Transactions of the American Fisheries Society 132:468–482, 2003

Rock Type and Channel Gradient Structure Salmonid Populations in the Oregon Coast Range

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Abstract.—The study objective was to investigate the response of salmonid populations to disturbance in Oregon Coast Range streams in two rock types, basalt and sandstone. Salmonid abundance was estimated in a total of 30 km of channel in 10 Oregon Coast Range streams with similar basin areas (14–20 km^2). These basins had a range of disturbance caused by timber harvest, fire, and salvage logging. Mean channel gradient in sandstone was 0.012 m/m, and pools were the dominant habitat type. Mean channel gradient in basalt (0.025 m/m) was twice that in sandstone, and riffles were the dominant habitat type. Mean percentages by length of pools, glides, and riffles were 47, 33, and 20%, respectively, in sandstone, compared with 24, 27, and 50% in basalt. Channel gradient and channel morphology appeared to account for the observed differences in salmonid abundance, which reflected the known preference of juvenile coho salmon *Oncorhynchus kisutch* for pools. Coho salmon predominated in sandstone streams, whereas steelhead *O. mykiss* and cutthroat trout *O. clarki* predominated in basalt streams. In sandstone, juvenile coho salmon were four times more abundant than age-0 trout (steelhead and cutthroat trout combined). In basalt, age-0 trout were five times more abundant than juvenile coho salmon. Steelhead and cutthroat trout aged 1 or older were more abundant in basalt streams than in sandstone. However, mean densities of all salmonids combined were not different between rock types. We failed to find a clear fish response to disturbance, but our study shows the importance of geology in the design of studies investigating the response of salmonids to timber harvest and suggests that streams in basalt and sandstone have different potential capacities for salmonid communities.

The effects on salmonid abundance of the frequent disturbance caused by forest practices have been a long-standing issue in the Pacific Northwest of the United States (Hicks et al. 1991b). Modifications to natural geomorphic processes attributable to timber harvest take place against a background of natural floods and wildfires, which have historically occurred less frequently than timber harvest but at unpredictable intervals (Reeves et al. 1995). The variable responses of salmonids have plagued investigations into the effects of timber harvest. In some circumstances, salmonids have been negatively affected (e.g., Hall et al. 1987; Schwartz 1991), whereas in others, there have been some positive responses (e.g., Murphy and Hall 1981; Hawkins et al. 1983; Hartman and Scrivener 1990). Still other studies have failed to find a salmonid response to logging (Bradford and Irvine 2000). Results from a long-term Carnation Creek study typify the variation: though logging appeared to increase the number of coho salmon *Oncorhynchus kisutch* smolts leaving the basin, increased sedimentation of spawning gravel led to a substantial reduction in numbers of chum salmon *O. keta* fry moving to sea (Tschaplinski 2000).

These variable responses may be attributable to differences in salmonid species, variation in forest practices, and differences in basin characteristics (Hicks et al. 1991b). For instance, rock type has a strong influence on channel morphology (Hack 1957; Keller and Tally 1979), as does large woody debris (Montgomery et al. 1995). Changes in channel morphology in response to timber harvest can affect salmonid distribution (Bisson and Sedell 1984; Tripp and Poulin 1986, 1992; Hogan and Church 1988), and latitude and climate can also modify the salmonid response (Hicks et al. 1991b).

Study design has contributed to the apparently variable responses of salmonids. Short study reaches, often used because of limited resources, are generally assumed to be representative, but may not encompass the range of densities within the stream. We attempted to overcome this problem by choosing as the spatial scale stream segments that were 3 km long. These segments largely conformed to the criteria of Frissell et al. (1986), as they represented the variability in physical habitat while maintaining uniform channel slope and bedrock type. Our stream segments also contained

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Received October 30, 2001; accepted October 8, 2002

enough channel units to provide a statistically valid application of double sampling (Hankin and Reeves 1988; Dolloff et al. 1993).

Streams can widen in response to timber harvest (e.g., Lyons and Beschta 1983; Tripp and Poulin 1986). As stream width is dependent on hydrological characteristics such as basin area and discharge (Brush 1961; Osterkamp and Hedman 1977), the study segments were matched for basin size rather than for stream width. Basin size was controlled by positioning the downstream ends of the stream segments above a tributary junction, which is an accepted longitudinal boundary for stream segments (Frissell et al. 1986).

The study objective was to investigate the response of salmonid populations to disturbance caused by timber harvest, fire, and salvage logging in Oregon Coast Range streams in two rock types, basalt and sandstone. The importance of this study is its attempt to isolate rock type as a factor causing some of the previously observed variable responses of salmonids to forest practices. Our hypothesis is that streams in basalt and sandstone have different potential capacities for salmonid communities, in the sense of Warren et al. (1979) and Frissell et al. (1986). By choosing streams with basins in uniform rock types and with a range of disturbance histories, but with similar basin areas, we also hoped to control for the effect of basin size on the response of salmonids to disturbance.

Methods

Study design.—In 1987, four streams in sandstone and four in basalt were selected for this study after an extensive search for second- and third-order streams with a range of disturbance levels in two uniform rock types in the Oregon Coast Range. The streams in basalt are located in the Cape Perpetua region (Figure 1A) and flow through basalt and pyroclastic rocks of the Toledo Formation (Wells and Peck 1961). Study segments in these basalt streams are within 15 km of the coast. The streams in sandstone are located in the lower Umpqua River (Figure 1C) and flow through rhythmically bedded sandstone of the Tyee and Fluornoy Formations (Wells and Peck 1961). In these sandstone streams, the study segments are situated 25−50 km from the coast. Sandstones are generally softer and more easily eroded than basalts and related volcanic rocks, but are less jointed than the basalts.

Two more streams were added to the study in 1988. The study segment of North Fork Wilson River near Tillamook (Figure 1B) flows through an area of basalt, breccia, and tuffs of the Tillamook Formation (Wells and Peck 1961) and is about 35 km from the coast. The study segment of North Fork Beaver Creek (Figure 1A) flows through sandstone of the Tyee Formation in the central Oregon coast north of Cape Perpetua, and is about 15 km from the coast.

Study segments averaged 3.03 km long (range, 2.83–3.39 km), and the downstream ends were located so that the basin area upstream was approximately 15 km^2 (Table 1). The resultant mean basin area was 16.9 km^2. Basin areas and lengths of the surveyed segments were similar between rock types. To compare habitat structure, channel morphology was surveyed in summer 1988 during periods when the discharges were the same in the two rock types (Table 1). Because of the length of time taken to survey each stream (3–5 d) and because there was only one survey team at work, streams had to be surveyed sequentially. Streamflows receded earlier in sandstone, so these streams were surveyed first (from 24 June to 19 July). Basalt streams were surveyed from 8 August to 14 September under streamflow conditions that were approximately equivalent to those of the sandstone streams. This ensured that the physical conditions were as comparable as possible and were largely independent of differences attributable solely to streamflow.

