

Fidelity and Survival of Juvenile Coho Salmon in Response to a Flood

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Abstract.—We compared the movement and spring out-migrant trap capture of 1,038 juvenile coho salmon *Oncorhynchus kisutch* tagged with passive integrated transponder (PIT) tags among four alcoves, seven backwaters, and six main-channel pool habitats after a 5-year flood. Sampling was conducted in November 1998 before the flood on 21 November and again in December, January, February, and March in selected habitat units. Along with out-migrant trapping during spring 1999, these repeated sampling efforts were used to measure the fidelity of juvenile coho salmon to particular habitat units, the immigration of coho salmon into those habitat units, and out-migration from them. Following the flood, fidelity and out-migrant trap capture were greater for juvenile coho salmon occupying alcoves (50% and 17.0%) than for those occupying backwaters (16% and 6.1%) or main-channel pools (7% and 2.7%). The out-migrant trap capture of juvenile coho salmon that had been PIT-tagged before the flood (16.1%; $N = 209$) was similar to that of fish PIT-tagged after the flood (15.3%; $N = 829$). This study corroborates previous research on the benefits of off-channel habitat to juvenile coho salmon and provides insight into the effects of flooding on these fish.

The mortality of juvenile coho salmon *Oncorhynchus kisutch* during their first winter in freshwater is highly variable and often substantial (Holtby 1988; Quinn and Peterson 1996). The survival and distribution of juvenile coho salmon have both been associated with available winter habitat (Bustard and Narver 1975a; Peterson 1982; Tschaplinski and Hartman 1983; Nickelson et al. 1992; Quinn and Peterson 1996). During winter, juvenile coho salmon select habitats with low water velocity (Bustard and Narver 1975b; Bisson et al. 1988) such as alcoves, side channels, backwaters, beaver ponds, riverine ponds, and deep rootwad-formed pools (Bustard and Narver 1975b; Tschaplinski and Hartman 1983; Nickelson et al. 1992). These habitats provide cover from predators and protection from high discharge, factors suggested to cause emigration and mortality of overwintering salmonids (Erman et al. 1988; McMahon and Hartman 1989; Sandercock 1991). In northern California, alcoves, backwaters, and

main-channel pools occur more commonly than other winter habitat types and were therefore chosen as study sites (Figure 1). Alcoves are formed by abandoned side channels and often maintain flow year round from springs, subterranean flow, or small tributaries. Alcoves are disconnected from the main channel, and fish typically only have access during high water stages. Water velocity in alcoves tends to be unmeasurable and mostly remains low (<30 cm/s) during high flows. Backwaters are formed from abandoned channels and scour around obstructions such as large woody debris. Backwaters are connected to the main channel during all stage heights but may become dry during low flows. Water velocity in backwaters tends to be low (<30 cm/s) during winter base flows but may be high (>60 cm/s) during high flows. The main-channel pools selected for this study were mostly formed by scour around large woody debris. Main-channel pools are within the main channel, fish have access at all stage heights, and current velocities range from moderate (<60 cm/s) to high (>60 cm/s).

Traditionally, the habitat preferences of juvenile

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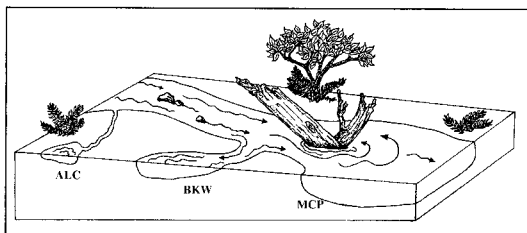


FIGURE 1.—Winter habitat types occupied by juvenile coho salmon in Prairie Creek, California; ALC = alcove, BKW = backwater, and MCP = main-channel pool.

salmonids during winter have been estimated by measuring their relative abundance among habitat types (Bustard and Narver 1975b; Swales et al. 1988; Nickelson et al. 1992; Swales and Levings 1989). Van Horne (1983) suggested that density is a misleading indicator of habitat quality, and Winker et al. (1995) proposed that in some systems movement data might be a more appropriate measure. If protection from floods is beneficial, habitats that provide refuge from velocity would presumably have higher site fidelity and the fish occupying these habitats should have higher survival to the smolt stage. Few measures of the reactions of juvenile coho salmon to floods in natural streams exist (e.g., Tschapinski and Hartman 1983; Shirvell 1994; Giannico and Healey 1998), and it is not clear if fidelity is related to survival or even if floods cause emigration or mortality. The objective of this study was to assess freshwater habitat quality by measuring fidelity, immigration, and spring out-migrant trap capture of juvenile coho occupying preferred habitat types following a flood.

