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Summer Habitat Utilization and Ecology of Cutthroat Trout Fry (*Salmo clarki*) in Cascade Mountain Streams[1]

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Emergent cutthroat trout fry (*Salmo clarki*) were observed in the margins, backwaters, and side channels, collectively called "lateral habitats," of three study streams with different riparian vegetation. Most fry remained in these lateral habitats until the end of their first summer. The abundance of cutthroat fry was proportional to the area of lateral habitat in each of the study streams. Average size and growth rate of fry were related to the effect of site elevation on stream temperature and the influence of riparian vegetation on the availability of invertebrate food. Lateral habitats are characterized by slow, shallow-water, abundant detritus and benthic invertebrate assemblages of high density. Stream margins and backwaters provide gradients of depth and velocity, cover, and access to food that are appropriate to the habitat requirements of fry. Because fry populations are closely related to the abundance and quality of lateral habitats in small streams, these habitats should be included in the assessment of habitat requirements of cutthroat trout.

Des alevins émergents de la truite fardée (*Salmo clarki*) ont été observés sur les bords, dans les remous ainsi que dans les chenaux latéraux, collectivement désignés sous le terme « habitats latéraux », de trois cours d'eau d'étude à végétation riveraine différente. La plupart des alevins restent dans ces habitats latéraux jusqu'à la fin de leur premier été. L'abondance d'alevins est proportionnelle à la superficie d'habitats latéraux dans chacun des cours d'eau étudiés. La taille et le taux de croissance moyens des alevins montrent un rapport avec l'effet de l'altitude sur la température de l'eau et l'influence de la végétation riveraine sur la disponibilité des invertébrés dont se nourrissent les alevins. Les habitats latéraux sont caractérisés par un écoulement lent, une eau peu profonde, des détritus en abondance et des communautés d'invertébrés benthiques en forte densité. Les remous et les bords des cours d'eau offrent gradients de profondeur et de vitesse du courant, couverture et accès aux aliments qui, tous, répondent aux nécessités de l'alevin en termes d'habitat. Puisque les populations d'alevins sont en étroite relation avec l'abondance et la qualité des habitats latéraux des petits cours d'eau, ces habitats devraient être considérés dans l'évaluation des nécessités en termes d'habitat chez la truite fardée.

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Young-of-the-year cutthroat trout (*Salmo clarki*) are conspicuous inhabitants of slow-water areas near the margins of streams in the Cascade Mountains of Oregon. Low-velocity habitats at the sides of the channel are important geomorphic features of headwater streams that retain nutritional resources and support dense populations of aquatic invertebrates. These lateral habitats are characterized by low-velocity heterogeneous substrate, abundant detritus, and structural protection from high stream discharge, a combination of morphological and hydraulic features that is unique among habitats in mountain streams.

Lateral habitats are important in the early life history of many stream fish, particularly salmonids. Lateral habitats are occupied by the fry of brook trout (*Salvelinus fontinalis*), rainbow trout (*Salmo gairdneri*), and Atlantic salmon (*Salmo salar*) (Keenleyside 1962; Symons and Heland 1978; Reiser and Bjornn 1979), coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) (Lister and Genoe 1970; Everest and Chapman 1972), and cutthroat trout (Bustard and Narver 1975; Aho 1977). These studies have reported the occurrence of salmonid fry in slow water along the margins of stream channels, but none has examined the physical characteristics of lateral habitats or the extent to which they are utilized by fry.

Lateral habitats have not been considered in geomorphic and fisheries classification of stream habitat structure. Stream sections have been classified on the basis of fluvial influences that form predictable sequences of main channel features such as pools and riffles (Keller and Melhorn 1978; Lisle 1986). Geomorphic studies of streams have emphasized main channel habitats that are larger than average stream width (Leopold et al. 1964; Richards 1976) and this level of resolution has been defined as the "channel unit" (Grant 1986). Lateral habitats are a subset of habitats defined at the channel unit scale, are smaller than average channel width, and generally have not been included in studies of geomorphology or fish habitat in streams. Fisheries research has focused on main channel habitats because of the biological significance of pools and riffles as fish habitat and for production of aquatic invertebrates (Chapman and Bjornn 1969; Mundie 1974; Binns and Eiserman 1979). Exclusive consideration of habitat features at the channel unit scale, however, is not sensitive to the habitat requirements of all life

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[1] Technical paper No. 8534 of the Oregon Agricultural Experiment Station.

TABLE 1. Physical characteristics of the study streams. Area and relative distribution of habitats in 100-m sections of the study reaches. Habitat area does not include exposed boulders or midchannel structures.

	Study stream		
	Mack	Quartz	Grasshopper
Riparian setting	Coniferous	Deciduous	Open
Drainage area (km^2)	5.4	9.7	7.6
Elevation (m)	805	515	880
Channel gradient (%)	10.0	5.3	10.0
Aspect	NNW	SSW	NNE
Stream area (m^2)	315	364	371
Pool area (m^2)	67	124	103
Percent pool	21	34	28
Riffle area (m^2)	193	161	194
Percent riffle	62	44	52
Lateral habitat area (m^2)	55	79	74
Percent lateral habitat	17	22	20

history stages of stream fish or appropriate for considering changes in habitat use in response to fluctuations in streamflow. Several studies, for example, have demonstrated the importance of lateral and off-channel areas as rearing and winter habitat for stream fish (e.g. Bustard and Narver 1975; Bisson et al. 1982; Sedell et al. 1982; Hartman and Brown 1987).

The effect of riparian vegetation on fish populations in streams of the Pacific Northwest has been studied by Aho (1977), Murphy and Hall (1981), and Hawkins et al. (1983) and the influence of riparian setting on pool habitat, prey availability, and trout growth was examined by Wilzbach (1985). Greater density and biomass of cutthroat trout was found in open stream reaches, a difference attributed to the effects of increased light on primary production, food availability, and foraging efficiency. These studies generally focused on age 1+ and older fish and main channel habitats. Patterns of habitat use by cutthroat fry and the effects of riparian setting on fry habitats have not been identified.

The objectives of this study were to examine the linkage between cutthroat fry populations and lateral habitats and to determine how habitat utilization and fry behavior change from the time of emergence to the beginning of high streamflow in fall. This study also examined the physical characteristics and nutritional resources of lateral habitats and the possible influences of riparian vegetation on habitat quality, fry growth, and fry population density.