The study basins had been subjected to a range of old and recent disturbance from timber harvest, fire, and salvage logging (Table 1). Fires occur frequently in the forests of the Pacific Northwest, and recur with an interval of about 200 years (Ripple et al. 2000). Much of the area of the Siuslaw National Forest, which includes Bob, Rock, Tenmile, Cape, Beaver, and Franklin creeks, was burned in a succession of fires between 1845 and 1890. The watershed of the North Fork Wilson River was burned in four major fires that destroyed large areas of the Tillamook State Forest between 1933 and 1951. The Big Creek watershed was burned in the Oxbow Fire of 1966. Salvage logging followed this fire and the fires in the Tillamook State Forest. For the purposes of this study, disturbance caused by extensive wildfire and subsequent salvage logging was considered to be equivalent to timber harvest followed by slash burning, which was a common practice associated with logging in the Oregon Coast Range.

Big, Halfway, and Paradise creeks are partly managed by the Bureau of Land Management and partly in private ownership. The basins of Bob, Rock, and Franklin creeks remained relatively un-

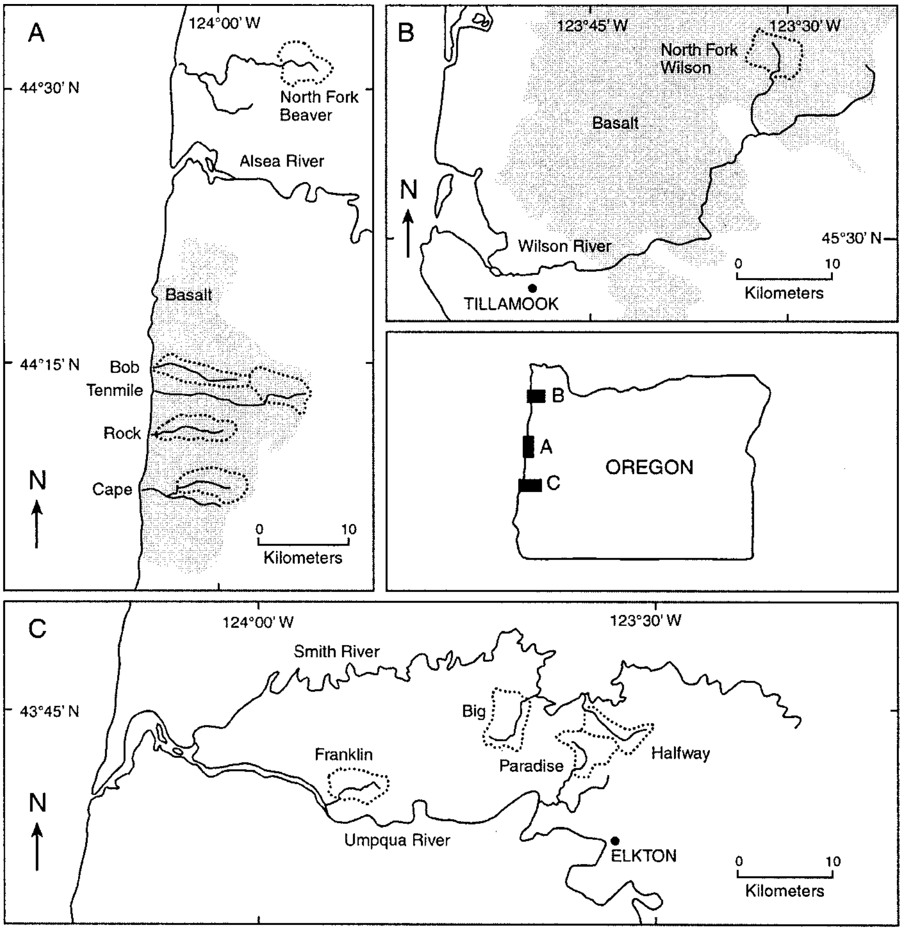

FIGURE 1.—Location of the study sites in the Oregon Coast Range: **(A)** the Cape Perpetua region and North Fork Beaver Creek, **(B)** the North Fork Wilson River, and **(C)** the lower Umpqua River basin. The basin boundaries of the surveyed stream segments are shown by the dotted lines, and the areas of basalt rock are shaded gray.

disturbed throughout the 20th century, whereas Cape Creek has been extensively disturbed by logging. A limited amount of timber has been harvested from the riparian zone of Rock Creek in the lower 1 km of the study reach.

The naturally occurring vegetation of the Oregon Coast Range is dominated by Douglas-fir *Pseudotsuga menziesii*. The vegetation around Bob, Rock, Cape, and North Fork Beaver creeks consisted of Douglas-fir, western hemlock *Tsuga heterophylla*, and western redcedar *Thuja plicata*, with Sitka spruce *Picea sitchensis* near the coast. Common hardwoods were red alder *Alnus rubra*, especially in logged and burned areas, bigleaf maple *Acer macrophyllum*, and vine maple *Acer circinatum*. Similar vegetation surrounded the study segments of Tenmile, Franklin, Halfway, Paradise, and Big creeks and the North Fork Wilson River, but without the Sitka spruce. Because of the location of timber harvest, red alder dominated the riparian zones of all the streams except Bob and Franklin creeks.

Salmonids common in small streams in this region are coho salmon, steelhead *O. mykiss*, and cutthroat trout *O. clarki* (Reeves et al. 1995). Most coho salmon smolts migrate out of Oregon Coast Range streams during April and May (Weitkamp et al. 1995). About 95% of these smolts are age 1; only about 5% migrate as age-2 smolts (Moring and Lantz 1975).

Channel morphology.—The stream channel in each segment was stratified longitudinally into individual channel units (pools, glides, or riffles) after the method of Bisson et al. (1982). The minimum length of channel units was one water surface width (3–6 m); smaller units were not indi-

TABLE 1.—Physical characteristics of the surveyed stream segments, including basin areas at the downstream ends and recent history of disturbance (i.e., timber harvest [eight basins] or fire followed by salvage logging [Wilson River and Big Creek]) for the study streams in the Oregon Coast Range. Water width was measured in 1988 at similar discharges in the two rock types (24 June to 19 July for sandstone, 8 August to 14 September for basalt). Means were calculated from square-root-transformed widths. The probability (*P*) of similarity of means between rock types (basalt or sandstone) was determined by analysis of variance.

