Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (Oncorhynchus clarki) during fall and winter

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Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter

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Abstract: To improve understanding of the significance of large woody debris to stream fishes, we examined the influence of woody debris on fall and winter movement by adult coastal cutthroat trout (*Oncorhynchus clarki*) using radiotelemetry. Fish captured in stream pools containing large woody debris moved less than fish captured in pools lacking large woody debris or other cover. Fish from pools lacking cover commonly moved to habitats with large boulders or brush, particularly during the day. Movements by fish over 1-day periods were strongly influenced by large woody debris or other elements providing cover. Fish initially found in habitats lacking large woody debris, large boulders, or brush cover moved the most extensively, while fish initially found in pools with large woody debris moved the least. Fish did not move extensively in response to a bankfull flood, although some moved to habitat downstream of large woody debris in tributaries or secondary channels. Habitat downstream of woody debris in the main channel was not used during the flood, apparently because of extreme turbulence. Overall, these observations provide additional evidence for the value of habitat complexity to some stream fishes and support previous observations of minimal effects of flooding on adult fish.

Résumé : Afin d'améliorer notre connaissance de l'importance des gros débris ligneux pour les poissons des cours d'eau, nous avons examiné, par radiotélémétrie, l'influence des débris ligneux sur les déplacements d'automne et d'hiver de truites fardées côtières adultes. Les poissons capturés dans les fosses de cours d'eau où se trouvaient de gros débris ligneux se déplaçaient moins que ceux capturés dans les fosses exemptes de tels débris ou d'un autre couvert. Les poissons des fosses sans couvert se déplaçaient généralement vers des habitats où se trouvaient de grosses pierres ou des broussailles, cela surtout pendant le jour. Les mouvements des poissons au cours d'une même journée étaient fortement influencés par la présence de gros débris ligneux ou d'autres éléments offrant un couvert. Les poissons des habitats exempts de gros débris ligneux, de grosses pierres ou de broussailles sont ceux qui se déplaçaient le plus tandis que ceux des fosses à gros débris ligneux se déplaçaient le moins. Les poissons ne se sont pas déplacés de façon importante suite à une crue affectant toute la rive, bien que certains se soient déplacés vers des habitats se trouvant en aval de gros débris ligneux, dans des tributaires ou des chenaux secondaires. Les habitats en aval des débris ligneux du chenal principal n'étaient pas utilisés pendant les crues, sans doute à cause de la turbulence extrême. De façon générale, ces observations confirment l'importance de la complexité de l'habitat pour certains poissons de cours d'eau et complètent des observations antérieures du peu d'effets des crues sur les poissons adultes.

[Traduit par la Rédaction]

Introduction

Large woody debris in streams affects the habitat of fishes. Scour around large woody debris can create pools, increasing the density of fishes that prefer pool habitat (Fausch and Northcote 1992). By increasing the visual isolation of individuals, woody debris may allow higher densities of territorial fishes (Dolloff 1986). Woody debris may also provide habitat with relatively low risk of predation (e.g., Angermeier and Karr 1984) or refuge from high water velocities (McMahon and Hartman 1989). In coastal, temperate-zone streams, large woody debris probably has its largest impact on predation risk and its greatest significance as a physical refuge in winter, when cold temperatures reduce swimming performance (Webb 1978) and high discharge increases water velocities. Indeed, during the winter, coho salmon (*Oncorhynchus kisutch*) in Oregon streams are most abundant in habitats usually associated with large woody debris, whereas they are more evenly distributed among habitats in other seasons (Nickelson et al. 1992*a*). Retention of coho salmon after winter freshets was positively related to the volume of woody debris in sections of Carnation Creek, British Columbia (Tschaplinski and Hartman 1983).

