

Empirical Review of Coho Salmon Smolt Abundance and the Prediction of Smolt Production at the Regional Level

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Abstract.—Regional habitat and fisheries management planning requires estimates of the capacity of watersheds to produce salmonids. To predict the average abundance of smolts of coho salmon *Oncorhynchus kisutch* produced by streams and rivers, we related estimates of smolt abundance to habitat features derived from maps and discharge records. We assembled a database of 474 annual estimates of smolt abundance from 86 streams in western North America for this analysis. We found that only stream length and to a lesser extent latitude were useful in predicting mean smolt abundance. The frequency distribution of annual estimates of smolt abundance from individual streams tended towards a normal rather than the more usual lognormal distribution; the median coefficient of variation in abundance was 37%. Our results are consistent with the view that, on average, smolt abundance is limited by spatial habitat, but that there is significant annual variation in abundance probably due to variation in habitat quality caused by climate, flow, or other factors. We conclude that forecasting smolt yield from stream length and latitude is feasible at the watershed or regional level, but that the precision of a prediction for a single stream is poor. A more detailed approach will be required for local forecasting.

For the watershed or region-wide management of salmonid populations and their habitats, estimates of the productive capacity of streams, rivers, and lakes in the watershed are required. In the case of coho salmon *Oncorhynchus kisutch*, a watershed can contain a great number of populations, because this species can occupy both large rivers and small streams (Sandercock 1991). Thus, estimating the potential productivity of a major watershed could entail a costly, detailed investigation of every stream in the basin (Nickelson et al. 1992; Beechie et al. 1994). If resources for detailed studies were not available, a predictive model that makes use of readily available sources of data would be useful for rough estimates of production.

The average number of coho salmon smolts produced annually by a stream is an appropriate measure of a stream's potential to produce coho salmon. In the few long-term studies of coho smolt production, no consistent relationship between smolt abundance and the number of parent spawners has been found, except at very low spawner abundance (Knight 1980; Holtby and Scrivener 1989). Coho smolt production, therefore, appears to be largely regulated by density-dependent factors, probably related to the quality and quantity of suitable rearing habitat in the stream. Early

workers hypothesized that rearing space during the low-flow period in summer may be the limiting factor (Neave 1949; Chapman 1965). However, only for one of four streams with sufficient data (Flynn Creek, Oregon; Knight 1980) has there been a significant correlation between late summer fry abundance and subsequent smolt production (Knight 1980; Andersen and Scrivener 1992). Recent studies (Brown and Hartman 1988; Nickelson et al. 1992) suggest that the abundance of suitable overwintering habitat could also limit coho smolt production.

Based on the hypothesis that the production of coho smolts is limited by the availability of suitable rearing space, Marshall and Britton (1990), using data collected up to 1979, described predictive models for smolt yield and found a correlation between smolt abundance and stream area or stream length. Baranski (1989) found a similar relationship for 10 Washington State streams, as did Holtby et al. (1990) for a slightly different data set. In this paper, we expand on these analyses of coho smolt production by first collating much of the available data for western North America and then by comparing smolt abundance to habitat variables that have been hypothesized to affect smolt production. The habitat variables we used were extracted from maps or discharge records, because we wished to assess the potential of readily available information for predicting mean smolt abundance. In addition, we analyzed the interannual variability in smolt abundance as well as fac-

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tors influencing the size and age of coho salmon smolts. Statistics are provided so that habitat managers can use our results for the estimation of potential coho salmon production in watersheds or regions.

Data Sources and Analysis

We collected data from studies that contained estimates of the total annual coho salmon smolt abundance for one or more years. We only considered estimates that were from calibrated index traps or from weirs or fences that sampled a large proportion of the outmigrant population. In the case of weirs, smolt abundance estimates are minimums because some smolts emigrate outside of the period of weir operation, and frequently some are not counted because of weir washouts or leaks. In some watersheds, estimates of both tributary and system-wide smolt production were available. These data are, therefore, not completely independent, as is assumed for statistical analyses. In most cases, each tributary contributed less than 15% of the system production, so we assumed the dependence of the system estimate on data for any individual stream was small and all data series from the system could be considered as independent. However, in four cases, estimates were not used in the analysis because of overlaps with other data series from the same system (see Appendix 1).

