

Stream Ecosystem Recovery Following a Catastrophic Debris Flow¹

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We studied recovery processes for 3 yr in Quartz Creek (Cascade Mountains, Oregon), a third-order stream catastrophically impacted by a February 1986 debris flow for which both predisturbance data and an upstream control reach were available. The debris flow altered channel geomorphology and destroyed riparian vegetation for 500 m, resulting in a reach with short, disordered channel units, low hydraulic retention, and an open canopy. High irradiance levels and reduced grazing by macroinvertebrates contributed to rapid accrual of benthic algae in the disturbed reach, which formed the bioenergetic basis for ecosystem recovery. Macroinvertebrates (mostly herbivores) recovered to upstream densities and taxonomic richness within 1 yr, although effects on community structure persisted into the second year. Cutthroat trout (*Oncorhynchus clarki*) populations were locally decimated by the disturbance, but by the following year, recruitment of young-of-the-year trout into the reach exceeded that of the upstream reach and populations had recovered to predisturbance densities. Despite the general rapid recovery of the biota within the disturbed reaches, most populations showed broad temporal fluctuations in abundance, suggesting that ecosystem stability was diminished by the debris flow. Long-term monitoring of Quartz Creek may yield additional insight into the role of episodic disturbance in stream ecosystems.

Nous avons étudié durant 3 ans les processus de rétablissement du ruisseau Quartz, situé dans les montagnes Cascade en Oregon, un cours d'eau de troisième ordre durement touché par une coulée de débris en février 1986. Des données sur ce cours d'eau prises avant cet événement de même que l'existence d'un tronçon non touché situé en amont pouvant servir de témoin ont facilité cette étude. La coulée de débris a transformé la géomorphologie du lit et a détruit la végétation riparienne sur 500 m; dans une partie du cours d'eau, elle a ainsi laissé une série de courts canaux désorganisés, réduit passablement la rétention hydraulique et dévasté le couvert végétal. Les taux élevés de rayonnement solaire et la diminution du broutage par les macroinvertébrés ont contribué à l'accroissement rapide de la quantité d'algues benthiques dans le tronçon perturbé; ces algues ont joué un rôle bioénergétique clé dans le rétablissement de l'écosystème. Les macroinvertébrés (surtout herbivores) ont retrouvé en une année les mêmes densités et la même diversité taxonomique que dans le tronçon témoin situé en amont, mais la structure des communautés n'était pas encore rétablie après la première année. En certains endroits, les populations de truite fardée (*Oncorhynchus clarki*) ont été décimées par cette perturbation, mais l'année suivante, le recrutement de jeunes de l'année y était supérieur à celui du tronçon témoin, produisant une densité de population équivalente à celle d'avant la coulée de débris. Bien que de façon générale le biote des secteurs touchés s'est rétabli rapidement, les abondances de la plupart des populations ont montré des fluctuations temporelles importantes, ce qui laisse entendre que la stabilité de l'écosystème a été réduite. La surveillance à long terme du ruisseau Quartz pourrait nous fournir d'autres renseignements sur les effets des perturbations occasionnelles sur l'écosystème des cours d'eau.

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Disturbance is a major factor determining the physical and biological organization of ecosystems (Connell 1978; Pickett and White 1985). A disturbance generally is defined as a discrete event that disrupts population, community, or ecosystem structure, often by changing resource abundance or the physical environment (Sousa 1984; Resh et al. 1988). In stream ecosystems, natural disturbance often is generated by floods of sufficient magnitude to scour attached microbiota from sediments (Fisher et al. 1982), remove or kill benthic macroinvertebrates (Siegfried and Knight 1977), and displace fish and other vertebrates (Meffe 1984). However,

because annual flooding is a normal event in most streams, many lotic organisms are adapted to this regular disturbance through behavioral features, life-history adjustments, or reproductive traits (Resh et al. 1988).

Catastrophic disturbance, such as severe hurricanes or intense wildfires, may overwhelm biotic resistance and elicit profound changes in ecosystem structure and function (Connell 1978). In streams, catastrophic disturbance is exemplified by debris flows (sometimes called debris torrents), which are mass movements of sediment and debris down stream channels that greatly alter both the streambed and adjacent riparian zone (Swanson et al. 1987). Unlike floods, which occur with some regularity in most streams (e.g. McElravy et al. 1989), debris flows are rare, unpredictable events (>50 yr recurrence interval; Swanson et al. 1987) that can severely affect aquatic biota.

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We studied recovery processes for 1 yr in Quartz Creek (Cascades Mountains, Oregon), a third-order stream catastrophically impacted by a February 1989 debris flow for which both pre-disturbance data and an upstream control reach were available. The debris flow altered channel geomorphology and destroyed riparian vegetation for 500 m, resulting in a reach with short, filamentous channel units, low instream vegetation, and an open canopy. High instream levels and rapid turnover of instream organisms resulted in rapid accrual of biomass along the disturbed reach, which formed the base for ecosystem recovery. Although instream biomass recovered to upstream levels and taxonomic richness within 1 yr, although effects on community structure persisted into the second year. Channel width, channel depth, and instream velocity were locally disturbed by the debris flow, but by the following year, settlement of young-of-the-year trout and other species exceeded that of the upstream reach and populations had recovered to pre-disturbance densities. Despite the general rapid recovery of the reach within the disturbed reaches, most populations showed broad temporal fluctuations in abundance, suggesting that ecosystem stability was diminished by the debris flow. Long-term monitoring in Quartz Creek may yield additional insight into the role of episodic disturbance in stream ecosystem recovery following a catastrophic debris flow.

Il nous avons étudié durant 1 an les processus de rétablissement de l'écosystème de la rivière Quartz, une rivière de troisième ordre des Cascades en Oregon, au cours d'un événement catastrophique qui a eu pour effet de modifier les caractéristiques de la rivière sur une distance de 500 m. Les données sur ce cours d'eau nous ont permis de comparer les caractéristiques de la rivière avant et après le débordement de la rivière. Le cours de la rivière a été affecté par le débordement de la rivière, ce qui a entraîné une réduction de la végétation riparienne et une modification de la géomorphologie du lit. Le débit de la rivière a également été affecté, ce qui a entraîné une augmentation de la biomasse le long du cours d'eau. Les niveaux élevés de biomasse le long du cours d'eau ont entraîné une accrual rapide de la biomasse le long du cours d'eau. Bien que la diversité taxonomique se soit rétablie à des niveaux supérieurs à ceux de la rivière contrôlée, les effets de la catastrophe ont persisté pendant plus d'un an. La largeur du chenal, la profondeur et la vitesse de l'eau ont été localement perturbés par le débordement de la rivière, mais au cours de l'année suivante, le recrutement de jeunes poissons et d'autres espèces a dépassé celui de la rivière contrôlée. Malgré le rétablissement rapide de la rivière dans les zones touchées, la plupart des populations ont montré de larges fluctuations d'abondance au cours de l'année. Le suivi à long terme de la rivière Quartz pourrait nous fournir des renseignements sur les effets des perturbations catastrophiques sur l'écosystème des cours d'eau.

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Catastrophic disturbance, such as severe hurricanes or debris avalanches, may overwhelm biotic resistance and elicit profound changes in ecosystem structure and function (Connell 1978). In streams, catastrophic disturbance is exemplified by debris flows (sometimes called debris torrents), which are mass movements of sediment and debris down stream channels that greatly alter both the immediate and adjacent riparian zone (Wasson et al. 1987). Lentic floods, which occur with some regularity in main streams (e.g. McHenry et al. 1989), differ from debris flow, catastrophic events (>50% reduction instream biomass) (Wasson et al. 1987) that can severely affect aquatic biota.

Disturbance is a major factor determining the physical and biological organization of ecosystems (Connell 1978; Pickett and White 1985). A disturbance generally is defined as a discrete event that disrupts population, community, or ecosystem structure, often by changing resources abundance or the physical environment (Sousa 1984; Keddy et al. 1985). In stream ecosystems, natural disturbances often are generated by floods of sufficient magnitude to scour streambeds, dislodge instream sediments (Fisher et al. 1981), remove or kill benthic macroinvertebrates (Siegfried and Knight 1977), and displace fish and other vertebrates (Muth 1984). However,

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In montane regions of the Pacific Northwest, major rainstorms can trigger landslides that deliver large pulses of sediment and debris to stream channels (Swanston and Swanson 1976; Swanson and Lienkaemper 1978). Landslides that enter small, steep tributaries often create a slurry of soil, water, boulders, and woody debris that travels down the channel as a debris flow. Debris flows may then enter mainstem reaches, often increasing in size as they mobilize materials already present in the channel. These flows can exceed 10 000 m³ in volume and travel distances ranging from metres to kilometres, depending on local conditions, at speeds greater than 10 m/s (Swanson et al. 1987). Debris flow usually stop where the channel widens, the gradient declines, or constrictions impede their movement, often terminating in a large accumulation of debris.