Observations of fish movement in the vicinity of large woody debris may illuminate the mechanisms of its significance to fishes. For example, where large woody debris provides refuge from high water velocity during floods,

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aggregations of individuals behind woody debris (McMahon and Hartman 1989) or relatively little movement by individuals occupying habitats with woody debris might be expected. Movement rates of territorial fish during baseflows might be relatively low at sites with large woody debris if it provides superior habitat (Winker et al. 1995).

To our knowledge, no winter field observations addressing these possibilities are available. Our objective in this study was to quantify the influence of large woody debris on movement and use of habitat by adult coastal cutthroat trout (*Oncorhynchus clarki*) across a range of discharges in fall and winter. In fulfilling this objective, we also added to the small number of observations of movement by individual stream fish during floods (e.g., Todd and Rabeni 1989; Matheney and Rabeni 1995).

Study site and methods

Little Jones Creek is a third-order tributary of the Middle Fork Smith River in northwestern California (41°51′N, 123°49′W), draining about 2750 ha of steep forested terrain. About 30% of the watershed has been logged in the last 50 years. The study reach, from 1400 to 3500 m upstream of the confluence with the Middle Fork Smith River, has a nearly complete canopy of red alder (*Alnus rubra*). Stream gradient in the study reach averages 1.8%. About 45% of the pools in the study reach were formed by scour adjacent to large woody debris >30 cm in diameter; the rest were adjacent to bedrock outcrops. The stream averaged 8 m in width during common winter flows of about 1.5 $m^3 \cdot s^{-1}$. At the site where we measured discharge during this study, depth averaged about 35 cm and velocity about 45 $cm \cdot s^{-1}$ at this flow. During a bankfull flood on 16–17 January 1998, discharge rose to about 45 $m^3 \cdot s^{-1}$. At the site where we measured discharge, stream width reached about 11 m during the flood, while depth averaged about 1.2 m and water velocities reached >2.7 $m \cdot s^{-1}$. Water temperature ranged 5.5–11.0°C during this study (February–March 1997 and October 1997 – February 1998). Coastal cutthroat trout is the only fish species in the stream.

We collected fish for the study by electrofishing in two kinds of habitats: pools formed by scour adjacent to bedrock, which contained little or no cover for fish (classified as "simple" habitat), and sites with abundant large woody debris ("complex" habitat). We usually collected fish at night because previous sampling efforts in winter suggested higher capture efficiency at night compared with daytime. On each collecting date (24 February 1997, 15 October 1997, 12 November 1997, 11 December 1997, and 9 January 1998), we implanted 1.2-g radiotransmitters in 8–10 fish, four or five fish from each of the two kinds of habitats. We tagged a total of 24 fish from simple pools and 22 fish from complex pools (three individuals were not included in the analyses because we were unable to make adequate observations on them). Cutthroat trout that received transmitters ranged from 177 to 236 mm fork length and from 60 to 138 g. Fish from the two habitat types were similar in size: both groups averaged 199 mm fork length and 89 g.

Transmitters were surgically implanted into the body cavity using the technique described by Young (1995). Transmitters and coiled antennae formed single units sealed in epoxy. They remained viable for about 30 days, and we tracked individual fish for an average of 29 days. We observed each fish during at least four 24-h visits to the site. During each visit, we located fish at least twice during the day and twice at night, with observations separated by at least 4 h. Usually, we made an initial daytime observation followed by two nighttime observations and a second daytime observation.

We were unable to follow this protocol during the bankfull flood on 16–17 January 1998, when logistical difficulties prevented us from gathering data rapidly enough to make the normal complement of observations. During that event, we were able to locate all fish with functional transmitters at least three times within 24 h, when discharge exceeded 30 $m^3 \cdot s^{-1}$ and stage was within 12 cm of the maximum attained during the flood.

We located fish by triangulation with a receiver and Yagi antenna while walking the streambank and wading. In general, we located fish within 1 m^2, as indicated by our success in recapturing fish with viable transmitters by electrofishing. Locations were occasionally less precise in the vicinity of large bedrock outcrops. For each observation, we determined the longitudinal position within the reach by referring to flagging placed every 25 m and noted the type of habitat occupied.

