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Summer Production of Coho Salmon Stocked in Mount St. Helens Streams 3–6 Years after the 1980 Eruption

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Abstract.—We monitored habitat use and summer production of stocked underyearling coho salmon *Oncorhynchus kisutch* from 1983 to 1986 in three streams affected by the 1980 eruption of Mount St. Helens, Washington. Two streams were in the blast area and one was on a volcanic mudflow terrace. Midsummer water temperatures frequently exceeded presumed stressful thresholds and occasionally surpassed the incipient lethal limit. Temperatures at the study sites (up to 29.5°C) may have been the highest ever recorded in small streams in western Washington. In addition, there was relatively little submerged cover and limited pool habitat. Despite the severe conditions created by the eruption, production rates of stocked coho salmon at all sites ranged from 15.1 to 143.8 mg/m^2·d (2.3–21.6 g/m^2 over an average 150-d summer period) and were equal to or greater than those measured in other streams of comparable size in the region. Coho salmon production in the streams was more strongly influenced by population biomass and density than by average individual growth rate. Production was also influenced by timing and average weight at stocking; larger fish stocked later in the summer had higher survival than smaller fish stocked earlier. Apparent summer mortality (true mortality plus emigration) may have been influenced by the presence of other salmonids. Coho salmon density at the end of summer was consistently lowest in the mudflow stream, the only site to have a large population of steelhead (anadromous rainbow trout *Oncorhynchus mykiss,* formerly *Salmo gairdneri*). We suspected that an abundance of both terrestrial and aquatic food was partly responsible for the high summer production of stocked coho salmon in what was an otherwise hostile environment.

The ecological effect of the 18 May 1980 eruption of Mount St. Helens was immediate and catastrophic. One consequence was a major reduction in resident and anadromous salmonid populations inhabiting the Toutle River system on the north and west sides of the mountain. Although losses of human life and property, commercial timber, and important fish and wildlife were considerable, the eruption created an unprecedented scientific opportunity to examine ecosystem recovery processes within a very large, massively disturbed area. Martin et al. (1986) reported that juvenile coho salmon *Oncorhynchus kisutch* released in selected Mount St. Helens streams during 1981 and 1982 suffered heavy summer mortality caused by high temperatures and unusually large diel temperature fluctuations. These extreme thermal conditions resulted from lack of shading caused by widespread destruction of trees during the explosive phase of the eruption or by removal of vegetation along streambanks during subsequent volcanic mudflows. Recovery of riparian vegetation was predicted to take from 5 to 20 years before third- and fourth-order streams would become adequately shaded for temperature control. Martin et al. (1986) also noted that sites in which large organic debris was absent or scarce lacked areas protected from high current velocities during storms and had the lowest winter survival rates for coho salmon parr. The authors speculated that high stream temperatures would act as a relatively short-term limiting factor and the absence of large organic debris would act as a long-term limiting factor to fish population recovery in the Toutle River basin, and that 50–75 years would be required for substantial amounts of debris to accumulate in stream channels.

Bisson et al. (1985) found that winter survival of stocked coho salmon during 1983 in a blast-area stream was similarly low, and they too attributed poor overwinter survival to lack of suitable habitat. However, they also observed that, despite high stream temperatures, summer survival and growth rates were similar to those reported for coho salmon populations elsewhere along the Pacific coast. These observations differed from the 1981 and 1982 experimental stocking results of Martin et al. (1986), in which high summer temperatures appeared to have a strong negative effect on coho salmon production. Bisson et al. (1985) suggested that, within several years of the eruption, other factors had begun to mitigate the effects of thermal extremes and that success in reestablishing coho salmon populations in the Toutle River system would be influenced by a variety of environmental variables related to posteruption ecosystem recovery.

In this paper, we describe the summer produc-

TABLE 1.—General features of study sites in three streams of the Toutle River drainage system near Mount St. Helens.

Feature	Hoffstadt Creek	Schultz Creek	Herrington Creek
Volcanic effect	Blast area	Blast area	Mudflow
Stream order (1:24,000)	4th	3rd	3rd
Watershed area (km²)	33	10	8
Reach surveyed (km)	2.2	1.1	1.6
Reach orientation	East–west	North–south	East–west
Average gradient (%)	2.4	4.0	1.4
Average wetted width (m)	4.6	3.1	2.5
Predominant substrate type	Bedrock	Boulder–bedrock	Cobble–sand
Cover[a]			
Large organic debris	Rare	Rare	Rare
Boulders, rock ledges	Moderate	Abundant	Moderate
Undercut banks	Rare	Rare	Rare
Overhanging vegetation	Rare	Rare	Moderate
Turbulence	Rare	Moderate	Rare

[a] Cover abundance was rated as follows: rare = 0–1 occurrence per 100 m; moderate = 2–10 occurrences per 100 m; abundant = greater than 10 occurrences per 100 m.

tion of experimental releases of hatchery coho salmon in three Mount St. Helens streams from 1983 to 1986. Our objective was to determine if survival, growth, and habitat use could be linked to riparian and stream recovery during this period 3–6 years after the eruption. In particular, we sought to document the production of coho salmon in streams where temperature reached levels that would be considered limiting to this species. A corollary objective was to examine the relative success of hatchery releases as other fish populations recolonized the area.

Methods

Study area.—Coho salmon were stocked in two streams in the volcanic blast area and in one stream on a volcanic mudflow terrace, all part of the Toutle River drainage system. The two blast-area streams, West Fork of Schultz Creek (hereafter called Schultz Creek) and Hoffstadt Creek, were tributaries of the Green River and the North Fork of the Toutle River, respectively. Study reaches in these streams were approximately 2 km upstream from the stream mouths. Monitoring began in Hoffstadt Creek in 1983 and in Schultz Creek in 1984. The mudflow-terrace stream, Herrington Creek, was a tributary of the South Fork of the Toutle River. Monitoring in Herrington Creek began in 1983; the study reach was a short distance above the stream's confluence with the South Fork. Although their watershed areas differed (Table 1), the study sites were typical of third- and fourth-order streams in the Toutle River basin in which most coho salmon spawning and summer rearing takes place.

