

Experimental Analysis of Microhabitat Selection by Juvenile Steelhead (*Oncorhynchus mykiss*) and Coho Salmon (*O. kisutch*) in a British Columbia Stream

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Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Can. J. Fish. Aquat. Sci.* 50: 1198–1207.

Replicate experiments were conducted in the Salmon River, British Columbia, during early summer 1990 to test the relative importance of velocity refuge, visual isolation, and overhead cover to microhabitat selection by steelhead (*Oncorhynchus mykiss*) parr and age-0 coho salmon (*O. kisutch*). Four types of artificial Plexiglas structures, the first three of identical construction, had different portions painted to provide increasing habitat complexity: velocity refuge alone, velocity refuge with visual isolation, all three features combined, and overhead cover alone. Steelhead parr selected structures with overhead cover alone or all three features significantly more often than those without overhead cover. Steelhead also selected structures adjacent to the swiftest velocities available and closest to other natural overhead cover, which accounted for most differences in use of the same structure in different locations. In contrast, few age-0 coho salmon used any structures. Those that did selected the three types of structures with velocity refuge about equally, but significantly more often than those with overhead cover alone, regardless of their location. Field experiments such as this hold promise for elucidating mechanisms of habitat selection by stream salmonids.

Des expériences répétées ont été effectuées dans la rivière Salmon, en Colombie-Britannique, au début de l'été 1990; elles avaient pour objet de tester l'importance relative des refuges contre le courant rapide, de l'isolation visuelle et du couvert pour le choix du microhabitat par des tacons de truite arc-en-ciel (*Oncorhynchus mykiss*) anadrome et par des cohos (*O. kisutch*) d'âge 0. Nous avons construit quatre types de structures artificielles en Plexiglas, dont les trois premières étaient identiques, et nous avons peint des parties différentes pour augmenter la complexité de l'habitat: refuge contre le courant seulement, refuge avec isolation visuelle, les trois caractéristiques combinées et le couvert seulement. Les tacons de truite ont choisi les structures avec couvert seulement ou avec les trois caractéristiques de façon nettement plus fréquente que celles qui n'avaient pas de couvert. Les truites ont aussi choisi les structures proches des courants les plus rapides et aussi les plus proches du couvert naturel, ce qui représentait la plupart des différences dans l'utilisation de la même structure en des lieux différents. Par contre, les saumons cohos d'âge 0 ont été peu nombreux à utiliser les structures. Ceux qui l'ont fait ont choisi de façon à peu près égale les trois types de structures avec refuge contre le courant, mais toutefois de façon nettement plus fréquente que celles qui offraient seulement un couvert, quel que soit leur emplacement. Les travaux de terrain comme celui-ci sont prometteurs pour l'étude des mécanismes du choix de l'habitat par les salmonidés dans les cours d'eau.

Received May 27, 1992

Accepted December 9, 1992
(JB499)

Reçu le 27 mai 1992

Accepté le 9 décembre 1992

Most of what has been discovered about the positions that salmonids hold in streams has been learned by observation. For example, early research showed that juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) undergo ontogenetic shifts in habitat selection, moving to faster and deeper water as they grow larger (Chapman and Bjornn 1969; Everest and Chapman 1972). Investigators have also described much about the average characteristics of microhabitat that salmonids use. Adult brown trout (*Salmo trutta*) are known to select shaded positions with low velocity (Gosse and Helm 1981; Bachman 1984; Clapp et al. 1990) whereas rainbow trout select relatively open positions in swifter currents (Cunjak and Green 1983; Baltz et al. 1991).

However, these observations give relatively little insight into why stream salmonids select certain positions over others. In contrast, more has been learned about these mechanisms by experimental manipulations, often under controlled conditions.

Research during the last 25 yr has shown that salmonids seek optimum conditions of depth and velocity for foraging, within the constraints of intraspecific and interspecific dominance hierarchies (Jenkins 1969; Fausch 1984; Fausch and White 1986; Hughes and Dill 1990; Hughes 1992a, 1992b). Moreover, stream fish must do all of this and not get eaten, i.e., they must also weigh the risk of predation (Dill and Fraser 1984; Power 1987; Lima and Dill 1990; Brown and Moyle 1991).

The experiments done to date suggest that physical structures forming habitat for stream salmonids provide three features relevant to the trade-offs among foraging, intraspecific and interspecific competition, and predation risk. These features are velocity refuge, visual isolation, and overhead cover (Campbell and Neuner 1985). Structures that afford *velocity refuge* allow fish to hold low-velocity positions adjacent to swifter currents and may thereby maximize their energy intake from drifting invertebrates while minimizing the cost of swimming to main-

tain position (Mundie 1969; Everest and Chapman 1972; Fausch 1984; but see Hughes and Dill 1990 for an alternative view). Structures that provide *visual isolation* from other fish can reduce agonistic behavior within intraspecific and interspecific dominance hierarchies and may thereby increase the density of fish that can occupy a given area (Kalleberg 1958; Mesick 1988). Lastly, structures that provide *overhead cover* afford hiding places and decrease visibility of salmonids to terrestrial and aquatic predators by reducing light beneath the structures, both of which are thought to reduce predation risk (Gibson and Power 1975; Helfman 1981).

Here I report the results of field experiments designed to test the relative importance of these three features to microhabitat selection by steelhead parr and coho salmon (*Oncorhynchus kisutch*) fry in a British Columbia stream. Most experiments aimed at discovering the relative importance of one or more of the features to stream salmonids have been done in the laboratory (Hartman 1963; Wilzbach 1985; Mesick 1988) or with fish that were constrained in outdoor channels (Butler and Hawthorne 1968; Baldes and Vincent 1969; DeVore and White 1978; McMahon and Hartman 1989), so the results may, to some degree, have been artifacts of handling or constraining fish. Two recent field experiments provided evidence that salmonids select certain conditions, but were unable to fully separate their relative importance due to constraints of the experimental design (Shirvell 1990) or because only one of the three features was manipulated (Cunjak and Power 1987).

