

Response of Young-of-the-Year Cutthroat Trout to Manipulation of Habitat Structure in a Small Stream

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Abstract.—In Mack Creek, a third-order stream flowing through a 450-year-old coniferous forest in Oregon's Cascade Mountains, population size of young-of-the-year cutthroat trout *Salmo clarki* was positively correlated with length of stream edge and area of lateral habitat. Lateral habitats included backwaters and eddies at the margin of the channel that made up 10–15% of total stream area. Lateral habitat area was reduced at higher or lower streamflow, but the length of channel perimeter formed by lateral habitats was never less than twice the length of the reach. In an experimental manipulation of lateral habitat before the emergence of young fish from the redd, an increase in lateral habitat area of 2.4 times the area observed in control reaches resulted in a 2.2-times greater density of age-0 cutthroat trout. Young-of-the-year fish were virtually eliminated from stream sections with reduced area of lateral habitat. Growth was not affected by the greater density of fish in reaches with enhanced lateral habitat.

Margins of small streams in the Cascade Mountains of Oregon are complex geomorphic structures that form unique habitats adjacent to main channel pools, riffles, and rapids. These areas are lateral to hydraulic features of the main channel and provide unique habitats for fish, invertebrates, and other aquatic organisms. Lateral habitats are characterized by low water velocity, heterogeneous substrates, abundant detritus, and structural protection from high discharge. This combination of physical and biotic conditions provides gradients of depth and velocity, cover, and access to invertebrate food. This makes lateral habitats particularly suited to the requirements of young-of-the-year cutthroat trout *Salmo clarki*. Cutthroat trout establish territories in lateral habitats upon emergence and do not move to main channel pools or riffles for several months (Moore 1987). Because cutthroat trout in these streams are residents that often complete their life history within a 20–100-m reach (Miller 1957; Wyatt 1959; Aho 1977), the availability and distribution of lateral habitats may significantly influence both the establishment and maintenance of cutthroat trout populations.

Use of lateral habitats by cutthroat trout in headwater streams is similar to the use of tributaries and flooded side channels by coho salmon *Oncorhynchus kisutch*, steelhead *Salmo gairdneri*, and cutthroat trout in larger drainage systems. Previous studies have frequently shown the occurrence of newly emergent salmonids in slow water at the edge of stream channels (Keenleyside 1962; Chapman 1966; Lister and Genoe 1970). The importance of off-channel pools, side chan-

nels, and tributaries for both rearing and winter habitat has been well documented (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Sedell et al. 1984; Hartman and Brown 1987). These studies have focused on the importance to juvenile salmonids of habitats adjacent to the main channel. However, the importance of lateral habitats to the establishment and subsequent abundance of juvenile populations has not been examined in natural stream channels.

In an earlier study of riparian influence on cutthroat trout populations, Moore (1987) observed that the abundance of age-0 fish was generally proportional to the area of lateral habitat in third-order streams. In the present study, our objective was to manipulate the stream margin in a natural stream and examine more rigorously the relationship between area of lateral habitats and the abundance of age-0 cutthroat trout. We hypothesized that increasing or decreasing the area of lateral habitat before alevins emerged would have a direct effect on subsequent abundance of age-0 fish. A second objective was to monitor the populations during the summer growth period and evaluate possible effects of density differences in the manipulated reaches on growth and production.

Methods

Mack Creek is a third-order stream in the H. J. Andrews Experimental Forest in Oregon's Cascade Mountains. Its upper section flows through a 450-year-old stand of conifers dominated by Douglas fir *Pseudotsuga menziesii* and western hemlock *Tsuga heterophylla*. The geomorphology of this small, steep channel (drainage area, 5.4

km²; gradient, 10.0%; average stream width in summer, 3.2 m) is controlled by large woody debris and boulders that form debris dams and cascades interspersed with pools and riffles. The distribution and hydraulic behavior of stream habitats were evaluated in the upper reach at 4–6-week intervals from July 1982 to January 1984, at which times the area of lateral habitats was mapped and the perimeter of the channel and length of lateral habitats were measured.