Sites were picked to represent a range of volcanic effects, riparian conditions, and stream habitat. Of the two blast-area streams, Schultz Creek was most heavily affected by the 1980 eruption. All standing trees in the watershed were blown down and many were burned or pulverized by the heat and force of the lateral explosion. The site also received a layer of tephra (coarse volcanic ash) that commonly exceeded 10 cm in depth. Hoffstadt Creek was near the periphery of the blast area and some trees remained standing, although nearly all were heat killed. Tephra deposition in the Hoffstadt Creek watershed was considerably less than in Schultz Creek. The mudflow terrace study site was unique in that it consisted of a channel formed when a mudflow dammed the mouth of Herrington Creek, forcing it to carve a new channel that ran parallel to the South Fork of the Toutle River for nearly 2 km. This site did not exist before the eruption. The watershed of upper Herrington Creek was relatively unaffected.

Vegetation at the time of the eruption consisted of mixed stands of conifers containing Douglas-fir *Pseudotsuga menziesii,* western hemlock *Tsuga heterophylla,* and western redcedar *Thuja plicata.* Forest stands were mosaics of recently logged and commercially regenerated forests. Before the eruption, streams were surrounded by young second-growth stands of Douglas-fir, and riparian zones were dominated by red alder *Alnus rubra.* After May 1980, virtually no large conifers or hardwoods remained standing next to any of the sites. Merchantable logs adjacent to Schultz and Hoffstadt creeks were removed soon after the eruption, and there were very few pieces of large organic debris on the mudflow terrace where the new Herrington Creek channel had formed.

Recovery of riparian vegetation in the blast area tended to occur more rapidly than on the hillslopes, and vegetative species richness was also greatest in riparian zones due to favorable microsites along streams (McKee et al. 1987). Early riparian colonizers included red alder, willow *Salix* spp., devil's club *Oplopanax horridum,* salmonberry *Rubus spectabilis,* swordfern *Polystichum munitum,* buttercup *Ranunculus uncinatus,* coltsfoot *Petasites frigidus,* fireweed *Epilobium angustifolium,* and pearly everlasting *Anaphalis margaritacea.* Herbaceous vegetation was abundant along the banks of Hoffstadt Creek and Herrington Creek at the beginning of the study in 1983, but by summer 1986 it was slowly being displaced by alder and willow, as well as by Douglas-fir planted in both watersheds. Vegetative recovery increased stream shading by 1986; however, both blast-area sites remained substantially open to direct solar radiation.

Riparian vegetation was initially slow to become established along Herrington Creek, apparently because the mixture of ash, cobbles, and boulders that formed the mudflow terrace was not a fertile substrate for early colonization and growth. In 1982, alder cuttings were planted on the banks of Herrington Creek. Survival was high; some alders had attained heights in excess of 3 m by 1986 and had formed a dense thicket next to the stream. These trees provided moderate shade, but canopy closure over Herrington Creek was incomplete. Martin et al. (1986) predicted that heights greater than 4.2 m would be necessary to shade third- and fourth-order streams completely near Mount St. Helens. During the 3–6-year posteruption period, Herrington Creek progressed from being the least shaded to the most vegetatively shaded study site.

The streams differed in substrate characteristics, but they all shared a scarcity of cover (Table 1). Hoffstadt Creek was influenced by a torrent of debris in early December 1981. The torrent originated as a landslide high in the watershed and swept through the entire length of the study reach, scouring the channel to bedrock in many places and removing nearly all of the pre-eruption large organic debris as well as trees that had been blown into the stream by the volcanic explosion. After the torrent, the only remaining cover in Hoffstadt Creek consisted of large cobbles and boulders, occasional bedrock ledges, and some surface turbulence. Schultz Creek did not experience a debris torrent after the eruption, but winter rainstorms scoured most of the tephra out of the channel, leaving a streambed dominated by boulders and bedrock. Herrington Creek continued to erode into the mudflow terrace during the study, and its substrate consisted of cobbles and occasional boulders in the matrix of volcanic mud. The rate of channel downcutting slowed in the latter study years as the bed gradually developed a substrate of gravel and cobbles.

Habitat and water quality.—We surveyed habitat composition at the start of the study in each stream and again in 1987 after the study had ended to determine the extent of channel change. The classification of different types of riffles and pools followed the system of Bisson et al. (1982) in which pools were identified as backwater, plunge, lateral scour, trench, or secondary channel pools, and riffles were identified as low-gradient riffles, rapids, or cascades. We measured lengths and widths of individual channel units to estimate relative abundances of different habitat types in each reach, expressed as a percent of total wetted surface area during summer.

We monitored water temperature with continuously recording thermographs placed near the downstream end of the study reaches. From 8 August through 21 October 1983, temperature in Hoffstadt Creek was measured with a 7-d mechanical thermograph (calibrated weekly and accurate to 1°C); in subsequent years, we used digital temperature recorders (calibrated bimonthly and accurate to 0.5°C) in all three streams. Summer 1983 was unusually cool and wet. Peak water temperatures during the period of measurement in Hoffstadt Creek exceeded 20°C on only a few occasions (Bisson et al. 1985), levels well below those measured in this stream by Martin et al. (1986) in 1981 and 1982. Water temperatures at the other study sites were not measured in 1983. Summer air temperatures from 1984 to 1986 were much warmer than in 1983, and water temperatures at all study sites also followed this pattern. Because more accurate monitoring instruments were used from 1984 to 1986 and because very high midsummer stream temperatures were observed during this interval, we have chosen to focus on the 1984–1986 data.

We sampled streamwater chemistry in Hoffstadt Creek and Herrington Creek at approximately monthly intervals during 1984. Chemical determinations included inorganic and organic nutrients (total phosphorus, ammonia-nitrogen, nitrate- plus nitrite-nitrogen, Kjeldahl-nitrogen, and total organic carbon) that could have influenced stream productivity. We preserved samples in the field with mercuric chloride (2.5 mL/500 mL) and assayed them in the laboratory with a Technicon autoanalyzer after filtering them to remove particulate material. Organic carbon samples were not preserved with mercuric chloride but were kept cold and filtered soon after being taken. A 10-mL subsample was oxidized to CO_2 in a sealed ampule and injected into an infrared CO_2 analyzer, in accordance with the procedure of Wetzel and Likens (1979). Turbidity was low at all study sites and was not measured.