Study Area

Two replicate experiments were conducted in separate 250-m reaches of the Salmon River, a productive, moderate-gradient tributary (~0.4% in the reach studied; McMynn and Vernon 1954) of the lower Fraser River in southwestern British Columbia. Fish distributions and habitat were described by Hartman (1965, 1968) and Hartman and Gill (1968). The two study reaches were located about 500 m apart, 2 km downstream from a site sampled by Hartman (1965, S-13 in his fig. 6). The river here consisted primarily of riffles and runs with cobble and gravel substrate and pools formed by large woody debris originating from the second-growth riparian forest.

Juvenile coho salmon and steelhead and a few juvenile and adult cutthroat trout (*Oncorhynchus clarki*) occurred in the reaches studied. Hartman (1968) found trout (steelhead and cutthroat combined) to age 3 based on scale annuli, most of which were <160 mm fork length (FL). Age-0 coho salmon captured by seining (3-mm-mesh) in the downstream study reach on 2 July 1990 averaged 59.5 mm total length (TL) (SE = 0.60, range 42–82 mm, $n = 162$). The age-0 steelhead captured were <60 mm TL and age-1 (hereafter parr) were >80 mm TL, based on a length–frequency histogram ($n = 93$).

Four runs in each study reach were chosen for the two experiments because Facchin and Slaney (1977) found the highest density of steelhead parr in this habitat type. The runs averaged 4.4 m wide (range 2.5–6.1 m) and 13 m long (range 4.5–32 m). They had mean depths of 28–49 cm (maxima 33–57 cm), mean substrate diameters of 2–7 cm (maxima 6–13 cm), and mean velocities of 12–32 $\text{cm}\cdot\text{s}^{-1}$ (maxima 35–65 $\text{cm}\cdot\text{s}^{-1}$). Water temperature ranged between 13.0 and 15.0°C during the first experiment (28 June to 6 July 1990) and between 13.5 and 17.5°C during the second (11–19 July 1990). Discharge was low and stable at both sites during experiments

(downstream reach: 0.16 $\text{m}^3\cdot\text{s}^{-1}$; upstream reach: 0.11 $\text{m}^3\cdot\text{s}^{-1}$). Underwater visibility averaged 5.1 m (range 4.2–6.3 m, $n = 10$). It was determined daily by measuring the distance through water at which a 13 × 18 cm white diving slate disappeared from view.

Methods

Design and Layout of Experimental Structures

The replicate experiments consisted of setting out artificial habitat structures that afforded fish different combinations of velocity refuge, visual isolation, and overhead cover and recording which ones were used by fish. The structures were constructed of three pieces of 6-mm-thick Plexiglas, two of which formed a T-shaped structure when viewed from above (Fig. 1). The T structure was 10 cm wide and 20 cm long and was buried so that 5 cm protruded above the substrate. The third piece was a 20 × 30 cm overhead cover centered above the T structure and suspended 10 cm above the bed on 6-mm-diameter steel legs.

Three different treatments were constructed by painting portions of the structures black. Unpainted structures provided only velocity refuge (hereafter treatment VR). However, because I suspected that clear structures might be difficult for fish to see when submerged, a 0.5-cm-wide black strip was painted along the edges of the leading piece of the T structure to provide a visual reference (Fig. 1). When the entire T was painted black the structure afforded velocity refuge and visual isolation (hereafter VR + VI). When all pieces were painted black the structure provided velocity refuge, visual isolation, and overhead cover (hereafter ALL). Each of these three treatments was hydraulically identical to avoid bias caused by altering flow patterns when adding features.

Pilot research conducted in mid-June indicated that some steelhead parr and coho presmolts selected overhead cover alone. Therefore, I designed a fourth treatment having a simple visual reference of the same dimensions as the leading piece of the T structure, placed beneath a black overhead cover identical to other treatments. The visual reference was a wicket (i.e., an inverted U) of 3-mm steel rod that was 10 cm wide, buried so that 5 cm protruded above the bed. This treatment afforded only overhead cover (hereafter OHC) with minimal velocity refuge. On three occasions, coho fry held positions directly downstream from a leg supporting an overhead cover, presumably using it as a velocity refuge (cf. Sutterlin and Waddy 1975), but neither species was ever observed to hold a position directly downstream from the wicket rod.

A set of four structures, one of each treatment, was set out in a 1 × 4 m plot in each of the four runs selected for each experiment. Runs in each study reach that had the highest steelhead parr densities were selected by underwater observation. Age-0 coho were abundant throughout. Plots were oriented with the long axis parallel to stream flow, and the boundaries were marked on the bed with nylon lines. In the first experiment, structures were placed in a line down the center of the long axis of the plot with their centers positioned 0.90 m apart and 0.65 m from the upstream and downstream plot boundaries. In the second experiment, structures were offset 10 cm from the centerline on alternate sides (Fig. 1) to minimize flow disturbance for adjacent upstream and downstream structures. Two runs used in the second experiment could not accommodate 1 × 4 m plots, so shorter, wider plots of 4 m^2 total area (2.7 × 1.5 m and 3 × 1.3 m) were used