The response of young-of-the-year cutthroat trout to manipulation of lateral habitat was studied in a 135-m reach approximately 1.5 km downstream from the upper section. The structure of the manipulated reach was similar to the upper reach (average width, 4.4 m; gradient, 8.2%). The riparian setting was composed of old-growth conifers on the west bank and a 15-year-old clear-cut region that contained small alder *Alnus rubra* and vine maple *Acer circinatum* mixed with young Douglas fir on the east bank. Although large woody debris was present in the manipulation reach, there were no debris dams spanning the channel. Cutthroat trout was the only fish species in both the upper and manipulation reaches.

Stream habitat definitions.—Lateral habitat comprises low-velocity areas (flow less than 4 cm/s) at the margins of the stream channel. Such areas are structurally and hydraulically distinct from main channel pools, riffles, and cascades. Lateral habitats are formed by structures, such as combinations of boulders and woody debris, that deflect flow away from the bank and act as hydraulic controls (Figure 1). These structures create eddies at the edge of the channel with low water velocity and zero slope of the water surface. Because lateral habitats are defined in the context of both structure and hydrology, variation in channel hydraulics at different discharges may cause the specific location of some lateral habitats to change within the active channel. At sufficiently high discharges, some lateral habitats may become part of main channel riffles or cascades.

Lateral habitats are classified, according to their morphology and orientation to the main channel, as stream margins, backwaters, and isolated pools. Stream margin habitat includes areas of shallow water and slow current along the stream edge with upstream or downstream structure but without lateral separation from the main channel. We defined stream margins operationally as lateral habitats with currents less than 4 cm/s in velocity and water less than 20 cm in depth. This combination of depth and velocity coincided with velocity tran-

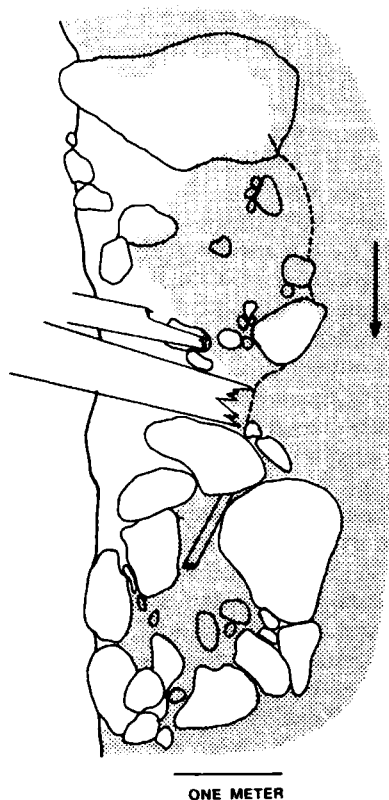


FIGURE 1.—Typical structure of stream margin (upper) and backwater (lower) lateral habitats with boulders and woody debris. Shaded area represents the wetted surface; bank is on the left, main channel on the right. The velocity transition between lateral and main channel habitats is represented by dotted lines. Arrow indicates the direction of streamflow in the main channel.

sitions that frequently occur between stream margins and riffles in third-order streams in the Cascade Mountains. The 20-cm depth was also used arbitrarily to distinguish between stream margin habitats and deeper, slow-water areas in adjacent main channel pools.

Backwaters are areas of slow-moving water that are further removed from the influence of the main channel than are stream margins. They may be either isolated pools in the active channel (off-channel backwaters) or connected to the main flow through gaps in boulders or wood that form the habitat. In backwaters, the opening to the main flow is narrower than the long axis of the habitat. The limited connection to the main flow distinguishes backwaters from stream margins. Depth in backwaters and isolated pools may exceed 20 cm.

Manipulation of lateral habitat.—The experi-

mental manipulation of lateral habitat was completed May 22, 1983, one week before cutthroat trout alevins began to emerge in lower Mack Creek. Nine stream sections were randomly assigned to one of three treatments: increased lateral habitat, reduced lateral habitat, and control (no change). Each section was 15 m long and each treatment was repeated three times.