Fish populations.—We planted young-of-the-year coho salmon (native Toutle River stock) from the Cowlitz River Salmon Hatchery at the upper end of each study reach. The actual stocking point was usually located below a waterfall or cascade that would have hindered upstream migration. However, the possibility of upstream movement out of the study reach existed in both Hoffstadt Creek and Herrington Creek. Inspection of the streams after stocking indicated that upstream movement was minimal. Most fish spread downstream from the initial point of entry and colonized the entire study reach within a few days. Because the streams lacked abundant pool habitat, it is likely that substantial numbers of coho salmon emigrated during the first 10 d (Bilby and Bisson 1987). In 1986, coho salmon were stocked in pools along the entire length of each reach instead of being planted at a single location. This procedure was thought to produce a more natural initial distribution.

Our intent was to establish coho salmon densities at or above the presumed carrying capacity of the streams (2–3 fish/m^2); therefore, uniform numbers were planted each year (Table 2). The lone exception was Herrington Creek, which received more coho salmon in 1983 than in subsequent years. The two blast-area sites were upstream from barriers to adult migration and contained no natural coho salmon populations, but Herrington Creek was available to spawning by anadromous salmonids and was extensively used by steelhead (anadromous rainbow trout *Oncorhynchus mykiss,* formerly *Salmo gairdneri*) throughout the study. We saw little evidence of natural coho salmon spawning in Herrington Creek from 1983 to 1985, but in 1986 and again in 1987, young-of-the-year coho salmon from natural spawning appeared in the stream. The extent to which naturally spawned coho salmon contributed to the total population in Herrington Creek was not known.

In addition to juvenile steelhead in Herrington Creek, other fish species inhabited the study streams. Coastal cutthroat trout *Oncorhynchus clarki* (formerly *Salmo clarki*) were always rare at the sites. They were present in Hoffstadt Creek in 1983, when a single age-4+ individual (apparently a survivor of the eruption) was captured. Numbers of cutthroat trout have since increased slightly in this stream. Cutthroat trout were occasionally observed in Herrington Creek throughout the study period and first appeared in Schultz Creek in 1986. Beginnning in 1985, rainbow trout were recorded in the two blast-area streams. These fish probably originated from plantings by the Washington Department of Game. Their occurrence above presumed barrier falls and their general appearance suggested that they were not anadromous. Herrington Creek also contained sculpins *Cottus* spp. and Pacific lamprey *Lampetra tridentata.* A single adult brown trout *Salmo trutta* was captured in Herrington Creek in October 1984 (Bisson et al. 1986), but no juveniles of this species have been found there.

We sampled fish populations twice after stocking in 1983 and 1984, and once after stocking in 1985 and 1986. We obtained habitat-specific population estimates by isolating individual channel units and electrofishing three times. In a few instances where pools were too large to use the backpack shocker effectively, we used a seine. Densities within individual riffles and pools were calculated by the removal summation procedure of Carle and Strub (1978). We estimated average density within the entire reach by multiplying habitat-specific density by the proportion of the total stream area occupied by each habitat type and summing these values for all habitat types present in the reach. We obtained weight esti-

TABLE 2.—Stocking dates and numbers and average weights of hatchery coho salmon released in three study sites near Mount St. Helens.

Location	Date	Number	Mean weight (g)
	1983		
Hoffstadt Creek	22 Jan	15,000	2.25
Herrington Creek	15 Apr	22,400	0.75
	1984		
Hoffstadt Creek	8 May	15,000	0.51
Schultz and Herrington creeks, each	21 May	15,000	0.51
	1985		
All study sites, each	12 Apr	15,000	1.06
	1986		
All study sites, each	19 Jun	15,000	3.69

mates from length–weight relationships determined each summer at the final population census.

Production calculations followed the numerical procedure of Chapman (1978), in which it was assumed that instantaneous rates of growth and apparent "mortality" (true mortality plus emigration) in the streams were exponential. We assumed further that the spatial distribution of coho salmon throughout a measurement interval was reflected in the relative proportions of fish observed in each habitat type, i.e., that all fish captured in a particular type of habitat had actually spent the entire interval there. Because coho salmon were not marked individually, these assumptions were untested.

Results and Discussion

Habitat Composition and Water Quality Changes

Pool habitat was scarce at all sites (Figure 1) owing to a combination of volcanic effects and loss of large organic debris. Lateral scour pools comprised the most abundant pool type in each of the streams, but were most common in Herrington Creek, the mudflow site. Plunge pools were the second most common pool type, followed by trench pools, in the two blast-area streams. Pools along the channel margins (backwater and secondary channel pools) were always rare. Riffle habitats, especially low-gradient riffles and cascades, were more abundant than pools.

The relative proportions of habitat types changed little from the beginning to end of the study (Figure 1). All habitat surveys were performed in August to minimize flow differences between years. Streamflow did not differ greatly between 1984 and 1987. However, the summer of 1983 was characterized by cool moist conditions, and stream discharge in Hoffstadt Creek appeared greater in 1983 than in 1987, when discharge was low. The disappearance of backwater and secondary channel pools from Hoffstadt Creek by the time of the 1987 survey may have been caused by exceptionally dry weather that eliminated these habitats. The relative proportion of cascade habitat increased at all sites over the period of study. The cause of this increase was not known, but the increase was usually accompanied by a decline in the abundance of low-gradient riffles and may have reflected downcutting by the stream through course volcanic deposits.