Methods

Prairie Creek, a third-order tributary to Redwood Creek in northwestern California (Figure 2), is almost entirely within Redwood National and State parks. Basin slopes range from 40% to 70% and support old-growth redwood *Sequoia sempervirens*, Sitka spruce *Picea sitchensis*, and Douglas fir *Pseudotsuga menziesii*. The understory is dominated by black huckleberry *Vaccinium ovatum*, red huckleberry *V. parvifolium*, and ferns *Polystichum* sp. Riparian vegetation almost completely covers the stream, and is predominately red alder *Alnus rubra*, big-leaf maple *Acer macrophyllum*, and salmonberry *Rubus spectabilis*. The climate in the region is characterized by wet, mild winters with rainfall between 135 and 200 cm and relatively dry summers.

We studied the headwater reach of Prairie Creek because human disturbances are low and the reach was accessible during moderate to high discharge. This study focused on a 6-km reach extending from Browns Creek upstream to Ten Taypo Creek (Figure 2). There are no barriers to fish movement within the study reach. In addition to coho salmon, the study reach contains chinook salmon *O. tshawytscha*, steelhead *O. mykiss*, coastal cutthroat trout *O. clarki clarki*, threespine stickleback *Gasterosteus aculeatus*, prickly sculpin *Cottus asper*, coast-range sculpin *C. aleuticus*, Pacific lamprey *Lampetra tridentata*, and Pacific brook lamprey *L. richardsoni*. The drainage area above the study reach is 10.36 km², and base discharge in the study reach between October and March is approximately 0.56 m³/s. Floods resulting from rainstorms occur frequently between October and March. Bankfull discharge is about 5.6 m³/s (Randy Klein, Redwood National Park, personal communication). The 21 November 1998 flood examined in this study had a peak discharge of 8.8 m³/s and a 5-year recurrence interval.

We surveyed Prairie Creek in early November 1998 after the watershed had received 15 cm of cumulative precipitation since 1 September (water year 1999) and winter habitat types were present. Alcoves, backwaters, and main-channel pools were flagged and measured for surface area and maximum depth (Table 1). We randomly selected 17 habitat units (4 alcoves, 7 backwaters, and 6 main-channel pools) from the 10 alcoves, 18 backwaters, and 105 main-channel pool units containing more than one juvenile coho salmon before the flood. The habitat units that were selected for study were located from 2,990 to 4,312 m upstream from the confluence with Browns Creek.

We initially sampled habitats between 11 and 18 November 1998 (preflood sampling). Sampling consisted of removing all juvenile coho salmon from selected units by multiple passes with one or two backpack electroshockers (Smith-Root, model 12). Sampling units were blocked with netting at the upstream and downstream ends and electroshocked to depletion, with a minimum of 4 passes. All the juvenile coho salmon captured were anesthetized with tricaine methanesulfonate (MS-222) before we recorded fork length (FL) to the nearest millimeter and wet weight to the nearest 0.01 g using an electronic balance (Mettler-Toledo, model BD202). All fish greater than 54 mm FL were tagged with 10-mm passive integrated transponder (PIT) tags. Tags were inserted into the

