefish *Prosopium williamsoni*, juvenile Pacific Lamprey, and juvenile Westslope Cutthroat Trout. Over the course of the study, we PIT-tagged 2,546 juvenile steelhead, 2,291 Chinook Salmon, and 2,281 Coho Salmon within the 10 side channels. The average FLs of steelhead and Chinook Salmon were 63 and 70 mm, respectively, in seasonally disconnected side channels; 56 and 79 mm, respectively, in connected side channels; and 63 and 77 mm, respectively, in partially connected side channels during the summer sampling period. No fish over 300 mm FL was found in seasonally disconnected or partially connected side channels, and only one large Brook Trout (315 mm) was found in connected side channels. Large Bull Trout, Mountain Whitefish, and Westslope Cutthroat Trout (>300 mm) were present in the main-stem Methow and Chewuch rivers (USGS, unpublished data) but were not found in these side channels.

Species-specific habitat conditions and species interactions were related to fish densities. Juvenile steelhead densities in pools were correlated positively with total cover (Pearson correlation: $r = 0.238$, $P < 0.001$) instream substrate (Pearson correlation: $r = 0.190$, $P = 0.005$), overhead large woody debris (Pearson correlation: $r = 0.203$, $P = 0.003$), overhead small woody debris (Pearson correlation: $r = 0.184$, $P = 0.007$), Coho Salmon densities (Pearson correlation: $r = 0.286$, $P = 0.005$), and Chinook Salmon densities (Pearson correlation: $r = 0.185$, $P = 0.005$). Steelhead densities in pools were negatively correlated with maximum depth (Pearson correlation: $r = -0.244$, $P = 0.001$), mean depth (Pearson correlation: $r = -0.223$, $P = 0.001$), and pool volume (Pearson correlation: $r = -0.200$, $P = 0.002$). Chinook Salmon densities were positively correlated with instream large woody debris (Pearson correlation: $r = 0.162$, $P = 0.015$), steelhead densities (Pearson correlation: $r = 0.366$, $P < 0.001$), and Coho Salmon densities (Pearson correlation: $r = 0.265$, $P < 0.001$); Coho Salmon densities were positively correlated with maximum depth (Pearson correlation: $r = 0.386$, $P < 0.001$), mean depth (Pearson correlation: $r = 0.438$, $P < 0.001$), total cover (Pearson correlation: $r = 0.243$, $P = 0.013$), instream substrate (Pearson correlation: $r = 0.256$, $P = 0.009$), and undercover banks (Pearson correlation: $r = 0.464$, $P < 0.001$). In summary, steelhead and Coho Salmon were correlated to total cover and multiple types of cover, while Chinook Salmon were significantly correlated with the presence of instream large wood debris.

Side Channel Type Comparisons

There were no significant differences between densities of steelhead (ANOVA; $F = 0.696$, $P = 0.507$, df = 2) and Chinook Salmon (ANOVA; $F = 0.596$, $P = 0.557$, df = 2) among the three types of side channels. Coho Salmon were present in high densities (0.2138 fish/m^2) in the middle and lower Methow

River during summer surveys, but were inconsistent and typically absent in the connected and partially connected side channels. In addition to fish densities, we compared smolt production rates among the different types of side channels. Kruskal–Wallis one-way ANOVA test showed the smolt production rates were not significantly different between side channel types for steelhead (Kruskal–Wallis ANOVA; $H = 0.421$, $P = 0.810$, df $= 2$) and Chinook Salmon (Kruskal–Wallis ANOVA; $H = 0.0457$, $P = 0.977$, df $= 2$), but were significantly different for Coho Salmon (Kruskal–Wallis ANOVA; $H = 6.966$, $P = 0.031$, df $=$ 2). Partially connected and connected side channels contained no more than one Coho Salmon smolt each over the course of the study. Disconnected side channels had a higher production rate for Coho Salmon smolt than did partially connected (Dunn's multiple comparison; $Q = 2.017$, $P = 0.044$) and connected side channels (Dunn's multiple comparison; $Q = 2.017$, $P = 0.044$). In seasonally disconnected side channels, the Coho Salmon smolt production rate (13.75 smolts per 100 m/tags per 100 m) was more than twice those of Chinook Salmon (4.83 smolts per 100 m/tags per 100 m) and steelhead (4.26 smolts per 100 m/tags per 100 m; Figure 3).