Although the proportions of different habitat types changed little during the study, the frequencies and average areas of individual channel units were altered sharply (Table 3). At all sites, the frequencies of both riffles and pools declined, and the average areas of individual channel units increased in 1987 compared to 1983–1984. On average, pool frequency declined 57% and riffle frequency declined 38%, whereas average individual pool area increased 270% and average individual riffle area increased 210% over the interval. Ap-

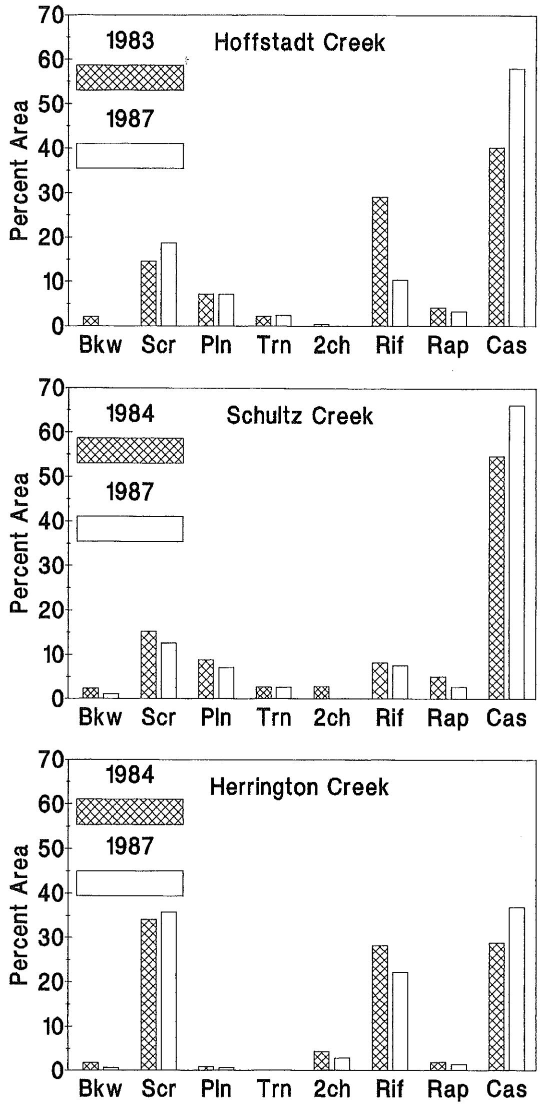

FIGURE 1.—Habitat composition in three Mount St. Helens streams, expressed as percent of total wetted surface area in summer of two different years. The habitat type designations are Bkw = backwater pool; Scr = lateral scour pool; Pln = plunge pool; Trn = trench; 2ch = secondary channel pool; Rif = low-gradient riffle; Rap = rapids, Cas = cascade.

TABLE 3.—Frequencies (number/km) and average areas (m^2) of individual pools and riffles in the study sites.

Year	Pools			Riffles		
	Frequency	Area	% of total stream	Frequency	Area	% of total stream
Hoffstadt Creek						
1983	44	32	27	49	80	73
1987	20	82	28	30	138	72
Schultz Creek						
1984	90	10	32	84	23	68
1987	35	29	24	52	62	76
Herrington Creek						
1984	71	18	41	75	25	59
1987	32	49	40	47	50	60

parent increases in surface area were not caused by flow differences; stream discharge during August 1987 was significantly less than in 1983 and slightly less than in 1984, based on gaging records from other small streams in southwestern Washington (K. Sullivan and J. D. Heffner, Weyerhaeuser Company, personal communication).

Summer water temperatures were high at all sites (Figure 2). July and August were almost always warmest; average daily maximum stream temperatures in the two blast-area streams usually exceeded 20°C. Overall, blast-area sites were slightly warmer than the mudflow-terrace site; of the two blast-area streams, Hoffstadt Creek tended to be warmest. Maximum air temperatures varied by month but were not significantly different when averaged over the entire summer, both among streams and among years.

Martin et al. (1986) measured diel fluctuations greater than 16°C in Bear Creek (near Hoffstadt Creek) in August 1981. They also reported that Bear Creek exceeded 25°C, the incipient lethal threshold for coho salmon (Brett 1952), on several occasions in both 1981 and 1982. This stream possessed the most extreme thermal conditions observed in their study. Our results indicated that the temperature regimes of Mount St. Helens streams remained severe from 1984 to 1986. In Hoffstadt Creek, which was slightly warmer than the other sites (Figure 2), temperature reached 29.5°C on three consecutive days in August 1984, when diel ranges of 17°C were recorded. During the same period, the daily maximum temperature and diel temperature range in Herrington Creek were 29°C and 17°C, respectively. These levels were observed when unusually warm weather caused peak air temperature to reach 42.5°C.

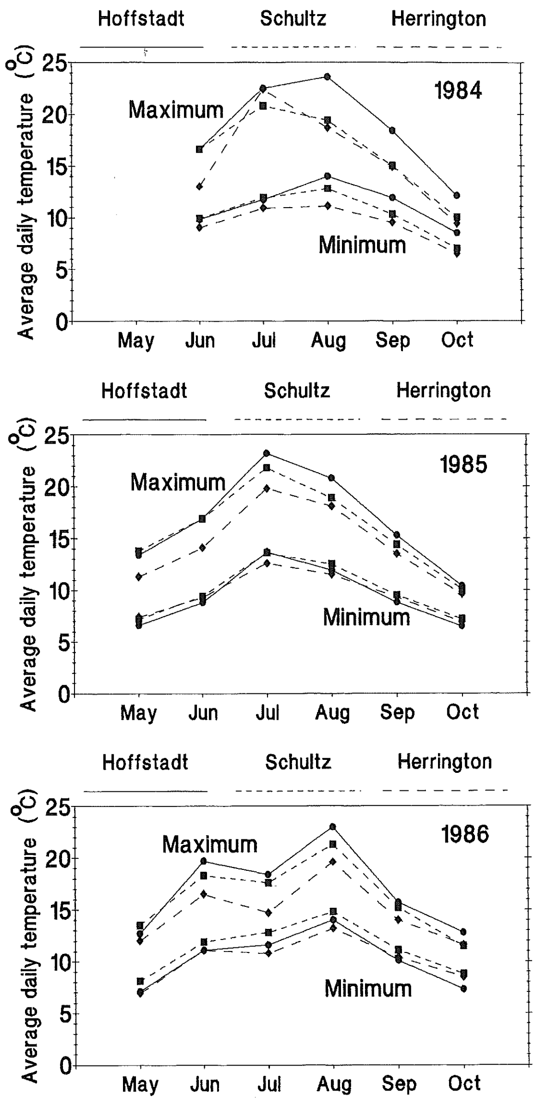

FIGURE 2.—Average monthly maximum and minimum summer water temperatures in three Mount St. Helens streams, 1984–1986.