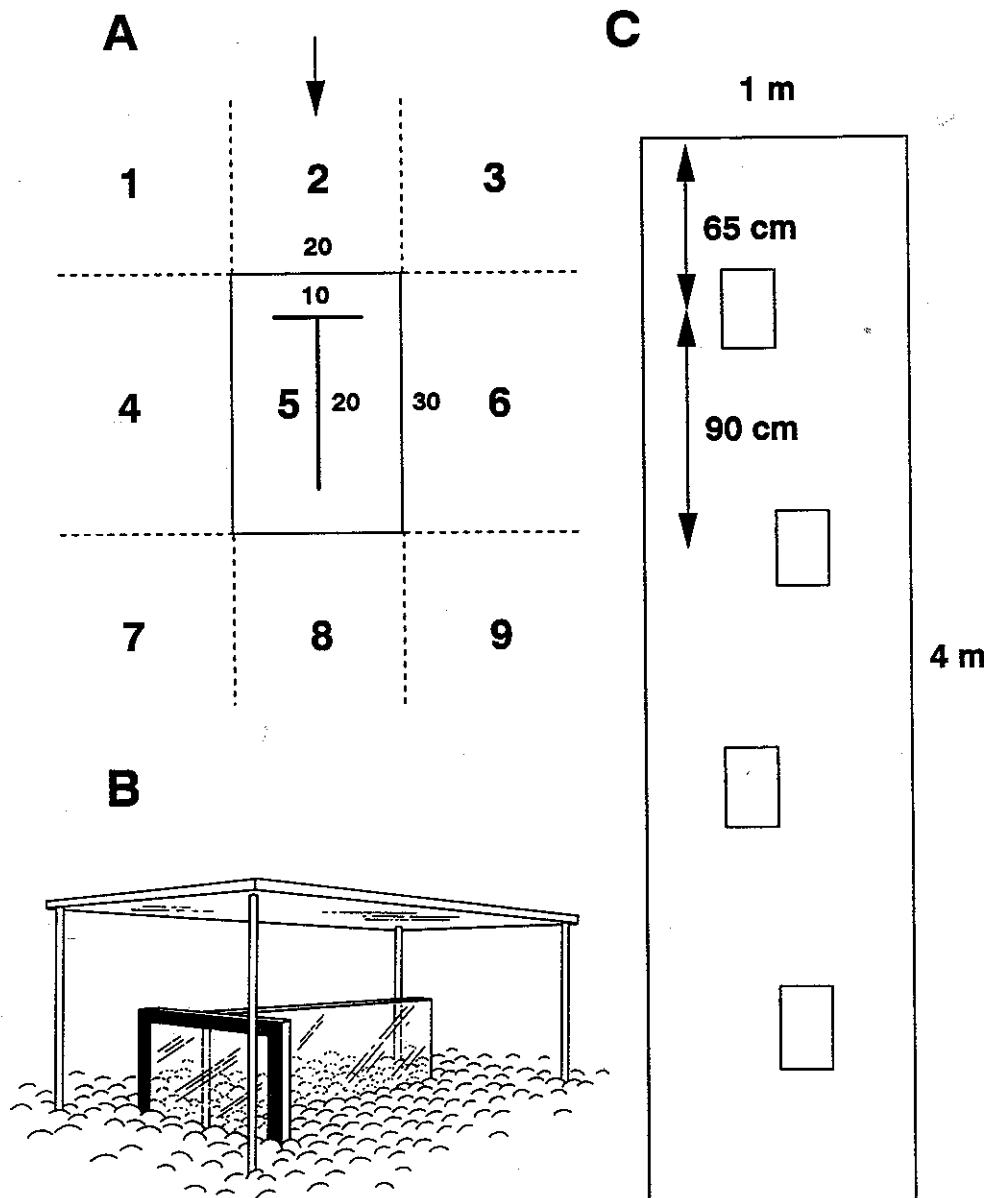


FIG. 1. Design and layout of structures used in experiments. (A) Top view showing orientation of structures to flow direction (arrow) and quadrats 1-9 in which fish were counted. Small numbers show dimensions (cm). (B) Three-dimensional side view of VR structure showing clear overhead cover and T structure with black stripe to provide a visual reference. The T structure is 5 cm high, and the overhead cover is supported 10 cm above the bed. (C) Layout of four structures in a 1 × 4 m plot in experiment 2. Structures were offset to the left and right of the midline to minimize disturbance to flow near adjacent structures.

instead. Complex channel morphology caused flow to change direction midway through the longer plot, so structures were arrayed down the centerline but oriented with their long axis parallel to local flow direction. In the shorter plot, structures were alternated along two lines parallel to flow that were spaced 0.7 m apart. The structures in each line were placed with their centers 0.9 m apart, and the edges of the most upstream and downstream structures were 0.3 m from the two adjacent plot boundaries.

Physical Measurements

The effects of treatments on the physical environment were measured during the last 2 d of observation of experiment 2.

Light above and beneath structures was measured with a Li-Cor model 185B meter and 192S underwater quantum sensor. Light was measured approximately 10 cm above, 2 cm beneath, and 5 cm beneath (for black overhead covers only) the center of each overhead cover immediately after fish counts were completed for each plot. On one day, light was also measured at positions of 10 steelhead parr (two or three per plot) that were beneath natural instream overhead cover or in the shade created by terrestrial vegetation. All fish were inside, or within 50 cm of, the plot boundaries.

Water velocity was measured upstream and to the sides of one T structure that was positioned near one of the plots in water 15 cm deep with uniform flow. Velocity was measured

($\pm 0.5 \text{ cm} \cdot \text{s}^{-1}$) using a Novonic Streamflo meter (Nixon Instrumentation Ltd., UK) that consisted of a 1-cm-diameter propeller on a thin wand. Four replicate velocity measurements (10-s integration) were made 2.5 cm above the bed of 1- to 2-cm gravel at each of 13 marked locations before and after the structure was carefully removed.

Water depths, water velocities, and substrate diameters were measured at each structure location the day before the last day of observation of each experiment (see below). Depths were measured 10 cm from each edge of the overhead cover (i.e., at locations of the numbers 2, 4, 6, and 8 in Fig. 1A). Water velocity 2 cm above the bed (hereafter bottom velocity) was measured with a Marsh-McBirney model 201 electromagnetic flow meter, 15 cm to the right and left of the leading corners of the overhead cover. A substrate particle was randomly selected from each of the thirty-six $0.3 \times 0.3 \text{ m}$ quadrats within each plot and its second-longest dimension measured as an index of mean diameter. Surface turbulence above each structure was scored in three classes: none (surface not rippled), slight (surface rippled but structure visible), and moderate (structure barely visible due to surface turbulence). I also measured the distance from each structure to the nearest natural overhead cover capable of concealing a 15-cm fish from overhead view, such as undercut banks and submerged logs, rootwads, or dense brush.

Observation Protocol

The number of coho fry and steelhead parr that were using each structure and the total number in each plot were counted at four 2-d intervals from the beginning of each 8-d experiment. Total counts of fish in each plot were also made immediately before structures were first placed. The fish were counted by underwater observation using a mask, snorkel, and wetsuit. I entered the water 10–30 m downstream from each plot and carefully moved upstream until the downstream plot boundary was sighted. I recorded the location of each fish in the plot as it came into view at the limits of underwater visibility (4–6 m). Many of the largest steelhead parr held positions away from natural or artificial overhead cover and were observed long before they became frightened and moved, which suggests that observations of habitat use were unbiased.