Although landslides typically affect <1% of a watershed in a particular episode, debris flows may influence >10% of the channel network because of their ability to move down stream courses (Swanson et al. 1987). Debris flows may scour channels down to bedrock, rearrange the existing streambed, or deposit new material on top of older sediment. Consequently, debris flows are major disturbances worldwide for streams in steep terrain or unstable geology (Swanson et al. 1987). In the forested landscapes of the Pacific Northwest, debris flow frequencies have increased due to logging, road and landing construction, inadequate road drainage, and other land-use practices that reduce hillslope stability and accelerate mass wasting (Swanson et al. 1987). However, the direct effects of debris flows on aquatic and riparian resources rarely have been evaluated.

In this paper, we report the effects of a debris flow on important physical, chemical, and biological attributes of Quartz Creek, a third-order stream in the Cascade Mountains of Oregon, USA. This stream had been studied intensively several years prior to the event and thus predisturbance information existed to help assess disturbance effects and rates of ecological recovery. Our objectives were to (1) document ecosystem recovery for 3 yr following the debris flow, (2) compare pre- and postdisturbance conditions in Quartz Creek, (3) relate patterns of biotic recovery to physical features of the environment, and (4) evaluate factors controlling rates of ecosystem recovery.

Study Area

Quartz Creek is a third-order stream located in the McKenzie River drainage on the west slope of the Cascade Mountains in Oregon and adjacent to the H. J. Andrews Experimental Forest (Fig. 1). The stream drains a 12-km² basin of mixed second-growth forest of Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*). Most of the lower basin was salvage logged in the 1940's following wildfire, although some recent harvest has occurred in upper portions of the basin. Quartz Creek flows approximately 6 km with an average gradient of 5% before emptying into Blue River Reservoir. Baseflow discharge ranges from about 0.05 m³/s in summer to about 1.0 m³/s in winter. Elevation varies from 370 to 1070 m within the basin and from 500 to 550 m at the study sites.

From 20 to 23 February 1986, the Quartz Creek basin received about 25 cm of rain in a 96-h period. The freezing level rose simultaneously and the intense rains melted much of the 25- to 50-cm snowpack in the area. In the early morning of 23 February 1986, the combined rain and snowmelt triggered a landslide in a clearcut near a first-order tributary to Quartz Creek (Fig. 1). The slide spilled into the tributary, traveled

about 500 m down the tributary, and swept into Quartz Creek, entraining additional woody debris, sediment, and water from the channel as it moved. Total mass of the debris flow was estimated at 5000 m³, which traveled at a velocity of between 5 and 10 m/s. The flow traveled 330 m in Quartz Creek before lodging as an accumulation of wood and sediment that spanned the stream channel. This debris dam measured about 40 m in length, 25 m in width, and 5 m in height and contained about 700 pieces of wood. A reach of about 200 m downstream of the debris dam was affected by the leading edge of the debris flow before the accumulation formed.

Upstream portions of Quartz Creek that were not affected by the debris flow experienced a major flood on 22–23 February 1986. Although Quartz Creek is not gauged for discharge, nearby stations provided some indication of flood magnitude. Two adjacent gauged streams, Lookout Creek and Blue River, had peak discharges of an estimated 8- to 10-yr average recurrence interval, based on 25 yr of hydrologic record (Friday and Miller 1984). The average return interval for the debris flow was much longer, probably in excess of 50 yr (Swanson et al. 1987).

We designated three reaches in Quartz Creek for intensive study (Fig. 1): (1) a reach *upstream* of both the tributary described above and a second tributary that had a smaller debris flow, which experienced only flooding on 22–23 February 1986, (2) the *debris flow* reach that was severely affected by both the debris flow and the flood, and (3) a reach *downstream* of the debris accumulation that was flooded and received moderate disturbance from sediment and debris that swept through before the accumulation stabilized. Reach lengths were 184 m (upstream), 276 m (debris flow), and 176 m (downstream). By chance, the debris flow occurred in a portion of Quartz Creek that had been studied during 1982–83 (Speaker 1985; Moore 1987). These previous studies provided physical and biological data on conditions prior to the debris flow.

Materials and Methods

Sampling Schedule

Water chemistry, algae, detritus, invertebrates, and fish were sampled in the three study reaches at 3- to 5-mo intervals between March 1986 and November 1988. We continue to take semiannual samples from Quartz Creek as part of the H. J. Andrews Long-Term Ecological Research Program. The sampling schedule was designed to represent seasonal conditions important to stream biota: late winter following high discharge, summer low flow period, and autumn detrital loading. Sampling was more frequent in the first year after the event to document the rapid physical and biological changes that often occur shortly after disturbance. On the first sampling date (26 March 1986), we did not sample the downstream reach; this site was added on the second sampling date (24 April 1986). Additional physical and biological parameters, including channel morphology, irradiance, hydraulics, and leaf abundance, were measured less frequently.

Physical Parameters

Geomorphology

Stream *reaches* in Quartz Creek were distinguished based on the degree of large-scale geomorphic disturbance described above. The stream channel and adjacent riparian surfaces were mapped for each reach during summer 1986. A 108-m segment

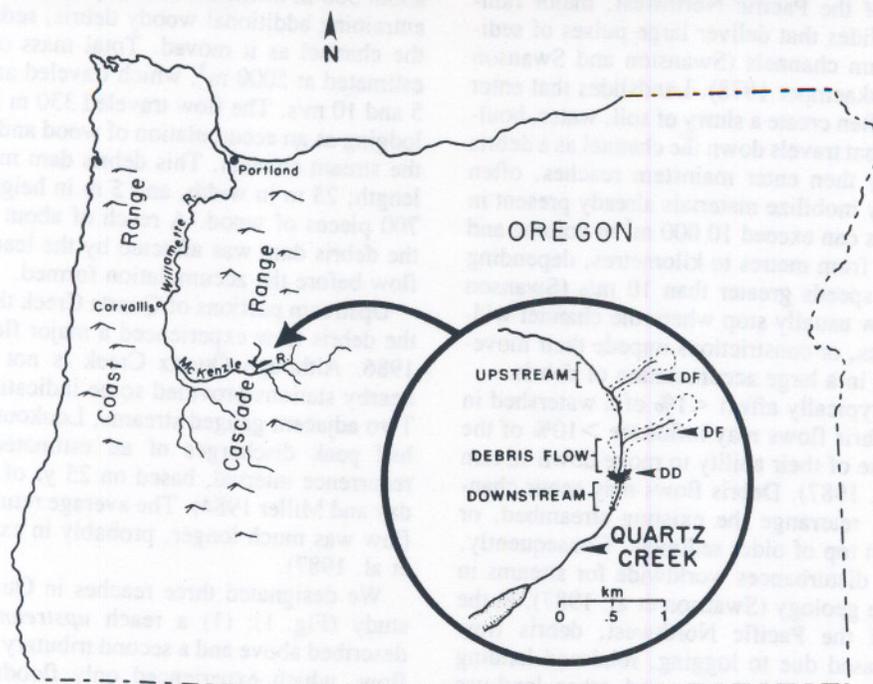


FIG. 1. Location of study sites in Quartz Creek, Oregon, USA. Dotted areas along Quartz Creek and its tributaries indicate zones of 1986 debris flow influence. DF = debris flow; DD = debris dam.

of the debris flow reach was mapped in 1983. Within the wetted channel of each reach, we determined the sequence and surface dimensions of its *channel units*. Channel units are distinct hydraulic and geomorphic features, formed during high flow, that span the channel and typically have lengths equal to several channel widths. Channel units given in increasing gradient are pools, riffles, rapids, cascades, bedrock falls, and boulder steps (see Grant 1986 and Gregory et al. 1991 for further description). For each channel unit, we then visually estimated the percent surface area of *subunits*. Subunits are discrete patches comprising each unit that are controlled by local structural and hydraulic features; these include stream margins, backwaters, secondary channels, and boulder eddies (grouped into "edge" habitats), pools ("slow-water" habitats), and riffles, chutes, and hydraulic jumps (grouped into "fast-water" habitats).

Irradiance

Light energy in the three study reaches was measured periodically from 1986 to 1988 with a Li-Cor quantum radiometer held at the water surface. Three stations within each reach were measured repeatedly.

Water chemistry

Water samples were collected on 13 occasions during 1986–88 from the three reaches and from the tributary where the debris flow started. Samples were filtered in the field, placed on ice, and analyzed within 48 h of collection. Chemical analyses focused on inorganic and organic forms of nitrogen and phosphorus. Ammonium nitrogen ($\text{NH}_4\text{-N}$) was analyzed by the hypochlorite oxidation method, and nitrate plus nitrite nitrogen ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$) was measured by the cadmium reduction technique (APHA et al. 1975). Reduced nitrogen was analyzed by Kjeldahl digestion and subsequent analysis of ammonium. Total dissolved nitrogen was calculated as Kjeldahl N + $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$. Orthophosphate ($\text{PO}_4\text{-P}$) was determined colorimetrically by the ammonium molybdate reaction, and total

phosphorus was analyzed by digestion and analysis as orthophosphate (APHA et al. 1975).