Differences in length among side channels were limited to juvenile Chinook Salmon in fall (ANOVA; $F = 7.297$, $P = 0.004$, df $= 2$). In fall, FLs of Chinook Salmon were found to be larger in partially connected side channels than in seasonally disconnected side channels (Holm–Sidak multiple comparison; $t = 3.628$, $P = 0.005$). No significant differences were found between seasonally disconnected and connected (Holm–Sidak multiple comparison; $t = 1.949$, $P = 0.128$) and partially connected and connected (Holm–Sidak multiple comparison; $t = 0.890$, $P = 0.384$) side channels. Fork lengths of juvenile steelhead were not significantly different between side channel types in both fall (ANOVA; $F = 3.189$, $P = 0.064$, df $= 2$) and spring (ANOVA; $F = 1.902$, $P = 0.177$, df $= 2$); differences were not significant for Chinook Salmon in spring (ANOVA; $F = 2.123$, $P = 0.150$, df $= 2$).

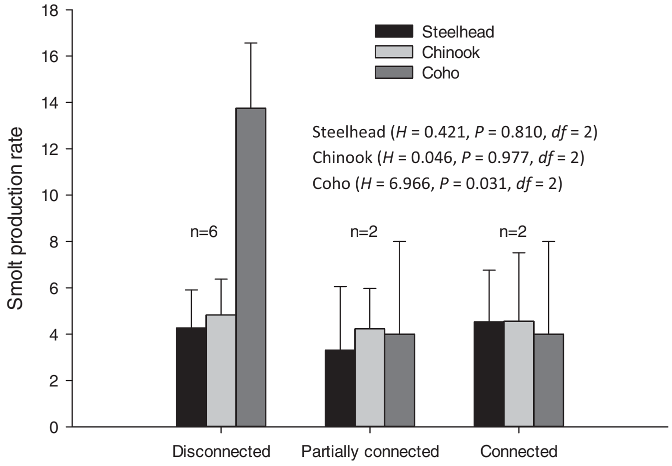

FIGURE 3. Smolt production rate (smolts per 100 m/tags per 100 m) of steelhead, Chinook Salmon, and Coho Salmon from the three types of side channels in the Methow River watershed with Kruskal–Wallis one-way ANOVA test. Smolts were detected by juvenile PIT-tag interrogators on the Columbia River during spring migration.

TABLE 1. Akaike's information criterion (AICc), corrected for a small sample size, for model selection results from three species of juvenile salmonids (steelhead, Chinook Salmon, and Coho Salmon). Phi = survival, p = detection efficiency, g = group (group 1 = pools > 100 cm deep, group 2 = pools < 100 cm deep), t = timing of sampling occasion, (.) = no groups or time effect.

Model	AICc	ΔAICc	AICc weight
Steelhead			
Phi(gt)p(gt)	1,393.21	0.00	1.00
Phi(t)p(t)	1,464.11	70.90	0.00
Phi(g)p(g)	1,537.90	144.69	0.00
Phi(.)p(.)	1,581.24	188.03	0.00
Coho			
Phi(gt)p(gt)	2,311.44	0.00	1.00
Phi(t)p(t)	2,595.46	284.01	0.00
Phi(g)p(g)	3,072.96	761.52	0.00
Phi(.)p(.)	3,242.11	930.67	0.00
Chinook			
Phi(t)p(t)	2,245.06	0.00	0.58
Phi(gt)p(gt)	2,245.68	0.62	0.42
Phi(.)p(.)	2,759.53	514.47	0.00
Phi(g)p(g)	2,762.09	517.03	0.00