Each fish position was mapped on an underwater slate, using the structures as points of reference. Locations of fish beneath or within 20 cm of the edge of the overhead cover for each structure were recorded in nine quadrats (Fig. 1). Lengths of steelhead parr were estimated within 25-mm size classes by comparing fish with substrate or structure features and later measuring the distances (cf. Fausch and White 1981). On two occasions during experiment 2, a cutthroat trout was observed using a structure. These data were included because the size, behavior and habitat selection of juvenile cutthroat observed throughout the reach were indistinguishable from those of steelhead parr.

Many fish, especially coho fry, that were not directly beneath structures nevertheless used one or more features afforded by them. For example, some fish held positions 10–20 cm upstream from structures providing velocity refuge, alone or with other features (i.e., treatments VR, VR + VI, or ALL) and were observed to use the structures as velocity refuges only. I defined structures as being used by fish if any of the features they afforded were used, based on the following criteria. Fish were judged to be using velocity refuge features only if their

head was positioned within 20 cm directly upstream or downstream from a T structure and their tailbeat frequency was substantially lower than in adjacent positions with ambient velocity. The difference in tailbeat frequency often could be observed when fish rose gradually in the water column to inspect drifting invertebrates and subsequently sank back to their focal point near the stream bed. Fish were recorded as using visual isolation features only if their body was within 5 cm upstream or to one side of a black T structure and within 2 cm of the bed, so that they were obscured from view by conspecifics on opposite sides of the structure. Fish were judged to be using overhead cover only if more than half their body length was beneath a black overhead cover, or in the shade provided by it. Only two fish, one coho and one steelhead, were observed doing the latter. All fish that were using all three features were directly beneath ALL treatment structures. Coho salmon that held positions $> 10 \text{ cm}$ above the stream bed, above or within 20 cm of a structure (i.e., floaters; Puckett and Dill 1985), were not counted as using them.

The four different types of structures were placed in random order in each of the four plots and randomly permuted after each day of observation according to a balanced set of Latin Squares unique to each experiment. This design ensured that each treatment occurred in a different upstream-to-downstream position in each run (or block) during every 2-d period and was randomly permuted to every position and run combination only once during the experiment (Gill 1978).

In addition to randomizing treatments within and among runs, I started observations at a different randomly selected run each day to control for bias due to time of day. Runs were observed in upstream order to avoid effects of increased turbidity on downstream visibility and fish behavior. After completing work in the most upstream run, I waited about 1 h to allow any turbidity to clear before beginning observations on the downstream run. Structures were cleaned of any periphyton and moved to their new locations soon after observations and measurements were completed for each plot. The work required about 7 h (~09:00–16:00) on each day of observation.

To determine whether the frequent disturbance of moving structures might bias the results, I set out an additional ALL structure in the center of a 1-m^2 "control" plot located within each experimental reach. This plot was observed at the same 2-d intervals as the others but was left undisturbed throughout the experiment.

Statistical Analysis

Fish response to structures was analyzed at three hierarchical levels: fish near structures (i.e., in quadrats 1–9, beneath or within 20 cm of the overhead cover), fish using structures (as defined above), and the specific features of structures used by fish (i.e., velocity refuge, visual isolation, overhead cover). Because at most two steelhead parr or coho fry were observed using any one structure simultaneously, data for the second level of analysis were nearly binary (i.e., the structure was used or not) rather than normally distributed, which precluded using analysis of variance based on the Latin Squares design (Gill 1978). Instead I used logistic regression (Hosmer and Lemeshow 1989), which is specifically designed to analyze effects of categorical and continuous variables on binomial response variables such as the proportion of structures used by fish. Separate logistic regressions were calculated for steelhead parr and coho fry, first based on five experimental factors (experiment,

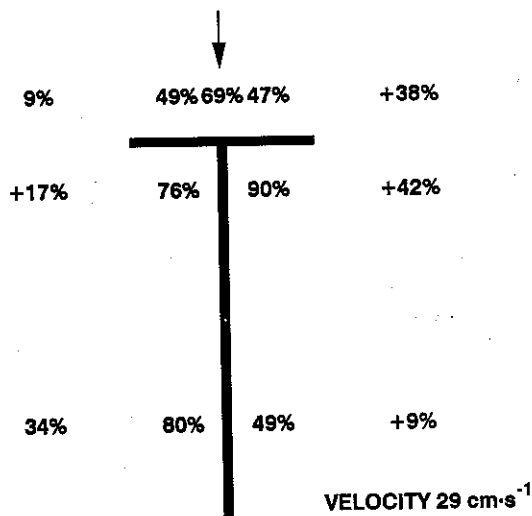


FIG. 2. Percentage velocity reduction around a T structure, based on measurements at 13 points before and after removing the structure. Percentage velocity increases are indicated by plus signs. Measurement points were oriented in three lines, 2.5 cm upstream and 2.5 cm downstream from the leading edge of the T and 5 cm upstream from the downstream end. The seven points closest to the T were all 2.5 cm from all Plexiglas surfaces and from each other. The six measurements to the right and left were arranged along lines parallel to flow that were 5 cm from the leading corners of the T. Ambient velocity of $29 \text{ cm}\cdot\text{s}^{-1}$ was measured at the junction of the two pieces, after the structure was removed.

day of observation, treatment, run, position within run) and then using five physical habitat variables (depth, velocity, substrate, distance to cover, surface turbulence). Although the logistic regression (unlike the balanced Latin Squares design) could not fully account for repeated measures effects, such as might be caused by a particular fish that selected overhead cover every day, it could detect other block and position-within-block effects that might prove to be important.

Results

Effect of Structures on Light and Water Velocity

The overhead covers greatly reduced light beneath them when painted black and had little effect when clear. Black overhead covers reduced ambient light (i.e., that measured above the structures) by an average of 99.8% (SE = 0.094, $n = 18$) 2 cm beneath the structure ($P < 0.0001$ by paired t -test after arcsine square-root transformation for percentages) and 99.1% (SE = 0.22, $n = 18$) 5 cm beneath the structure (i.e., 5 cm above the stream bed) ($P < 0.0001$). In contrast, light 2 cm beneath clear overhead covers was not significantly different from ambient light ($\bar{x} = 0.5\%$ higher beneath structures, SE = 13.5, $n = 16$, $P = 0.66$) but varied greatly in some cases due to shadows that affected only one measurement. Light above all types of structures averaged 4100 lx (SE = 847, range 360–18 900, $n = 34$) and averaged 4.6 lx (SE = 1.03, range 0–11, $n = 18$) 2 cm beneath black overhead covers, when measured during the last 2 d of experiment 2. Light measured at positions of 10 steelhead parr beneath natural overhead cover, or in the shade of overhanging vegetation, averaged 198 lx (SE = 228, range 0–556).