Hydraulics

We measured hydraulic features of Quartz Creek with fluorescent dye tracers. We released a known amount of fluorescein dye (generally 5 g/L, w/v) into a turbulent area of the channel. Water samples were collected 50 or 100 m downstream at 15- to 60-s intervals, depending on discharge. Dye concentration in each sample was measured with a fluorometer. Discharge was calculated based on dye dilution (Replogle et al. 1976). Hydraulic residence time (HRT) was calculated as the time required for 95% of the dye to move through the reach.

On 18 March 1987, we released dye into the upstream reach, the debris flow reach, and through the debris dam. Dye releases were conducted sequentially upstream to prevent contamination of downstream study reaches. An additional five dye releases were conducted in different sections of the debris flow reach during both summer and winter baseflow, 1986–88. Predisturbance data were provided by nine dye releases conducted in the debris flow reach during 1983 (Speaker 1985).

Biological Parameters

Organic matter

Benthic detritus was sampled using an enclosed McNeil sampler (123 cm²) driven 10 cm into the streambed. Contents of the sampler were evacuated and all detritus larger than 0.7 μm was retained using a combination of sieves and filters (Whatman GF/F). To determine ash-free dry mass (AFDM) of detritus, each sample was dried for 24 h at 55°C, weighed, combusted for 12 h at 500°C, and reweighed. On each sampling date within each reach, we collected five samples from each of riffle (= fast-water), pool (= slow-water), and backwater (= edge) habitats in a stratified random sampling design ($N = 15$ for each reach). Care was taken to distribute the samples over the entire length of each reach. Using the habitat proportions generated

TABLE 1. Amounts and proportions of stream subunits for the three study reaches of Quartz Creek in July 1986. Subunit areas were determined for reaches of 184 m (upstream), 276 m (debris flow), and 176 m (downstream). These percentages were used to calculate weighted means and variances for benthic detritus and macroinvertebrates.

Subunit	Upstream	Debris flow	Downstream
Fast-water habitat			
Total area (m ²)	411.2	548.1	407.0
Area/100 m	233.5	198.6	220.8
Percent area	53.4	50.4	53.9
Slow-water habitat			
Total area (m ²)	235.7	342.3	204.5
Area/100 m	133.8	124.0	111.0
Percent area	30.6	31.5	27.1
Edge habitat			
Total area (m ²)	123.2	197.1	143.5
Area/100 m	70.0	71.4	77.9
Percent area	16.0	18.1	19.0

from subunit estimations (Table 1), we calculated a weighted average detritus load (\bar{x}_w) and variance of the mean (s_w^2) for each reach (simplified from Krebs 1989) as

$$\bar{x}_w = \sum_{i=1}^3 p_i \bar{x}_i$$

and

$$s_w^2 = \sum_{i=1}^3 p_i^2 s_i^2/n_i$$

where p_i is the proportion of the total reach represented by habitat i , \bar{x}_i and s_i^2 are the observed mean and variance for habitat i , and n_i is the sample size for habitat i . The standard error of the weighted mean is calculated as s_w (Krebs 1989).

On 18 November 1987, we measured the densities of fallen leaves within the active stream channel. Five 1-m-wide transects were established perpendicular to the channel at random locations within each reach. Leaves were counted in every 1-m² quadrat along each transect while noting if the quadrat sampled wetted channel or nonwetted active channel (= active channel shelf).

Benthic algae

Standing crop of benthic algae was measured by extraction of the pigment chlorophyll *a*, an indicator of algal abundance. Five sets of three rocks (10–20 cm in diameter) were randomly collected from riffles of each reach on each sampling date. Rock sets were bagged, placed on ice in the field, and frozen within 8 h. Within 4 wk of collection, rocks were soaked in buffered 90% acetone for 24 h. Extracted chlorophyll *a* was measured with a spectrophotometer using the trichromatic method (Strickland and Parsons 1968). Rock surface area was determined by wrapping each rock in aluminum foil, weighing the foil, and estimating area from known areal weight of foil. This estimate was halved to adjust for surface area exposed to solar radiation (normally about 50% of the rock).

Macroinvertebrates

Benthic macroinvertebrates were sampled using a modified Hess sampler (510 cm²) with 250- μ m-mesh screen. On each sampling date, 15 Hess samples were collected from each reach using the same stratified random sampling approach described for detritus. Samples were preserved immediately in 95%

ethanol and later sorted in the laboratory. Samples visually estimated to exceed 2000 animals were subsampled (1/4 or 1/8) using a sample splitter. All invertebrates were enumerated and identified to the lowest taxonomic level possible (usually genus), except for Chironomidae and Oligochaeta, which were not identified to lower levels. Weighted average density and variance of macroinvertebrates were calculated for each reach as for detritus.

Fish populations

Only one species of fish, cutthroat trout (*Oncorhynchus clarki*) (formerly *Salmo clarki*), was found in Quartz Creek. Stream lengths of 150 m (upstream and downstream reaches) and 250 m (debris flow reach) were repeatedly sampled for trout. To determine trout population density, trout were counted by direct observation while snorkeling in March and June 1986 only whereas double-pass electroshocking was used for all subsequent estimates. During snorkeling, a diver swam upstream from the bottom to the top of the reach recording the number of trout. Fish were assigned to fry (0+ yr or young-of-the-year) or adult (1+ yr and older) age classes based on size. A second diver repeated this procedure about 1 h later. The mean of the two observations was used in population estimates; no verification with electrofishing was conducted on these two dates. During electroshocking on all later dates, sequential 50-m lengths were blocked with nets at both ends and fish were sampled using the double-pass method (Armour et al. 1983). All fish were anesthetized, measured for total length (± 1 mm), weighed for wet mass (± 0.05 g), revived, and returned to the reach. In June 1987 and June 1988, newly emerged fry were not electroshocked because their small size made them highly sensitive to shocking. However, because young fry are found almost exclusively along shallow stream margins (Moore and Gregory 1988a), we made visual fry counts within each reach. One observer walked upstream along each streambank recording the number of fry; these are probably underestimates of true fry numbers.

Statistical Analyses

Several statistical methods were used to analyze physical and biological data. For nonrepeated measures, we used analysis of variance (ANOVA) and the Student–Newmann–Keuls (SNK) multiple range procedure on log-transformed data to test for differences in means among the three reaches. For repeated measures and inventories, graphical methods were used to reveal temporal trends in abundance. Size–frequency plots of trout populations were used to follow cohorts over time. Regression techniques were used to analyze some parameters such as hydraulics. For all tests, differences were considered significant at the $p < 0.05$ level. It should be noted that because reaches were not replicated (i.e. one debris flow was studied), these tests only establish statistical differences among reaches and we cannot attribute differences solely to the disturbance.

Results

Initial Observations

The upstream reach of Quartz Creek experienced a flood on 22–23 February 1986, but physical alteration of the site was minimal in comparison with downstream reaches subjected to the debris flow. Dense riparian vegetation, large boulders, and wood debris contributed to a heterogeneous stream channel

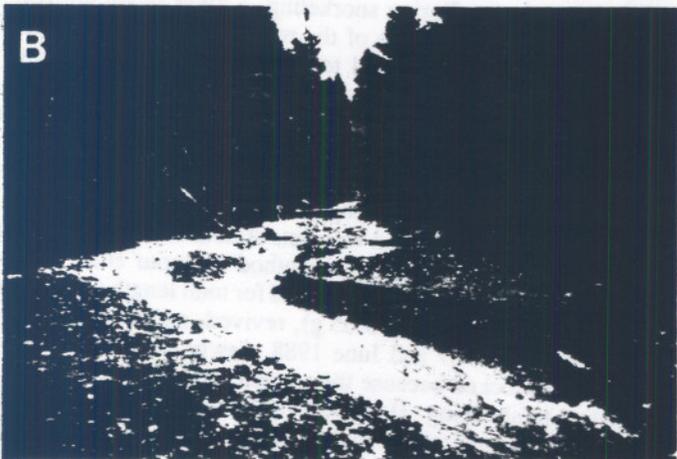


FIG. 2. Photographs of three study reaches in Quartz Creek taken approximately 1 mo after the debris flow. (A) Upstream reach, showing alder canopy and high channel roughness; (B) debris flow reach, showing open canopy and low channel complexity; (C) downstream reach, showing debris dam and open canopy.

in the upstream reach (Fig. 2A). Many aquatic organisms probably survived the flood alone.