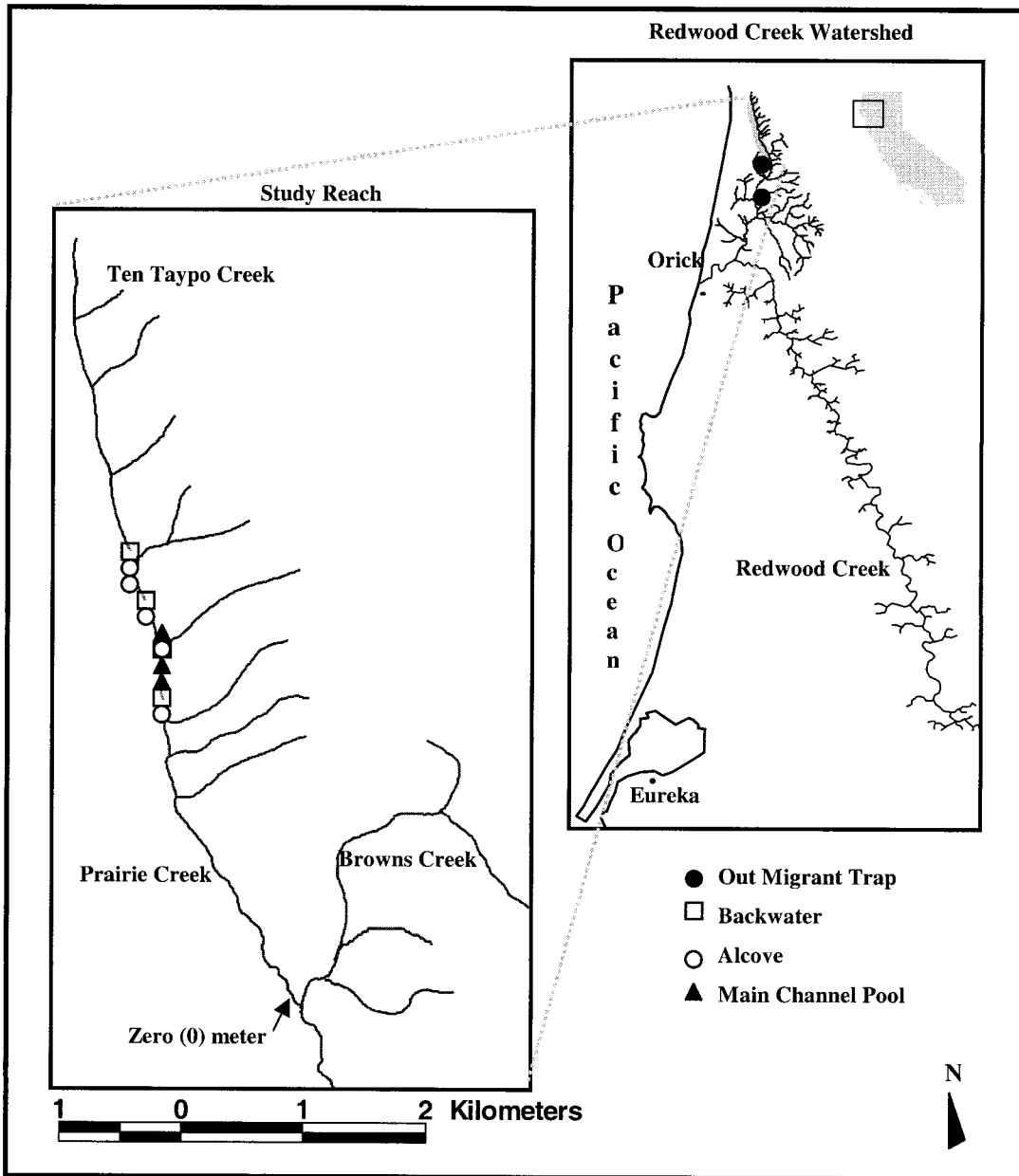


FIGURE 2.—Map of Prairie Creek, California.

body cavity anterior to the pelvic fin with a 12-gauge hypodermic needle. When a scanner is placed adjacent to a fish that has been PIT-tagged, a unique 10-digit alphanumeric code is displayed, which allowed us to collect data on individual fish. We recorded the code and unit of origin for each tagged fish, then clipped the adipose fin to aid identification. Fish were then allowed to recover and returned to their original habitat. Eleven per-

cent of the fish were too small to be tagged and were not given any mark. No mortalities resulting from handling were observed, and tag loss was about 5%.

All 17 habitat units sampled in November were again sampled between 11 December and 18 January 1999 (postflood sampling) to determine the effect of the flood on fidelity and immigration in habitat units. The methods of postflood sampling

TABLE 1.—Characteristics of preferred winter habitat types studied in Prairie Creek, California. Habitat data were collected at winter base flow. The same number of habitat types were sampled before and after a 5-year flood on 21 November 1998.