We also collected water temperature and stream-flow data because of their potential significance to fish movement. A data logger positioned near the middle of the study reach recorded water temperature every 15 min during the study. In November 1997, we placed a staff gage in the stream and measured stage during subsequent visits to the study site. We measured discharge on 20 occasions to establish a stage–discharge relationship. To obtain information on discharge in Little Jones Creek when direct measurements were unavailable, we attempted to predict stage at Little Jones Creek using the stage of the mainstem Smith River at a U.S. Geological Survey gage 28 km downstream. We performed a series of regressions using the stage of the mainstem Smith River from 0 to 6 h after our observations of stage at Little Jones Creek and used the strongest relationship to predict stage in Little Jones Creek. For this analysis, we used a set of 55 observations of Little Jones Creek stage made on separate days.

We compared the site fidelity of fish captured from complex versus simple pools in several ways. First, we computed the proportion of observations where each fish was in the specific habitat where it was initially captured. We transformed these proportions (arcsin square root) and then compared fish from the two kinds of habitats with a t test. Second, we compared the distance between the point of capture and the point of last observation for fish from the two kinds of habitats, also using a t test. A $\log(x + 1)$ transformation of these distances homogenized the variances of the two treatments. Finally, we examined the subsequent use of different habitat types by fish captured in the two different types of pools. For this comparison, we recognized four habitat types: (*i*) "open" habitat with no large (>75 cm long axis) boulder or wood cover for fish, (*ii*) pool habitat with cover provided by large woody debris, (*iii*) riffle or run habitat with cover provided by brush or alder roots, and (*iv*) riffle or run habitat with cover provided by boulders (>75 cm long axis). Habitats classified as open often included areas with unembedded cobbles and small boulders that probably provided cover for fish (Meyer and Griffith 1997). The open habitat category also included both fast- and slow-water habitats.

We also compared the movement behavior of fish from different kinds of habitats by analyzing changes in their positions during the 1-day observation periods. We measured these changes in two ways. First, we quantified the length of stream over which individual fish were observed during each period. Second, because significant nighttime movements by fish sometimes resulted in little "net movement" from one day to the next, we calculated the change in position of individual fish on successive days. Because some fish rarely were observed in the habitat where they first were captured, and most fish used various types of habitat over the course of our observations, we included the habitat type occupied by fish when first located during the 1-day observation periods as a factor in the analyses. We used the four habitat types described above to classify these and employed an analysis of covariance design that accounted for repeated observations of individual fish (Table 1). River stage and water temperature were included as covariates in these analyses.

Because only one bankfull flood occurred during this study, we

Table 1. Outline of the analysis of covariance used to analyze movement by radiotagged adult coastal cutthroat trout over 1-day observation periods in Little Jones Creek, California.

Source of variation	df	Error term
Capture site habitat	1	Fish within capture site habitat
Fish within capture site habitat	41	
Initial habitat (at beginning of 1-day observation periods)	3	Fish within capture site habitat × initial habitat
Initial habitat × capture site habitat	3	Fish within capture site habitat × initial habitat
Fish within capture site habitat × initial habitat	27	
Stream stage	1	
Water temperature	1	
Error	105	
Total	182	

used a descriptive approach to our observations during this event. We compared the locations of the 12 fish with functioning transmitters during the flood (16–17 January 1998) with their preflood positions (12 January 1998). We also categorized the preflood positions of fish based on the presence or absence of large woody debris and contrasted the responses to the flood of these two groups of fish.

Results

The stage of Little Jones Creek was well predicted by the stage 1 h later at the U.S. Geological Survey gage 28 km downstream on the mainstem Smith River (r^2 = 0.96). Therefore, we combined direct observations and computed predictions of stage for use as a covariate in analyses of fish movement. Stage at our gage ranged from 55 to 95 cm during our observations of radiotagged fish, except for the bankfull flood when it reached 145 cm.