In the debris flow reach, our qualitative observations 48 h after the flood and debris flow indicated severe physical changes including canopy removal, loss of wood debris, and reorganization of channel sediments (Fig. 2B). The aquatic fauna and flora probably were completely lost from the reach. Even 2 d after the event, landslide sediment continued to enter

Quartz Creek from the tributary, which scoured the streambed or buried substrates. At that time, we found no macroinvertebrates and no macroscopic algal growth on the surfaces of stones in the debris flow reach. We assume that all fish in the debris flow reach were killed or displaced downstream; dead trout were found high on the streambanks downstream.

Riparian vegetation of the downstream reach was removed or battered by the leading edge of the debris flow, but some channel complexity was retained by existing and delivered wood and boulders (Fig. 2C). A portion of the stream biota probably survived in this reach but ecological recovery of the disturbed reaches began with a greatly diminished aquatic biota.

Response in Physical Features

Channel geomorphology

The channel unit sequence in the upstream reach was characterized by alternating cascades (25–40 m long) and pools (5–10 m long) arranged in a stairstep fashion, with few riffles or rapids (Fig. 3). This pattern is typical of many high-gradient streams in the Cascade Mountains (Sullivan et al. 1987).

The debris flow substantially affected channel morphology of Quartz Creek. Prior to the disturbance, the upper 108 m of the debris flow reach was composed predominantly of short pools (38% of reach length) and cascades (37%), with a shorter distance of riffles and rapids (23%) (Fig. 3). After the debris flow, the reach had a disordered sequence of channel units. Pools in the upper 108 m were reduced to 14% of reach length and riffle/rapid distance was increased to 43%. In the lower part of the debris flow, channel units were longer and included several large pools formed in deep sediments trapped behind the debris accumulation. The downstream reach, which was partially buffered by the debris dam, was composed mostly of long rapids and cascades, with only two pools.

Stream gradient in the debris flow reach before the disturbance was 5.3% but declined to 3.4% after the debris flow; this is due mainly to deposition of 2–6 m of sediment and wood in and behind the debris dam, which reduced overall reach gradient. Gradient in the upstream reach was 6.3%, which was similar to that in the debris flow reach before the event. The downstream reach had a gradient of 3.2% after the disturbance, possibly also associated with sediment deposition.

Despite disturbance-induced changes in the channel unit sequence and in gradient, all three reaches contained similar proportions of subunit habitats (Table 1). In all reaches, fast-water habitat comprised 50–54% of total reach area, pool habitat formed 27–32% of the area, and edge habitat was 16–19%. Thus, subunit quantities indicated a high degree of reach similarity in aquatic habitat, even soon after the debris flow. However, there were qualitative differences in habitat. For example, edge habitat in the disturbed reaches was mostly associated with deep eddies created around large particles in midchannel areas, such as boulders delivered by the debris flow. In the upstream reach, much of the edge habitat occurred along stream margins, such as in shallow backwaters, within side channels, and around wood debris.

Riparian characteristics

Prior to the debris flow, all three reaches had closed riparian canopies dominated by 40- to 50-yr-old alder trees and diverse understory vegetation that heavily shaded the stream. The debris flow removed a 5- to 15-m swath of trees and understory plants on each side of the stream along the entire length of both the

Quartz Creek Channel Unit Organization

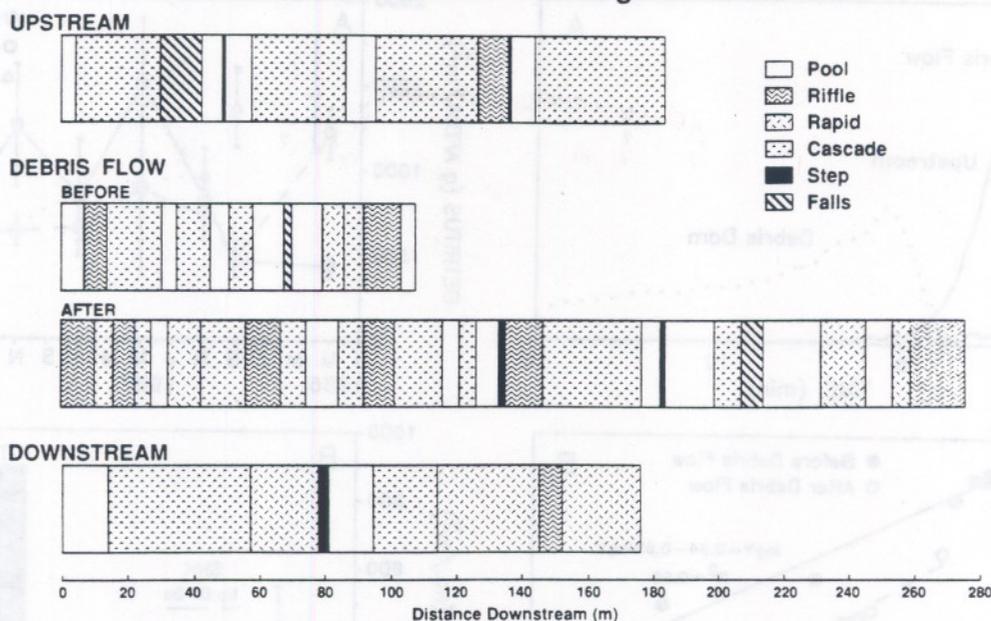


FIG. 3. Sequence of channel units in the three study reaches of Quartz Creek following the flood and debris flow of 1986. The before-disturbance (1983) sequence for the upper 108 m of the debris flow reach is presented for comparative purposes. Lateral dimensions of the channel units are not drawn to scale.

TABLE 2. Concentrations of selected nutrients in the three study reaches and tributary of Quartz Creek during 1986–88. Mean \pm SE and range (in parentheses) are expressed in $\mu\text{g/L}$; $N = 11\text{--}13$.

Nutrient	Upstream	Debris flow	Downstream	Tributary
Total P	20 \pm 1 (15–27)	20 \pm 2 (13–33)	19 \pm 1 (12–30)	30 \pm 3 (18–49)
PO ₄ -P	10 \pm 1 (8–13)	11 \pm 1 (8–14)	10 \pm 1 (7–13)	16 \pm 1 (7–20)
Total N	24 \pm 4 (5–65)	28 \pm 3 (7–50)	26 \pm 7 (7–46)	43 \pm 8 (18–114)
Organic N	17 \pm 5 (0–63)	18 \pm 3 (2–34)	15 \pm 2 (1–29)	23 \pm 4 (4–60)
NH ₄ -N	3 \pm 1 (1–5)	3 \pm 1 (2–8)	3 \pm 1 (0–6)	4 \pm 1 (1–7)
NO ₃ -N + NO ₂ -N	4 \pm 1 (1–11)	6 \pm 1 (2–17)	7 \pm 2 (1–18)	16 \pm 5 (1–49)

debris flow and downstream reaches. This resulted in a 15- to 40-m-wide canopy opening (including the stream channel) in the two disturbed reaches, which greatly increased solar radiation reaching the stream but potentially reduced detritus loading.

Irradiance at the stream surface was substantially higher in the disturbed reaches than in the upstream reach. For example, photon flux density was generally less than $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the upstream reach, compared with $500\text{--}2500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the debris flow and downstream reaches at the same time. These large differences in irradiance were significant (Wilcoxon $p < 0.05$; $N = 12$) and persisted throughout the 3-yr study of Quartz Creek. By 1988, however, alder seedlings were growing on most riparian surfaces within the disturbed reaches and beginning to shade stream margins.

Water chemistry

In general, nutrient concentrations were consistently low in all three study reaches of Quartz Creek (Table 2). Orthophosphate (PO₄-P) concentration averaged about $10 \mu\text{g/L}$ in all three reaches and total dissolved phosphorus was about $20 \mu\text{g/L}$. Concentrations of inorganic nitrogen forms also were low in Quartz Creek, which is typical of streams in the Cascade Mountains. Ammonium (NH₄-N) generally was less than $5 \mu\text{g/L}$ in all reaches. Nitrate plus nitrite (NO₃-N + NO₂-N) averaged $4 \mu\text{g/L}$ in the upstream reach, but was slightly higher in the debris flow and downstream reaches at $6\text{--}7 \mu\text{g/L}$. Levels of total nitrogen and total organic nitrogen were less than $30 \mu\text{g/L}$ in all three reaches of Quartz Creek.

Nutrient concentrations were generally 25–50% higher in the tributary where the debris flow began than in Quartz Creek (Table 2), perhaps due to release of nutrients from the clearcut and landslide area coupled with diminished vegetative uptake of those nutrients. Higher nitrate concentrations in the tributary may also reflect increased nitrification associated with greater supply of dissolved organic nitrogen; however, nutrient contribution by the tributary to Quartz Creek was probably minor because tributary discharge ($< 0.01 \text{ m}^3/\text{s}$) was low relative to Quartz Creek ($> 0.05 \text{ m}^3/\text{s}$).