Methods

Study Sites

We investigated the ecology of cutthroat trout fry in third-order streams in or near the H. J. Andrews Experimental Forest in the Cascade Mountains of Oregon. The utilization of lateral habitats by cutthroat trout and the morphology of stream edges were studied in 100-m sections of three streams in different riparian types: a 450-yr-old coniferous stand, a 40-yr-old alder-dominated (*Alnus rubra*) deciduous stand, and an open, herb-, and shrub-dominated site that had been clearcut logged. Study sites were selected at streams with different riparian settings but with similar geomorphic and basin characteristics (Table 1). Cutthroat trout was the only species of fish in the study reaches.

At Mack Creek, the coniferous site, riparian vegetation was dominated by old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Quartz Creek, the deciduous site, was logged during the 1940's and red alder has formed a partial canopy over the stream channel. Grasshopper Creek, the open site, was clearcut in 1977 and riparian vegetation was dominated by herbs such as colts-foot (*Petasites frigidus*) and fireweed (*Epilobium angustifolium*) and shrubs such as willow (*Salix sitchensis*).

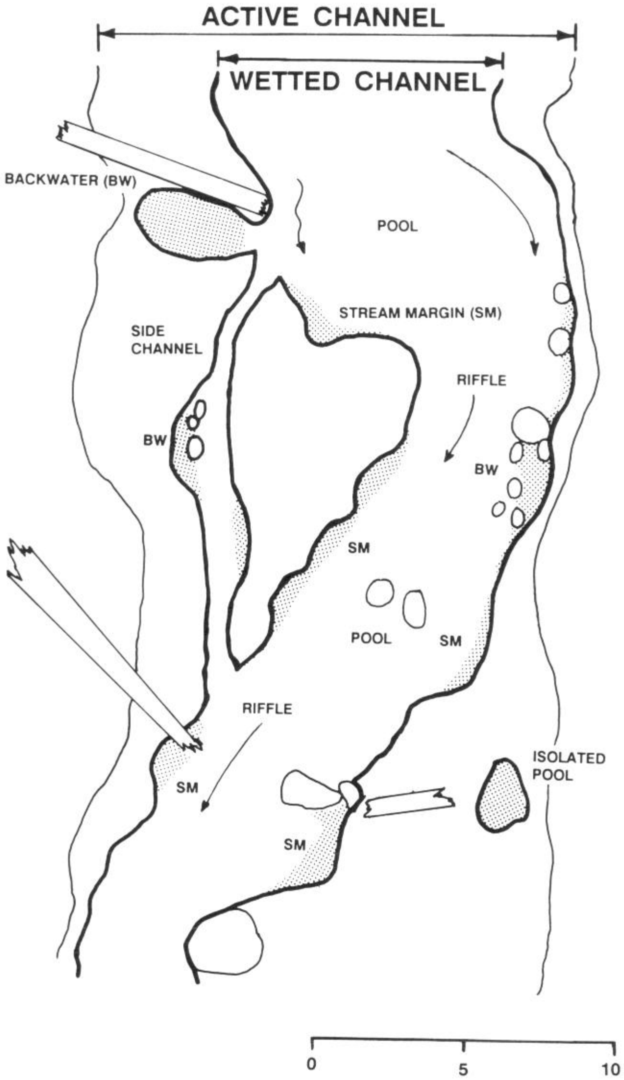

FIG. 1. Habitat structure of a hypothetical stream reach. Lateral habitats are shaded.

Stream channel habitat, hydraulics, and substrate were mapped at each site during July and August 1982. Mapping began by constructing a string grid over the active channel surface. The grid was marked at 1-m intervals and used to align a frame of PVC tubing that was placed on the stream bed. Within each square metre delineated by the frame, habitat and hydraulic class, large woody debris, and substrate size distribution were recorded. During the summer of 1983, the distribution of habitats was reevaluated and the availability of substrates and fish cover within lateral habitats was mapped.

The stream at the coniferous site was located in a smaller drainage and had less surface area in the 100-m reach than the streams at either the deciduous or open sites (Table 1). The stream at the coniferous site also had the smallest total area in pool and lateral habitats. Habitat composition of the study reaches was relatively constant from June to October in both

1982 and 1983 (Moore 1987). Coarse woody debris derived from riparian vegetation is a major geomorphic feature in the forested reaches influencing channel structure and creating debris dams. Coarse woody debris was most abundant and evenly distributed at the coniferous site. Remnant debris from the previous coniferous stand was also abundant at the deciduous site. Coarse woody debris was largley absent from the stream channel in the open site, a result of stream cleaning after timber harvest.

Midchannel stream temperature was continuously monitored at each site by recording thermographs. Water temperature and oxygen concentration were measured in 20 lateral habitats at each site after each census of fry populations. Oxygen concentration was measured with a YSI portable oxygen meter calibrated to oxygen saturation for the elevation and temperature of each site.

Stream Habitat Definitions

Because lateral habitats have not been rigorously defined, we developed a classification system based on structural properties of lateral habitats observed in the streams of the Cascade Mountain Range. Lateral habitats are distinguished according to morphology, hydraulics, and orientation to the main channel and classified as stream margins, backwaters, and isolated pools (Fig. 1).

Stream margin habitats are defined as areas of shallow water and slow current along the stream edge without structural separation from the main channel. In stream margins, the long axis of the habitat feature is generally parallel to the main flow. Structures such as boulders and woody debris that deflect flow away from the bank can create abrupt transitions in velocity between stream margins and the main channel. In the study streams, we delineated stream margins as lateral habitats with current velocity less than 4 cm/s and depth less than 20 cm. This combination of depth and velocity coincided with velocity transitions that frequently occur between stream margins and riffles in third-order streams in the Cascade Mountains. This depth was also used arbitrarily to distinguish between stream margin habitat and slow-water areas in adjacent main channel pools. Although stream margins were not physically separated from the main channel, hydrologic exchange between stream margins and the main flow was limited. The movement of water within stream margins may be either an eddy or parallel flow in the main channel.

Backwaters are areas of slowly moving water that are further removed from the influence of the main channel than are stream margins. Backwaters may be isolated pools (off-channel backwaters), or pools connected to the main flow through gaps in the boulders and/or wood that form the habitat. The limited connection to the main flow distinguishes backwaters from stream margins. In backwaters, the opening to the main flow is narrower than the long axis of the habitat. Depth in backwaters and isolated pools may exceed 20 cm. Large boulders and woody debris are the primary structural elements of off-channel backwaters. At high streamflow, most off-channel backwaters become connected to the main channel.

Stream margin and backwater habitats have been described as alcoves, eddys, drop zones, edge pockets, and off-channel pools (Salli 1974; Keller and Swanson 1979; Cummins et al. 1980; Swanson and Lienkaemper 1981; Sedell et al. 1984). We use the term lateral habitat to describe all of these habitat types and the terms stream margin, backwater, and isolated pool to distinguish among each type. Because they are defined in the context of both structure and hydrology, the specific location of some lateral habitats within the active channel may change because of variation in channel hydraulics at different discharges.