Habitat type	Number sampled	Number in study reach	Average, surface area, m ² (\pm SD)	Average maximum depth, m (\pm SD)
Alcove	10	10	28 (\pm 29)	0.57 (0.45)
Backwater	18	18	32 (\pm 50)	0.52 (0.28)
Main channel pool	20	105	117 (\pm 81)	0.94 (0.45)

were identical to those used in the first sampling effort. All fish with adipose clips were scanned with a hand-held scanner (Destron Fearing, model MPR). Fork length, wet weight, and unit of capture were recorded for each fish. For fish recaptured in habitats other than those where they were originally tagged, the minimum distances moved (m) were recorded. During postflood sampling an additional group of juvenile coho salmon were PIT-tagged in the original 17 habitat units and in 31 new units using the same methods as in the first visit. Between 18 February and 12 March 1999 (late winter), all 48 habitat units were sampled for either a second or third time using the same methods as in the postflood sampling to determine fidelity. No additional fish were tagged during the late winter sampling.

Fidelity, immigration, and the density of juvenile coho salmon were measured in all habitat units sampled during postflood sampling. Fidelity was defined as the proportion of fish tagged during pre-flood sampling that were recaptured in the same unit during postflood sampling. We defined immigration as the proportion of fish captured in a unit that were not tagged during the first sampling effort. Immigration rates of over 100% occurred when more fish immigrated into a unit than were present during initial sampling. Fish that escaped tagging during the initial visits may bias immigration rates, but efforts were made to ensure depletion during sampling and the bias is assumed to be equal among habitat types. Density was defined as the number of juvenile coho salmon in a habitat unit divided by the total surface area of that habitat unit. Differences in fidelity, immigration, and the density of juvenile coho salmon among alcoves, backwaters, and main-channel pools were tested using a one-way analysis of variance (ANOVA) with individual habitat units as experimental units. When statistical differences were detected, planned comparisons were used to test for differences among the means of the three habitat types. For planned comparisons, we con-

trolled the experimentwise error rate at 0.05 using the Bonferroni method (Sokal and Rohlf 1995).

Downstream-migrant traps were installed on Prairie Creek to measure out-migrant trap capture of tagged juvenile coho salmon occupying the sampled habitat types. The out-migrant trap capture ratio was considered an estimate of survival and is defined here as the proportion of fish tagged in the habitat units that were subsequently captured at either of two out-migrant traps. A fyke trap with a 1.2-m-wide opening and a rotary screw trap 1.5 m in diameter were operated continuously from 5 February to 21 June 1999. The fyke trap was at the downstream end of the study reach, and the rotary screw trap was located 7,450 m below the study reach (Figure 2). We removed the fyke trap during high discharge events and the screw trap when discharge fell below about 0.14 m³/s, but at least one trap was fished each day during the period. After 25 June, the fyke trap was fished 3 d per week to monitor any late-season downstream migration. Trap efficiencies were estimated to be about 33% using a Cormack–Jolly–Seber resighting structure. To ensure that the out-migrant trap capture analysis reflected differences among habitat types, only PIT-tagged fish that occupied specific habitat units were considered in the analysis. Fish were considered to have occupied a habitat unit if they were observed there during at least two sampling visits. Out-migrant trap capture estimates were biased by an unexpected portion of the population rearing for a second year in freshwater; these fish were not used in the analysis. Thus, out-migrant trap capture was a minimum estimate of survival owing to the presence of age-2 out-migrants and an out-migrant trap efficiency of less than 100%. Out-migrant trap capture estimates were considered an accurate means of comparing the relative survival among habitat types, assuming that trap efficiency and age composition were similar among habitat types.

Differences in out-migrant trap capture among alcoves, backwaters, and main-channel pools and

TABLE 2.—Number of juvenile coho salmon tagged with passive integrated transponders in alcove, backwater, and main-channel pool habitat units originally sampled before and after a 5-year flood in Prairie Creek, California, plus the number subsequently captured at out-migrant traps.

Habitat type	Number of fish tagged		Number of fish recaptured in original habitat				Number of fish captured at out-migrant traps ^c	
			11 Dec 1998–18 Jan 1999		18 Feb–12 Mar 1999			
	Preflood ^a	Postflood ^b	Tagged preflood	Tagged postflood	Tagged preflood	Tagged postflood	Tagged preflood	Tagged postflood
Alcove	55	189	24	46	18	60	11	30
Backwater	72	329	22	23	12	38	10	50
Main-channel pool	82	319	7	52	0	29	10	61
All of above	209	837	53	121	30	127	31	141

^a 11–18 Nov 1998.

^b 11 Dec 1998–18 Jan 1999.