Measurements upstream, downstream, and on each side of the leading piece of a T structure showed that a velocity of

$29 \text{ cm}\cdot\text{s}^{-1}$ was reduced an average of 66% (range 47–90%) within 2.5 cm upstream and within 2.5 cm of the longitudinal piece downstream (Fig. 2). In contrast, water velocity was up to 42% higher 5 cm to the sides of the leading piece, most likely because flow was shunted around it. Thus, measurements of light and velocity around structures indicated that the velocity refuge and overhead cover features had the desired effect on the physical environment.

Fish near Structures

Experimental plots had high average densities of both steelhead parr (experiment 1: $\bar{x} = 0.9\cdot\text{m}^{-2}$; experiment 2: $\bar{x} = 1.3\cdot\text{m}^{-2}$) and coho fry (experiment 1: $\bar{x} = 4.6\cdot\text{m}^{-2}$; experiment 2: $\bar{x} = 5.6\cdot\text{m}^{-2}$) when structures were present. However, there was no indication that fish were attracted into plots by the structures because about the same numbers were present before and after the structures were placed. Single counts of steelhead parr made immediately before structures were placed were always within the range of those made when structures were present ($\bar{x} = 4.4$ parr per plot, SE = 0.5) for all eight plots used in both experiments. For coho fry, this was true for four of eight plots ($\bar{x} = 20.7$ parr per plot, SE = 1.2). For two of the other four plots, counts made before structures were placed were two fish less than the lowest count with structures present, but in the other two plots, counts made before structures were placed were one and four fish more than the highest counts afterwards. Overall, these data suggest that few coho were attracted into the plots by structures.

The most general hypothesis to test about fish response to structures is whether fish in plots chose positions near structures over those in the surrounding natural habitat. For example, fish might display a general thigmotactic response to structures (cf. Hartman 1963; DeVore and White 1978) or derive benefit from velocity refuges or proximity to escape cover. If so, one would expect a higher density of fish beneath and within 20 cm of the structures (i.e., in quadrats 1–9; Fig. 1) than the average for the plot as a whole. The density of coho fry near structures was not significantly different from that in the whole plot ($P = 0.22$ and $P = 0.37$ for the two experiments by paired t -test; $n = 16$ each), suggesting that coho were not generally attracted to positions near structures. Density of steelhead parr was significantly greater in quadrats 1–9 than in the whole plot in experiment 1 ($P = 0.01$) but not in experiment 2 ($P = 0.49$). However, failure to reject the null hypothesis of no general preference for positions near structures does not preclude the possibility that fish used certain locations or types of structures more than others. For example, density of steelhead was significantly higher in the strip upstream, beneath, and downstream from structures (i.e., in quadrats 2, 5, and 8) than in adjacent strips to the right and left in both experiments ($P \leq 0.0002$ by paired t -test for both). Moreover, because most (76%) steelhead in quadrats 1–9 were either upstream or beneath structures, and the majority (63%) were also using the structures (as defined above), only relationships between steelhead using structures and the five experimental factors were analyzed by logistic regression. A similar analysis was conducted for coho.

Use of Structures by Steelhead

Steelhead parr used structures with overhead cover and all three features significantly more often than structures with velocity refuges alone or combined with visual isolation (Fig. 3;

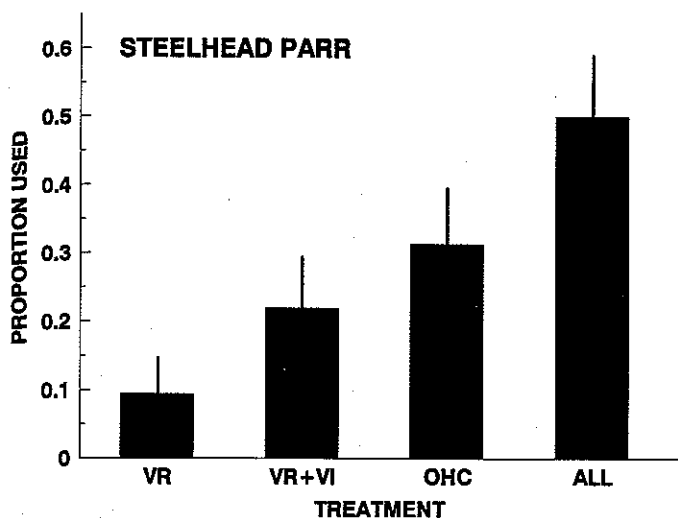


FIG. 3. Proportion of structures of four different treatment combinations that were used by steelhead parr. Vertical lines show +1 SE. Treatments were velocity refuge (VR), velocity refuge and visual isolation (VR + VI), overhead cover (OHC), and all three features combined (ALL).

$P = 0.0009$ for contrast of VR and VR + VI versus OHC and ALL treatments). However, the effects of visual isolation added to velocity refuge (VR versus VR + VI, $P = 0.15$) and of velocity refuge and visual isolation added to overhead cover (OHC versus ALL, $P = 0.086$) were not significant. These three a posteriori contrasts were judged significant at $P = 0.017$ to control the experimentwise error rate at $P = 0.05$.

Logistic regression indicated that, of the five experimental factors tested (experiment, day, treatment, run, position), only treatment, run, and position accounted for significant variation in the proportion of structures used ($P < 0.015$ for likelihood-ratio (LR) chi-square tests of models with individual variables versus intercept only). Moreover, a model with these three variables accounted for no less variation than one with all five ($P = 0.79$ by LR chi-square) and was the most parsimonious based on Akaike's Information Criterion (AIC; Akaike 1985). None of the two-way interactions between treatment and other main effects (e.g., experiment-by-treatment) were significant ($P > 0.13$ by LR chi-square for interactions added to the five-variable model). Interactions with run and position were not considered further because different runs were used in each experiment.