Stream margin habitat area was increased by moving cobble and small boulders into short rows approximately perpendicular to the bank, thus forming deflectors that slowed current. Backwaters were created by making semicircular rows of rocks along the stream bank. Existing backwater and stream margin habitats were enhanced where possible by providing greater protection from fast current and by increasing depth near the edge. Lateral habitats were reduced by cutting off and filling in existing backwaters, and by arranging cobbles in rows parallel to the channel margin. Small boulders near the stream margin were pushed towards midchannel, decreasing edge roughness and eliminating some lateral habitats. Shrub and herb cover along the bank was trimmed to equalize the abundance of plant cover in each of the treatments. After the manipulation was complete, stream width, depth, and velocity were measured in each section. The reach was mapped and the areas of pool, riffle, rapid, and lateral habitats were measured in each section. Streamflow in the manipulation reach was $0.17 \text{ m}^3/\text{s}$ at the time alevins began to emerge. The maximum discharge during the study period ($0.32 \text{ m}^3/\text{s}$) occurred during a rainstorm on July 2, 1983. After this event, streamflow decreased gradually throughout the summer but was never lower than $0.09 \text{ m}^3/\text{s}$.

Observations of age-0 cutthroat trout.—Observations of juvenile cutthroat trout began when alevins started to emerge from the substrate and continued at 2- or 3-week intervals through the summer growth period (June–October 1983). The abundance of age-0 cutthroat trout in each treatment section was evaluated by survey along the bank and by snorkeling observations. Observations of age-1 and older fish were not made. The most efficient method of observing fish immediately after emergence and in areas where stream geometry precluded entry of a diver was that of crawling upstream along the bank, looking between and beneath cobbles. Fish were captured by slowly moving a small dip net in front of the fish, then moving a meter stick toward the fish from behind until the fish was startled and swam for-

ward into the net. This method was successful in 95% of capture attempts when the fish first emerged, but capture efficiency decreased to only 70% as the fish grew larger near the end of the study period. Each fish caught was measured quickly for total length and returned to the same location where it was captured. Released fish typically sought crevice cover in the substrate. If a fish was not captured, its length was estimated by comparing its size to an adjacent particle in the substrate and using a small ruler taped to the dip net to measure the length of the particle. After a capture or capture attempt, the observer moved upstream until another fish was encountered. The behavior of released fish, the ability to follow the movement of individual fish, and the upstream progression of the observer made it unlikely that fish would be captured more than once during each census.

A final census was conducted at the end of the summer season by a combination of electrofishing and snorkeling. Fish were collected from each section, starting at the downstream end of the reach, with a backpack electroshocker; they were sorted by habitat and treatment type, and held in buckets until they could be weighed and measured. After electrofishing was completed, a diver collected any remaining age-0 cutthroat trout and these fish were added to the census.

Biomass of age-0 cutthroat trout at each sampling time was estimated from a length–weight regression of data from the October census. Instantaneous growth rate and production (Ricker 1975) were calculated from the weight estimates. Differences in abundance, length, and biomass between treatments were tested by analysis of variance or Kruskal–Wallis procedures (Sokal and Rohlf 1981). Correlations between abundance and mapped habitat area or stream channel perimeter were determined by regression techniques.

Results

Lateral Habitat Structure in the Old-Growth Reach

Stream geomorphology in the old-growth section of Mack Creek was dominated by large boulders and wood that increased flow resistance and created complex channel margins. More than 50% of the active channel surface was composed of boulders greater than 32 cm in diameter and woody debris greater than 2 m in length. The edge of the wetted channel was also formed primarily by boulders and wood. Straight segments of the stream edge were rare and only occurred where the chan-

nel was constrained by bedrock or ran along gravel bars. Lateral habitats were formed by the processes of erosion, deposition, and channel alteration associated with clusters of boulders and wood at the channel margin.