^c Mar–Jun 1999.

between the preflood and postflood tag groups were tested using log-linear model analysis, which effectively tested survival among habitat types and tag groups. When significant models for survival were found, effect Z-values were examined to further analyze the relationships among the three habitat types before and after the flood.

Results

In November 1998 (preflood), 209 juvenile coho salmon were tagged in 17 habitat units, with 55

fish tagged in alcoves, 72 in backwaters, and 82 in main-channel pools (Table 2). In December 1998 (postflood), 62 fish that had been tagged before the flood were recaptured. After the 21 November flood, a total of 171 juvenile coho salmon were tagged in the original 17 habitat units, and 666 were tagged in 31 new habitat units. In January, February, and March sampling, 83 fish tagged before the flood and 248 tagged after the flood were recaptured in their original habitat units. The flood resulted in major channel rearrangement in portions of the study reach and turned two sampled backwater pools and one sampled alcove into main-channel habitat. Channel migration during the flood created two new alcoves and one new backwater, which were subsequently sampled. There were no observed changes following the flood in the 14 sampled habitat units that were not eliminated by channel migration.

The fidelity of juvenile coho salmon to habitat units differed among habitat types (Figure 3; one-way ANOVA: $F_{2,14} = 4.11$, $P = 0.039$). Fish occupying alcove habitat prior to the flood had the greatest fidelity (50%), followed by those in backwaters (16%) and main-channel pools (7%) (planned comparison: $t_{14} = 3.235$, $P = 0.006$). Juvenile coho salmon occupying alcoves in post-flood sampling to March also had the highest fidelity (33%), followed by fish in backwaters (14%) and those in main-channel pools (8%) (one-way ANOVA: $F_{2,33} = 6.199$, $P = 0.005$; planned comparison: $t_{33} = 6.307$, $P < 0.001$). There were no differences in the preflood densities of juvenile coho salmon among habitat types (one-way ANOVA: $F_{2,16} = 0.693$, $P = 0.516$), though there were higher densities of fish in alcoves after the flood (one-way ANOVA: $F_{2,16} = 11.37$, $P = 0.001$). Immigration rate variances could not be

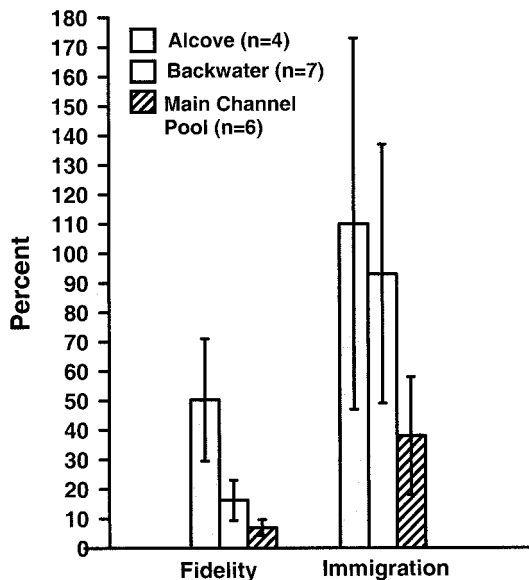


FIGURE 3.—Mean percent fidelity and immigration of juvenile coho salmon in Prairie Creek, California, following a flood; bars indicate standard errors. Data are from 55 juvenile coho salmon that were PIT-tagged in alcoves, 72 that were PIT-tagged in backwaters, and 82 that were PIT-tagged in main-channel pools.

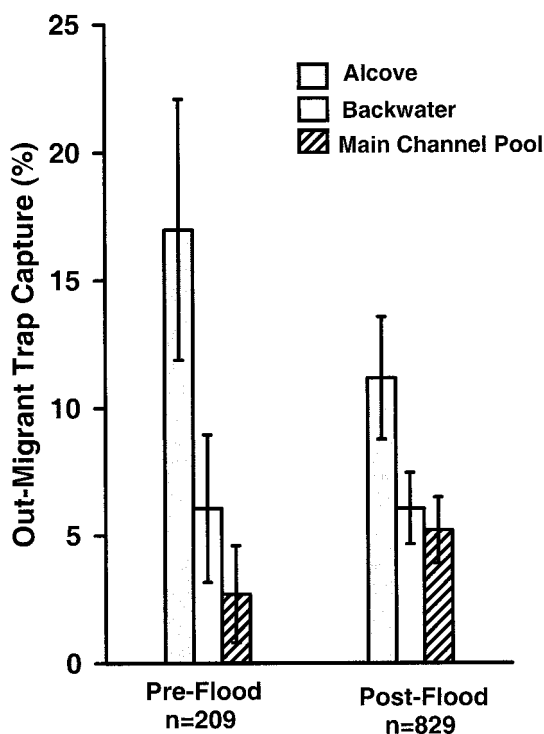


FIGURE 4.—Total percent out-migrant trap capture of juvenile coho salmon tagged before and after a 5-year flood in Prairie Creek, California; bars indicate standard errors.