Stream and *P*-value	Basin area (km^2)	Channel gradient (m/m)	Stream discharge in Jun–Sep 1988 ($L \cdot s^{-1} \cdot km^{-2}$)	Mean water surface width (m)	Percentage of basin area disturbed	Duration of disturbance
			Basalt			
Bob	16.1	0.0213	3.66	4.6	5	1950–1960
Rock	15.6	0.0238	7.38	4.7	6	1930–1962
Tenmile	17.1	0.0320	4.87	4.6	32	1959–1986
Cape	16.7	0.0205	8.08	5.5	78	1946–1986
Wilson	18.4	0.0295	4.24	4.2	100	1933–1951
Means	16.8	0.0254	5.65	4.7		
			Sandstone			
Franklin	14.5	0.0178	1.80	3.3	15	1963–1972
Halfway	19.1	0.0097	3.08	4.3	47	1950–1988
Beaver	15.7	0.0101	8.02	5.2	49	1957–1987
Paradise	20.1	0.0147	4.13	4.7	59	1950–1988
Big	16.1	0.0087	2.04	4.2	100	1951–1966
Means	17.1	0.0122	3.81	4.3		
P	0.777	0.002	0.237	0.346		

vidually classified. Channel units were classified as pools, glides, or riffles by water surface slope identified visually and by maximum depth measured with a wading rod. For each channel unit, active-channel width was measured as the distance between permanent, woody vegetation.

We minimized the variability inherent in visual classification of channel units (Kaufmann et al. 1999) in four ways. Discharge was matched between streams as much as possible when the physical surveys were carried out in 1988 (Table 1), all channel unit identification was carried out by one of us (B.J.H.), and the length of each channel unit was measured with a hip chain. Finally, channel units were identified by two criteria: water surface slope and maximum water depth.

Pools had water surface slopes less than 0.005 m/m and maximum water depths of 0.40 m or greater. Glides had slopes greater than or equal to 0.005 m/m but less than 0.015 m/m and maximum depths less than 0.40 m. Riffles had slopes of 0.015 m/m or greater and maximum depths less than 0.30 m. The water surface slopes of a subsample of channel units were measured initially with a 5×-magnifying Abney level to verify the visual classification. Thereafter, slopes were measured only for channel units whose classification was not immediately obvious.

To estimate stream channel gradient at the segment scale, the fall in altitude was measured between contours along the blue-line length of the surveyed stream segment on 1:24,000-scale maps with 12.2-m (40-ft) contour intervals. Stream order was determined by the blue-line method from the same maps. The streams had low sinuosity; channel lengths measured on the ground with a hip chain divided by the straight-line distance between the upstream and downstream ends of the stream segments ranged from 1.01 to 1.67. Stream discharge was measured at the downstream end of each surveyed stream segment in October 1987, when it had become apparent that discharges in the two rock types were very different. Discharges were measured several times in early summer 1988 so that the physical habitat surveys could be conducted with similar streamflows. Discharge was calculated from water depths and mean velocities measured at 10 points equally spaced across a uniform cross section by the method of Buchanan and Somers (1969). Mean velocity at 0.6 of depth from the surface was measured with a flowmeter fitted with a magnetic inductance current sensor.

The dominant substrate was identified visually as the substrate size-class that covered the greatest area, which was usually more than 50% of the total wetted area of a channel unit. Substrate size was measured where the size-class was not immediately obvious. Substrate size was assigned to phi-classes after the scale of Lane (1947). Mean dominant substrate size was calculated from the phi sizes (–$\log_2$ transformed data; Krumbein 1938). Substrate size frequency distributions were, for the most part, normal. Bedrock was recorded separately from particulate substrate when it was the dominant substrate. Pieces of large woody debris greater than 0.1 m in diameter and greater than 2 m long in the active channel were counted for each channel unit.

Corrected dive counts of salmonids.—Estimates of salmonid numbers were stratified into the three channel unit types (pools, glides, and riffles) based on the two-phase sampling methods of Hankin and Reeves (1988) as modified by Dolloff et al. (1993). In the first phase of sampling, a diver (BJH) counted salmonids in a systematic subsample of each stratum (every 5th pool, 5th glide, and 10th riffle), working from downstream to upstream within the study segments. Proportions of the main-stem channel dived were about 15% of the total number of channel units. The few side channels present were not included in the fish counts. Age-0 steelhead could not be distinguished from age-0 cutthroat trout, and therefore both were classed together as age-0 trout. Age-classes of steelhead of age 1 and older also could not be distinguished, so were categorized as age 1+; cutthroat trout were treated similarly.

In the second phase of sampling, we estimated the bias of dive counts by comparing removal electroshocking population estimates with dive counts between 16 August and 20 September 1988. We used 44 channel units (8 pools in basalt and 10 in sandstone, 6 glides in basalt and 8 in sandstone, and 6 riffles in each rock type) for these bias estimates. Each end of a channel unit was blocked with a 5-mm-mesh net, and then a dive count of the salmonids was made. Within 1 h of the dive count, we captured the salmonids by electroshocking without replacement, making three passes of equal effort. Numbers of age-0 trout, juvenile coho salmon, age-1+ steelhead, and age-1+ cutthroat trout were estimated from the catches for each pass with the maximum likelihood procedure REMOVAL in the program CAPTURE (White et al. 1982). These population estimates were compared with the paired dive counts to estimate the correction factor, $\hat{R}$ (Dolloff et al. 1993), from the equation

$$\hat{R} = \frac{\sum_{i=1}^{n'} y_i}{\sum_{i=1}^{n'} x_i},$$

where y_i is the number of fish estimated by removal electroshocking in each channel unit, x_i is the number of fish counted by the diver in those units, and n' is the number of channel units with paired electroshocking population estimates and dive counts. Estimates of salmonid numbers and their variances in each stratum in each 3-km segment were extrapolated from counts of fish per channel unit based on the equations in Dolloff et al. (1993). The fork length (FL) of fish caught by electroshocking was measured to the nearest millimeter.

Statistical procedures.—For analysis of variance (ANOVA), analysis of covariance (ANCOVA), discriminant function analysis, and calculation of correlations, the program SYSTAT 7.0 was used (Wilkinson 1997). For ANCOVA, the difference between rock types was tested, with disturbance as the covariate. Pearson's product-moment correlation coefficients are reported for all correlations, and probabilities were calculated with the Bonferroni adjustment (Wilkinson 1997). To overcome nonnormality, means of active-channel and water surface widths were calculated from square-root-transformed data.

Results

Channel Morphology and Rock Type

Mean channel gradients in basalt (0.025 m/m) were twice those in sandstone (0.012 m/m) for drainage basins of the same area (Table 1). At comparable streamflows, the mean water surface widths were not different between rock types (Table 1). However, mean active-channel width was marginally wider in basalt than in sandstone.