Although average water temperatures did not change significantly over the study period, there was a slight but statistically significant reduction in daily maximum temperatures at Hoffstadt Creek and Herrington Creek (analysis of variance; $P < 0.05$). More marked was the reduction in diel temperature fluctuations that took place at all sites (Figure 3). Average diel fluctuations in summer declined 11, 21, and 37% in Hoffstadt Creek, Schultz Creek, and Herrington Creek, respectively, from 1984 to 1986 (all reductions were significant at $P < 0.05$). Reductions were greatest in July and August, the warmest months. The extent

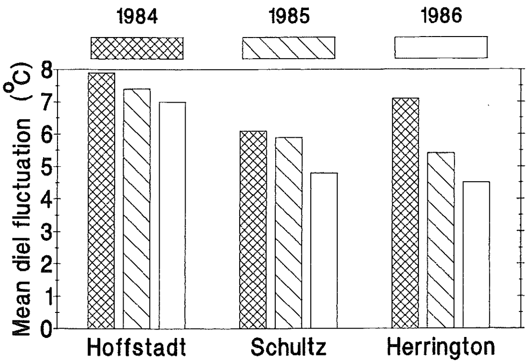

FIGURE 3.—Average diel temperature fluctuations in three Mount St. Helens streams, 1984–1986.

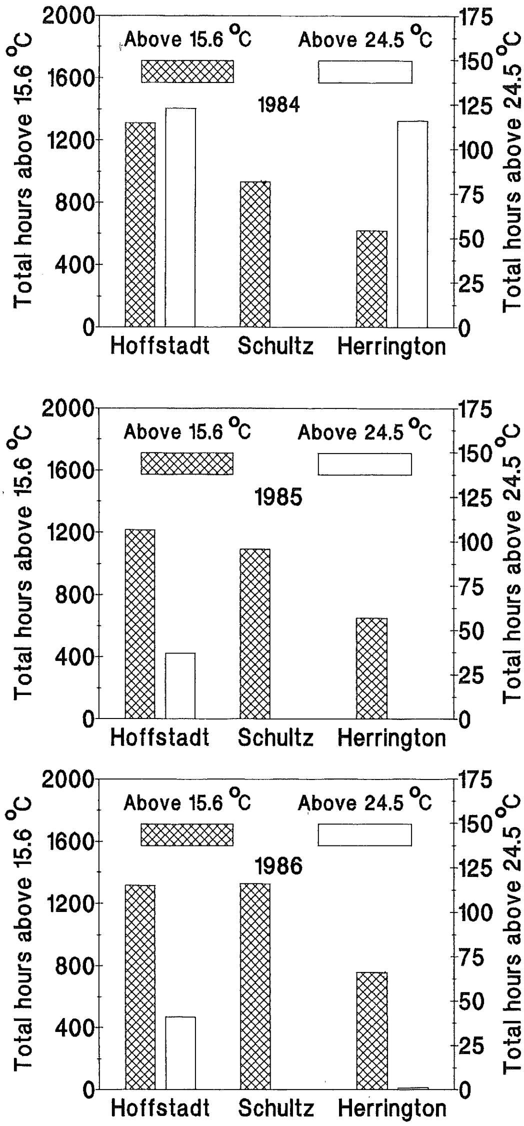

FIGURE 4.—Cumulative hours from May to October, 1984–1986, during which stream temperature exceeded 15.6°C and 24.5°C in three Mount St. Helens streams.

of reductions in diel temperature variation appeared to be strongly influenced by the amount of vegetative shading, which was greatest in Herrington Creek and least in Hoffstadt Creek.

We took 15.6°C to be a threshold for temperature stress (at the time of this study, the Washington Department of Natural Resources used 60°F [15.6°C] as the basis for identifying "temperature sensitive" streams) and 24.5°C to be a conservative estimate of incipient lethal temperature for juvenile coho salmon, based on results of laboratory tolerance studies (Brett 1952; Averett 1968). With these estimated thresholds of thermal stress and lethality, we found that the two blast-area streams experienced more severe conditions than the mudflow stream (Figure 4). Averaged over the entire summer, temperature remained above 15.6°C from 25 to 35% of the time in Hoffstadt and Schultz creeks, while Herrington Creek exceeded 15.6°C from 15 to 20% of the time. The duration of time above 15.6°C did not decline at any of the sites from 1984 to 1986, but in Schultz Creek there was a significant increase over these 3 years (analysis of variance; $P < 0.05$) that may have been related to a minor rise in peak air temperatures in the Schultz Creek watershed. Although the duration of time above 15.6°C did not decrease coincidentally with vegetative recovery along streambanks, there was a reduction of time above 24.5°C in Hoffstadt Creek and Herrington Creek (Figure 4), the two sites with east–west orientation. Some of the apparent reduction was caused by an unusually hot period in August 1984 that was not repeated in subsequent years. However, there were occasional hot periods in both 1985 and 1986, during which temperatures at these sites did not climb above 24.5°C for very long, if at all. We believe that part of the reduction in cumulative time above the incipient lethal level was associated with riparian recovery.

In summary, we found that (a) summer temperatures at all sites were often well above levels considered optimal for juvenile coho salmon rearing and, in some cases, exceeded the incipient lethal level for extended periods; (b) the blast-area sites were slightly warmer than the mudflow site, Hoffstadt Creek being the warmest of the three streams; and (c) there was a gradual reduction in average diel temperature fluctuation and duration

TABLE 4.—Coho salmon production statistics for three Mount St. Helens streams from 1983 to 1986.