TABLE 2. Number of fry observed in 100-m reaches of each riparian site in 1983.

Census interval	Coniferous	Deciduous	Open
June 23	—	16	—
June 26–30	49	67	—
July 7–14	60	24	14
July 22–Aug. 4	42	21	78
Aug. 11–13	—[a]	41	47
Aug. 31–Sept. 3	36	53	46
Oct. 6–8	23	73	69

[a] No census at the coniferous site during this interval.

Observations of Trout Fry

Habitat use, behavior, and population density of cutthroat fry were evaluated by bank survey and underwater observation from June to October 1983. Fry closest to the edge were more effectively observed by bank surveys. Crawling upstream along the bank, looking for fry between and beneath cobbles, was most efficient for observing young fry immediately after emergence and in areas where stream geometry precluded entry of a diver. Fry in pools, riffles, and shallow water near the stream edge were also observed by snorkeling. This approach was more efficient when the diver could look upstream from the lower end of a pool with an unrestricted view of the entire stream width. Fry quickly adjusted to the presence of a diver and usually resumed feeding activity within 30 s from the time the diver entered the stream segment or habitat unit.

Observations of fry distribution were initated when fry started to emerge from the substrate and continued at 2- or 3-wk intervals through the summer growth period. Snorkeling or bank observations were made of all habitats in each reach. Because fry were observed repeatedly throughout the summer, only nondestructive techniques were used to evaluate population size and habitat utilization. Marking or tagging was not used because fry were very small (20–25 mm) and easily injured at the start of the study period. Because no marking was used, mortality, immigration, and emigration of fry in the study reaches could not be measured directly.

Physical characteristics of the habitat were measured where each fish was first observed. If the fish was not disturbed, its position was assumed to be the focal point. The focal point is the position most frequently occupied by an individual fish and is generally the locus of feeding behavior. Velocity was measured with a Montedoro Whitney (folded magnetic field) current meter. Habitat type, stream depth, distance to the nearest stream edge, distance to nearest cover, cover type, and substrate size distribution were also recorded. Use of cover and substrate was determined by direct observation of fry where they maintained focal feeding positions.

At each observation interval, a team of a diver and bank observer worked upstream from the lower end of the reach and attempted to capture each fry they encountered. Fry were captured by slowly moving a small dip net in front of the fish and then placing a meter stick behind the fry and moving closer until the fry was startled and swam forward into the net. This method worked equally well for both diver and bank observer;

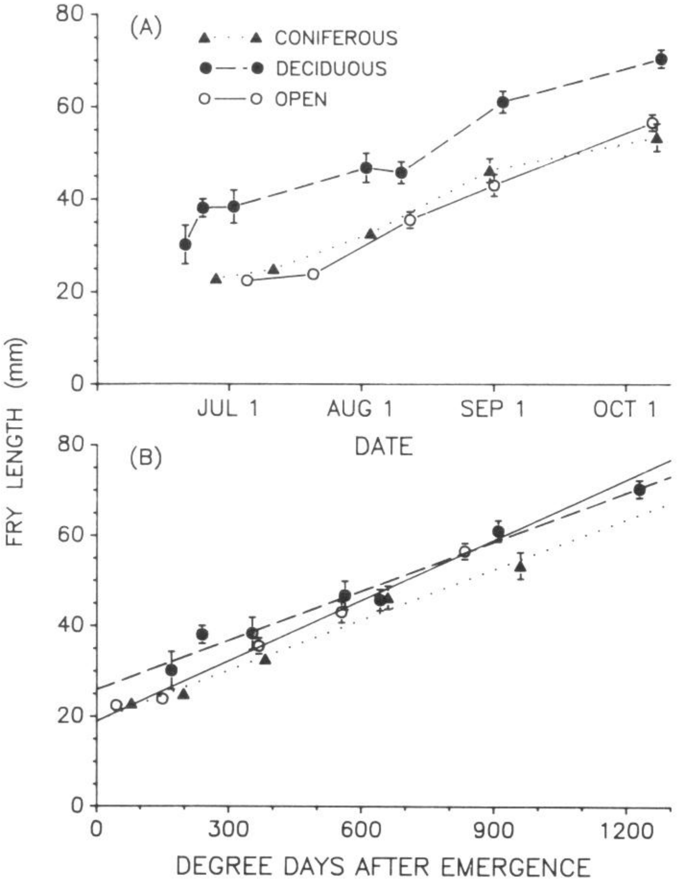

FIG. 2. (A) Fry length from June to October 1983 in the coniferous, deciduous, and open reaches. (B) Fry length versus accumulation of temperature degree days in the riparian study reaches. Coniferous reach fry length $y = 0.037x + 19.0$, $r^2 = 0.982$; deciduous reach $y = 0.036x + 25.8$, $r^2 = 0.972$; open reach $y = 0.045x + 18.8$, $r^2 = 0.980$. Bars are 95% C.I.

95% of capture attempts were successful when the fry first emerged, but capture efficiency decreased to only 70% as the fish grew larger near the end of the study period. After capture, each fry was measured quickly for total length and then returned to the stream at the position where it was first observed. Released fish usually swam to cover in the substrate. We attempted to capture all fry in each habitat unit, but if a fish was not captured, its length was estimated by comparing its size with an adjacent particle in the substrate and then measuring the length of the particle with a small ruler taped to the dip net. Because of the progressive upstream movement of the observation team and the behavior of released fish, it was unlikely that a fish would be counted more than once during each census.

A final census of fry was conducted for all habitats in each reach at the end of the summer season using a combination of electrofishing and snorkeling. Fish were collected by electroshocking, sorted by habitat, and held in buckets until they could be weighed and measured. Any fry not captured by electrofishing were then censused by snorkeling and collected by hand netting.

Benthic invertebrates were sampled from backwaters and stream margins to evaluate the potential for food production at each site. Invertebrates were collected from 10 lateral habitats at each site using a modified Hess sampler with a 250-μm mesh. All samples were processed using a dissecting microscope at 50× magnification. A small sample ($N = 36$) of fry was collected from reaches downstream from the intensive study sections for analysis of gut contents. Fry were collected when they were first observed after emergence, in midsummer, and at the end of summer when they began to occupy different habitats. Each fish was captured with a dip net and immediately preserved in 90% ethanol solution for later dissection and identification of prey items.