Survival in seasonally disconnected side channels were compared between two types of pools according to maximum depth (<100 cm and ≥100 cm). The group and time model ranked highest of the four models by ΔAICc for both steelhead and Coho Salmon, indicating that a combination of time and depth class of pool best described survival in the side channels (Table 1). The time-only model ranked the highest for juvenile Chinook Salmon. The ΔAICc for the time-only model and the group and time model with Chinook Salmon was less than 1, indicating little difference between the two models. All other models had essentially no support, their ΔAICc values being greater than 70. Fish in deep pools had higher survival than fish in shallow pools in all but one season for steelhead and Coho Salmon and in two seasons for Chinook Salmon (group and time model; Figure 4). During periods of disconnection, fish emigration was not possible, resulting in estimates of true survival. The average true survival (i.e., no emigration during disconnection) between summer and fall in deep pools was 74% and 44% in shallow pools for steelhead; 72% and 46%, respectively, for Chinook Salmon; and 88% and 74%, respectively, for Coho Salmon. The average true survival between fall and spring in deep pools was 52% and 44% in shallow pools for steelhead; 50% and 50%, respectively, for Chinook Salmon; and 68% and 38%, respectively, for Coho Salmon. Between spring and summer when these side channels reconnected, the average apparent survival (movement and survival) for steelhead was 25% in deep pools and 1% in shallow pools; for Chinook Salmon and Coho Salmon, apparent survival was essentially 0% in either pool-depth class.