The amount of pool, glide, and riffle habitat reflected the steeper channel gradients in basalt. Stream segments in basalt had fewer pools than those in sandstone, but similar numbers of glides and riffles (Table 2). Also, streams in basalt had only half the length of pool habitat of streams in sandstone, but more than twice the length of riffle habitat, largely because riffles were longer in basalt (Table 2). These differences in channel morphology showed no relationship with disturbance as a covariate ($P \geq 0.677$). Percentage of the channel length as riffle was closely correlated with channel gradient in basalt ($r = 0.98$, $P = 0.004$, $N = 5$) but not in sandstone ($r = 0.48$, $P = 0.409$, $N = 5$).

Dominant substrate size was larger in basalt than in sandstone, and larger in riffles than in pools or glides (Figure 2). Mean size of the dominant substrate in basalt riffles corresponded to large cob-

TABLE 2.—Mean number and percentage ±95% confidence limits of pools, glides, and riffles in Oregon Coast Range streams in basalt and sandstone areas, as determined at the same discharges in 1988. The *P*-value is the ANOVA determination of the probability that the means are the same between rock types; $N = 5$ streams in each rock type.

Habitat type	Rock type		*P*
	Basalt	Sandstone	
	Number in 3 km		
Pool	53 ± 11	87 ± 28	0.014
Glide	50 ± 12	60 ± 12	0.145
Riffle	80 ± 12	70 ± 18	0.240
	Percentage by length		
Pool	24 ± 7	47 ± 9	<0.001
Glide	27 ± 5	33 ± 4	0.036
Riffle	50 ± 9	20 ± 6	<0.001

bles (length of median axis, 128–255 mm) and appeared to be related to disturbance. Riffle substrate in basalt became coarser with increasing disturbance, whereas in sandstone it became finer (Figure 3). The relationship between mean size of the dominant substrate in riffles in phi units and percent disturbance for each rock type was $y = -7.53 + 0.00654x - 0.000150x^2$ for basalt ($r^2 = 0.88$, $P = 0.018$, $N = 5$) and $y = -7.05 - 0.00683x + 0.000174x^2$ for sandstone ($r^2 = 0.98$, $P = 0.002$, $N = 5$).

Rock type appeared to influence stream discharge; streamflows in summer receded more severely in the sandstone streams than in the basalt streams. Mean water surface width was greater in basalt than in sandstone in 1987, consistent with the higher discharges in basalt streams (Table 3). Mean October streamflow in basalt was 4.62 $L \cdot s^{-1} \cdot km^{-2}$ in 1987 and 5.91 $L \cdot s^{-1} \cdot km^{-2}$ in 1988, and mean October streamflow in sandstone was 0.11 $L \cdot s^{-1} \cdot km^{-2}$ in 1987 and 0.99 $L \cdot s^{-1} \cdot km^{-2}$ in 1988. Sections of the surveyed segments of Franklin and Big creeks were completely dry in 1987. The summer of 1987 was particularly dry; between 21 and 30 October, the unregulated Wilson River near Tillamook and the Siletz River at Siletz had 7-d duration low flows with 50-year recurrence intervals (U.S. Geological Survey record; Wellman et al. 1993).

Discharge for Beaver Creek, the coastal sandstone stream, was lower than for any basalt stream but was greater than the other sandstone streams, suggesting that there is an interaction between rock type and distance inland. Stream discharge was not influenced by disturbance (ANCOVA; $P = 0.987$). Stream discharge receded severely in 1987 as a result of the long, dry summer, whereas discharge recessions were less severe in 1988 (Table 3). By the end of the summer 1987, many riffles in sandstone streams were completely dry, with water remaining mostly in residual pools. The ranges of mean annual precipitation in the vicinity of the stream basins between 1980 and 1999 for the two

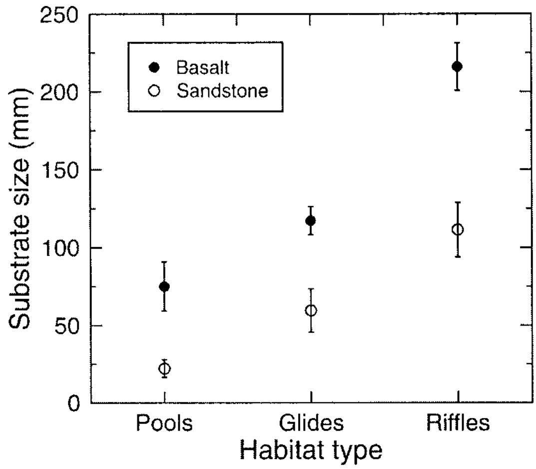

FIGURE 2.—Means and 95% confidence intervals of the dominant substrate sizes in pools, glides, and riffles in basalt and sandstone streams in the Oregon Coast Range.

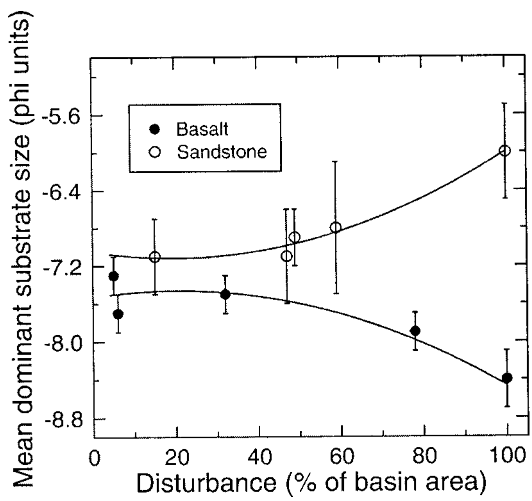

FIGURE 3.—Relationship of the mean size of dominant substrate in riffles to the percentage of basin area disturbed by fire and timber harvest in basalt and sandstone streams in the Oregon Coast Range. The mean phi size of substrate is the negative of the $\log_2$ transformation of the length (mm) of the median axis (Krumbein 1938). Vertical bars are 95% confidence intervals.

TABLE 3.—Mean water surface width, stream discharge, pool frequency, loading of large woody debris (LWD), and number of debris scour pools in basalt and sandstone streams in the Oregon Coast Range. The probability (*P*) of similarity of means between rock types was determined by ANCOVA, with disturbance as the covariate. Within rock types, basins are listed in order of increasing disturbance (i.e., timber harvest or fire followed by salvage logging).