TABLE 3. Cutthroat trout fry density in 100-m riparian study reaches in summer (1983). Average number of fry after emergence was complete excluding July 14 and Aug. 3 data from the deciduous reach because of poor conditions for observation. Coniferous, $n = 5$; deciduous and open, $n = 4$.

Site	Reach (fry/100m)	Reach area (fry/m^2)	Lateral habitat area (fry/m^2)
Coniferous	42.0	0.13	0.76
Deciduous	58.5	0.16	0.74
Open	60.0	0.16	0.81

Results

Fry Populations in the Riparian Study Reaches

Immediately after emerging, fry established territories in lateral habitats that were maintained until the end of summer. The density of fry in each reach was generally highest in early summer after emergence was complete (Table 2). The ability to observe fry varied with weather conditions. For example, overcast and light rain on July 14 and August 3 at the deciduous reach created unfavorable conditions for observation, and comparatively few fry were censused. The combination of electrofishing and visual counts employed in the October census was probably the most efficient method of counting fry. More fry were counted at this census in the deciduous and open reaches than in the preceding census (increases of 38 and 50%, respectively). The reason for the low number of fish captured at the coniferous site could not be determined.

Cutthroat trout fry emerged earliest at the deciduous site, starting by June 1. The first fry at the coniferous site appeared about 3 wk later. Fry at the open reach began emerging about 1 mo after fry in the deciduous reach. Emergence continued for 1–3 wk after the first fry were observed in each stream. The sequence of emergence corresponded to differences in stream temperature during the time trout eggs were developing in the gravel. During the development of trout eggs, average stream temperature was about 5°C warmer at the deciduous site than at the open site and about 3°C warmer than at the coniferous site.

Fry Growth

From June to October, the length of cutthroat fry in the study streams increased threefold and weight increased more than 30-fold. Fry in the deciduous reach emerged earlier and maintained greater average length than fry in the coniferous and open reaches (Fig. 2A). Fry in the open reach had the smallest average length for most of the summer. However, relative to temperature, the greatest rate of increase in fry length was at the open reach (Fig. 2B). Growth rate per degree-day, expressed as the slope of the length versus degree-day regression, was greater at the open site than in either forested reach (test of slope difference $p < 0.05$). Differences in temperature between

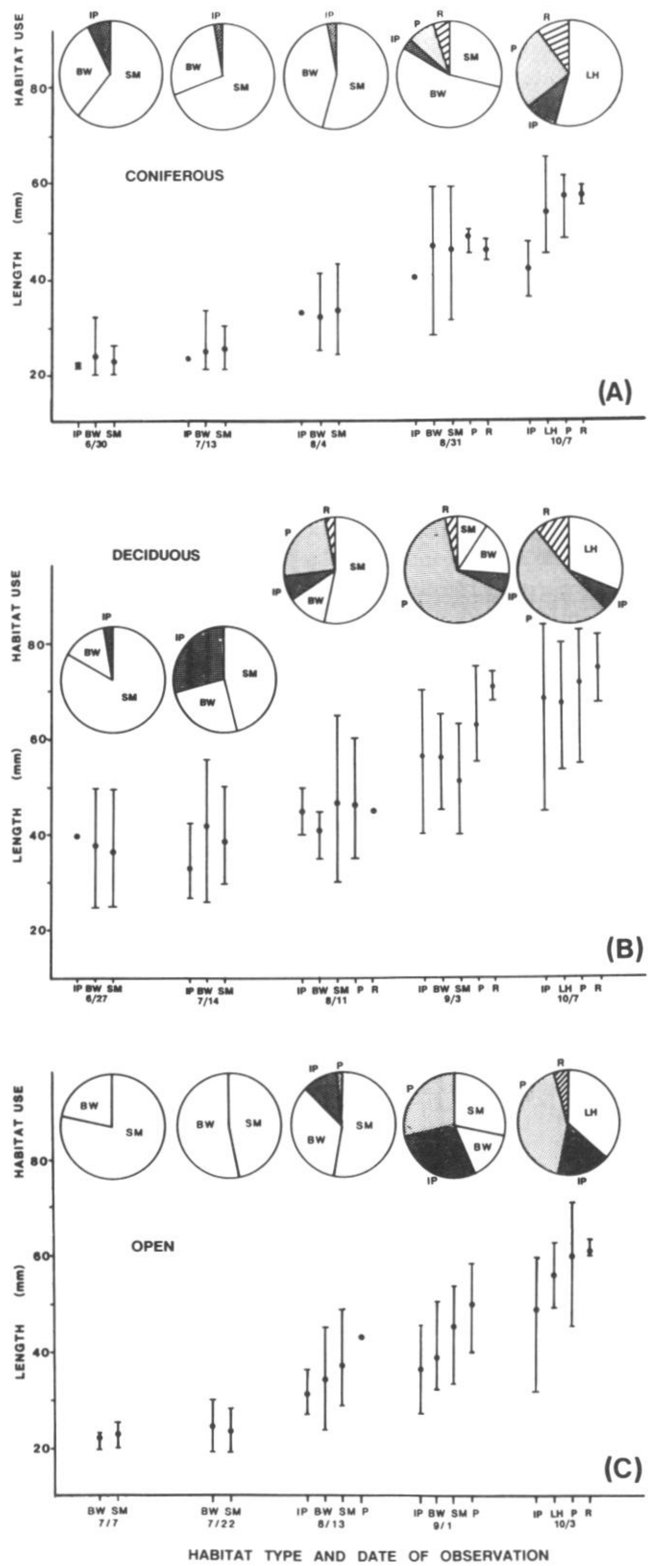

FIG. 3. Changes in habitat use and habitat specific lengths of fry in the (A) coniferous, (B) deciduous, and (C) open reahces. Habitat use expressed as percentage of fry observed in each habitat type. Bars show mean and range of length for each habitat on each date. BW = backwater, IP = isolated pool, SM = stream margin, P = pool, R = riffle, LH = stream margin and backwater combined at final census.

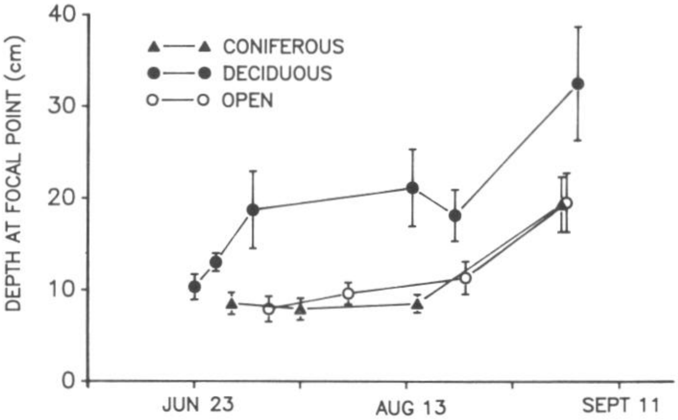

FIG. 4. Stream depth at focal position of fry during June–September 1983 (mean for each site and 95% C.I.).

reaches largely reflected differences in site elevation and were not an influence of shading by the riparian canopy. The sum of mean daily temperature (degree-days) from the time of emergence to final sample was much higher at the deciduous site (1223 degree-days) than at either the coniferous (957 degree-days) or open (831 degree-days) reaches.