Statistic	Hoffstadt Creek	Schultz Creek	Herrington Creek
1983			
Interval	22 Jun–23 Oct		15 Apr–25 Oct
Mean biomass (g/m^2)	4.2		2.2
Mean density (number/m^2)	1.4		0.9
Growth rate (%/d)	0.4		1.1
Production (mg/m^2·d)	17.9		24.1
Survival (%)	48.8		9.6
1984			
Interval	8 May–3 Oct	21 May–26 Sep	21 May–9 Oct
Mean biomass (g/m^2)	2.7	1.9	0.9
Mean density (number/m^2)	1.2	0.9	0.5
Growth rate (%/d)	1.6	2.1	1.7
Production (mg/m^2·d)	34.4	37.7	15.1
Survival (%)	39.5	8.6	6.5
1985			
Interval	12 Apr–11 Sep	12 Apr–15 Aug	12 Apr–10 Sep
Mean biomass (g/m^2)	1.8	4.5	2.4
Mean density (number/m^2)	0.4	1.2	0.5
Growth rate (%/d)	1.2	1.4	1.3
Production (mg/m^2·d)	21.2	67.9	32.0
Survival (%)	5.9	16.9	6.5
1986			
Interval	19 Jun–5 Sep	19 Jun–2 Sep	19 Jun–11 Sep
Mean biomass (g/m^2)	6.0	11.1	6.3
Mean density (number/m^2)	1.0	1.6	0.9
Growth rate (%/d)	1.2	1.3	1.0
Production (mg/m^2·d)	68.4	143.8	64.6
Survival (%)	30.5	25.7	23.2

of time above 24.5°C that was coincidental with recovery of streamside vegetation.

Total dissolved phosphorus was near or below detectable concentrations (0.01 mg/L) in both Hoffstadt Creek and Herrington Creek throughout 1984, except in late autumn, when dissolved phosphorus concentrations reached approximately 0.07 mg/L at both sites. Ammonia-nitrogen concentrations were always low (<0.05 mg/L) and there were no consistent differences between the two streams. Nitrate-nitrogen concentrations in Hoffstadt Creek ranged from 0.1 to 0.6 mg/L and were well above those in Herrington Creek (<0.05 mg/L). Nitrate concentrations in Hoffstadt Creek were also much higher than typical nitrate-nitrogen levels reported from other western Washington streams (Thut and Haydu 1971; Fredriksen et al. 1975). Possible explanations for the high nitrate-nitrogen concentrations in Hoffstadt Creek include decreased uptake of nitrate by the surrounding forest after it was killed by the volcanic blast, decomposition of organic material buried by tephra deposits, and increased rates of microbial nitrification. Kjeldahl-nitrogen concentrations at both sites usually ranged from 0.02 to 0.12 mg/L. Kjeldahl levels were greatest in Herrington Creek early in 1984 but, by summer and throughout the rest of the year, they were greatest in Hoffstadt Creek. Dissolved organic carbon was almost always greater in Herrington Creek than in Hoffstadt Creek, possibly reflecting the forested condition of most of the Herrington Creek watershed. In general, nutrient concentrations were similar to those in streams not affected by the Mount St. Helens eruptions, with the exception of high nitrate levels in Hoffstadt Creek.

Coho Salmon Production

The production rate of coho salmon in the streams generally increased over the study period (Table 4). Overall, production did not differ greatly among streams except in 1985 and 1986, when the production rate in Schultz Creek was approximately double that of the other two sites. Because the stocking dates and measurement intervals varied, total production during summer was standardized to a 150-d interval for comparative purposes. There was a 10-fold difference in total production between the lowest estimate (2.3 g/m^2 in Herrington Creek, 1984) and highest estimate (21.6 g/m^2 in Schultz Creek, 1986); however, the trend toward higher levels of production in the

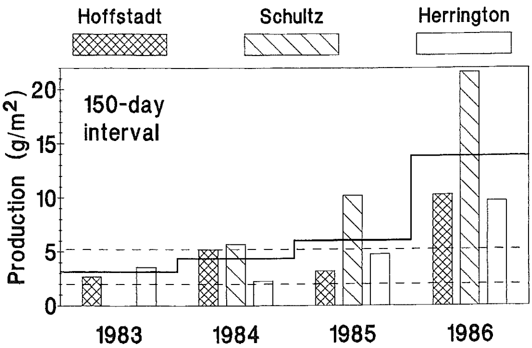

FIGURE 5.—Estimated coho salmon production over standardized 150-d summer periods from 1983 to 1986. The broken horizontal lines denote upper and lower limits of coho salmon production observed in the Deschutes River system by Bilby and Bisson (1987). The stepped horizontal line denotes annual averages for the study streams.

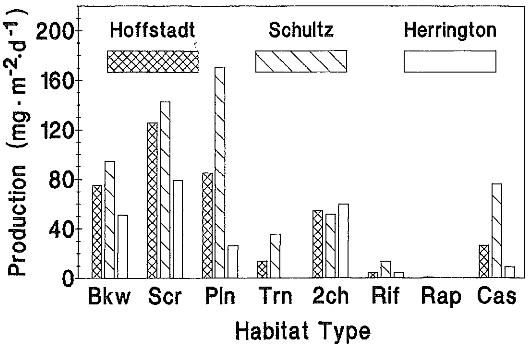

FIGURE 6.—Habitat-specific production rates of coho salmon in three Mount St. Helens streams, averaged over 1983–1986 for Hoffstadt and Herrington creeks and over 1984–1986 for Schultz Creek. Bkw = backwater pool; Scr = lateral scour pool; Pln = plunge pool; Trn = trench; 2ch = secondary channel pool; Rif = low-gradient riffle; Rap = rapids; Cas = cascade.

latter years of the study was evident at all sites (Figure 5).

Production estimates were equal to or greater than summer production estimates for wild age-0+ coho salmon in streams of similar size in the region (Chapman 1965; Burns 1971; Dolloff 1983). In what were probably the most similar experimental conditions to this study (hatchery fish stocked at relatively high densities in two streams draining the west slope of the Cascade Range), Bilby and Bisson (1987) found that coho salmon production in summer ranged from 2.05 to 3.95 g/m^2 in an old-growth forested watershed and from 4.63 to 5.28 g/m^2 in a watershed that was mostly clear-cut. Their study took place in 1982 and 1983 in the headwaters of the Deschutes River, Washington, less than 100 km from the Toutle River sites. With the exception of 1986, which was characterized by high production at all our Toutle River sites, production in Hoffstadt Creek and Herrington Creek fell into the range of values observed by Bilby and Bisson (1987) in watersheds that were not affected by the 1980 Mount St. Helens eruption (Figure 5). Production in Schultz Creek was always above this range.