Hydraulic retention

Dispersion and movement rates of fluorescein dye in Quartz Creek provided information on reach hydraulics. Hydraulic residence time (HRT), a relative index of reach heterogeneity, was calculated as the time required for 95% of the dye to move through a designated reach. Over 50-m reaches, HRT was 3.1 min in the debris flow reach compared with 4.8 min in the upstream reach (Fig. 4A), indicating lower hydraulic retention in the disturbed reach. Dye released through the complex debris dam indicated long hydraulic retention, with a 95% passage time of 23.4 min.

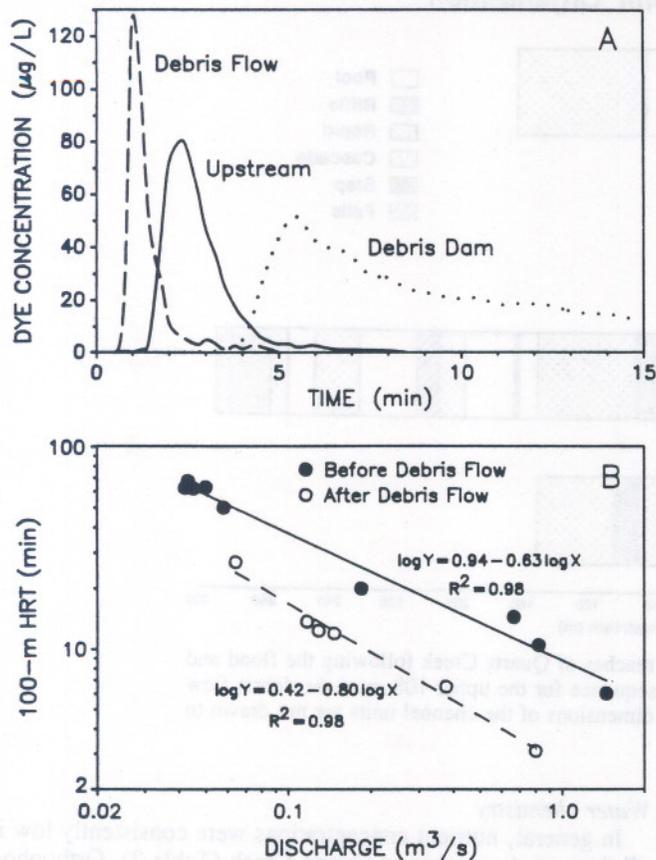


FIG. 4. Hydraulic features of Quartz Creek, determined from releases of fluorescein dye into the channel. (A) Dye concentration over time at 50 m downstream of the release point for the debris flow and upstream reaches, and within the debris accumulation; (B) 95% hydraulic residence time (HRT) for 100-m reaches in the debris flow reach, before and after the disturbance, at different discharges.

Using data from a series of 100-m dye releases conducted in 1983 and 1986–88, HRT was compared with discharge in the debris flow reach before and after the disturbance (Fig. 4B). The debris flow reduced HRT to about one third of the predisturbance residence times over a range of discharges. Logarithmic regression analysis indicated that although the slopes were similar, the HRT intercept value before the event ($a = 0.94$) declined substantially after the debris flow ($a = 0.42$). Thus, the debris flow substantially reduced HRT at all discharges, apparently by simplifying channel structure and eliminating large pools.

Response in Biological Features

Benthic detritus

The mean abundance of benthic detritus generally varied from 0.5 to 1.5 kg/m^2 in all three study reaches of Quartz Creek (Fig. 5A). Detritus was about 0.5 kg/m^2 in the upstream reach for most of 1986, probably because the severe flood of February 1986 removed stored detritus. From autumn 1986 to autumn 1988, however, the upstream reach showed marked seasonal fluctuations of up to 1 kg/m^2 in mean detrital standing crop, probably reflecting seasonal loading and removal of detritus. Detritus appeared to increase in the autumn with input of deciduous leaves and decline from winter through summer as organic matter was removed by high flow, decomposition, or consumption.

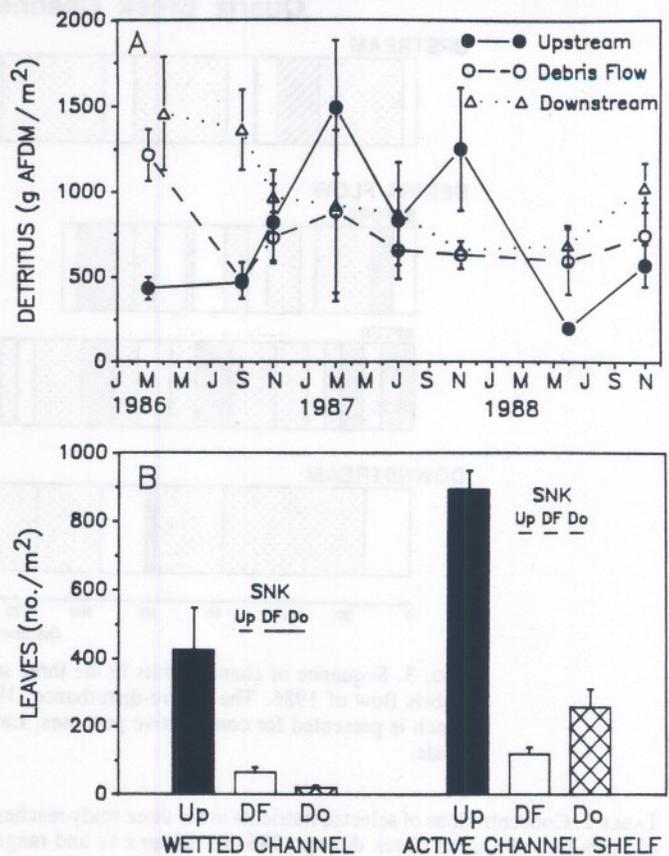


FIG. 5. Mean abundance (\pm SE) of detritus in the three study reaches of Quartz Creek. (A) Standing crop of benthic detritus from 1986 to 1988; (B) density of fallen leaves in the wetted channel and on the active channel shelf in November 1987. SNK = results of a Student–Newmann–Keuls test where different underscores indicate significantly different mean densities ($p < 0.05$).

In contrast, the debris flow and downstream reaches showed little seasonality in detrital standing crops (Fig. 5A). Detritus was abundant at $>1 \text{ kg/m}^2$ in the disturbed reaches soon after the disturbance, probably the result of delivery of organic matter by the debris flow. After autumn 1986, detritus declined to relatively constant levels near 0.6 kg/m^2 , probably because streamside sources of deciduous vegetation were removed by the debris flow while organic matter retention was reduced in the disturbed sites. This constant residual level of detritus may be due to on-site production of algal detritus during spring and summer, coupled with some import of autumn leaf detritus from upstream reaches. Predisturbance measurements of benthic detritus were made in March 1983 by Speaker (1985), who reported a habitat-weighted average of 588 g/m^2 within the debris flow reach.

Leaf litter

Leaves in the wetted channel and on the active channel shelf represented current and potential sources of aquatic detritus for the different reaches (Fig. 4B). The wetted channel comprised 43–47% of the active channel in Quartz Creek when leaves were sampled in November 1987. In both zones, densities of leaves were 5–10 times higher in the upstream reach than in the debris flow or downstream reaches. In all three reaches, leaf densities were at least twice as high on the active channel shelf than in the wetted channel.

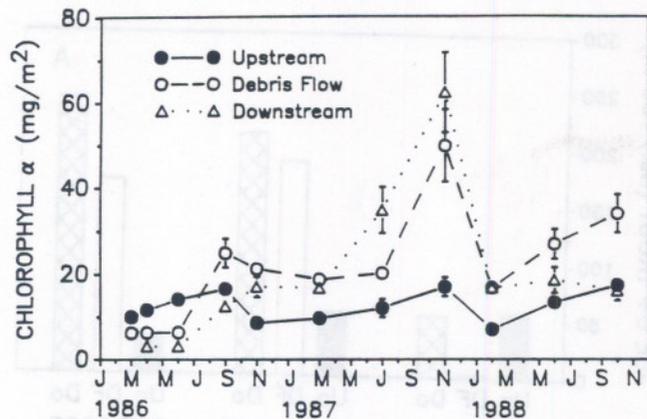


FIG. 6. Mean abundance (\pm SE) of algal chlorophyll *a* in the three study reaches of Quartz Creek from 1986 to 1988.

Benthic algae

Chlorophyll *a* abundance was used as an index of algal standing crop. During the 3-yr study, the amount of chlorophyll *a* was relatively constant in the upstream reach, varying from 8 to 16 mg/m² (Fig. 6). In the debris flow and downstream sites, chlorophyll *a* levels were low shortly after the disturbance but increased rapidly. By November 1986, mean chlorophyll *a* levels in the disturbed sites were two times higher than in the upstream site. These differences persisted into 1987, and by November 1987, mean chlorophyll *a* was about three times higher in the disturbed sites (50–60 mg/m²) than in the upstream site (15 mg/m²). Late rains in 1987, coupled with relaxation of grazing pressure in the autumn, probably accounted for these high chlorophyll *a* levels. In 1988, differences in chlorophyll *a* diminished among sites, but the debris flow reach maintained the highest chlorophyll *a* levels. In all three reaches, chlorophyll *a* levels were lowest in winter.