Fish condition factor ($K = W/L^3 \times 10^5$) was greater at the deciduous reach than at either the coniferous or open reaches (deciduous>coniferous or open, $p<0.05$, Kruskal–Wallis). Average condition factor was 1.09 at the deciduous site, 0.97 at the coniferous site, and 0.98 at the open site. At the end of summer, total biomass of fry was 0.91 g/m^2 at the deciduous reach, 0.13 g/m^2 at the coniferous reach, and 0.39 g/m^2 at the open reach.

Habitat Utilization

The abundance of fry in each reach was proportional to the area of lateral habitat. The deciduous and open reaches had approximately 30% more lateral habitat and averaged 29% more trout fry than the coniferous reach (Table 3). Fry established territories in lateral habitats that provided visual or spatial distance from other fry. In stream margins, over 85% of the fry occurred as single individuals within a habitat unit. In cases where two or more fry occupied the same stream margin, cobbles and woody debris created complexity and visual isolation within the habitat. In some backwaters, especially off-channel backwaters that physically prevented emigration, fry often occurred in groups. Less than 40% of the fry in off-channel backwaters occurred as single individuals, and as many as 10 fry were observed in one backwater.

All fry occupied lateral habitats exclusively for at least 1 mo after emergence (Fig. 3). The sequence of habitat utilization was the same in each reach. Immediately following emergence, about 65% of the fry were in stream margins, 30% in backwaters, and 5% or less in isolated pools. Fry did not move from these habitats for about 6 wk, but the characteristics of their habitats changed. As discharge decreased during the summer, some stream margins became backwaters, and some backwaters became isolated pools. As a result of lower stream levels, the proportion of backwaters and isolated pools increased relative to total lateral habitat. Because the fry did not move from their initial habitats, the number of fish observed in backwaters and isolated pools increased to about 50% of the total. Fry were not moving from stream margins to backwaters and isolated

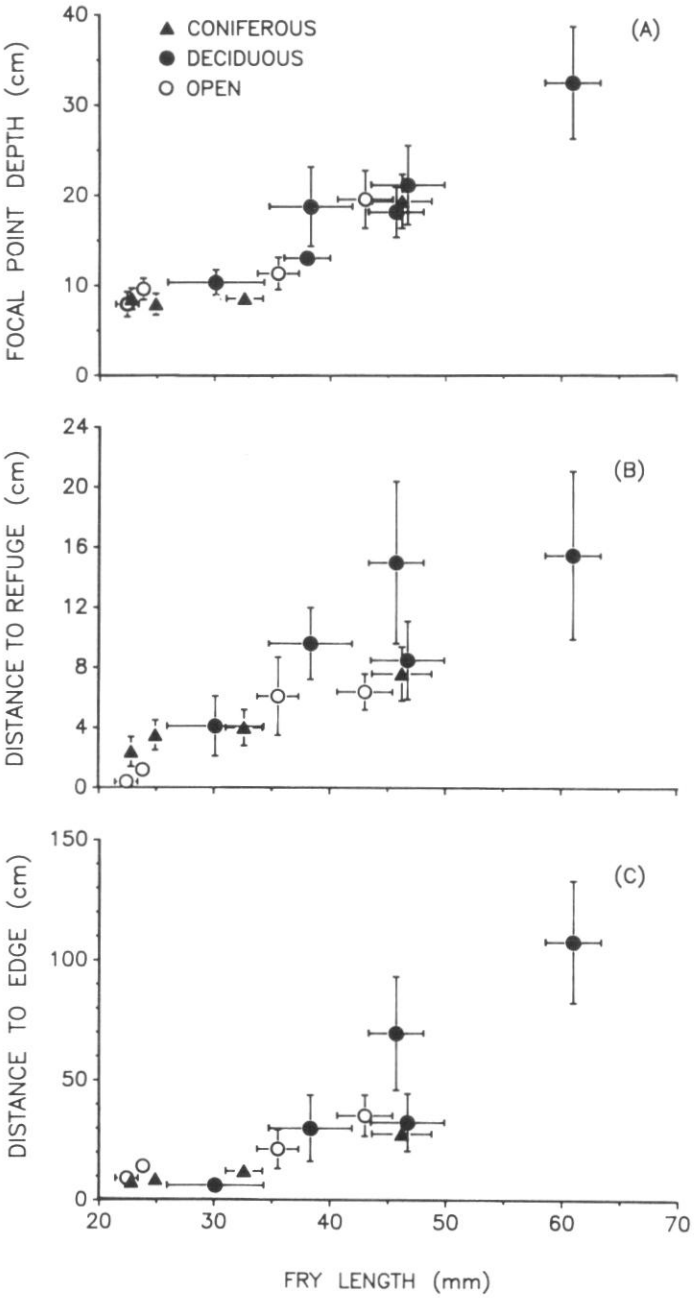

FIG. 5. Changes in (A) focal point depth, (B) distance to refuge, and (C) distance to stream edge associated with increasing length of fry (mean for each site and 95% C.I.).

pools, but rather the stream margins occupied by trout became backwaters and isolated pools as flows decreased.

In late summer, stream discharge was at its lowest level and the contrast between lateral habitat velocity and pool velocity was at its minimum. During this time, some of the larger fry in the stream margins moved to pools. As a result, the proportion of fry in stream margins decreased. Fry in backwaters were less likely to move, and fry in isolated pools could not move to other habitats. The average length of fry was not significantly different among habitat types in the forested reaches (ANOVA, $p > 0.05$), and mortality due to drying of lateral habitats was not observed. In the open reach, fry in isolated pools and backwaters were significantly shorter than fry in other habitats (ANOVA, $p < 0.01$), and some fry were stranded in isolated pools that had become dry.

In October, 65% of the fry remained in lateral habitats at the coniferous reach and 53% remained in lateral habitats at the open site, but only 38% of the fry population were found in lateral habitats at the deciduous reach. Smaller fish stayed closer to the edge in lateral habitats, and the largest fry were most likely to migrate to pools and riffles. Fry at the deciduous reach were larger than in the open or coniferous reaches, and as a result, a larger proportion of the fry population at the deciduous reach moved from lateral habitats to pools and riffles at the end of summer than in the open or coniferous sites.