Cutthroat trout captured in pools with large woody debris exhibited greater site fidelity than fish from pools lacking cover. Fish from pools with large woody debris occupied the habitats where they were captured twice as often on average as fish from pools lacking cover (81% (N = 21, SE = 5) versus 40% (N = 22, SE = 8); t test, P < 0.01). Similarly, the site of capture and final location were identical for 71% of fish from pools with large woody debris compared with 23% of fish from pools lacking cover. Excluding one fish from a pool without woody debris that travelled about three times further than any other fish (978 m), fish from pools without woody debris were last located an average of 90 m from their capture sites versus an average of 32 m for fish from pools with large woody debris (t test, P < 0.01). The relatively low site fidelity of fish captured in pools lacking cover is reflected in their greater use of large-boulder and brush habitat than fish from pools with large woody debris (Fig. 1). Fish captured in habitats lacking cover were particularly unlikely to use such habitats during the day. Indeed, fish from both types of capture sites used habitat that we classified as open more often at night than during the day: the day/night difference in the proportion of observations in open habitat differed significantly from zero for both groups (N = 21 and 22; paired t tests, P < 0.002 for both). The other three habitat types, which all provided cover, were occupied more often during the day than at night.

Habitat strongly influenced fish movement during the 1-day observation periods (Fig. 2). Fish initially located in open habitats at the start of an observation period travelled over longer sections of stream than did fish first located adjacent to large woody debris, while fish first located at boulders and brush moved intermediate distances ($F_{3,27}$ = 6.50, P < 0.01). Fish exhibited similar patterns of net movement, the difference in their locations during daytime observations on successive days ($F_{3,27}$ = 4.33, P < 0.02) (Fig. 2). For both total and net movement, the effect of the initial location of fish during an observation period was independent of where fish were captured (P > 0.35 for the interaction terms). From one day to the next, we rarely observed movement of cutthroat trout out of pools containing large woody debris. However, we commonly found fish that occupied the same habitat on successive days outside that habitat during intervening nighttime observations. Water temperature was a significant covariate with a positive slope in the analyses of both total and net movement (P = 0.03 for both response variables), while stage was not (P > 0.25 for both response variables). As might be predicted based on the difference in site fidelity, fish initially captured in pools with large woody debris exhibited less total movement than fish from open habitats ($F_{1,41}$ = 9.84, P < 0.01), although net movement was not different for fish from the two types of capture sites ($F_{1,41}$ = 2.65, P = 0.11).

During the flood, 11 of the 12 fish with functional transmitters responded with minor changes in position compared with the sites that they occupied 4 days before. One fish captured in simple habitat on 9 January 1998 was detected 70 m upstream of that capture site on 12 January 1998 and then 900 m further upstream in a tributary during the flood. Given the upstream movement by this fish prior to the flood and the behavior of other fish, we cannot confidently interpret this lengthy upstream movement as a response to the flood. Excluding this individual, during the flood, fish occupied sites an average of 17 m from those occupied 4 days before (N = 11, SE = 7). The positions of fish did not reveal a pattern in their direction of movement in response to the flood: we found five fish downstream and four upstream of their preflood positions, while two fish did not alter their longitudinal positions. Cutthroat trout apparently also moved little during the flood. Net movement of fish for the two daytime observations during the flood, on 16 and 17 January 1998, averaged only 4 m. We found seven fish in the same locations on both days, and the greatest net movement by an individual was 20 m.

The five fish that occupied pools with large woody debris on 12 January 1998 all occupied those same sections of stream during the flood. However, at a finer spatial scale, several of these fish occupied habitat during the flood that

Fig. 1. Habitats occupied by radiotagged adult coastal cutthroat trout in Little Jones Creek, California, during fall and winter. Data are categorized by two types of capture sites: (*i*) pools formed by large woody debris (LWD) and (*ii*) pools formed by scour adjacent to bedrock that contained little or no cover for fish (open). Percentages in the top panel are based on 364 observations of 21 fish, equally divided between day and night. Percentages in the bottom panel are based on 380 observations of 22 fish, also equally divided between day and night.