Because of the irregularity of the stream edge, total channel perimeter and the perimeter of lateral habitats were very high relative to reach length. The maximum values of lateral habitat length and total channel perimeter occurred when streamflow was between 0.15 and 0.20 m³/s (Figure 2), discharges that were typical of streamflow during late May, June, and July. The average length of the channel perimeter was 5.5 times greater than the length of the reach.

The area of lateral habitat was also greatest in early summer, making up 15% of total stream area in the old-growth reach. Stream margins made up the largest proportion (59%) of the area in lateral habitats, followed by backwaters (28%) and isolated pools (13%). The area of lateral habitats was reduced both by low water in late summer and by storm flows from the main channel during winter. Lateral habitat area decreased 10–30% during late summer when streamflow was lowest. Despite fluctuations in area caused by changes in streamflow, lateral habitats were the most persistent of all stream habitats in the reach. Velocity and depth varied less in proportion to changes in streamflow in lateral habitats than in pools or riffles (Moore 1987).

Manipulation of Lateral Habitat Structure

In lower Mack Creek, manipulation of stream edge structures altered the areas of lateral habitats

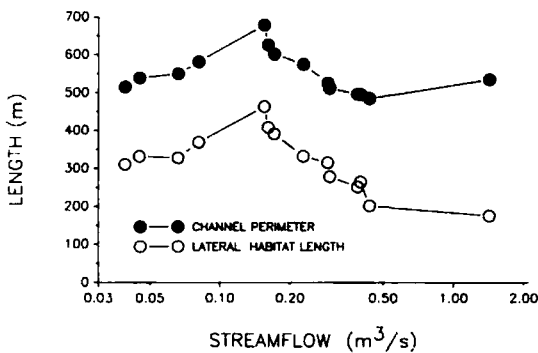


FIGURE 2.—Effect of streamflow on the length of stream edge (channel perimeter) and on the perimeter of lateral habitats (lateral habitat length) in a 100-m reference reach of the old-growth section of Mack Creek, Oregon. The range of discharge is from summer low flow (<0.05 m³/s) to conditions characteristic of storm events with a frequency of two or three times per year (1.55 m³/s).

TABLE 1.—Channel characteristics and average habitat distribution (SE) in habitat manipulation reach of Mack Creek, Oregon, on July 21, 1983. Areas of individual habitats were combined in each treatment segment and expressed as mean area ($N = 3$) and percent of total segment area.

Channel measurement	Treatment		
	Control (no change)	Increased lateral habitat	Reduced lateral habitat
Stream width (m)	4.4 (0.4)	5.4 (0.1)	3.7 (0.1)
Depth (m)	0.2 (0.8)	0.2 (0.9)	0.2 (1.0)
Velocity (m/s)	0.2 (0.0)	0.2 (0.0)	0.2 (0.1)
Stream area (m ²)	66.6 (5.9)	80.2 (1.3)	55.6 (1.0)
Area of pools (m ²)	6.7 (1.6)	8.3 (1.0)	8.6 (4.0)
% pools	10.1	10.3	15.5
Area of riffles (m ²)	50.3 (5.6)	53.4 (0.7)	43.5 (3.5)
% riffles	75.6	66.6	78.1
Area of rapids (m ²)	3.1 (0.5)	3.0 (0.5)	2.6 (0.5)
% rapids	4.6	3.7	4.7
Area of lateral habitats (m ²)	6.5 (0.6)	15.6 (1.1)	0.9 (0.2)
% lateral habitats	9.7	19.5	1.7

but had little effect on the areas of other habitat types (Table 1). After the manipulation, increased-lateral-habitat sections had 2.4 times more area of lateral habitat than control sections, and control sections had 7.2 times more area of lateral habitat than reduced-lateral-habitat sections. The channel perimeter of the 15-m treatment segments averaged 63 m in the control sections, 89 m in the increased-lateral-habitat sections, and 41 m in the reduced-lateral-habitat sections. Total stream area was greatest in sections where area of lateral habitat was increased. Average stream depth and average water velocity were similar in all treatments.