Fry Behavior and Changes in Focal Point Parameters

Most fry remained in lateral habitats until they were at least 50 mm long, but fry often moved to areas of faster, deeper water within lateral habitats as they grew. Focal point velocity, depth, and distance from the edge increased gradually until fry began to move out of lateral habitats into pools and riffles. With the shift in habitat utilization, focal point parameters increased abruptly. When fry moved from lateral habitats to pools and riffles the average focal point velocity, depth, and distance from the edge increased at least twofold.

Newly emerged fry exhibited swimming behavior (regular tail movements and rheotaxis) at velocities too low to be measured with the current meter (velocity less than 1 cm/s). Fry were obviously responding to velocity differences within lateral habitats, but the velocities were either too low to be measured or occurred in areas that were too small to place the probe of the current meter.

Only fry 30 mm and longer were observed at velocities greater than 1 cm/s. The average focal point velocity never exceeded 2 cm/s in any reach. Many fry, regardless of length, remained in slow water. Fry that moved out of lateral habitats to faster water (>5 cm/s) were generally longer than 55 mm. Only about 35% of the total number of fry were observed at velocities greater than 1 cm/s, and no fry were observed at velocities greater than 15 cm/s.

Fry maintained focal points near, but not on, the stream bottom in areas of shallow water. Fry were first observed in shallow water between 6 and 12 cm deep. Fry moved to deeper water as they grew, but most fry remained in water less than 20 cm deep for at least 6 wk after emergence (Fig. 4). Average focal depth increased rapidly from mid-August to early September, especially at the deciduous reach, but the average depth was always less than 35 cm. Focal point depth was positively correlated with fry length at each site (average depth (cm) $= 0.59 \times$ average length (mm) $- 6.86$, $p<0.025$, $r^2=0.906$, $n=13$; Fig. 5A). Exceptions to the general pattern of fry length and focal point depth occurred when some of the larger fry remained in shallow water. Many larger fry remained at depths less than 40 cm, but only fry longer than 50 mm were found at depths greater than 40 cm.

Fry usually had a retreat or refuge for avoiding capture. When disturbed, fry moved to crevices in substrates or beneath overhanging boulders and wood. Unless they were further disturbed, fry usually returned to their original focal position within 1 min. Refuges were located within 1–50 cm of the focal point. Newly emerged fry stayed within 5 cm of cover. Distance to cover increased as fry grew, but average distance to cover never exceeded 8 cm at the coniferous and open reaches or 16 cm at the deciduous reach (Fig. 5B). Interstices of cobble and rubble substrate were used as refuges by 30–42% of the fry. Larger substrates and roughness features that formed

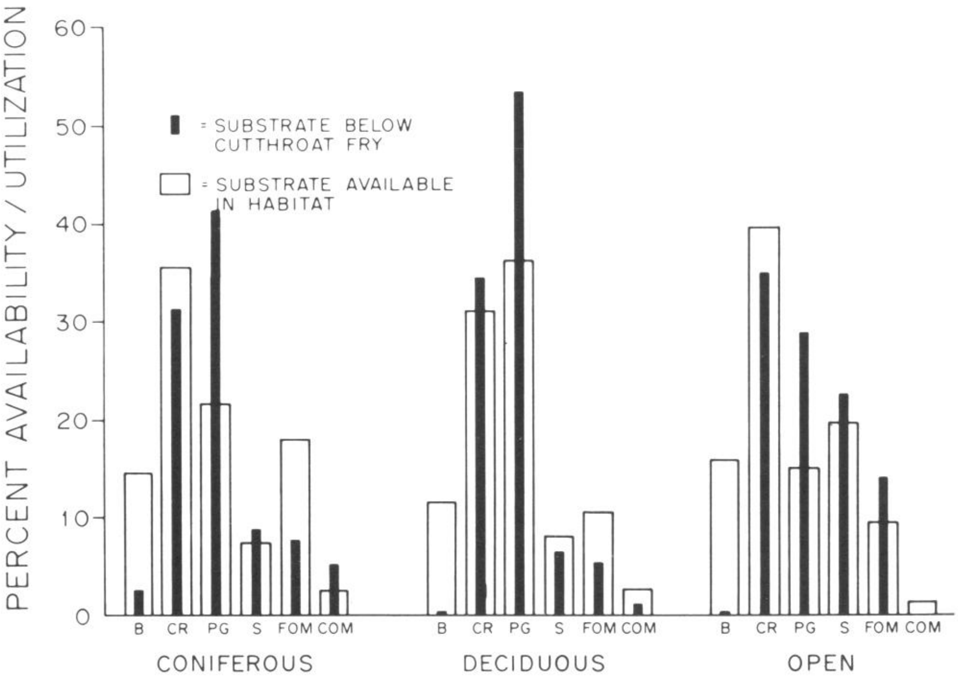

FIG. 6. Substrate composition of lateral habitats and substrate utilization by fry in each of the riparian reaches. B = bedrock, CR = cobble-rubble, PG = pebble-gravel, S = sand, FOM = fine particulate organic matter, COM = coarse particulate organic matter.

TABLE 4. Substrate composition of the wetted channel (WC) and lateral habitats (LH) in summer (percent in each size class). Substrate size classes were sand–FOM (<0.1 cm in diameter), pebble–gravel (0.1–8 cm), cobble–rubble (8–32 cm), and boulder–bedrock (>32 cm).

	Coniferous		Deciduous		Open	
	WC	LH	WC	LH	WC	LH
Boulder–bedrock	56.5	15.1	52.6	12.4	72.5	15.7
Cobble–rubble	24.7	36.2	18.5	31.7	13.3	41.2
Pebble–gravel	11.3	22.3	25.3	36.1	10.4	15.0
Sand–FOM	7.5	26.4	3.6	19.8	3.8	28.1

boundaries of lateral habitat were also frequently used. About 25% of the fry used refuges beneath boulders and 18% escaped beneath large wood debris.

Newly emerged fry were observed within 15 cm of the stream edge at each riparian site. The distance from the focal point to the shoreline increased slowly for most of the summer then increased rapidly when fry began to move to main channel habitats. The increase in distance to the edge was related to increased fry length (Fig. 5C). All fry less than 50 mm long were located within 80 cm of the edge. Conversely, more than 80% of fry 60 mm and longer were located at least 1 m from the nearest stream edge.