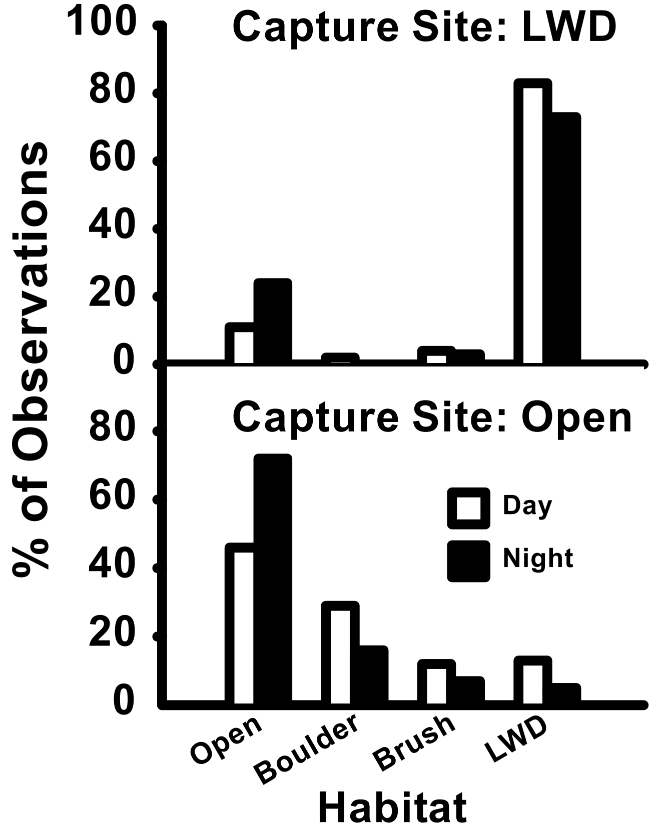
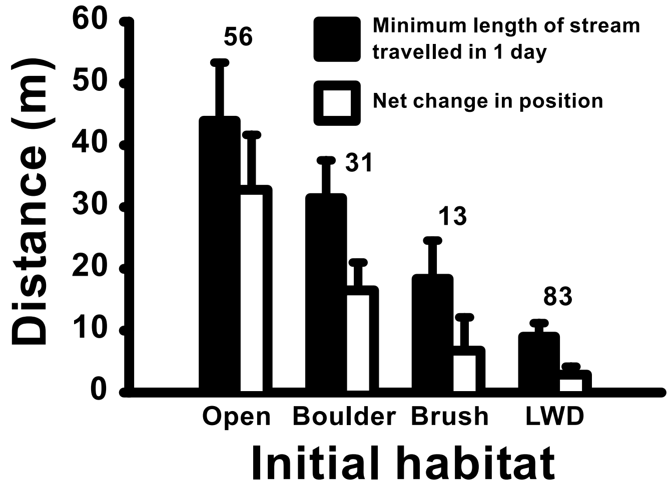


Fig. 2. Movement by radiotagged adult coastal cutthroat trout in Little Jones Creek, California, during fall and winter. Minimum stream length travelled is the distance covered by fish in 1 day, based on an initial daytime observation followed by two nighttime observations and a second daytime observation. Net change in position indicates the distance between the sites occupied by fish during two daytime observations on successive days. Numbers above the bars indicate sample size, and error bars are 1 SE; both of these reflect values for data from all fish combined. LWD, large woody debris.



they never used at lower flows. Also, none used the areas immediately downstream of large woody debris, where they were usually found at lower flows. During the flood, most areas in the main channel immediately downstream of large woody debris were sites of extreme turbulence, sometimes exacerbated by oscillations of the debris itself.