The previous analysis indicated that use of structures by steelhead parr depended not only on the type of structure (treatment), but also on its location (i.e., run and position). I therefore used logistic regression to determine whether any of the five physical habitat variables (depth, average bottom velocity, diameter of substrate beneath structures, surface turbulence, distance to nearest natural overhead cover) could account for differences due to structure location. After accounting for the differential effect of treatments, the proportion of structures used was significantly related only to velocity and distance to nearest cover ($P < 0.007$ by LR chi-square for both versus model with treatment alone), which themselves were not significantly correlated ($r = -0.171$, $P > 0.05$, $n = 128$). However, because the relationships were not logistic, especially for distance to cover, these continuous variables were transformed to categorical by dividing the observations into four sets of about equal sample size each (Fig. 4) as suggested by Hosmer and

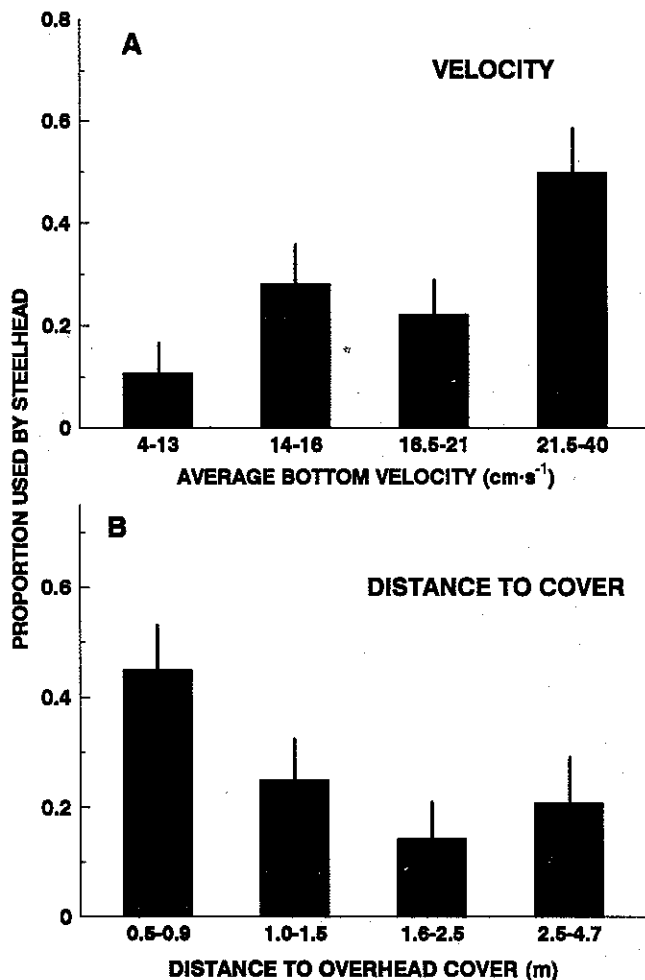


FIG. 4. Proportion of structures used by steelhead parr, divided into four classes by (A) average bottom velocity and (B) distance to nearest natural overhead cover. Vertical lines denote +1 SE. Bottom velocity was measured 2 cm above the bed and 15 cm to the right and left of the leading edge of each overhead cover. Natural overhead cover included undercut banks and submerged logs, rootwads, and dense brush.

Lemeshow (1989). The resulting regression, which included treatment, velocity, and distance to cover, accounted for about as much information (AIC = 135.7) as the former one containing treatment, run, and position (AIC = 132.5), indicating that the physical habitat variables accounted for most of the variation in structure use due to different locations. Single a posteriori contrasts showed that steelhead selected structures located adjacent to swifter velocities ($>21 \text{ cm}\cdot\text{s}^{-1}$, $P = 0.003$) and within 0.9 m of natural overhead cover ($P = 0.02$) significantly more often than those in lower velocities or farther from cover.

The disturbance of moving structures every 2 d probably had little effect on their use by steelhead, based on observations of the ALL structure in the 1-m² "control" plot. In experiment 1, no steelhead parr ever colonized the structure, probably due to low ambient velocity, whereas in experiment 2, one or two parr were observed beneath it on each observation day. In neither case, therefore, was there any change during the experiment. On one occasion in each experiment the number of steelhead in a plot was counted twice, at 3- and 5-h intervals, and on another day counts were made 4 h apart in a control plot.

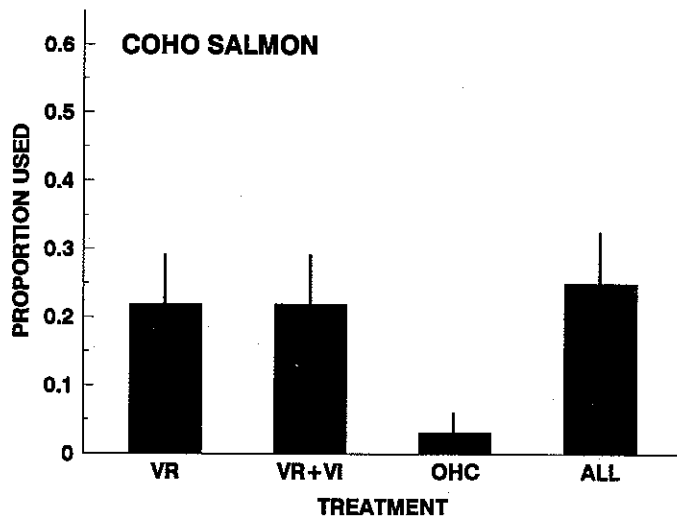


FIG. 5. Proportion of structures of four different treatment combinations used by age-0 coho salmon. Vertical lines denote +1 SE. Treatment combinations are as in Fig. 3.

In all three cases the number of parr in the plot and the number in quadrats 1-9 near structures varied by only one fish or were identical for the two counts, suggesting that time of day also had little effect on the results.

Although a few age-0 steelhead were observed in the plots, none were ever beneath structures or used any of the features they provided. Densities were low ($\bar{x} = 1.2$ per plot, SE = 0.2, range 1-5 per plot, $n = 32$), probably because this age class generally occupies riffles during the first months after emergence (Hartman 1965).

Use of Structures by Coho

Age-0 coho used the three structure types that had velocity refuges (VR, VR + VI, and ALL) significantly more often than structures with overhead cover alone ($P = 0.029$ by a posteriori contrast; Fig. 5). Of the five experimental factors tested by logistic regression, only treatment and day of observation accounted for significant variation ($P < 0.04$ by LR chi-square for each versus the model with intercept alone). Moreover, a model with treatment and day accounted for no less variation than other more complex models with three to five main effects ($P = 0.67$ or greater by LR chi-square) and was the most parsimonious based on AIC. There were no significant interactions between treatment and other variables.