Manipulation of lateral habitats led to substantial changes in fish density; age-0 cutthroat trout exhibited an immediate and sustained response to the alteration of lateral habitat. In the first census following emergence, average numbers of age-0 fish per 15-m section were 26.7 in the increased-lateral-habitat treatment, 13.3 in the control treatment, and 3.0 in the reduced-lateral-habitat treatment. This relative distribution did not change in four subsequent observations during the summer (Figure 3). The difference between treatments was highly significant at each observation date (least significant difference of means = 4.9; $P < 0.001$).

In the increased-lateral-habitat sections, a 2.4-fold increase in area of lateral habitat resulted in a 2.2-fold increase in the average number of age-0 fish (Table 2). Straightening stream sections reduced the area of lateral habitat 86% and resulted

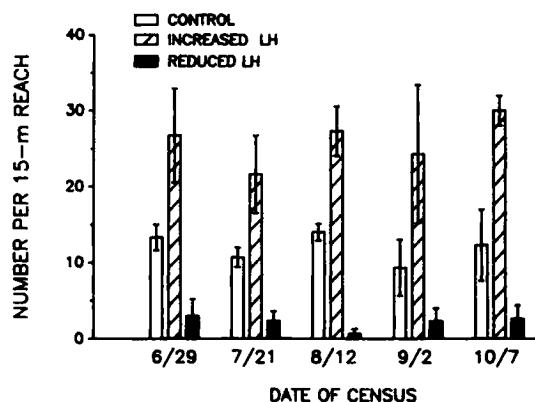


FIGURE 3.—Average numbers of age-0 cutthroat trout in the three control, three increased-lateral-habitat (LH), and three reduced-lateral-habitat treatments during each census of the habitat manipulation reach, Mack Creek. Error bars are ± 2 SE. Dates are month/day.

in an 83% reduction in average number of age-0 cutthroat trout. Density per unit of stream area showed the same relationship: higher in increased-lateral-habitat sections and lower in reduced-lateral-habitat sections.

Measures of the areas of lateral habitats were the best indicator of juvenile abundance in the manipulation reaches. The number of age-0 fish in each of the treatment sections was highly correlated with the area of lateral habitat ($r = 0.983$), perimeter length of lateral habitat ($r = 0.956$), total channel perimeter ($r = 0.900$), and stream area ($r = 0.829$). Abundance was also positively related to the area of riffles ($r = 0.655$), but was poorly related to the area of pools ($r = -0.066$) or rapids ($r = 0.122$) in each treatment.

The pattern of habitat use was the same in each of the manipulation sections and in the old-growth section of Mack Creek. After emergence, juveniles established territories in lateral habitats exclusively and remained there for at least 6 weeks. Although the number of age-0 fish per treatment did not change, there were changes in habitat use within each section. By the end of summer, some age-0 fish had moved laterally in the direction of adjacent midchannel pools and riffles (Figure 4). Juveniles that established territories in the reduced-lateral-habitat sections of the manipulation reach were observed in the few remaining pockets of shallow, low-velocity water at the stream edge.

We hypothesized that the difference in abundance between treatments would become smaller in successive observations as the fish grew larger, streamflow decreased, and the contrast between

TABLE 2.—Population density of age-0 cutthroat trout in each of three habitat manipulation treatments in Mack Creek, Oregon. Densities are means (SE) of five observations in each of three 15-m reaches per treatment, July–October 1983.

Density measure	Treatment		
	Control (no change)	Increased lateral habitat	Reduced lateral habitat
Number per treatment	11.9 (0.8)	26.0 (1.4)	2.2 (0.4)
Number/m ² of stream	0.18 (0.01)	0.33 (0.03)	0.04 (0.01)
Number/m ² of lateral habitat	1.83 (0.08)	1.67 (0.27)	2.37 (0.04)

velocity and depth in lateral habitats and main channel pools and riffles was reduced. By the end of summer, decreased streamflow had created potential foraging sites and areas of lateral habitat in the reduced-lateral-habitat sections, but additional age-0 fish were not observed in these areas. This suggested that movement between treatment sections did not occur. Because fish were not marked, however, movement of individual fish could not be detected and the degree of movement between treatment sections could not be demonstrated objectively.