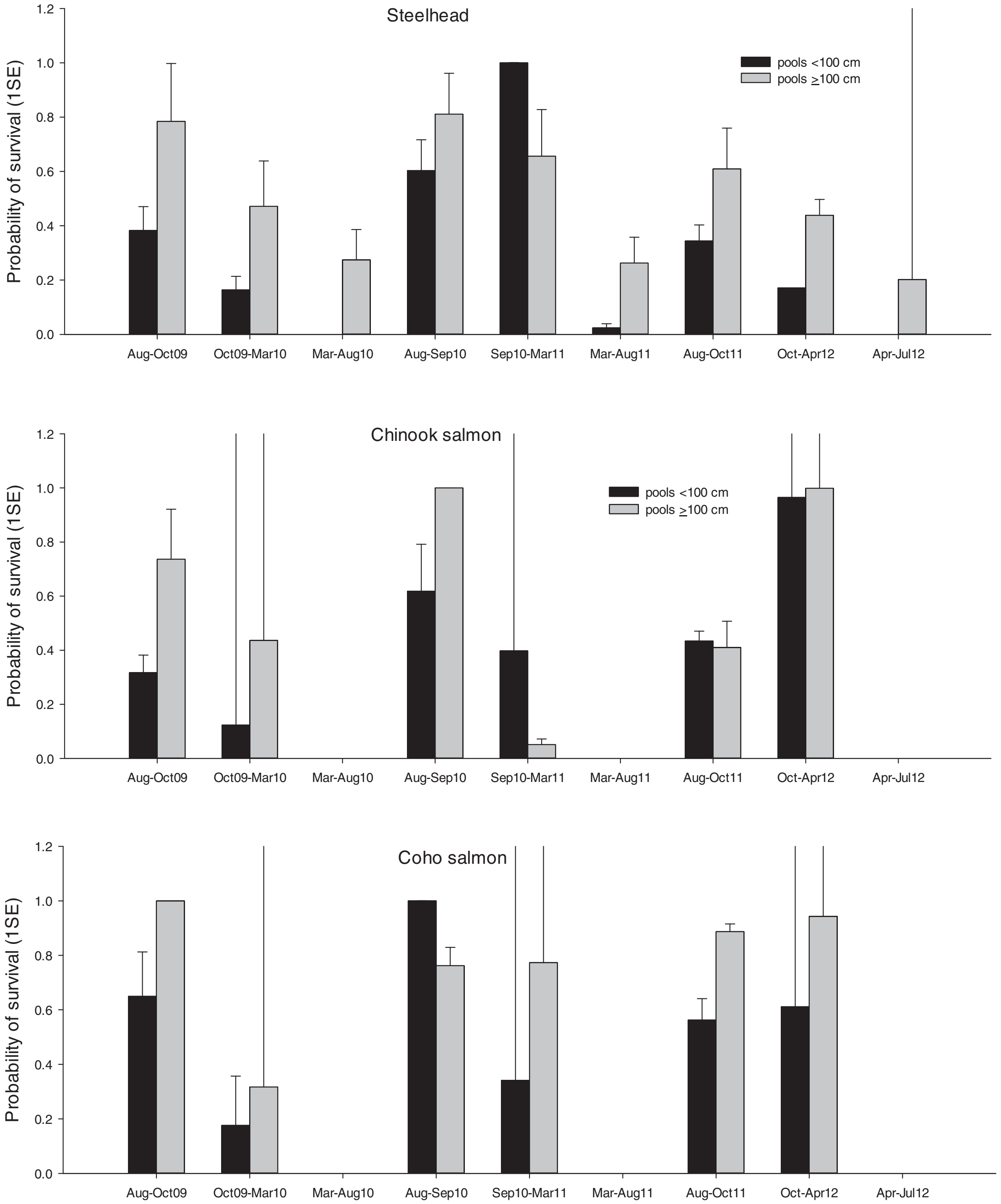

FIGURE 4. Survival of juvenile steelhead, Chinook Salmon, and Coho Salmon in six seasonally disconnected side channels in the Methow River watershed.

Side Channel, Tributary, and Main-Stem Lateral Margin Comparisons

Steelhead and Chinook Salmon in the Methow River watershed were found to inhabit three stream categories: all types of side channel, tributary, and main-stem lateral margin. For steelhead, densities in side channels, tributaries, and main-stem lateral margins differed (Kruskal–Wallis ANOVA; $H = 27.853$ $P < 0.001$, df = 2), being larger in side channels than in main-stem lateral margins (Dunn's multiple comparison; $Q = 4.561$, $P < 0.001$), but no differences in densities were

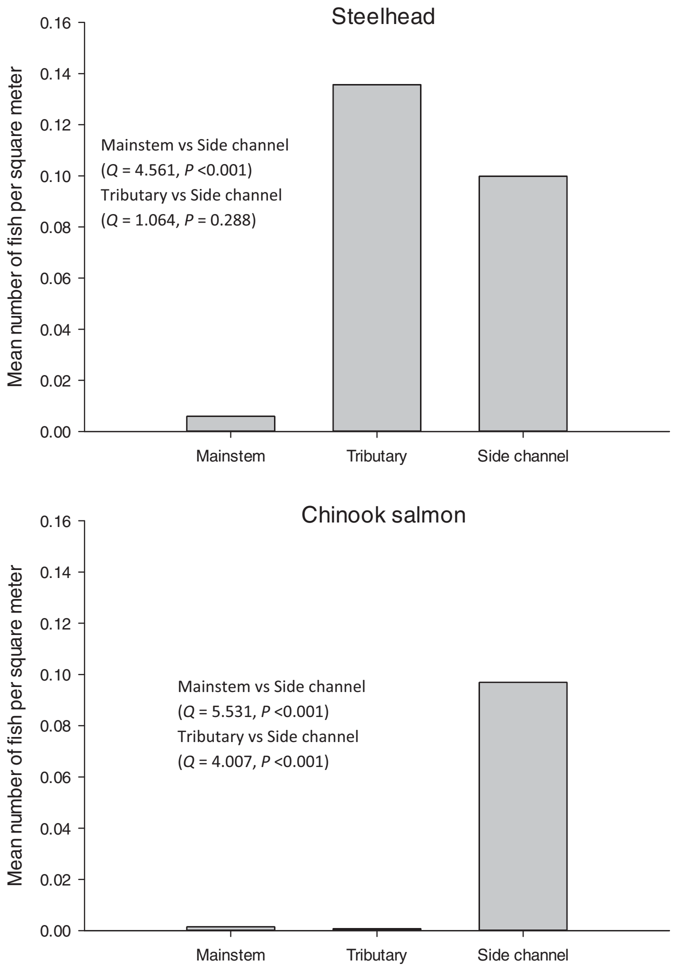

FIGURE 5. Mean fish per square meter of steelhead and Chinook Salmon in main-stem lateral margins, tributaries, and side channels in the Methow River watershed with results from Dunn's comparison test after a Kruskal–Wallis one-way ANOVA test was found to be significant ($\alpha < 0.05$; steelhead: $H = 27.853$, $P < 0.001$, df = 2; Chinook: $H = 37.286$, $P < 0.001$, df = 2).