Substrate Utilization

Within lateral habitats, cutthroat trout fry were most likely to maintain a focal point that was above heterogeneous substrate. At least 65% of the fry in each stream were observed over mixtures of cobble, rubble, pebbles, and gravel (Fig. 6). Fry were rarely seen in proximity to smooth, homogeneous substrates, such as boulder surfaces or uniform patches of sand or fine particulate organic matter. The extent of selection for substrate size classes within lateral habitats can be compared based on substrate utilization and substrate availability. This was measured by a modification of Ivlev's (1961) electivity calculation

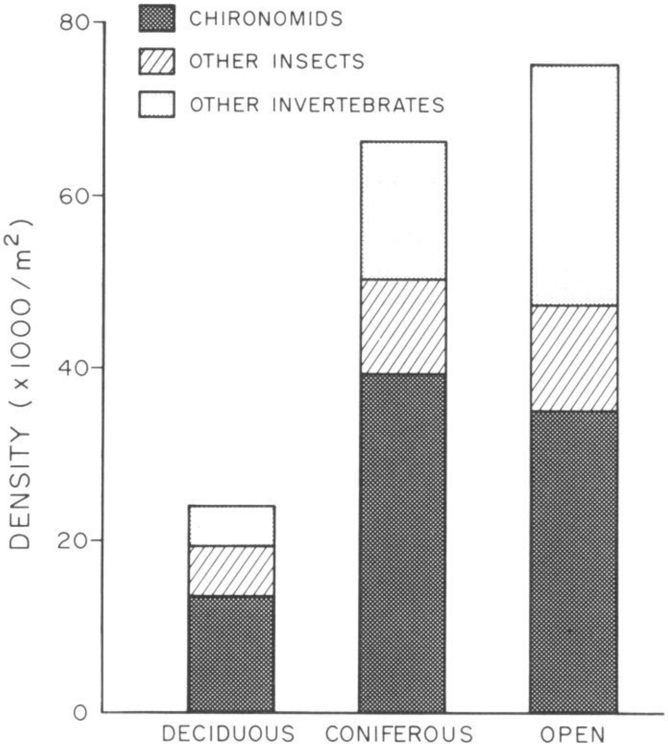

FIG. 7. Abundance of benthic invertebrates in lateral habitats at each of the riparian sites (average of 10 samples at each site collected June 1983).

$$E = (r - p)/(r + p)$$

where E = electivity, r = proportion of use, and p = proportion in environment. Electivity ranges from -1 to $+1$; -1 indicates the strongest negative selection, +1 indicates the strongest positive selection. Electivity for pebble–gravel substrates was 0.32 at the coniferous reach, 0.19 at the deciduous reach, and 0.44 at the open reach. Electivity for pebble–gravel substrates was greater than for any other substrate class. Differences in electivity between the three reach types were related primarily to differences in the availability of pebble–gravel substrates within lateral habitats (Fig. 6). The open site had the largest value for electivity of pebble–gravel substrate, but this value was influenced by the low availability of this substrate class. Pebble–gravel availability was lowest at the open reach and a greater proportion of fry utilized cobble and rubble substrate than pebble–gravel. Electivity for pebble–gravel substrate was low at the deciduous reach because availability and utilization were both high.

Lateral habitats contained a greater percentage of the substrates associated with high electivity than other habitats of the same reach. Compared with the substrate distribution of the entire wetted channel, lateral habitats had more cobble, rubble, pebble, and gravel substrates (Table 4). Boulders were the most abundant substrate in each of the reaches, but in lateral habitats, substrates in the 1.0- to 16.0-cm size range comprised more than 50% of the surface.

Temperature and Dissolved Oxygen

Water temperature in lateral habitats was always within 1.5°C of the temperature observed in the main channel. Midsummer temperature in isolated pools was expected to be warmer than the main channel because of the long hydraulic residence time in off-channel backwaters. However, there were no temperature differences between isolated pools and the main channel at either of the forested reaches, and isolated pools were generally cooler in summer than the main channel at the open reach. The greatest difference in maximum temperature was at the open site where in August, afternoon temperatures in backwaters averaged 14.4°C and the main channel average was 13.5°C. On the same date, isolated pools were 1°C cooler than the main channel.

Dissolved oxygen concentrations were near saturation in stream margins and backwaters throughout the summer (9.0–11.5 mg O_2/L depending on the elevation and water temperature of each site). Isolated pools were significantly lower in dissolved oxygen than other lateral habitats or the main channel (ANOVA, $p<0.05$), but average oxygen concentrations were never lower than 7.5 mg O_2/L. The lowest oxygen concentration recorded (6.1 mg O_2/L) was taken in early fall at the deciduous site in an isolated pool that was filled with decomposing alder leaves.

Benthic Invertebrates and Diet of Fry

Lateral habitats supported benthic invertebrate communities that were characterized by a high abundance of chironomids, microinvertebrates, and other detritivores (Fig. 7). Chironomid density exceeded 50 000 individuals/m^2 in some backwaters and average density for all lateral habitats was nearly 30 000/m^2. Microinvertebrates, predominantly oligochaetes, hydracarinid mites, ostracods, and harpacticoid copepods, had an average density of nearly 20 000/m^2. Macroinvertebrate populations were dominated by collector–gatherer and shredder functional groups. These insects are associated with the abundant detritus stored in lateral habitats (Moore 1987). Collector–gatherers comprised nearly 80% of the total number of invertebrates in lateral habitats. The collector–gatherer group included the abundant chironomids, but even if chironomids were excluded, collector–gatherers represented more than 50% of the remaining total. Although the average invertebrate density in lateral habitats was comparatively lower at the deciduous site than at either the open or coniferous reaches ($p<0.05$, Kruskal–Wallis), this density represents a relatively high abundance, particularly when compared with pool or riffle habitats in the same reach (R. Wildman, Department of Fisheries and Wildlife, Oregon State University, unpubl. data).

Invertebrate assemblages characteristic of lateral habitats comprised an important part of the diet of fry. Chironomid midge larvae were an especially important food of newly emerged fry. In fry less than 30 mm long, 45–100% of the total number of prey items consumed were chironomid larvae. As fry grew, the percentage of chironomid larvae in the diet decreased ($p<0.01$, $r=-0.567$, $n=36$) but they remained an important food item. In fry of all sizes, chironomid larvae occurred in nearly 90% of the stomachs examined. Fry consumed over 30 different prey taxa, but chironomids, ephemeropterans, and ostracods numerically dominated the gut contents, constituting 88% of the total number.

Discussion

Immediately upon emergence from the gravel, cutthroat trout exhibit adaptive behaviors that position the fish in stream habitats appropriate to the size and metabolic capacity of the fry. Stream margins and backwaters are particularly suited to the habitat requirements of cutthroat trout fry, providing appropriate gradients of depth and velocity, cover, and access to invertebrate food. Because fry do not move for several months once they establish territories in lateral habitats, the quality of the habitat is critical for growth and survival.