Stream and statistic	Mean water surface width in 1987[a] (m)	Stream discharge in October ($L \cdot s^{-1} \cdot km^{-2}$)		Pool frequency in Jun–Sep 1988 (number/100 m)	Percentage of channel units with bedrock as the dominant substrate	Abundance of LWD[b]		Number of debris scour pools per 100 m	Mean active-channel width (m)
		1987	1988			(pieces/100 m)	(pieces/m^2)		
Basalt									
Bob	4.6	2.73	6.14	1.68	8.6	23.1	0.021	0.27	11.0
Rock	4.7	5.13	8.15	1.90	5.3	19.7	0.017	0.28	11.6
Tenmile	4.6	5.28	3.81	1.36	6.0	18.3	0.019	0.17	9.7
Cape	5.5	5.33	7.96	2.11	9.3	43.7	0.035	0.16	12.4
Wilson			3.48	1.81	13.0	12.5	0.010	0.00	12.6
Means	4.8	4.62	5.91	1.77	8.4	23.4	0.020	0.18	11.5
Sandstone									
Franklin	3.3	0.14	0.21	4.13	4.9	21.7	0.019	0.20	11.4
Halfway	3.8	0.26	0.94	2.42	48.4	37.0	0.037	0.27	9.9
Beaver			3.25	1.95	47.0	18.6	0.019	0.10	9.7
Paradise	3.6	0.05	0.45	2.82	62.7	18.0	0.019	0.20	9.4
Big	3.2	0.00	0.12	2.76	45.5	18.0	0.020	0.06	9.2
Means	3.5	0.11	0.99	2.82	41.7	22.6	0.023	0.17	9.9
P-value									
Rock type	0.004	0.001	0.005	0.034	0.013	0.911	0.682	0.779	0.059
Disturbance	0.417	0.459	0.447	0.676	0.227	0.996	0.948	0.007	0.751

[a] Calculated from square-root-transformed widths.
[b] Minimum size of wood was 0.1 m in diameter × 2 m long.

rock types overlapped substantially (range, 183–313 cm for basalt and 133–217 cm for sandstone).

The difference between rock types was tested for several variables by ANCOVA, with disturbance as the covariate. Pool frequency, as measured at similar streamflows between June and September in 1988, was greater in sandstone than in basalt but was not related to disturbance (Table 3). Bedrock was more predominant in sandstone than in basalt, and its occurrence was not influenced by disturbance. Abundance of large woody debris in the active channel was also not different between rock types and was not influenced by disturbance. However, individual pieces of wood were generally shorter and less effectively positioned in the channel in Big Creek and the Wilson River compared to streams with little logging. As a consequence, there were fewer debris scour pools (DSPs) in the disturbed streams, but the frequency of DSPs was not different between rock types (Table 3).

Habitat-Specific Densities

There was a fourfold difference in the bias correction factors for dive counts ($\hat{R}$) among the species, age-classes, and habitats (Table 4). The correction factors were lowest for juvenile coho salmon and age-0 trout in pools, and highest for steelhead aged 1+ in shallow-water habitats (glides and riffles; Table 4). Even where estimates of $\hat{R}$ were greater than 1.5, the correlation between dive counts and population estimates was generally high. However, age-1+ cutthroat trout in pools had the poorest correlation (Table 4) because population estimates were three or fewer fish in each channel unit. There was no difference between the mean $\hat{R}$ values for the two rock types (ANOVA $P = 0.098$); therefore, $\hat{R}$ values were derived from combined data from both rock types.

Comparisons between dive counts and population estimates were not valid for juvenile coho salmon in riffles or for age-1+ cutthroat trout in glides and riffles because there were too few fish in each channel unit surveyed in one or both rock types. To rectify this, we used the $\hat{R}$ value for coho salmon in glides for coho salmon in riffles and the $\hat{R}$ values for age-1+ steelhead in glides and riffles for age-1+ cutthroat trout in the same habitats. These substitutions made little difference to the overall density estimates because coho salmon were seldom seen in riffles and cutthroat trout occurred at low densities throughout. Also, the behavior of cutthroat trout in riffles in response to

TABLE 4.—Bias correction factors ($\hat{R}$) for dive counts of salmonids in Oregon Coast Range streams by species, age-class (ages 0 and age 1 and older [age 1+]), and habitat type showing Pearson correlations (r) between dive counts and removal electroshocking population estimates. The $\hat{R}$ values are the mean removal electroshocking population estimates divided by the mean dive counts for each habitat stratum, species, and age-class; N is the number of comparisons with valid population estimates contributing to each estimate. Age-0 trout comprise both steelhead and cutthroat trout.

Species and age class	Population estimate	Dive count	$\hat{R}$[a]	N	r	Bonferroni P
Pools						
Juvenile coho salmon	173	149	1.16	15	0.92	<0.001
Age-0 trout	336	303	1.21	17	0.98	<0.001
Age-1+ steelhead	73	39	1.87	16	0.79	<0.001
Age-1+ cutthroat trout	24	15	1.60	16	0.59	0.016
Glides						
Juvenile coho salmon	19	8	2.38	14	0.88	<0.001
Age-0 trout	241	159	1.52	14	0.86	<0.001
Age-1+ steelhead	10	4	2.50	13	0.84	0.001
Age-1+ cutthroat trout	3	1		12		
Riffles						
Juvenile coho salmon	1	0		12		
Age-0 trout	121	68	1.78	12	0.96	<0.001
Age-1+ steelhead	27	5	5.40	11	0.94	<0.001
Age-1+ cutthroat trout	1	0		12		

[a] Empty cells indicate that some species and age-class were found in too few channel units to calculate a meaningful $\hat{R}$.

the diver was the same as that of steelhead, so the $\hat{R}$ values are likely to be similar.

Mean number of fish per channel unit varied widely between habitat types and rock types, and in some instances, between years (Table 5). These values were the basis of extrapolation of the dive counts to total fish numbers. Age-0 trout were spread throughout all habitat types but were especially abundant in riffles in basalt. Juvenile coho salmon were largely restricted to pools but also occupied glides in sandstone. Age-1+ steelhead occupied all habitats but were three to eight times more abundant in pools in basalt than in sandstone. Riffles were especially important for age-1+ steelhead, partly because of the large proportion of this habitat type in basalt. Age-1+ cutthroat trout were much more abundant in basalt streams than in sandstone and were restricted to pools in sandstone.

Salmonid Density and Rock Type

To compare the differences between rock types, we calculated mean salmonid densities by combining results from both years, with results from the Wilson River and Beaver Creek excluded. Mean total densities of salmonids of all species and ages were not discernibly different between rock types because of the variability among streams (Table 6). However, the density of juvenile coho salmon was 10 times greater in sandstone than in basalt. The densities of age-1 fish, however, were greater in basalt than in sandstone.

Fish densities were broadly similar between years within rock types, but in basalt streams there were about three times more juvenile coho salmon in 1987 than in 1988 (Table 7). The streams added in 1988 were compared with the streams originally surveyed. The North Fork Wilson River had greater numbers of age-0 trout than other basalt streams, but similar densities of other species and age-classes (Table 7). Salmonid densities in the North Fork Beaver Creek were similar to those in other sandstone streams, apart from greater numbers of age-1+ fish.