Pool habitat types sustained higher levels of coho salmon production than riffle types (Figure 6), usually by a factor of two or more. Backwater, lateral scour, and plunge pools were most productive (Duncan's multiple-range test; $P < 0.10$); trench and secondary channel pools were the least productive of the pool types. Production rates in cascades were not significantly different from those of secondary channel or trench pools. Low-gradient riffles and rapids were least productive of all habitat types.

The trend toward increasing production over the study did not appear to be related to changes in habitat composition (Figure 1). The relative proportions of the most productive pool types did not increase in any of the streams. Although there was a slight increase in the proportions of cascades (which sustained moderate levels of production) and corresponding reductions in low-gradient riffles (which sustained low levels of production), we believe these relatively minor changes were unlikely to have caused the magnitude of increase in coho salmon production observed at the sites from 1983 to 1986. In addition, there were no obvious changes in either the amount of instream cover or substrate characteristics that would have influenced production.

Success of the experimental coho salmon releases was influenced by the timing and size of fish at stocking. Survival over summer was strongly associated with average weight at stocking in Schultz Creek ($r = 0.97$) and Herrington Creek ($r = 0.95$), and weakly associated with stocking weight in Hoffstadt Creek ($r = 0.27$). Larger fish also tended to be those that were planted later in the year (Table 2), and it was not possible to determine whether higher survival rates resulted from larger initial size, later introductions, a combination of both factors, or chance.

Bilby and Bisson (1987) found that smaller coho salmon stocked earlier in the year emigrated more rapidly than larger fish stocked later in the year. Scrivener and Andersen (1984) noted that earlier

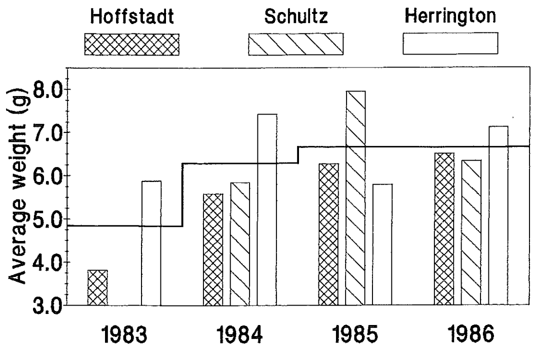

FIGURE 7.—Average weight of coho salmon in three Mount St. Helens streams at end of summer, 1983–1986. The stepped horizontal line represents the mean of the streams for each year.

emergence in spring of wild coho salmon in Carnation Creek, British Columbia, could result in increased downstream movements during freshets. We suspect that emigration from the study reaches accounted for most of the apparent mortality in Mount St. Helens streams, and that larger fish entering the streams in June were less likely to move out of the sites than those released in April or May. The relatively high survival in 1986 could have resulted from scattering the release locations in selected pools along the entire study reach of each stream; this may have reduced the initial intensity of competition and allowed more fish to establish foraging territories within the area.

Production rate was also affected by initial population size. With one exception, the streams were stocked with equal numbers of fish each year, but differences in average weight at stocking led to large differences in initial population biomass. These initial differences usually carried through the summer; biomass at stocking and mean biomass over the summer were highly correlated (r = 0.89, 0.99, and 0.90 for Hoffstadt, Schultz, and Herrington creeks, respectively). Coho salmon production in the streams was more strongly influenced by biomass and density than by average growth rate, a finding similar to that of Hawkins (1986) for ephemerellid mayflies in western North America.

Although average individual growth rates were not significantly correlated with production, there was a trend toward increased average weight at the end of summer (Figure 7). Coho salmon at the end of summer in 1985 and 1986 weighed 40% more than at the end of summer in 1983. In addition, average weights during 1985 and 1986 in the Mount St. Helens streams were nearly twice as great as those reported by Bilby and Bisson (1987) for nearby Deschutes River tributaries, where average coho salmon weights at the end of summer ranged from 3.0 to 4.2 g.

TABLE 5.—Average densities (number/m^2) of fishes in three Mount St. Helens streams during the last summer population census, 1983–1986.

Species	Density		
	Hoffstadt Creek	Schultz Creek	Herrington Creek
1983			
Coho salmon	1.25		0.44
Steelhead–rainbow trout			1.16
Cutthroat trout	<0.01		0.01
Sculpins			0.17
Total	1.25		1.78
1984			
Coho salmon	1.01	0.42	0.20
Steelhead–rainbow trout			0.97
Cutthroat trout	0.01		<0.01
Sculpins			0.66
Total	1.02	0.42	1.83
1985			
Coho salmon	0.15	0.83	0.20
Steelhead–rainbow trout		0.13	0.52
Cutthroat trout	<0.01		<0.01
Sculpins			0.47
Total	0.15	0.96	1.20
1986			
Coho salmon	0.78	1.26	0.71
Steelhead–rainbow trout		0.45	0.58
Cutthroat trout	0.02	<0.01	0.01
Sculpins			0.49
Total	0.80	1.71	1.80

The presence of other species may have caused a reduction in the summer survival of coho salmon in Herrington Creek, the mudflow stream. This site was used for rearing by large numbers of juvenile steelhead throughout the study (Table 5), and, except in 1986, steelhead were numerically dominant over coho salmon. Riffle habitat types predominated in the reach (Figure 1), and these conditions would have favored juvenile steelhead, which prefer riffles and displace coho salmon competitively where the two species are sympatric (Hartman 1965). Densities of coho salmon in Herrington Creek at the end of summer were often less than in the other two streams. However, the total density of all fish species in Herrington Creek was in every case greater than in either of the blast-area sites. The effect of resident rainbow trout on the coho salmon population in Schultz Creek during 1985 and 1986 was not obvious. In both years, Schultz Creek possessed a higher coho salmon density than the other sites and, in both these years, there were more coho salmon in Schultz Creek than in 1984, when rainbow trout were not present.

Coho salmon survived and grew at all sites during all years, even when temperatures exceeded the incipient lethal threshold. We saw no evidence of mortality when peak stream temperature climbed above 24.5°C, nor did we observe signs of lethargic or moribund behavior, such as those witnessed by Martin et al. (1986) in the first 2 years after the 1980 eruption. A few dead coho salmon were observed in Hoffstadt Creek in late summer 1986, but these deaths did not occur during extreme temperature peaks.