found between side channels and tributaries (Dunn's multiple comparison; $Q = 1.064$, $P = 0.288$; Figure 5). Juvenile Chinook Salmon densities also differed between side channels, tributaries, and main-stem lateral margins (Kruskal–Wallis ANOVA; $H = 37.286$, $P < 0.001$, df = 2), being higher in side channels than in tributaries (Dunn's multiple comparison; $Q = 4.007$, $P < 0.001$) or in main-stem lateral margins (Dunn's multiple comparison; $Q = 5.531$, $P < 0.001$).

DISCUSSION

Side Channel Use

All of the side channels we sampled in the Methow River contained juvenile steelhead and Chinook Salmon. They had low numbers of, or no, large predatory species (>300 mm FL) such as Bull Trout, Brook Trout, resident Rainbow Trout, and Westslope Cutthroat Trout, which were known to be in the main-stem Methow River (USGS, unpublished data). The lack of these fish in the seasonally disconnected side channels could represent a refuge for young-of-year fish in comparison with habitats that maintain their connection to the main-stem river. In side channels that maintain a connection to the main-stem juvenile fishes could be vulnerable to predatory fishes, by either juvenile fish emigration or predatory immigration. Sommer et al. (2001) speculated that increased off-channel habitat could reduce the possibility of encountering predators. Stevens and DuPont (2011) found aggregations of salmonids 300 mm or longer in connected side channels and noted that they were more likely to be found in deeper pools (≥ 2 m). Gido et al. (2000) found that adult radio-tagged Rainbow Trout move into connected side channels during increased flows. The seasonally disconnected side channels primarily contained small young-of-year salmonids. On the basis of PIT tag fish movement and fish lengths, we found that these side channels would typically empty out of the previous year's fish while simultaneously filling up with young-of-year fish during the spring high-water connection. Seasonally disconnected side channels contained high densities of young-of-year steelhead, Chinook Salmon, and Coho Salmon, but were especially important for the production of Coho Salmon smolts. Offspring from recently reintroduced Coho Salmon were apparent in the seasonally disconnected side channels of the middle and lower Methow River, but colonization had not been fully established in the Upper Methow River and the Chewuch River. This most probably accounted for the higher smolt production in seasonally disconnected side channels, which were mostly in the middle and lower Methow River, over partially connected and connected side channels that were limited to the upper sections of the Methow River watershed. With increases in Coho Salmon probable with intensive basinwide reintroduction, we might expect increased interactions with ESA-listed steelhead and Chinook Salmon.

Side Channel Type Comparisons

While we did not find significant differences of steelhead and Chinook Salmon densities or smolt production rates between the three types of side channels, this study focused on juvenile fish and not the potential uses of side channels for adults, such as spawning or feeding areas. Partially connected and connected side channels could provide additional spawning habitat that is not possible in seasonally disconnected side channels because of the timing of disconnection. Evidence of potential spawning use in these side channels was found in the upper Methow River. One of the connected side channels (rkm 87) contained several spring Chinook Salmon redds during fall spawning for each year of the study (USGS, unpublished data). In addition, Eiler et al. (1992) found that most Sockeye Salmon *O. nerka*, a species rarely found in the Methow River, returned to the main-stem river and used side channels for spawning. Seasonally disconnected side channels were generally not available to adult Chinook Salmon, Coho Salmon, and possibly steelhead (depending on the timing of high flows) during spawning, thus limiting the amount of potential spawning habitat represented by side channels.

Emigrants of steelhead, Chinook Salmon, and Coho Salmon from seasonally disconnected side channels contributed to the watershed's smolt production, even with low survival during periods of disconnection in pools less than 100 cm deep, which made up 88% of the habitat units. The low apparent survival from spring through the summer in seasonally disconnected side channels (essentially zero for Chinook Salmon and Coho Salmon) from just before connection in spring to just after disconnection in summer was probably due to fish emigrating from the side channel rather than a result of low survival. This was evident by juvenile fish tagged in the seasonally disconnected side channels that were later detected as smolts in the Columbia River. Since all three side channel types produced similar rates of steelhead and Chinook Salmon smolts, an increase in young-of-year survival in seasonally disconnected side channels could increase the number of smolts produced.