equalized so statistical analysis was not possible, but rates were slightly higher in alcove habitat (Figure 3). The detected movements of juvenile coho salmon from one habitat unit to another were mostly in the downstream direction and varied between 10 and 1,992 m ($N = 9$, mean = 516.6 m). The sample size of detected movements by individual juvenile coho salmon was considered to be too small for detailed analysis.

Altogether, 31 (14.8%) juvenile coho salmon that were tagged before the flood and 141 (16.8%) tagged after the flood were captured at out-migrant traps. The habitat types occupied prior to out-migration significantly affected out-migrant trap capture (log-linear analysis: $\chi^2_2 = 13.54$, $P = 0.0011$). We found no effect of the flood on out-migrant trap capture (log-linear analysis: $\chi^2_1 = 0.22$, $P = 0.6365$). The interaction of habitat type and flood had no effect on out-migrant trap capture (log-linear analysis: $\chi^2_1 = 1.81$, $P = 0.405$). The out-migrant trap capture of juvenile coho salmon occupying alcoves before the flood was 17.0% ($\pm 5.1\%$); for those occupying backwaters it was 6.1% ($\pm 2.9\%$), and for those occupying main-

channel pools it was 2.7% ($\pm 1.9\%$; Figure 4). Out-migrant trap capture of fish occupying alcoves after the flood was 11.2% ($\pm 2.4\%$); for those occupying backwaters it was 6.1% ($\pm 1.4\%$), and for those in main-channel pools it was 5.2% ($\pm 1.3\%$). Examination of the effect Z-values suggested that differences in out-migrant trap capture among habitat units was due to high trap capture of juveniles occupying alcoves (effect Z-value = 3.56) and low trap capture of fish occupying main-channel pools (effect Z-value = -2.14). Fifty-two percent of the fish tagged prior to the flood and captured at out-migrant traps were not recaptured in either of the two subsequent sampling efforts in habitat units and thus did not rear exclusively in the habitat where they were tagged. Eighty percent of the juvenile coho salmon originally tagged in main-channel pools and captured at out-migrant traps were not recaptured in either of the two subsequent sampling efforts in habitat units. The figures for fish originally tagged in backwaters and those originally tagged in alcoves were 60% and 19%, respectively.

Discussion

We found that juvenile coho salmon occupying alcove habitat had higher fidelity and densities following a flood than those occupying backwater or main-channel pool habitat. Higher fidelity and densities in off-channel habitat (alcoves and backwaters) may explain the conclusions of Swales et al. (1988) and Nickelson et al. (1992) that juvenile coho salmon prefer off-channel habitat types during the winter. Tschaplinski and Hartman (1983) found that sections of a creek with adequate winter habitat maintained higher numbers of juvenile coho salmon than sections without adequate winter habitat. Our results indicate that particular sections of creek may maintain higher numbers by virtue of increased fidelity in off-channel habitats, such as alcoves and backwaters. However, capture rates in main-channel habitat may also be lower due to lower electroshocker efficiency in main-channel pools, which tend to be larger and deeper than other habitat types.

We detected juvenile coho salmon movement either during or following the flood. Movement by salmonids in response to high discharge has been previously documented (Shirvell 1994; Giannico and Healey 1998). Eighty percent of the juvenile coho salmon tagged in main-channel pools that were captured in out-migrant traps did not rear exclusively in the habitat where they were tagged. Fish initially occupying main-channel pools may

have increased their chances of survival by migrating to other types of habitat, as the nine fish that we detected moving from one habitat unit to another were doing. The measured densities of juvenile coho salmon in off-channel habitat may not indicate the number of fish that utilize that habitat solely during peak discharge. The juvenile coho salmon occupying main-channel pools that did survive may have located a velocity refuge in microhabitats during the flood, as has been observed with juvenile coho salmon in artificial stream channels (Taylor 1988) and cutthroat trout in the wild (Harvey et al. 1999). We captured juvenile coho salmon tagged in the main channel on the floodplain during a February 1999 overbankfull discharge, indicating that juveniles move from the main channel to avoid high discharge, as was observed by Harvey et al. (1999).