In contrast with the fish that had occupied pools with large woody debris, only two of seven fish that occupied habitats lacking large woody debris before the flood (12 January 1998) remained within those sections of stream during the flood. One of these two fish utilized habitat with low water velocity immediately below a tributary inflow, while the second occupied habitat among flooded alders near the streambank opposite the thalweg.

Overall, the 12 fish with transmitters occupied five types of habitat during the flood: (*i*) downstream of woody debris in tributaries or secondary channels (five fish), (*ii*) upstream of large woody debris in the main channel (two fish), (*iii*) open areas of low water velocity along the bank opposite the thalweg in pools formed by woody debris (two fish), (*iv*) flooded alders along the edges of straight sections of channel (two fish), and (*v*) below a tributary confluence in a pool formed adjacent to bedrock (one fish). All of these sites were along the stream margin and appeared to offer microhabitats with water velocities <15 $cm \cdot s^{-1}$, while water velocity along the thalweg during the flood was consistently >2.2 $m \cdot s^{-1}$.

Discussion

Habitat strongly influenced movement by adult cutthroat trout in Little Jones Creek during our fall–winter study period. Overall, during nonflood stream flows, fish captured at sites with large woody debris moved less than fish from pools lacking cover, and radiotagged fish found at sites with large woody debris were less mobile over 1-day observation periods independent of the type of habitat where they were captured. This lower vagility near large woody debris may simply reflect reduced movement of individuals when they encounter high-quality habitat. However, other processes appear to be involved in winter habitat selection by cutthroat trout in Little Jones Creek: extreme concentrations of fish in pools with woody debris are not apparent during moderate discharge, and a winter experiment revealed similar numbers of juvenile and adult cutthroat trout in pools lacking cover and pools where cover (including woody debris) was artificially enhanced (B.C. Harvey and J.A. Simondet, unpublished data). Perhaps lower movement rates in the vicinity of large woody debris reflect territorial defense of superior habitat by dominant individuals (Winker et al. 1995). Aggressive behavior by salmonids under winter conditions has been observed previously (Gregory and Griffith 1996).

Large woody debris and other elements providing habitat complexity appeared to be important to all the fish in this study. Cutthroat trout from pools lacking large woody debris or other cover were often found outside the specific habitats where they were captured. These fish commonly occupied higher-gradient habitats with large boulders or sites with large woody debris or brush, particularly during the day. The availability of large boulders appeared to be important to the fish that we captured in pools without cover. Such boulders were rare in the study reach, yet most were utilized by the relatively small number of radiotagged fish.

Our method of categorizing habitat necessarily underestimated the significance of habitat that can provide cover for cutthroat trout. Because of our inability to resolve the positions of fish on a spatial scale <1 m^2, habitat that we classified as open included areas with unembedded cobbles and small boulders. In Little Jones Creek (B.C. Harvey and J.A. Simondet, unpublished data) and elsewhere (e.g., Cunjak 1988; Griffith and Smith 1993), salmonids may conceal themselves within such substrate during the winter.

Even with our inclusion of some habitats providing cover in the open category, significant day/night differences in the use of open habitat were apparent. These differences probably reflect the diel pattern of concealment during the day and emergence at night, which has been observed in salmonids primarily during the winter (e.g., Heggenes et al. 1993; Valdimarsson et al. 1997) but also in summer (Gries et al. 1997; Gries and Juanes 1998). In Little Jones Creek, cutthroat trout apparently carry out this diel pattern both by remaining continuously in habitats providing cover and by moving from habitats providing cover during the day to habitats lacking cover, principally pools, at night.

The fitness consequences of occupying habitat with large woody debris during the winter remain unclear. Several authors have suggested that seasonal increases in risk of predation may promote greater nocturnal activity in salmonids (Fraser et al. 1993; Heggenes et al. 1993). In some areas, predation risk may be more severe in winter because swimming performance is reduced at low temperatures and predators may be more abundant. Both otters (*Lutra canadensis*) and common mergansers (*Mergus merganser*) have been observed in fall and winter, but not in summer, at Little Jones Creek, and one of the radiotagged fish in this study located in open habitat was consumed by a merganser. Occupying complex habitat and moving infrequently may reduce the risk of mortality when predation pressure is particularly severe.