Length-frequency analyses indicated that there were several age-classes of steelhead and cutthroat trout in the study streams but that coho salmon were predominantly age 0. Length-frequency and scale analyses were used to identify the age-0 trout caught by electroshocking in August and September. These fish ranged from 34 to 90 mm FL (mean ± 95% confidence interval, 61.0 ± 0.9 mm, N = 659). Coho salmon ranged from 48 to 94 mm FL (mean, 72.1 ± 1.1 mm, N = 259). Mean size of coho salmon was significantly greater (ANOVA; $P < 0.001$) than the mean size of age-0 trout.

Differences in the sizes of the larger basins of which the study segments were a part, or in dis-

TABLE 5.—Mean corrected dive counts of salmonids in pools, glides, and riffles in eight Oregon Coast Range streams in basalt and sandstone areas in 1987 and 1988 excluding the Wilson River and Beaver Creek. Mean numbers of fish per channel unit are the products of the uncorrected dive counts and the bias correction estimates ($\hat{R}$) from Table 3 and represent the grand means by rock type calculated according to the procedures in Dolloff et al. (1993).

Channel units (*N*), species, and age-class	Mean number per channel unit		
	Pools	Glides	Riffles
Basalt 1987			
N	45	40	30
Juvenile coho salmon	15.6	3.3	1.1
Age-0 trout	12.4	18.5	27.6
Age-1+ steelhead	6.8	5.6	15.8
Age-1+ cutthroat trout	3.2	2.1	1.4
Basalt 1988			
N	47	40	30
Juvenile coho salmon	6.6	1.3	0.6
Age-0 trout	13.6	18.4	32.9
Age-1+ steelhead	9.9	5.4	14.2
Age-1+ cutthroat trout	3.5	1.8	3.8
Sandstone 1987			
N	78	42	22
Juvenile coho salmon	55.0	63.3	8.8
Age-0 trout	7.3	8.6	4.5
Age-1+ steelhead	2.3	4.3	0.0
Age-1+ cutthroat trout	0.9	0.1	0.0
Sandstone 1988			
N	76	46	20
Juvenile coho salmon	36.6	31.1	2.6
Age-0 trout	9.9	13.4	5.2
Age-1+ steelhead	1.3	0.7	0.5
Age-1+ cutthroat trout	0.6	0.0	0.0

tance from the coast, could have been confounding influences on the salmonid assemblages. To investigate these possible flaws, a discriminant function based on the areal densities of age-0 trout and juvenile coho salmon and age-1+ steelhead and cutthroat trout was calculated for 1987 and 1988 for each stream (Wilkinson 1997). Rock type was used as the grouping variable, and the streams from which the discriminant function was derived excluded the Wilson River and Beaver Creek. The resulting canonical discriminant function was:

$$\begin{aligned}\text{Canonical score} &\\ = 0.134 &+ 0.256(\text{age-0 trout number/m}^2)\\ &+ 1.945(\text{juvenile coho salmon number/m}^2)\\ &- 4.147(\text{age-1+ steelhead number/m}^2)\\ &- 27.54(\text{age-1+ cutthroat trout number/m}^2).\end{aligned}$$

Streams in basalt and sandstone were classified 100% correctly using this function ($N = 16$, $P = 0.033$). Canonical scores calculated from this function were positive for sandstone streams and negative for basalt streams (Table 7).

Both streams that were added to the study in 1988 (Wilson River and Beaver Creek) showed patterns of salmonid abundance similar to those of other streams in the respective rock types. The canonical score calculated from the discriminant function was −0.037 for the Wilson River (basalt) and 0.187 for Beaver Creek (sandstone), consistent with the scores for the original streams (Table 7). The variables most strongly correlated with the canonical scores were channel gradient ($r = -0.69$; $P = 0.002$), density of juvenile coho salmon ($r = 0.83$; $P < 0.001$), density of age-1+ steelhead ($r = -0.74$; $P = 0.001$), and density of age-1+ cutthroat trout ($r = -0.82$; $P = 0.001$).

Influence of Disturbance and Rock Type

The relation of age-0 salmonid abundance (trout and coho salmon combined) to disturbance was not consistent. In 1988, there were more age-0 salmonids in heavily disturbed streams than in streams with little disturbance (Figure 4; Table 7). There was no difference between rock types (ANCOVA: $P = 0.531$; $N = 10$), but abundance was significantly related to disturbance ($P = 0.031$ for disturbance as a covariate). In 1987, the abundance

TABLE 6.—Mean density ± 95% confidence limits of salmonids in basalt and sandstone streams in the Oregon Coast Range excluding the Wilson River and Beaver Creek. Values are for four streams in each rock type in 1987 and 1988 combined ($N = 8$). The *P*-value is the ANOVA determination of the probability that the means are the same between rock types.

Species and age-class	Density (number/m^2)		*P*
	Basalt	Sandstone	
All species and ages	0.458 ± 0.239	0.812 ± 0.424	0.108
Juvenile coho salmon	0.048 ± 0.042	0.624 ± 0.429	0.007
Age-0 trout	0.257 ± 0.123	0.155 ± 0.084	0.126
Age-1+ steelhead	0.119 ± 0.085	0.027 ± 0.018	0.023
Age-1+ cutthroat trout	0.033 ± 0.021	0.006 ± 0.003	0.008

TABLE 7.—Salmonid densities in basalt and sandstone streams in the Oregon Coast Range in summer 1987 and 1988. The canonical score was derived from the abundance of each salmonid category by rock type. Within rock types, basins are listed in order of increasing disturbance (i.e., timber harvest or fire followed by salvage logging).

	Density ($fish/m^2$)					
Stream	Age-0 trout	Juvenile coho salmon	Age-1+ steelhead	Age-1+ cutthroat trout	All species	Canonical score
Basalt 1987						
Bob	0.10	0.016	0.022	0.008	0.15	−0.12
Rock	0.27	0.053	0.081	0.039	0.44	−1.10
Tenmile	0.20	0.038	0.029	0.016	0.28	−0.30
Cape	0.40	0.159	0.311	0.043	0.91	−1.93
Sandstone 1987						
Franklin	0.33	0.618	0.067	0.011	1.03	0.84
Halfway	0.02	0.709	0.033	0.006	0.77	1.22
Paradise	0.10	0.386	0.050	0.011	0.55	0.40
Big	0.14	1.802	0.008	0.003	1.96	3.56
Basalt 1988						
Bob	0.03	0.004	0.041	0.012	0.08	−0.35
Rock	0.24	0.000	0.162	0.079	0.49	−2.65
Tenmile	0.43	0.063	0.204	0.053	0.75	−1.94
Cape	0.40	0.047	0.106	0.015	0.56	−0.53
Wilson	1.65	0.000	0.077	0.010	1.74	−0.04
Sandstone 1988						
Franklin	0.20	0.065	0.013	0.005	0.29	0.12
Halfway	0.09	0.541	0.012	0.002	0.65	1.10
Beaver	0.14	0.424	0.062	0.020	0.65	0.19
Paradise	0.09	0.443	0.022	0.005	0.56	0.79
Big	0.25	0.428	0.008	0.004	0.70	0.89

of age-0 salmonids was not associated with either rock type ($P = 0.160$) or disturbance ($P = 0.136$).