The effect of day was significant because, for both experiments combined, only one age-0 coho was observed using any structure on the first experiment day compared with six to nine coho on subsequent days. This might lead one to suspect that use of structures by coho increased through time. However, use of the ALL structures in control plots did not change during either experiment (no coho were observed using them), and the number of coho in control plots did not increase with time. Counts on successive days were 5, 5, 6, 7, and 6 for experiment 1 (two counts on day 2) and 4, 4, 4, and 3 for experiment 2.

The proportion of structures used by coho was not significantly related to any of the five physical habitat variables, after accounting for the effects of treatment ($P > 0.1$ for all by LR chi-square). This was expected because neither the effects of run nor those of position were significant in the logistic regression based on experimental factors alone.

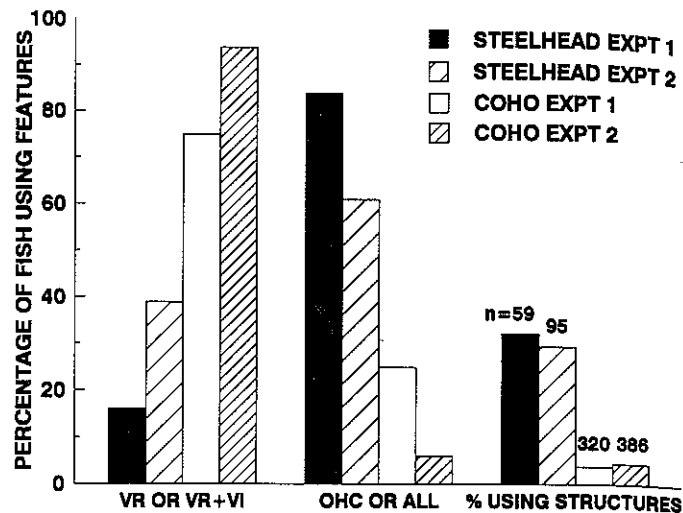


FIG. 6. Percentage of the steelhead parr and coho salmon fry occupying structures in experimental and control plots that were using velocity refuge features, with or without visual isolation, versus those using overhead cover or all three features. The set of bars at the right shows the percentage of all fish counted in plots that were using any structure.

Features Used by Fish

Analysis of the specific features that steelhead and coho used corroborated results on the types of structures fish used. In both experiments, a high percentage of the steelhead parr that occupied structures (including those in control plots) used overhead cover or all three features (70% for both experiments, $n = 47$; Fig. 6), rather than velocity refuge alone or in combination with visual isolation. All steelhead using overhead cover or all three features were directly beneath structures, except for one fish positioned adjacent to an overhead cover in the shade it provided. In contrast, all but one of those using velocity refuge features, with or without visual isolation, held positions directly upstream from structures. In five cases, two steelhead parr were observed simultaneously using opposite sides of the black T beneath a structure having all three features. In one other case, two steelhead were observed simultaneously using a structure providing overhead cover alone.

Nearly the opposite was found for coho fry. On average, 86% of those using structures ($n = 29$) selected the velocity refuge feature alone (none used visual isolation). Only one of these fish, and three others using overhead cover alone or all three features, held positions directly beneath structures. Of all fish observed in experimental and control plots, about a third of the steelhead parr occupied structures (30 and 32%) whereas very few of the coho observed used structures (4% in both experiments). Most of the steelhead using structures with overhead cover (OHC of ALL treatments) were among the smaller parr observed in the plots, although the proportion was not significantly different from expected (29 of 33 using overhead cover were <150 mm versus 116 of 154 observed in plots; $P = 0.10$ by G -test).

Most steelhead parr that were not using structures held positions beneath or within about 30 cm of natural overhead cover located near the plot boundaries or in shade from overhanging terrestrial vegetation. For example, one plot was crossed by a 10-cm-diameter branch suspended about 10 cm above the bed, beneath which two to four steelhead parr held positions during each observation.

Discussion

Steelhead Parr

During early summer, steelhead parr selected artificial habitat structures that provided overhead cover significantly more often than those with velocity refuge alone or with visual isolation (Fig. 3). Physical measurements confirmed that the structures having all three features reduced light to low levels and substantially decreased water velocity (Fig. 2), and their design ensured that fish holding positions close to opposite sides of the same structure were visually isolated.

The experiments indicated that, of the three features, overhead cover and the low light it provided was the most important relative to the others. Shirvell (1990) also inferred from his field experiment using simulated rootwads that steelhead parr selected positions in a coastal British Columbia stream primarily in response to low light levels. However, although I found that overhead cover was the primary feature selected, the data also suggest that both velocity refuge and visual isolation contributed to use of structures by parr. For example, 30% of the steelhead using structures in both experiments selected velocity refuge features alone, or combined with visual isolation, and all but one of these held positions directly upstream from structures. Moreover, 21% of the parr using structures were visually isolated from a conspecific positioned on the opposite side of a black T, beneath a structure with all three features. Experiments by other investigators have also shown that various other stream salmonids selected locations beneath or within the most complex cover available, especially during winter (Hartman 1963; DeVore and White 1978; McMahon and Hartman 1989).

Other physical features adjacent to the structures also were important predictors of steelhead parr use. Steelhead selected structures that were adjacent to the swiftest velocities in the plots (21–40 cm·s⁻¹; Fig. 4). Such velocity refuges adjacent to relatively swift currents that provide abundant drifting invertebrates may allow fish to optimize foraging (Fausch 1984). Steelhead also selected structures that were within about 1 m of other pieces of natural overhead cover such as undercut banks and submerged logs, rootwads, or dense brush. Moreover, most of the steelhead parr observed in the plots that were not using structures (69% on average) held positions adjacent to or beneath this natural overhead cover, or in other shaded positions, suggesting that steelhead selected positions with light below some threshold.