For pools less than 100 cm deep within disconnected side channels, potential causes for the low survival may include low dissolved oxygen, predation, lethal water temperatures, available food resources, or lack of water. Henning et al. (2006) found that dissolved oxygen concentrations decreased in wetlands throughout the season and approached lethal limits for Pacific salmonids by May or June each year. Giannico and Hinch (2003) found that higher water temperatures reduced carrying capacity and production of Coho Salmon smolt, and Peterson (1982) speculated that predation from avian and mammalian predators were a main cause of winter mortalities in fish. Additionally, Swales and Levings (1989) hypothesized that competition for food and space may control the mix of species. Lack of available food does not appear to have been a factor in fish survival in our side channels in that a companion study by Bellmore et al. (2013) on food webs in the side channels of the upper and middle Methow River revealed that steelhead and Chinook Salmon consumed less than 65% of the potential food available in any of the side channels ($n = 5$) they sampled.

Side Channel, Tributary, and Main-Stem Lateral Margin Comparisons

We found that side channels play an important role in salmonid production in the Methow River watershed. Salmonid densities in side channels were initially either similar to or higher than those in other categories of stream types. Side channels contained higher densities of steelhead than did main-stem lateral margins and had similar densities as in tributaries. The high densities of juvenile steelhead in side channels contradict results of some earlier studies that found minimal use of steelhead in side channels (Swales and Levings 1989; Morley et al. 2005). Side channels also contained the highest densities of juvenile Chinook Salmon, and seasonally disconnected side channels had high densities of Coho Salmon. Restoration actions to improve the factors that are currently limiting off-channel habitat, such as dike removal and wood incorporation (Methow Subbasin Plan 2004), have great potential to improve salmon populations in the Methow River watershed.

Stream Restoration

When designing side channels, managers should keep system-based processes in mind. Fixing specific habitat characteristics instead of the underlying problems could result in eventual project failure (Beechie et al. 2010). We found that side channels with pools deeper than 100 cm had improved survival of young-of-year salmon over pools less than 100 cm deep, and that side channels held large densities of young-of year salmonids. In addition, we found that large wood or total cover proved to be important to fish densities for all three target species. Increasing wood in these side channels in addition to riparian restoration could provide temporary structures to improve habitat until natural sustainable processes could be restored. The importance of large wood for juvenile salmon has been well documented (Roni and Quinn 2001; Mossop and Bradford 2004). Large wood has been found to provide fish cover, scour pools, and provide organic substances to increase invertebrate and periphyton production (McMahon and Hartman 1989; Coe et al. 2009). Proper wood placement will probably increase pool depth through scour while creating fish cover and increasing potential food availability. The increased pool depth also would probably increase salmon survival. We believe that mechanisms for creating deeper pools should be incorporated in designs for treating seasonally disconnected side channels rather than directly deepening pools. Creating deeper pools without solving the underlying mechanisms in the side channels could lead to pools filling in and wasting valuable restoration dollars.

Floodplain restoration will probably be more successful if it is focused on creating a diversity in habitat types because habitat types have complementary values and habitat use may be species-specific (Grift et al. 2003). Additionally, Paillex et al. (2009) recommended maintaining or creating diversity in side channel types based on connectivity to preserve diversity in biological characteristics. Bisson et al. (2009) and Beechie et al. (2010) emphasized that restoration should adhere to process-based principles and should restore the drivers of the ecosystem function, not just treat the symptoms of the degradation. While targeting species-specific individual habitat enhancement projects could lead to a more efficient means of salmon recovery on the site level, creating or maintaining a diversity of side channels with different levels of connectivity should provide the greatest overall benefit to multiple species and life stages within the watershed. However, targeting full connectivity of side channels may not be feasible (e.g., if lack of water availability) or not be desirable because of risk (e.g., flooding, stream capture, bank stabilization). In this case, providing higher quality and sustained habitat in partially connected and seasonally disconnected side channels should be evaluated as an alternative.

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