Many stream salmonids occupy the highest velocity water their swimming ability and the availability of velocity shelter will allow, thereby increasing their exposure to drifitng prey (Chapman and Bjornn 1969; Lister and Genoe 1970; Fausch 1984). The movement of cutthroat fry from areas of slow current in early summer to faster water in pools and riffles at the end of summer is consistent with this concept. The hydraulic properties of lateral habitats create areas of low velocity particularly suited to the requirements of newly emerged fry. Subsequent changes in focal point depth, distance to the edge, and distance to refuge in cutthroat trout fry are related to increased swimming ability with growth.

Riparian Influence on Fry Populations

Riparian vegetation and the effect of site elevation and aspect on water temperature were important influences on cutthroat trout fry populations. Growth rate was highest at the open site, but the average size was greatest at the deciduous reach. Fry at the coniferous site had the smallest average size and poorest condition factor. Productivity of lateral habitats, access to invertebrate prey, and temporal stability of habitat characteristics are all potentially influenced by the effect of riparian vegetation on energy inputs and channel structure (Swanson et al. 1982; Wilzbach et al. 1986; Moore 1987).

The higher growth rate of cutthroat fry at the open reach may have resulted from the effect of increased light on primary production, invertebrate production, and prey capture efficiency. Open sites have a higher standing stock of benthic algae (Lyford and Gregory 1975; Moore 1987) and a greater abundance of herbivorous, multivoltine invertebrates (Grafius 1976; Hawkins et al. 1983). Because of the short generation time of these animals, production relative to standing stock may be greater than at sites with detrital based invertebrate assemblages. The coniferous site also had a high standing stock of invertebrates, however; this food source may be less available to fry because shading by the canopy may reduce the ability of fry to locate and to capture prey. Foraging efficiency of trout was lower in streams in old growth forests than in streams with more open riparian settings (Wilzbach 1985).

Fry at the deciduous reach may have been larger because of the effect of temperature on the timing of emergence and the metabolic efficiency of fry. For rainbow trout, development of eggs to hatching requires 50 d at 7.3°C and 25 d at 12°C (Bardach et al. 1972). If cutthroat trout eggs develop at a similar rate, eggs spawned at the same time would hatch 2–3 wk earlier at the deciduous reach than in the other reaches. This interval corresponds to the sequence of initial observations of fry in each of the reaches. In a similar manner, the increased stream temperature associated with an open canopy has accelerated the development of eggs and timing of emergence of coho salmon in Carnation Creek, British Columbia (Scrivener and Andersen 1984).

As stream temperatures increase from 5 to 15°C, the difference between standard metabolism and active metabolism increases 1.5 times in cutthroat trout (Dwyer and Kramer 1975). Defined as ''scope'' for activity and growth (Fry 1947), this difference means that a greater portion of food energy is available for growth and less is required for standard metabolism than at colder temperatures. This relationship only applies when food is abundant (Bisson and Davis 1976; Wurtsbaugh and Davis 1977), and the standing crop of invertebrates at the deciduous reach was lower than in the other reaches. However, this apparent contradiction may not apply to the deciduous reach. Warmer temperatures at the deciduous reach may shorten invertebrate generation time and increase invertebrate production relative to standing stock biomass (Benke 1984). This effect of temperature particularly applies to midges and *Baetis* mayflies (Mackey 1977), the most important food of fry in these streams.

Habitat Complexity

The formation and maintenance of lateral habitat is dependent on structures that divert streamflow and create spatial and hydraulic diversity at the channel margin. Such complexity is derived from the geomorphic structure of the valley floor, large boulders, and large woody debris. Geomorphic features that create edge complexity and form fry-rearing habitat in summer also create the largest and most persistent refuge habitat in winter (Moore 1987). Debris dams and large wood along the margin of the channel create lateral habitats that undergo smoother, more predictable changes in volume and velocity with increased streamflow than do lateral habitats formed by boulders and cobbles. At the open site, lateral habitats are formed by boulders without the additional stabilizing influence of large woody debris. The open site, however, has an abundance of boulders, many more than 3 m in diameter. In drainages not supplied with large boulders, removal of the canopy and woody debris from the channel may result in reductions in the quality of lateral habitats and lower populations of fry and adult fish.

Attempts to increase winter carrying capacity by enhancing winter habitat require structures that are not only appropriate for the behavior of the fish, but are also appropriate to the behavior of the stream. Artificial off-channel habitats have been used by salmonid fry in small streams (Bustard and Narver 1975), but experimental refuges have often failed because they could not withstand high flows or have served as sediment traps during bedload movement (Mason 1976). Habitat ''improvement'' directed at increasing pool depth at the expense of edge heterogeneity may reduce fry populations and decrease winter carrying capacity for all age classes (Everest et al. 1984).

Incorporation of Lateral Habitats into Stream Habitat Models

Because habitat requirements of cutthroat fry change significantly during the summer and throughout the year, models that prescribe habitat parameters based on limited probability-of-use data, such as Instream Flow Methodologies (Bovee and Cochnauer 1977), may inadequately consider the habitat requirements of fry populations. The focal point velocities measured in this study were much lower than velocities described for cutthroat trout fry in a habitat suitability index proposed by Hickman and Raleigh (1982). Such indices may be improved if they incorporate the utilization of areas of very low velocity by recently emerged fry. Instream flow models have also focused on the effects of changing flow on main channel habitats and relatively uniform cross sections (Bovee 1982; Morhardt 1986). As a result, they are not sensitive to the complexity of habitat structure characteristic of the margins of small streams or to the rapidly changing habitat requirements of cutthroat fry.

Management of stream salmonids must recognize temporal changes in habitat utilization within both cohort and population. Fishery biologists and geomorphologists alike have focused on the characteristics of main channels and have largely ignored the unique properties of channel margins and secondary channels in small streams. But like floodplain ponds, sloughs, and secondary channels in large rivers (Sedell et al. 1984; Welcomme 1985), lateral habitats in streams make a unique contribution to fishery resources because they increase habitat diversity and provide rearing areas and refuge from high flow. The reduced velocities, shallow depths, and greater complexity of these lateral areas of the active channel contribute to their ecological importance as depositional zones for organic matter, rearing areas for invertebrates and fish, and refuges for most stream organisms during floods. Stream margins, backwaters, and secondary channels are critical habitats for the fry of many salmonids, and these lateral areas provide the major rearing habitat for cutthroat trout in streams of the Cascade Mountains of Oregon.

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