Floods of the magnitude we observed have been assumed to cause emigration and mortality of juvenile salmonids (Sandercock 1991). We found that trap capture during the spring out-migration was similar for fish tagged before and after the flood. It is possible that subsequent discharge events influenced the survival of fish tagged after the flood, as there were three subsequent periods of high discharge later in the same winter. None of the later peaks, however, was comparable to the November flood in magnitude. Because the downstream-migrant traps were placed relatively high in the watershed, the fate of fish displaced during the flood could not be assessed. It is possible that displaced fish found adequate or even superior habitat in stream reaches below the traps.

While higher fidelity rates, density, and trap capture indicate beneficial winter rearing in alcove habitat, the differences in immigration rates were inconclusive. Slightly lower immigration rates and densities in main-channel pools following the flood suggest that these habitat units were not providing adequate winter habitat, resulting in a net loss of fish in these units. Immigration rates of over 100% in alcove and backwater habitat units suggest that these habitats were accessible during the flood and probably not at carrying capacity before the event.

The benefits of alcoves were evident both for the pre-flood and post-flood tag groups. Either the benefits of alcove habitat are independent of high discharge or subsequent flows had effects on the population similar to those of the flood. If the benefits of alcoves are independent, then having a velocity refuge may not be the primary advantage to rearing in alcove habitat. Clearly, in years of low

discharge alcoves are not going to be as important, simply because of limited access at low stage height. If the fidelity and survival of fish occupying alcoves were high simply because of flow dynamics, we would expect backwaters to have high fidelity and survival rates as well. However, while alcoves and backwaters have similar flow dynamics at winter base flows, during periods of high flow alcoves maintain low water velocities whereas backwater currents often become turbulent (personal observation). Lower than expected fidelity and survival of fish rearing in backwaters may indicate the importance of habitat that offers a velocity refuge during high flows. Food availability may also be an important factor affecting fidelity. Though aquatic drift is rare in alcoves, terrestrial input from overland flows may be an adequate food supply. During high flows we observed juvenile coho salmon eating large numbers of earthworms and arachnids, indicating that high flows may be an important feeding opportunity for fish in off-channel habitats, as was observed by Minakawa and Kraft (1999). Differences in diet among juvenile coho salmon occupying winter habitat need to be explored because they may help to explain variable fidelity rates. It is also possible that to some degree fish were simply trapped in alcoves, resulting in higher measurements of fidelity.

Interactions with other species can also dictate habitat use (Glova 1986; Bisson et al. 1988). Juvenile coho salmon's use of off-channel habitat may reduce competition with cutthroat trout in a main-channel habitat. Although there were higher densities of cutthroat trout in main-channel pools than in off-channel habitat, it is not clear whether this reflects the displacement or emigration of coho salmon or is unrelated to the presence of the coho salmon.

While growth of fish is another important indicator of habitat quality, no differences in growth were found among habitat types (Ethan Bell, unpublished data). Though alcove habitat appeared to be superior to other types, there were only 10 alcove habitat units in the 6-km study reach, and thus they comprised only a small portion of all habitat units and supported only a small portion of the population. However, the proportion of the population occupying alcove habitat during sampling visits may not reflect the degree of utilization during high discharge. To properly interpret the benefits of off-channel habitat, observations of microhabitat shifts during high flows are recommended.

Erman et al. (1988) attributed the mortality of young-of-the-year brown trout *Salmo trutta* to an increase in flow and streambed mobilization associated with high discharge in a confined channel in the Sierra Nevada. In contrast to Sierra Nevada streams, Prairie Creek has a low-gradient alluvial channel and migrates through a riparian zone dominated by old-growth redwood. As the channel migrates, abandoned side channels become backwaters and alcoves, large trees are recruited into the channel, and the result is a system with complex main-channel and off-channel habitat. This high habitat complexity may have reduced the detrimental effects of the flood. These results support assertions by Cunjak (1996) that stream management should focus on maintaining habitat complexity at all discharges rather than on maintaining a few selected habitat types at low discharge.

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