Facchin and Slaney (1977) found significant positive correlations between steelhead parr density and various size classes of boulders (>30 cm in diameter) in riffles of another Fraser River tributary nearby. They observed parr using positions downstream from boulders in turbulent water of riffles and the upstream portions of runs and surmised that the fish were selecting locations that afforded velocity refuges and overhead cover. Like Shirvell (1990), I suspect that complex structure provides different functions under different circumstances. For example, based on Facchin and Slaney's (1977) results, steelhead parr might have used the velocity refuge or visual isolation features of structures that lacked overhead cover (i.e., VR and VR + VI) more had they been placed in riffles, whereas in runs with little surface turbulence the overhead cover feature was most important. Surface turbulence was, at most, moderate and varied relatively little among structures, which may be the reason that it accounted for little variation in structure use by steelhead.

Neither day of experiment nor time of day noticeably affected fish use of structures. Numbers of steelhead and coho using permanent ALL structures in control plots were unchanged during both experiments, and replicate counts of steelhead in a few plots revealed little change between about 09:00 and 16:00. Numbers of steelhead and coho in plots also changed little before and after structures were placed, indicating that few fish were attracted into plots by the structures. These observations suggest that results were not an artifact of gradual acclimation to structures or of diurnally shifting preferences of fish for structures.

Coho Fry

In contrast with steelhead parr, only a small proportion of the age-0 coho in the plots used any structure (4% in both experiments). Those that did selected the three treatments that provided velocity refuge (i.e., VR, VR + VI, and ALL) significantly more often than the one with overhead cover alone (Fig. 5), and most used the velocity refuge feature of structures they occupied (Fig. 6). Shirvell (1990) also concluded that coho fry of similar size, and studied during the same months, selected positions primarily based on low velocity, regardless of whether this required moving to deeper or shallower positions when stream flow was purposely manipulated. Mundie (1969) found that simple current deflectors greatly increased the number of coho fry that remained in an experimental outdoor channel with swift ambient velocity, compared with two channels without deflectors that had swift or slow average velocity. Together, these results suggest that velocity refuges are the most important feature selected by age-0 coho during early summer.

Much of the reason that so few age-0 coho, which averaged about 60 mm TL, used structures may be that velocity refuges and visual isolation were generally plentiful in the cobble and large gravel substrate that was abundant in most plots. In addition to coho that defended velocity refuges near the stream bed in regions of the plot with faster velocity, there were many other "floaters" (Puckett and Dill 1985) that milled about in the water column in regions with slower velocity, regardless of their proximity to structures or other natural cover. Mundie (1969) proposed that in swift velocities where invertebrate drift is unidirectional, larger coho defend individual positions whereas in lower velocities, coho live in loose aggregations and scramble for food, as has been observed by others (cf. Fausch and White 1986; C.S. Shirvell, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, personal communication).

Differences reported here in microhabitat selected by coho fry and steelhead parr are supported by the findings of other investigators (e.g. Hartman 1965; Bisson et al. 1988). Bisson et al. (1988) proposed that these differences were related to body and fin morphology, coho being better adapted to hold low-velocity positions and steelhead better adapted for swifter currents. However, coho also undergo ontogenetic and seasonal shifts in habitat use, and so may have used structures more had experiments been conducted at another time. For example, complex structure that provides overhead cover, velocity refuge, and visual isolation has been shown to be important for coho during winter (Bustard and Narver 1975), especially during freshets (Tschaplinski and Hartman 1983; Swales et al. 1986; McMahon and Hartman 1989), and during the spring seaward migration as smolts (McMahon and Holtby 1992).

Implications for Management and Further Research

The results reported here will be useful for fishery biologists throughout the Pacific Northwest who attempt to enhance hab-

itat for steelhead parr (e.g., Ward and Slaney 1979, 1981). Some may argue that use of certain microhabitat features by steelhead during early summer does not substantiate their importance for survival because bottlenecks that limit populations may occur during other seasons, especially winter (Bustard and Narver 1975). However, while this may be true, it is unlikely that microhabitat requirements during summer are generally unimportant to stream salmonids. Instead, the two are probably linked to varying degrees in different populations. For example, survival of juvenile salmonids that overwinter in streams may strongly depend on body growth during the previous summer, as Hunt (1969) found for brook trout (*Salvelinus fontinalis*) in Lawrence Creek, Wisconsin. Similarly, ocean survival of anadromous salmonids has been shown to increase with body weight at smolting (Bilton et al. 1982; Ward et al. 1989). Thus, survival, and ultimately fitness, may be closely related to body growth during summer, which in turn depends on quality of foraging positions, constraints of the dominance hierarchy, and trade-offs with predation risk.

Observational data on microhabitat use of stream salmonids are prevalent in the literature (e.g., Murphy et al. 1989; Heggenes et al. 1991a, 1991b). These data are widely used to construct models for predicting how man's perturbations of flow and channel structure affect the amount of suitable habitat for fish and, by inference, fish abundance (Bovee 1986; Fausch et al. 1988). However, unanticipated correlations and interactions among variables may render models based on observations alone misleading in many cases and ultimately produce poor predictions of how stream salmonids will respond to perturbations. Although such observations have provided empirical evidence suggesting which microhabitat features are important to stream salmonids, these data should now be used to generate critical hypotheses for experimentation, preferably in the field. We have much to learn from replicated field manipulations of habitat features, even based on simple experiments like those described here (see also Angermeier and Karr 1984). Such field experiments, and others in more controlled environments where investigators focus on closely simulating the natural environment (e.g., McMahon and Hartman 1989), hold promise for elucidating mechanisms of habitat selection by stream salmonids on which sound management of lotic ecosystems can be based.

Acknowledgments

Tyson Bull provided able field and laboratory assistance for the project, which was done while the author was on sabbatical leave in Resource Ecology and the Departments of Zoology and Forest Sciences at the University of British Columbia. I thank Bruce Ward and Tom Northcote for securing funding, providing equipment and advice, and making my sabbatical and this research possible. Peter Larkin, Pat Slaney, Geoff Scudder, Gordon Smith, and Lynne Bonner also gave advice or assisted with funding. I am grateful to J. Neufeld and B. Morris for kindly allowing access to study sites through their land. Gary White and Ken Burnham provided statistical advice, and Cole Shirvell, Tom Northcote, Nick Hughes, Bruce Ward, Jim Grant, Chas Gowan, and an anonymous reviewer made helpful suggestions that substantially improved the paper. This research was funded by the Habitat Conservation Fund of the British Columbia Ministry of Environment, Fish and Wildlife Branch.

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