Macroinvertebrates

One month after the flood and debris flow, macroinvertebrate densities were low at all sites, averaging <2000 animals/m² (Fig. 7A). Invertebrate abundance at the upstream site remained relatively constant at about 3000/m² through March 1987, but then increased to >10 000/m² in November 1987 before declining again in 1988. At the debris flow and downstream sites, invertebrate abundance fluctuated greatly, exhibiting summer – early autumn maxima and winter minima. In the summer of 1986 and from 1987 to 1988, mean invertebrate abundances at the disturbed sites were double those of the upstream site. In general, invertebrate densities at all sites were highest in the second year (1987) after the debris flow, reaching about 20 000/m² in the disturbed reaches and 12 000/m² at the upstream site.

Taxonomic richness of invertebrates at the upstream site was about 50 taxa shortly after the flood, and increased to 70–80 taxa during the following year (Fig. 7B). The number of taxa in the debris flow and downstream reaches was quite low shortly after the disturbance (25–35 taxa), but increased rapidly during the first summer. From November 1986 to June 1988, taxon richness was similar among the three reaches. Richness declined from November 1987 to June 1988 in all reaches, possibly associated with the effects of high flows that winter.

Fish populations

Trout populations were locally decimated by the 1986 debris flow. In October 1983, cutthroat trout density in the debris flow

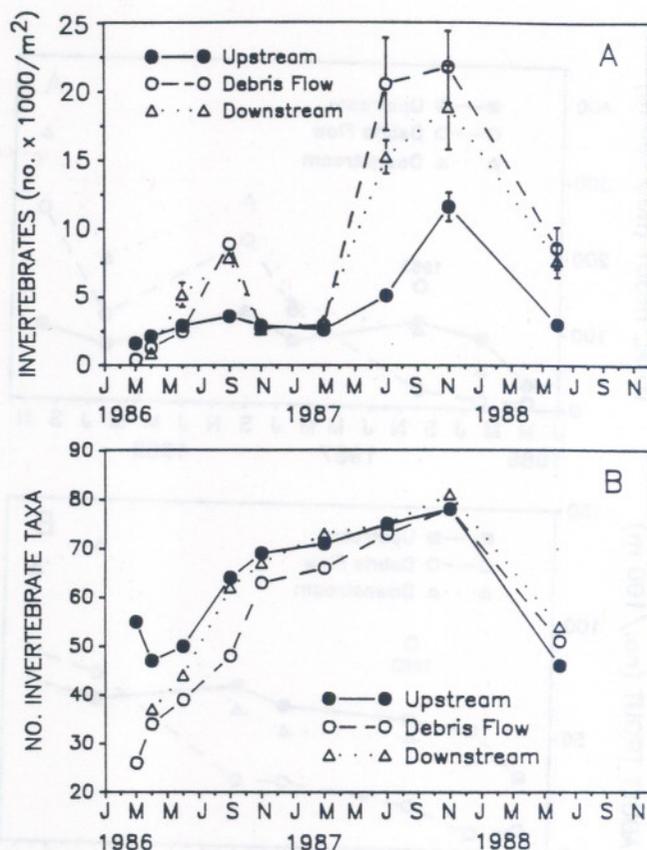


FIG. 7. Macroinvertebrate assemblages in the three study reaches of Quartz Creek from 1986 to 1988. (A) Mean density (\pm SE) of all macroinvertebrates; (B) total number of taxa found in each reach.

reach was 146 fish/100 m of stream length (Moore 1987). One month after the disturbance (March 1986), trout density in the debris flow reach was only about 10 fish/100 m and remained <20 fish/100 m throughout 1986 (Fig. 8A). Trout density in the upstream reach was about 100 fish/100 m in June 1986 and stayed near that level for the entire 3-yr study. Densities in the downstream reach were intermediate between the other two reaches. In 1987 and 1988, trout densities increased markedly in the debris flow and downstream reaches, and by October 1988, densities in the disturbed reaches were about double those of the upstream reach.

Adult cutthroat trout (1+ and older fish) and cutthroat fry (0+ fish or young-of-the-year) showed different responses to the debris flow. The upstream reach had the highest densities of adult trout in 1986 and 1987, averaging 50–70 fish/100 m (Fig. 8B). In contrast, densities of adult trout remained low in the debris flow site (<30/100 m) and intermediate in the downstream reach (40–50/100 m). In 1988, however, adult trout densities in the disturbed reaches increased sharply, especially in the downstream reach, and exceeded those of the upstream reach.

Cutthroat trout fry emerge from their gravel redds in May–June. Because some fry had not yet emerged at the time of the June sampling, the early autumn sample provided the best estimate of annual fry production (Fig. 9A). The upstream reach produced similar numbers of fry each year from 1986 to 1988 (30–50 fry/100 m), which is close to 1983 densities in the debris flow reach (61 fry/100 m). The debris flow reach produced very few fry in 1986 whereas normal densities were observed in the downstream reach (50 fry/100 m). In 1987 and 1988, the debris

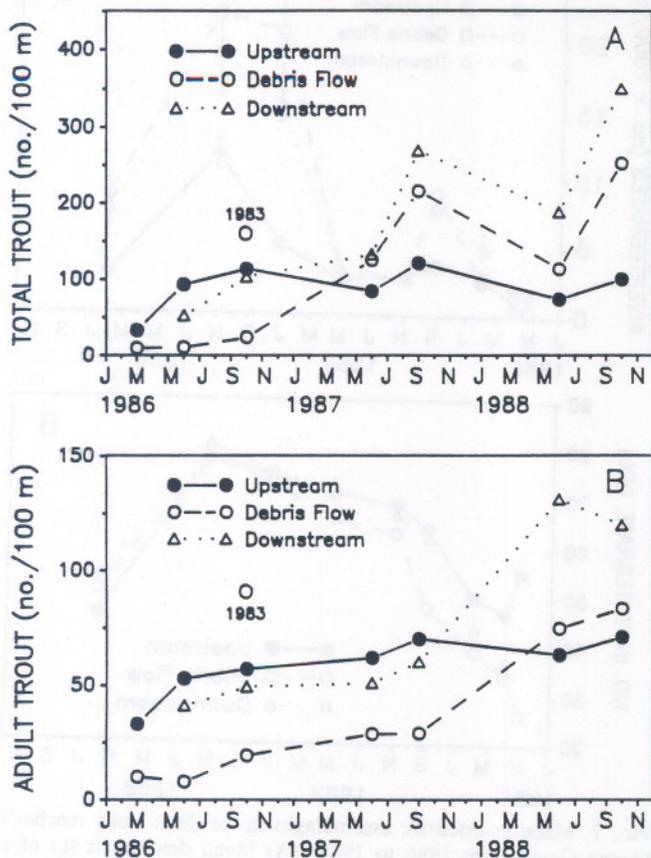


FIG. 8. Cutthroat trout populations in the three study reaches of Quartz Creek from 1986 to 1988. (A) Total trout abundance (fry plus adults); (B) abundance of adult trout only. Unconnected point refers to 1983 trout density in the debris flow reach.

flow and downstream reaches had high fry densities (approximately 200 fry/100 m), some four times greater than in the upstream reach.

Growth rates of fry also varied considerably among reaches (Fig. 9B). In the upstream reach, fry reached similar mass in the autumn of each year (approximately 2.5 g). In contrast, fry were 50–100% larger in the disturbed reaches during autumn of 1986 and 1987, indicating higher growth rates. However, this difference declined over time, and in 1988, fry size did not differ significantly between the upstream and downstream reaches, and fry were only about 10% larger in the debris flow reach.

Overwinter survival of fry was examined by comparing numbers of 0+ trout in the fall with numbers of 1+ trout the following spring (the same cohort) using size–frequency plots (summarized in Fig. 10). Numbers of 1+ trout in spring 1987 were 25–40% higher than 0+ trout densities in fall 1986 (except in the downstream reach), indicating immigration of fish into these reaches after the flood or debris flow. Lower than average rainfall in 1986–87 (resulting in low winter flows) probably also enhanced overwinter survival of fry. In 1987–88, cohort densities declined over the winter, but survival was twice as high in the upstream reach (only 35% of 0+ cohort lost) as in the debris flow reach (69% lost) or downstream reach (67% lost). High rainfall in 1987–88, and resultant high winter flows, probably contributed to low fry survival in the disturbed reaches.