Density Effects on Growth and Production

Growth of young-of-the-year cutthroat trout was not affected by the differences in the number of fish in each manipulation treatment. From June to October, the mean length of age-0 fish increased from about 20 to 60 mm (Figure 5A), but, for any census period, the average length was not significantly different between treatments ($P > 0.10$; Kruskal–Wallis test).

Total biomass of age-0 cutthroat trout was higher in the increased-lateral-habitat sections than in either the control or reduced-lateral-habitat sections (Table 3). In October, when age-0 fish were captured by electrofishing and weighed for the first time, average total biomass in the 15-m-long stream reaches was 0.846 g/m² in the sections with increased lateral habitat, 0.432 g/m² in the control sections, and 0.116 g/m² in the sections with reduced lateral habitat (least significant difference of mean biomass = 0.187; $P < 0.01$).

Because the abundance was much greater in the increased-lateral-habitat sections and there were no significant differences in size, biomass of young-of-the-year cutthroat trout accumulated much more rapidly in the increased-lateral-habitat sec-

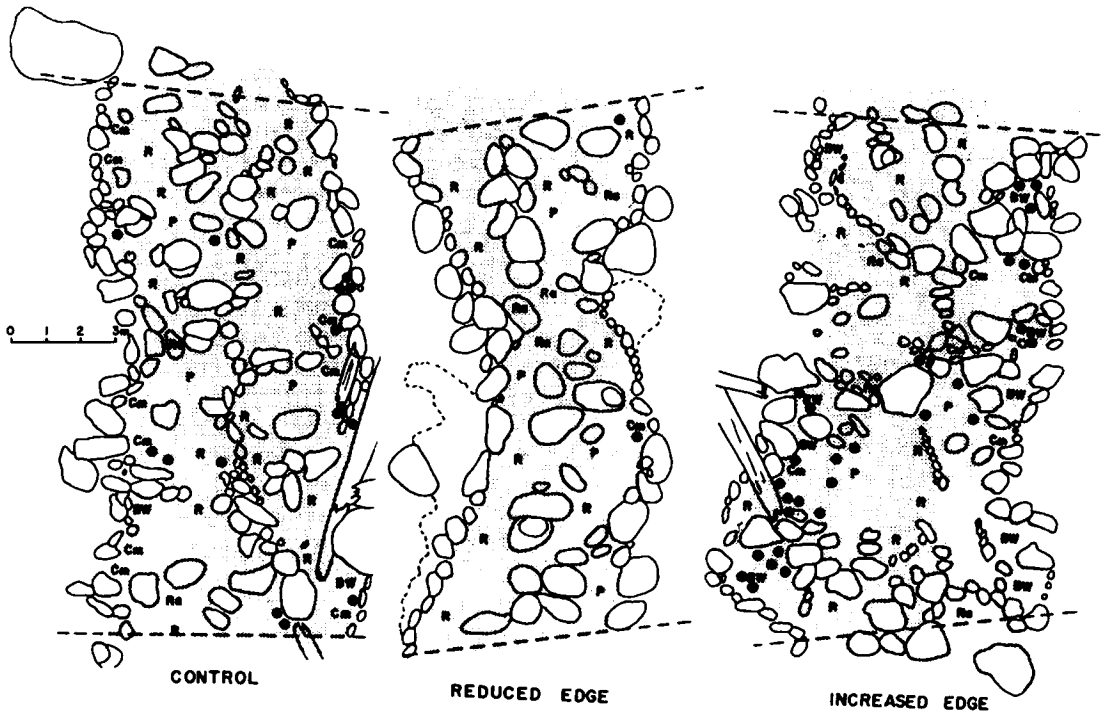


FIGURE 4.—Positions of individual age-0 cutthroat trout (filled circles) in three representative treatment sections of Mack Creek, Oregon, during the September 2, 1983, census. Shaded areas represent the wetted channel. Dotted lines in the reduced-edge section indicate locations of lateral habitat before the manipulation. Habitat abbreviations are P = pool, R = riffle, Ra = rapid, Cm = stream margin, and BW = backwater.