The abundance of age-1+ trout (steelhead and cutthroat trout combined) was different between rock types in 1988 (ANCOVA; $P = 0.036$) but not in 1987 (ANCOVA; $P = 0.173$). The mean density (±1 SE) of age-1+ trout in 1988 was 0.152 ± 0.041 $fish/m^2$ for basalt and 0.031 ± 0.013 $fish/m^2$ for sandstone ($N = 5$ for each rock type). In 1987, Cape Creek had far more age-1+ steelhead than any other stream (Table 7). The abundance of age-1+ trout was unrelated to disturbance (ANCOVA with disturbance as a covariate: $P = 0.286$ in 1987 and $P = 0.443$ in 1988).

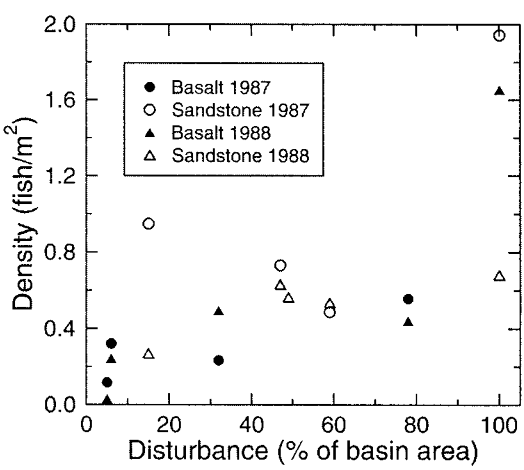

FIGURE 4.—Combined densities of juvenile coho salmon and age-0 steelhead and cutthroat trout in 1987 and 1988 in basalt and sandstone streams in the Oregon Coast Range versus the percentage of basin area disturbed by fire and timber harvest.

Discussion

Physical Habitat

In these similar-sized basins, rock type had a profound influence on substrate size and channel gradient. Substrate was larger in basalt than in sandstone, consistent with other comparisons of rock types (e.g., Hack 1957), and channel gradients in basalt were, on average, twice those in sandstone. Consequently, riffle habitat dominated streams in basalt, whereas pools dominated streams in sandstone. Small Oregon Coast Range streams (drainage area, 0.87–3.47 km^2) showed a similar result (Connolly and Hall 1999), with mean gradient in small streams in basalt (0.0536 m/m; $N = 9$) steeper than that of small streams in sandstone (0.0336 m/m; $N = 7$; ANOVA; $P = 0.010$).

Rock type also influenced summer stream discharge and water surface width. Streamflows receded much more severely in sandstone basins than in basalt basins. Rock type is known to influence water yield in the Oregon Coast Range; because of its fractured, jointed nature, basalt yields more water than sandstone (Frank and Laenan 1977; Curtiss et al. 1984). In addition, the riparian zones in sandstone were generally dominated by alder and maple. Alder has been implicated in lowered summer streamflows in response to timber harvest in the Oregon Cascades (Hicks et al. 1991a). The coastal location of our basalt streams probably contributed some orographic rainfall that the inland sandstone streams did not receive, which might have confounded the rock type comparison. However, streamflows in the coastal sandstone stream (Beaver Creek) in October 1988 were lower than streamflows in any of our basalt streams.

Salmonid Assemblages

The salmonids responded to the differences in channel gradient that were caused by rock type. In the steeper-gradient basalt streams, with their greater proportion of riffle habitat, salmonid assemblages were dominated by steelhead and cutthroat trout. In the lower-gradient sandstone streams, with their greater proportion of pool habitat, salmonid assemblages were dominated by coho salmon. These results support our initial hypothesis that streams in basalt and sandstone have different potential capacities for salmonid communities in the long term. Similarly, in Drift Creek in the Oregon Coast Range, juvenile coho salmon were largely absent from reaches with channel gradients greater than 0.04 m/m, and the proportion of reach length composed of pools was inversely related to gradient (Schwartz 1991). Basin-scale comparisons in western Washington also showed an inverse relationship between coho salmon abundance and channel gradient estimated from maps (Sharma and Hilborn 2001). However, comparisons of watersheds over a wider scale in Alaska, British Columbia, Washington, and Oregon did not show the same relationship with channel gradient (Bradford et al. 1997).

One implication of our findings is that the restoration of salmonid habitat and efforts to maintain wild salmonid runs should recognize differences in potential capacity caused by channel morphology, and species recovery plans should be adapted accordingly. For instance, the pool habitats that juvenile coho salmon frequent can be more easily created or enhanced in low-gradient streams than in high-gradient streams. High-gradient streams naturally limit coho salmon; therefore, in such streams, habitat management should probably focus on steelhead and cutthroat trout.

The distribution of coho salmon and trout among the habitat types in our study was consistent with the known habitat preferences of juvenile coho salmon and trout (e.g., Hartman 1965; Bisson et al. 1988). The mean and range of lengths of juvenile coho salmon in our study suggest that nearly all were age 0. Juvenile coho salmon were present mainly in pools in basalt, but in sandstone, they occurred in riffles in small numbers, as well as in pools and glides (Table 5). Age-0 trout were present in all habitats in sandstone at similar abundances, but were more abundant in riffles in basalt than in pools or glides. In Lake Ontario streams in New York in June, juvenile coho salmon used deep habitats (mean depth, 0.61–0.73 m) compared to age-0 steelhead, which used shallow habitats (0.09–0.15 m; Sheppard and Johnson 1985). These depths correspond to habitats identified elsewhere as pools and riffles (Jowett 1993). In the northwestern United States, cutthroat trout used depths and velocities similar to those used by steelhead (Bisson et al. 1988).

The length and quality of riffle habitats were very different between the rock types. In sandstone, riffles are very vulnerable to reductions in discharge and thus were the first habitats to dry in summer 1987; many riffles in sandstone dried completely that summer (Hicks 1990). In basalt, large substrate size in riffles, combined with substantial summer streamflows, provided considerable habitat diversity through high relative roughness (in the sense of Thorne et al. 1985), where cobbles and boulders protruded through the water surface. High relative roughness in riffles probably caused the high value of $\hat{R}$ for age-1+ steelhead (5.40) and the inefficiency of dive counts for the larger fish.