The only observed behavioral response to elevated temperature was an aggregation of coho salmon into a cool water plume created by inflowing groundwater in Schultz Creek. This aggregation took place when water temperature exceeded about 22°C. We do not know if use of cool water refuges such as groundwater seeps constituted an important survival mechanism enabling coho salmon to withstand peak stream temperatures at Mount St. Helens. Bilby (1984) described the occurrence of cool water pockets in a western Washington stream, but found that they were relatively rare.

Increases in coho salmon production and average end-of-summer weight corresponded with a gradual decline in diel temperature variation and, for Hoffstadt and Herrington creeks, with a reduction in the total number of hours during which stream temperature exceeded the incipient lethal threshold (Figure 4). Production was greatest in Schultz Creek, the only study site where lethal temperatures were never recorded. It is possible that recovery of riparian vegetation adjacent to the streams led to reduced diel temperature ranges and slightly lowered peak temperatures, both of which may have positively influenced production. However, it was impossible to separate the influence of these two trends from the confounding effects of factors such as size at stocking.

Circumstantial evidence suggests that high coho salmon production during the study period was made possible, in part, by increasing food resources. Several observations point to this conclusion. First, there was a noticeable increase in vigorously growing herbaceous vegetation along the streams over the years. The herb- and shrub-dominated riparian communities supported populations of terrestrial arthropods that were visually very abundant and active during summer. Mispagel and Rose (1978) found terrestrial invertebrates to be more diverse among ground-level vegetation than among tree canopies, and Mundie (1969) documented the importance of surface drifting terrestrial insects to the diet of coho salmon.

The second observation supporting an elevated-food hypothesis was that the amount of algae growing in the channels during late spring and summer appeared to be exceptionally high. Each stream was open to considerable direct solar radiation, and high light levels in combination with summer temperatures and elevated nitrogen concentrations would have supported high algal growth rates (Stockner and Shortreed 1978; Gregory 1980; Jasper and Bothwell 1986). Elevated nitrate-nitrogen concentrations in blast-area streams may have stimulated primary production, because west-slope Cascade Range streams draining watersheds with volcanic parent material are likely to be nitrogen-limited (Thut and Haydu 1971; Gregory 1980). Hawkins et al. (1983) and Perrin et al. (1987) demonstrated that increased primary production can lead to greater fish production in streams where the forest canopy has been opened or which have received inorganic nutrient additions.

The third observation suggesting that food was abundant in the Mount St. Helens streams was based on growth rates of the fish themselves. Temperatures at the sites were often in a range that would have favored low food conversion efficiency. At low food levels, most of the energy consumed would have been used to support metabolic functions with relatively little left for growth (Warren and Davis 1967; Averett 1968). Relatively high population densities would have created a strong demand on available food resources; in some cases, competition with other fish species would also have been involved. In spite of these constraints, average growth rates of coho salmon at the sites usually fell into a range of 1–2%/d (Table 4). To sustain such growth rates at high population densities and high temperatures would have required an abundance of available food. In an unpublished study of Clearwater Creek in the Mount St. Helens blast area, C. P. Hawkins (Utah State University, personal communication) reported that the densities of Chironomidae and *Baetis* spp. mayflies have reached very high levels where suitable cobble habitat occurs. These two insect groups are prone to entering the drift and both are important components of the diet of juvenile coho salmon in streams (Mundie 1969).

These observations all point to food as being an important factor mediating the effects of summer temperature extremes. With abundant food, the coho salmon populations may have been better able to resist disease, predation, or other factors that could have contributed to loss of fitness. Studies of salmonid populations elsewhere in the region have suggested that food abundance can mask or override the effects of environmental degradation (Murphy et al. 1981; Hawkins et al. 1983; Wilzbach 1985). It is possible that in the early posteruption period, food availability in the Mount St. Helens streams had not recovered to levels that existed from 1983 through 1986; this could help explain the difference between our study results and those of Martin et al. (1986).

Our study dealt strictly with the performance of hatchery coho salmon from stocking until the end of summer. It was our original intent to follow the experimental populations through the winter; however, efforts to monitor smolt production with fyke nets were largely unsuccessful. We therefore do not know if winter survival rates at the sites were affected by elevated temperatures or increased food abundance. Martin et al. (1986) measured low winter survival in Mount St. Helens streams where cover was lacking, compared with streams where cover was abundant. Low coho salmon densities in winter were observed in reaches of Carnation Creek where large organic debris had been removed (Tschaplinski and Hartman 1983; Hartman et al. 1987). Mason (1976) found that large increases in coho salmon biomass resulting from supplemental food additions during summer in a British Columbia stream did not lead to elevated smolt yield the following spring. This was believed to be caused by winter losses due to lack of cover during storm flows. Some of the apparent mortality in all of these cases resulted from downstream movements of fish out of the study areas. The extent to which emigrants contributed to total smolt production from the watersheds was poorly known, and may have depended on availability of off-channel overwintering sites (Peterson 1982; Brown 1985). Over the period of study, we did not observe significant entrainment of new large organic debris or other cover structures into the streams, and we suggest that lack of suitable winter habitat continues to be an important limiting factor for coho salmon that reside in volcanically affected portions of the Toutle River drainage.

Beschta et al. (1987) and Gregory et al. (1987) summarized the complicated interactions that accompany temperature and productivity increases caused by removal of forest canopy and alteration of riparian vegetation during logging and reforestation. These interactions potentially can result in a cycle of temporarily elevated fish production as the riparian community passes through early successional stages. Although the stream channel and riparian changes caused by the 1980 Mount St. Helens eruption were more extreme than those brought about by logging activities, many of the stream ecosystem responses to such factors as increased light and nutrients were similar. Environmental factors that regulated summer coho salmon production 1–2 years after the eruption did not appear to be as important 3–6 years after the disturbance. Continued long-term monitoring of streams near Mount St. Helens will reveal if and when new factors become limiting to both summer and winter coho salmon production, and will provide a unique opportunity to examine stream habitat and population recovery processes on a very large scale.

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