tions than in the control or reduced-lateral-habitat sections (Figure 5B). Growth rates were similar in the control and increased-lateral-habitat sections, being highest in early summer and declining slightly at the end of the sample period (Table 3). Growth rates calculated for the reduced-lateral-habitat sections were more variable and generally lower than in the other treatments, except for a large increase during the interval from August 12 to September 2. Total production from June 29 to October 7 in the increased-lateral-habitat sections was 95 and 824% higher than in the control and reduced-lateral-habitat sections, respectively (Table 3).

Discussion

The strong correlation between lateral habitat area and number of age-0 cutthroat trout in a reach ($r = 0.983$) underscores the importance of lateral habitats in the early life history of these fish. Tests of coho salmon response to lateral habitat have shown increased carrying capacity of introduced juveniles in artificial rearing channels with enhanced edges (Mundie 1969) and have demon-

strated that both coho salmon and cutthroat trout juveniles introduced into lateral habitats remain there through winter high flows (Bustard and Narver 1975). In our study, increased lateral habitat resulted in increased population density of native cutthroat trout in a naturally stocked stream where fish residence in both habitat and reach was entirely volitional.

The density of juvenile cutthroat trout in a stream reach depends on the availability of suitable habitats and the competition for these territories. Habitat choice by juvenile salmonids has been explained by the mechanisms of competition for food and space in territories (Mason and Chapman 1965) or for focal positions that maximize exposure to food and minimize energy expenditure (Everest and Chapman 1972). Based on these ideas, Bachman (1984) and Fausch (1984) proposed that focal positions in areas of low velocity adjacent to faster current would have the greatest potential for net energy gain. The structure of lateral habitats results in velocity transitions near the stream margin that create profitable focal positions. Increasing the area of lateral habitat in a

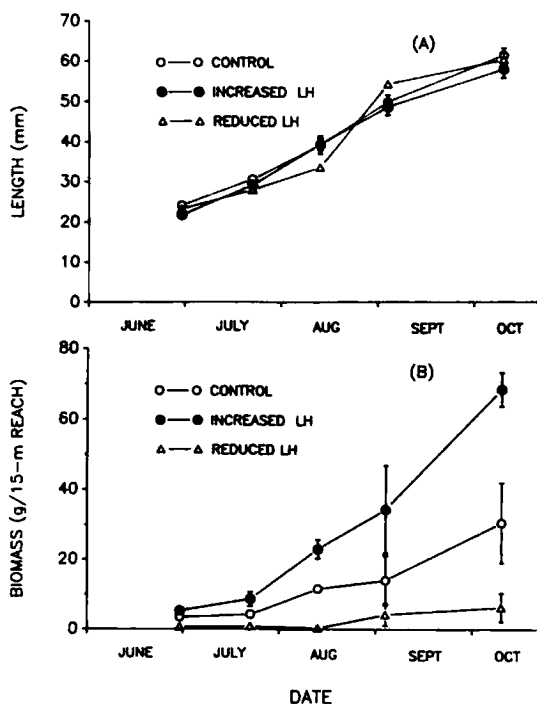


FIGURE 5.—Increase in length of age-0 cutthroat trout (A) and accumulation of biomass (B) in three treatment sections in the manipulation reach of Mack Creek, Oregon, during summer 1983. Treatments include no change (control), and increased and decreased areas of lateral habitat (LH). Error bars are ± 2 SE.

reach has the effect of increasing the availability of focal positions and, therefore, of increasing the number of juvenile fish. Stream edge heterogeneity provides space for processes of segregation and isolation to operate. Increasing the area of lateral habitats provides more territories for resident fish and reduces downstream emigration.