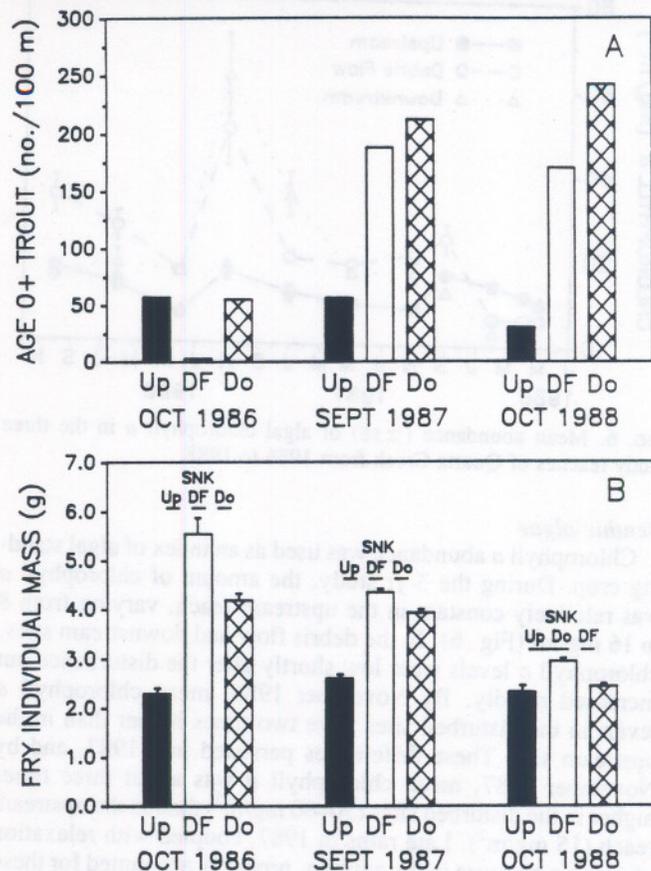


FIG. 9. Cutthroat fry populations in the three study reaches of Quartz Creek from 1986 to 1988. (A) Fry population density in the autumn of each year; (B) mean size (\pm SE) of individual fry, as wet mass, in the autumn of each year. SNK = results of a Student–Newmann–Keuls test where different underscores indicate significantly different mean masses ($p < 0.05$).

Discussion

Value of Natural Experiments

Major disturbances such as the debris flow in Quartz Creek provide unique opportunities to assess ecosystem processes as part of "natural" experiments (Connell 1978; White and Pickett 1985). Such disturbances have realistic intensity and spatial extent, and ecological recovery patterns are a function of natural ecosystem resistance and resilience. However, three problems often hinder the evaluation of natural disturbance: (1) lack of predisturbance information or representative control systems, (2) limited knowledge of the timing, extent, and immediate effects of the event, and (3) inability to assess recovery processes over sufficiently broad spatial and temporal scales (Sousa 1984).

In Quartz Creek, these limitations were minimized by a combination of events. First, because the disturbance occurred in a previously studied stream reach, a substantial amount of predisturbance information was available. A suitable upstream control area also was located, which provided a parallel comparison over time with the debris flow disturbed areas. Second, we examined debris flow impact just 48 h after it occurred and were able to gauge its origin, mass, velocity, and distribution in the watershed. Immediate effects were assessed with qualitative observations, and quantitative sampling was initiated 1 mo after the event. Third, ecosystem recovery was

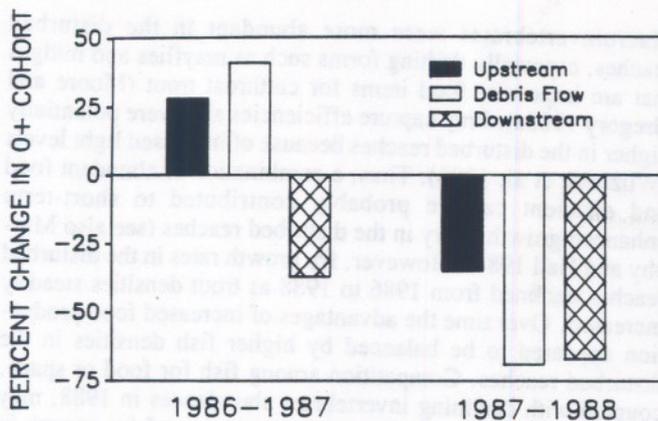


FIG. 10. Change in numbers of 0+ cohort of cutthroat trout between autumn and the following spring for 1986-87 and 1987-88 in the three study reaches of Quartz Creek. Positive change indicates net immigration whereas negative change indicates net mortality and emigration.

evaluated over broad spatial and temporal frameworks; we monitored over 600 m of Quartz Creek for 3 yr after the event. We will continue to monitor ecosystem recovery of Quartz Creek as part of the Long-Term Ecological Research Program at the H. J. Andrews Experimental Forest.

Stream Ecosystem Responses

Template for ecological recovery

The backdrop for physical and ecological recovery of Quartz Creek involved two spatial scales of disturbance and two levels of disturbance intensity. The flood in Quartz Creek occurred on a basin-wide scale but with only moderate intensity, as shown in the intact riparian vegetation and channel structure of the upstream reach. Refuge for organisms from the flood alone was available within lateral habitats and among coarse substrates. In contrast, the debris flow was intense but relatively localized, as shown in its dramatic impacts on a 500-m reach. In a confined area, riparian vegetation was destroyed and refuge for aquatic organisms was scarce or absent. Thus, two scales of disturbance mosaics emerged from the Quartz Creek flood and debris flow, each eliciting different recovery processes.

Geomorphic and hydraulic changes in Quartz Creek were obvious and immediate consequences of the debris flow. The staircase sequence of pools and cascades typical of these montane streams changed to series of short, disordered units or longer, high-velocity units such as rapids and riffles. Sediment was eroded from the upper end of the debris flow reach and deposited at the lower end behind the debris accumulation, resulting in local reduction of stream gradient. During late summer and early autumn, streamflow went entirely subsurface through the deep sediments up to 50 m behind the debris dam. Surface flow reappeared only at the lower end of the debris dam.

Hydraulic retention in these streams normally is high because of good pool development, heterogeneous stream margins, and high channel roughness (Speaker 1985). Channel morphology was altered by the debris flow and hydraulics were simplified, resulting in rapid transport of water through the disturbed reach. Such declines in hydraulic retention can create a more rigorous environment for aquatic biota and may reduce nutrient retention (Lamberti et al. 1989). Thus, the debris flow created a channel of greatly modified geomorphic and hydraulic character.

The downstream reach also experienced a flood and mud flow, but much of the organic debris was deposited in the massive accumulation just upstream. Thus, the scouring and depositional action of the debris flow was diminished by the debris dam. It is likely that a significant proportion of the fauna and flora survived in this reach because of the lower intensity of the disturbance. The rapid biotic recovery of the downstream reach also may be related to the hydraulic "buffering" effect provided by the debris dam during subsequent high flow. However, the downstream reach may experience lingering detrimental effects of the debris flow because the debris dam may trap coarse sediments that would normally be delivered to the reach. The debris dam itself may variably act as either a source of organic matter for the downstream reach or as a sink for entrapment of detritus transported from upstream.

Basis of ecological recovery

Stimulation of primary production coupled with residual storage of detritus appeared to provide the trophic basis for ecological recovery in Quartz Creek. After September 1986, algal standing crop was consistently higher in the disturbed reaches. Such stimulation may have resulted from increased nutrient concentrations or light levels, or both. Disturbance in drainage basins often is associated with increases in dissolved nutrient concentrations (Likens et al. 1970). However, the debris flow disturbed only plant communities associated with the valley floor, and upslope nutrient cycling was not disrupted. As a result, we observed no significant increases in nitrogen or phosphorus concentrations in Quartz Creek.

Increased light levels are a more likely cause of enhanced primary production in Quartz Creek. Removal of streamside vegetation greatly increased irradiance levels in the debris flow and downstream reaches. Because benthic primary production in small forested streams is limited primarily by low light levels (Gregory 1980), opening of the canopy in Quartz Creek apparently stimulated algal production. This enhanced primary production occurred in spite of very low nutrient concentrations in the disturbed reaches.

The abundance of benthic detritus often is an important determinant of trophic structure in stream ecosystems (Vannote et al. 1980; Cummins et al. 1989). In Quartz Creek, the debris flow removed local riparian sources of leaf detritus (as shown in leaf densities), yet the disturbed reaches had moderate standing crops of benthic detritus. This may be because algae contributed to detritus pools in the disturbed reaches, or there was significant import of detritus from upstream reaches. Alternatively, this detritus may represent recalcitrant material in long-term storage within the sediments. Thus, increased primary production, coupled with a residual supply of detritus, probably formed the bioenergetic basis for stream ecosystem recovery from the debris flow.

Recovery of invertebrate assemblages

Macroinvertebrate populations in Quartz Creek recovered rapidly from the February 1986 disturbance. Within 6 mo, invertebrate densities in the debris flow impacted reaches exceeded those of the upstream reach. Within 9 mo, taxonomic diversity of the disturbed reaches equaled that of the upstream reach. However, in 1987, densities in all three reaches were higher than in 1986, probably indicating that recovery processes from the large flood were still ongoing. Apparently, some invertebrate populations recovered from the localized debris flow within 1 yr whereas more time was needed for com-

plete recovery of the invertebrate assemblage from the basin-wide flood.