Seasonal shifts in use of habitat by stream fishes, including cutthroat trout (Brown and Mackay 1995), are widely recognized. If predation risk is relatively less significant in other seasons, shifts away from large woody debris based on a balancing of predation risk and food acquisition may be common, even for fish highly ranked in dominance hierarchies. Such shifts might explain similar patterns of retention of individually tagged cutthroat trout in pools with and without large woody debris in Little Jones Creek from one summer to the next (Harvey 1998), even if pools with large woody debris provide superior habitat during part of the year. The wide variation in movement and use of habitat by cutthroat trout observed during this study may represent strategies with similar fitness consequences.

During the flood of January 1998, Little Jones Creek appeared to provide adequate habitat for adult trout over most of the study reach, even though water velocity in the thalweg consistently exceeded 2.2 $m \cdot s^{-1}$. The modest responses to flooding of cutthroat trout (this study) and other adult stream fishes (Todd and Rabeni 1989; Matheney and Rabeni 1995) provide partial explanation for minor differences between fish assemblages before and after floods (e.g., Matthews 1986; Lobón-Cerviá 1996), even though eggs and young-of-the-year fishes of some species are readily displaced and killed during flooding (e.g., Seegrist and Gard 1972; Harvey 1987). Perhaps only extreme events in relatively large channels cause significant displacement of post-young-of-the-year salmonids (Jowett and Richardson 1989). Apparently, in many settings during floods, stream fishes readily exploit habitats with relatively low water velocities along stream margins (e.g., Ross and Baker 1983; Jowett and Richardson 1994; this study).

During the flood, the majority of adult cutthroat trout that we located occupied habitat influenced by woody debris. However, fish occupied different habitats near woody debris in the main channel than they did in secondary channels and a tributary. In the smaller channels, fish occupied positions downstream of woody debris. This coincides with the observation that coho salmon occupied habitat downstream of artificial root masses during high flow in 0.9-m-wide stream channels (McMahon and Hartman 1989). In the main channel of Little Jones Creek, however, extreme turbulence downstream of large woody debris appeared to render these areas uninhabitable. Similarly, Nickelson et al. (1992*b*) hypothesized that high turbulence may have accounted for their finding that the addition of brush to plunge pools in Oregon streams did not increase the density of coho salmon, unlike the addition of brush to less-turbulent pools. When fish occupied habitat close to large woody debris in the main channel of Little Jones Creek, they were positioned upstream. Fish also occupied areas of low water velocity in the main channel along the bank opposite large woody debris. Areas of low water velocity may be relatively common during bankfull conditions in pools formed by large woody debris because woody debris may significantly deflect the flow more often than do bedrock outcrops (Lisle 1986). However, the study reach of Little Jones Creek contained several pools with large areas of low water velocity during flood conditions where bedrock did significantly deflect the flow. This observation weakens the hypothesis that cutthroat trout in the study reach would be habitat limited during floods if large woody debris were absent. Low overall movement by cutthroat trout in open habitat during the flood, and their use of the floodplain along straight sections of channel, also do not support the hypothesis that cutthroat trout are limited by the abundance of woody debris during flooding.

Overall, the extensive use of habitat associated with large woody debris, large boulders, and brush by cutthroat trout during fall and winter parallels previous studies of other salmonids (Tschaplinski and Hartman 1983; Cunjak and Power 1986). Our observations are also consistent with the hypothesis that fish assemblages in hydraulically complex stream reaches are more resistant to flooding (Pearsons et al. 1992). Finally, our observations support Cunjak's (1996) suggestion that stream habitat complexity should be maintained or restored to assure adequate winter habitat for stream fishes.

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