The larger size of juvenile coho salmon than age-0 trout in our study streams is consistent with their earlier emergence (Coe 2001) and with previous observations of size differences between the species (Hartman 1965). Larger size, aggressive behavior, and tendency to school in midwater suit coho salmon well to pool habitats. Conversely, the smaller age-0 trout are more benthically oriented, seeking refuge close to the stream bed and in the interstices between cobble substrates, which makes basalt streams, with their coarse substrate and extensive riffles, ideal trout rearing habitat. In summer, age-0 steelhead are more likely to occupy riffles, whereas coho salmon occupy pools (Hartman 1965).

The density of age-0 salmonids in 1988 was positively related to disturbance in our study, but the abundance of age-1+ steelhead and cutthroat trout was unrelated to disturbance. Our study is not unusual in showing an increased abundance of juvenile salmonids in disturbed streams. Outmigrant coho salmon smolts increased in abundance following logging in Carnation Creek as a response to the higher water temperatures (Hartman and Scrivener 1990). A number of other studies have shown increased abundance of juvenile salmonids following logging (Murphy and Hall 1981; Bisson and Sedell 1984; Hall et al. 1987), but frequently such increases are short-lived. High abundance in summer was offset by low overwinter survival in logged streams in southeast Alaska (Johnson et al. 1986). Regardless of timber harvest history, the presence of woody debris improved overwinter survival in that region (Murphy et al. 1986). In the Queen Charlotte Islands, coho salmon fry in logged stream reaches had higher densities and faster growth rates than in unlogged reaches, but mass wasting and poor overwinter survival nullified any gains from logging (Tripp and Poulin 1992).

In contrast to studies in which juvenile salmonids increased in abundance after logging, the abundance of cutthroat trout in the clear-cut stream in the Alsea Watershed Study was substantially reduced following logging. Age-0 trout recovered to prelogging densities 23–30 years later. However, density of trout aged 1 and older immediately following logging was 40% of prelogging density, and 23–30 years later averaged only 20% of the prelogging value. The densities of juvenile coho salmon were largely unaffected by logging (Gregory et al., in press).

The frequency of DSPs in our study was inversely related to disturbance, whereas overall pool frequency and woody debris were unrelated to disturbance. Debris scour pools comprised only 16% or less of the total number of pools in each stream, but can be disproportionately valuable habitats because of their use in summer by juvenile coho salmon (Hicks 1990; Rosenfeld et al. 2000). Our findings differ from those of Bilby and Ward (1991), who found that streams in old-growth forest had greater pool frequency than streams in clear-cuts or second-growth forest, even though our range of wood loadings were similar for equivalent stream width. This suggests that wood was not the most important pool-forming factor in our streams, where wood loadings were generally low by the criterion of Montgomery et al. (1995) (<0.03 pieces/m^2). The authors concluded that wood was a major factor in pool formation in southeast Alaska and Washington.

Pool frequency can be reduced by timber harvest (Bisson et al. 1992), and Reeves et al. (1993) argued that loss of pool habitat and replacement with riffle habitat caused by logging favors age-0 trout at the expense of age-1+ salmonids. In small Oregon Coast Range streams, density of large woody debris appeared to best explain the variation in abundance of cutthroat trout above barriers, in the absence of other salmonids (Connolly and Hall 1999).

We did not identify the factors that controlled the abundance of age-0 salmonids, but disturbance appeared to cause different physical responses in the two rock types. Riffle substrate was coarser in basalt but finer in sandstone in highly disturbed basins. Low flows in summer appear to have controlled salmonid abundance in sandstone, but were unlikely to have been a limiting factor in basalt. Drought in late summer and autumn 1987 severely reduced the streamflows in sandstone (Table 3), and the ratio of the abundance of age-1+ salmonids in 1988 to the abundance of age-0 trout in 1987 (a crude measure of overwinter survival) was positively correlated with streamflows in October. Whether this result is a general feature of sandstone streams or was merely the response of these particular streams to an extreme event, we cannot tell.

Stochastic events, such as extreme climatic events (droughts and storms), and variable salmonid escapement could swamp the effects of geology and land management on salmonid abundance in streams. The coho salmon runs along the Oregon coast north of Cape Blanco during our surveys were very depressed, with returns per spawner below replacement (Weitkamp et al. 1995). The extreme and consistent differences in juvenile coho salmon abundance between rock types, despite the depressed state of the Oregon coho salmon stocks, suggest that the basalt and sandstone rock types do indeed have different capacities for salmonids.

Streamflow can control the extent of the upstream spawning migration of salmonids (Everest et al. 1985). Coho salmon adults normally return to the mid-Coast Range streams of Oregon from late October through January (Weitkamp et al. 1995). The drought in 1987 was at its most severe in October. Low flows blocked the access of spawning coho salmon to the middle reaches of Franklin Creek, causing a low abundance of juvenile coho salmon in the following summer (1988). Our study streams in sandstone appear to offer good habitat for age-0 salmonids in spring and early summer, but juvenile survival in late summer and the upstream extent of spawning adults in these streams can be severely reduced in dry years.

Our work highlights the difficulties in designing studies that will show unambiguous responses to disturbance. The streams selected for such studies must have adequate basin areas and freedom from barriers to fish migration so that the full expression of salmonid assemblages for the region is possible. These basins should be of similar size so that the hydrological responses are comparable. Also, landscape factors, such as underlying rock type and topography, need to be as similar as possible within the sites that are to be grouped on this basis. Finally, the disturbance regime needs to be comparable between the groups, especially with respect to its timing, and the sites should be adequately replicated. Meeting all of these requirements in practice is not possible, so ultimately any study of this type will be a compromise between the idealized objectives and the realities of the available sites and study resources.

In conclusion, this study has also shown the importance of underlying rock type in determining the capacity of Oregon Coast Range streams for different salmonid communities. Future studies need to recognize the influence of rock type on channel gradient, substrate, and stream habitat, which are likely to ultimately control the salmonid assemblages. Disturbance may also accentuate the natural differences in salmonid assemblages, providing conditions that favor age-0 trout in basalt and juvenile coho salmon in sandstone.

Acknowledgments

We would like to thank the New Zealand Government and the U.S. Forest Service, Pacific Northwest Research Station, for financial support during this study. The study was undertaken as part of the requirements of the degree of Ph.D. for B.J.H., and the manuscript benefited considerably from the comments of G. Reeves and D. Hankin. We also thank D. Bateman, S. Paustian, and an anonymous reviewer for their valuable comments. J. Williams of the U.S. Geological Survey, Oregon, helped with the low-flow analysis.

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