We propose that increased invertebrate densities in the disturbed reaches were a direct response to increased primary production. In 1986, invertebrate assemblages in the debris flow and downstream reaches were composed mostly of herbivorous taxa. Chironomid midge larvae and baetid mayflies, which tend to be early colonists of disturbed stream habitats (Lamberti and Moore 1984), were particularly abundant in the impacted reaches. This rapid recolonization probably occurred primarily by drift of larvae from upstream areas and oviposition by adults. In 1987, less mobile grazers such as glossosomatid caddisflies and pleurocerid snails, and various detritivores and predators, were found in low densities within the disturbed reaches. This longer term recolonization probably occurred by a combination of drift, oviposition, and benthic movement (Williams and Hynes 1976), which brought less vagile taxa into the disturbed reaches. In Quartz Creek, the highest chlorophyll *a* levels and the highest invertebrate densities were both observed in late 1987, suggesting a tight linkage between primary and secondary production. Previous studies in streams of the Pacific Northwest also have reported higher macroinvertebrate densities and algal biomass in reaches with open canopies as compared with shaded reaches (Murphy et al. 1981; Hawkins et al. 1982).

Recovery of fish populations

Two years after the debris flow, trout populations in the disturbed reaches had recovered to levels equal to or exceeding those in the upstream reach. Fish population recovery appeared to be related to (1) immigration of 1+ trout during the first year after the disturbance and (2) enhanced recruitment of fry in the second and third years. Fry were virtually eliminated in the debris flow reach during 1986 but were abundant in 1978 and 1988, thus contributing to large 1+ cohorts in each succeeding year in spite of poor overwinter survival. Thus, high fry recruitment in summer apparently compensated for increased winter losses.

Low fry density in the debris flow reach during 1986 was probably related to timing of the debris flow and the life history and behavior of cutthroat trout. In Cascade Mountain streams, age 2+ and older trout typically spawn from February to April and fry emerge from redds about 8 wk later (Behnke 1979; Moore and Gregory 1988a). Any redds built prior to the February 24 debris flow undoubtedly were destroyed by the event, as were most fish of reproductive age. Thus, in 1986 there was little reproduction within the debris flow reach and few fry migrated into the reach, as cutthroat fry tend to remain close to their spawning areas (Moore and Gregory 1988b). Other studies also have shown that eggs and juveniles of salmonids are affected more strongly by lotic disturbance than are adults (Hanson and Waters 1974; Seegrist and Gard 1972).

In the downstream reach, populations of both fry and adults recovered more rapidly than in the debris flow reach. Both fish and some redds probably survived downstream because of lighter disturbance, and more reproductive adults were present in 1986 to contribute to first-year fry recruitment. Unlike the debris flow reach, upstream movement of adult fish into this reach was unimpeded by a debris dam.

In 1986 and 1987, trout fry grew to larger size in the open disturbed reaches than in the shaded upstream reach. This pattern may be related to (1) food abundance, (2) food capture rates, and (3) total fish abundance in the disturbed reaches.

Macroinvertebrates were more abundant in the disturbed reaches, especially drifting forms such as mayflies and midges that are important food items for cutthroat trout (Moore and Gregory 1988a). Prey capture efficiencies also were potentially higher in the disturbed reaches because of increased light levels (Wilzbach et al. 1986). Thus, a combination of abundant food and efficient capture probably contributed to short-term enhanced growth of fry in the disturbed reaches (see also Murphy and Hall 1981). However, fry growth rates in the disturbed reaches declined from 1986 to 1988 as trout densities steadily increased. Over time the advantages of increased food production appeared to be balanced by higher fish densities in the disturbed reaches. Competition among fish for food or space, coupled with declining invertebrate abundances in 1988, may have resulted in density-dependent limitation of fry growth in Quartz Creek.

Disturbance in Stream Ecosystems

Most stream ecosystems are subjected to disturbance by floods that occur anywhere from several times per year (Fisher 1983) to several times per decade (Harr 1981). In montane streams of the Pacific Northwest, floods occur once every 1–2 yr on average, normally in the late autumn through early spring. Compared with other major disturbances such as wildfire or hurricanes (Connell 1978), flood disturbance in streams is frequent and relatively predictable. Stream organisms are adapted to this flood disturbance regime and have evolved various behavioral or reproductive strategies to minimize death or displacement or to ensure population recovery (e.g. Siegfried and Knight 1977; Fisher et al. 1982; Meffe 1984). In contrast, debris flows are rare, episodic events that may influence a particular stream reach only once every 50–200 yr or even longer (Swanson et al. 1987). These events have varying areal extent, high intensity, and low predictability. Loss of organisms during debris flows appears to be severe.

Sousa (1984) proposed that ecosystem recovery following disturbance is a function of (1) resistance of extant species to the disturbance, (2) influx rates of new organisms, (3) characteristics of the disturbance, including severity and time of occurrence relative to organism life history, and (4) features of the disturbed patch, including size, location, and internal heterogeneity. In Quartz Creek, we presume that the debris flow overwhelmed the resistance of most organisms in directly affected areas, as seen in the abrupt and severe reduction in plant and animal abundance. Colonization of the disturbed area thus was primarily a function of immigration rates of nearby organisms.

The rate of biotic recovery varied with the trophic level, proximity, and dispersal ability of colonists. Microbial and algal propagules are nearly always present in stream water (Lamberti and Resh 1987), and their downstream transport provides a continual source of colonists. Algal immigration and colonization provided the propagules for algal growth, and the enhanced light levels of the disturbed reaches favored rapid recovery of algal standing crop in Quartz Creek.

Recovery of consumer populations was slower than for algae, but still relatively rapid. Initial (first-year) recolonization by macroinvertebrates consisted primarily of vagile herbivores, but by the second year a fuller complement of trophic groups had recolonized the disturbed areas. This rapid recolonization may have been related to (1) physical stabilization of the channel, (2) increased food availability, such as periphyton, and (3)

recovery of individual populations following recolonization. For invertebrates, the lower intensity but more extensive effects of the flood may have been more important to recolonization dynamics than the higher intensity but less extensive debris flow.

Among the biota, recovery of fish populations was the most gradual and occurred both by immigration into the disturbed reaches and reproduction within the reach. Fry grew rapidly in the disturbed reaches during benign summer conditions, but about two thirds were eliminated by rigorous winter conditions and possibly predation. Winter fry loss in the disturbed reaches probably was related to the more rigorous hydraulic conditions and reduced overwintering habitat in the affected areas. During high flow, availability of lateral habitat as refuge is critical to the survival of cutthroat trout fry (Moore and Gregory 1988b).

Although the debris flow in Quartz Creek had severe local effects, the size of the disturbance (approximately 0.5 km of mainstem length) was small compared with some debris flows that may move for several kilometres or more in stream channels (Swanson et al. 1987). Its occurrence in February was prior to the major spring dispersal period for aquatic invertebrates (Williams and Hynes 1976) and cutthroat trout (Wyatt 1959). Disturbance size and timing thus favored rapid recolonization of the affected reaches. In general, this rapid recolonization may reflect some preadaptation to episodic disturbance imparted by adaptation to physically similar but more regular and frequent disturbance (i.e. floods).

Concluding Remarks

Stream ecosystem properties are closely linked to the structure of riparian vegetation and to the valley floor processes influencing plant succession (Hynes 1975; Vannote et al. 1980; Minshall et al. 1983; Gregory et al. 1991). Valley floors are dynamic portions of the landscape that are frequently affected by fluvial and terrestrial disturbance. Disturbance modifies valley floors through physical rearrangement of geomorphic surfaces, destruction of riparian vegetation, and direct removal of stream biota. The Quartz Creek study suggests that recovery of stream ecosystems from major disturbance is a complex process linked to postdisturbance stabilization of geomorphic surfaces, regrowth of riparian vegetation, development of heterogeneous hydraulic environments, and recolonization potential of aquatic organisms.

There is growing recognition that long-term studies are needed to examine complex ecological processes (Schlosser 1982; Callahan 1984). This 3-yr study of Quartz Creek documents the early phases of ecological recovery from a severe disturbance. Organismal abundances and ecological processes in the disturbed segment of Quartz Creek continue to fluctuate broadly, an indication that ecosystem stability (sensu Connell and Sousa 1983) has not yet been achieved. However, overall rates of recolonization of the disturbed areas were rapid, indicating high resilience in lotic biota that reflects ecological responses shaped by the frequent disturbance in stream ecosystems. Long-term monitoring of ecosystem properties in disturbed systems such as Quartz Creek should contribute substantially to our understanding of disturbance ecology.

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