Behaviors associated with the establishment of dominance hierarchies and competition for focal positions clearly influence patterns of habitat use by juvenile stream fishes (Jenkins 1969; Fausch 1984). However, newly emergent juveniles must

also develop behaviors that reduce exposure to predation and the risk of downstream displacement from the reach. In an 18-year study, Elliott (1985) concluded that survival during the period immediately following emergence had the greatest influence on brown trout *Salmo trutta* population density. In the Cascade Mountains, cutthroat trout emerge during a period of declining streamflow after the winter rainy season. However, velocity in main channel habitats easily exceeds the swimming capacity of 20–30-mm-long cutthroat trout. If the margins of the stream channel are abrupt and have either deep water or fast current, juvenile cutthroat trout will be displaced downstream until they reach suitable habitats.

Evidence from our study suggests that limited dispersal of emergent juveniles may be an adaptive behavior for resident trout populations. In contrast, lack of dispersal by stocked juveniles results in density-dependent effects that suppress growth and lower survival (Egglishaw and Shackley 1980; Hume and Parkinson 1987). Although we made no direct measure of mortality, we found no effect of density on abundance in successive observations, and growth was unaffected by the density differences associated with each treatment. Immediate occupation of lateral habitats and lack of dispersal maintain populations of age-0 cutthroat trout in reaches where resident adult fish have spawned successfully. Analysis of substrate size distributions in headwater streams (Moore 1987) and our recent observations of spawning behavior of cutthroat trout in these streams have shown that both the availability of spawning gravel and selection of spawning sites occur in or near lateral habitats. When cutthroat trout spawn in lateral habitats, alevins may emerge directly into appropriate territories.

When emergence occurs from midchannel spawning sites, dispersal mechanisms may also result in the establishment of territories in lateral habitats. Bams (1969) observed that emerging sockeye salmon *Oncorhynchus nerka* do not im-

TABLE 3.—Mean biomass ($\bar{B}$, g/100 m²), instantaneous growth rate (G), and production (P , g/100 m²) of age-0 cutthroat trout for each of three habitat manipulation treatments in Mack Creek, Oregon.

Interval	Increased lateral habitat			Reduced lateral habitat			Control (no change)		
	$\bar{B}$	G	P	$\bar{B}$	G	P	$\bar{B}$	G	P
Jun 29–Jul 21	8.73	0.639	6.05	0.56	0.353	0.20	5.84	0.613	3.58
Jul 21–Aug 12	19.73	0.742	14.64	0.85	0.432	0.37	11.95	0.613	7.33
Aug 12–Sep 2	35.71	0.591	21.10	4.15	1.150	4.77	19.23	0.519	9.98
Sep 2–Oct 7	64.16	0.485	31.12	9.53	0.268	2.55	33.42	0.495	16.54
Total			72.91			7.89			37.43

mediately swim to the surface to fill their air bladders, a prerequisite for normal swimming and feeding. Instead, they remain near the bottom and swim laterally in short bursts, then sink to the bottom and rest. They continue this behavior and make progressive movements toward the side of the channel until they eventually come to shallow areas near the stream edge. The flow characteristics of lateral habitats and structure of the stream channel increase the probability that emerging salmonids exhibiting this behavior will eventually be located in lateral habitats.

We do not propose the construction of lateral habitats like those we used in this manipulation as a form of habitat improvement in small streams. Instead, we favor the maintenance of complex structure in stream channels that results in the development of a variety of lateral and main channel habitats. In the old-growth section of Mack Creek, this function is derived from the interaction of large woody debris from the riparian forest with the geomorphology of the stream bed. For stream enhancement projects to be successful, objectives must be identified and channel modifications must be designed to provide habitat characteristics appropriate for all stages of the early life history of stream fish. Enhancement effort focused on the development of spawning areas and midchannel pools may be insufficient to achieve desired objectives if lateral rearing areas are not abundant. If natural or human-induced events degrade available habitat for juvenile salmonids, stream rehabilitation managers should consider lateral habitat complexity as well as main channel habitats.

Acknowledgments

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