Some systems contained lakes that we treated as extensions of the stream, and we converted the perimeters of such lakes into equivalent stream lengths. We felt this conversion was justified because surveys of juvenile coho salmon in lakes suggest the fish inhabit nearshore habitat and are rarely found in the pelagic zone (Swales et al. 1988). We excluded systems where lakes made up more than half of the rearing length, because our analysis focused on stream, rather than on lake, production. We excluded data from small ground-water-fed side channels and sloughs. Finally, we excluded some recent studies from streams in the southern portion of the range because the observed very small spawning escapements would have been unlikely to fully seed rearing habitats. In all, data were collected for 86 systems.

The total number of smolts migrating each year, and when available, smolt age and mean length by age were compiled. If smolt age was not recorded and the stream was south of 48°N, we assumed all smolts were age 1, because all emigrants that had been aged south of 48°N were yearlings.

Habitat Variables

We selected several habitat variables that we thought might be related to coho salmon smolt production. Two variables we did not include were stream area, which was not available for many systems, and the degree and type of land use in the drainage basin. The latter would have been difficult to collect because our data extended back to the 1930s, and quantifying land use over this period would require extensive historical investigation of human activity in each watershed. We used the following habitat data in this analysis.

Stream length.—The length of stream available to rearing coho salmon juveniles upstream from the trapping site was often described in the source report. For British Columbia streams, detailed information was also available in FHIIP (1991) catalogues. In other cases, the upstream limit of coho salmon rearing was estimated from an examination of stream gradient on topographic maps (usually 1:50,000 or 1:63,360 scale). For larger systems, we assumed all small tributaries of low gradient (<3%) were used by coho juveniles. Stream lengths were measured on a digitizing tablet.

Stream gradient.—The mean gradient of stream used for rearing was calculated from contour lines on the topographic maps. In the case of short, low-gradient streams for which we could not estimate the gradient from maps, we assumed a value of $0.001 \text{ m} \cdot \text{m}^{-1}$.

Valley slope.—Streams located in broad, flat floodplains may possess more off-channel habitat that has been shown to be important for rearing juveniles (e.g., Brown and Hartman 1988). We attempted to index this potential by estimating the steepness of the valley walls adjacent to the stream. To do this, we first located points on topographic maps where contour lines crossed the stream. We then measured the distance, perpendicular to the stream, from each point to the next contour line beside the stream, on both sides of the valley. The slope of the valley was calculated from the average of the two distances and the elevation change between contour lines. On some streams, measurements were made at points half way between the contour lines crossing the stream, and it was assumed the elevation change from this point to the next contour line parallel to the stream was half the contour interval. When possible, we repeated this process at five points along the length of the stream and averaged the estimates. For some short streams where the valley slope could not be

TABLE 1.—Bivariate correlations between habitat variables used in the analysis of streams and rivers. For each pair of variables, r is listed above P ; $N = 83$ in all cases. Gradient is the average stream gradient. Valley is the average valley slope adjacent to the stream. Minflow and maxflow are the ratios of the lowest and highest monthly flows to the mean annual discharge. Yield is water yield ($\text{m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-2}$).

Correlate	$\text{Log}_e(\text{gradient})$	$\text{Log}_e(\text{valley slope})$	$\text{Log}_e(\text{latitude})$	$\text{Log}_e(\text{minflow})$	$\text{Log}_e(\text{maxflow})$	$\text{Log}_e(\text{yield})$
$\text{Log}_e(\text{length})$	-0.42 <0.001	0.17 0.12	-0.10 0.37	0.29 0.008	-0.17 0.12	0.16 0.15
$\text{Log}_e(\text{gradient})$		0.48 <0.001	0.17 0.11	0.27 0.01	-0.34 0.002	0.28 0.01
$\text{Log}_e(\text{valley slope})$			-0.10 0.35	0.52 <0.001	-0.42 <0.001	0.45 <0.001
$\text{Log}_e(\text{latitude})$				0.22 0.04	-0.10 0.36	0.32 0.003
$\text{Log}_e(\text{minflow})$					-0.70 <0.001	0.66 <0.001
$\text{Log}_e(\text{maxflow})$						-0.58 <0.001

estimated because no contour lines crossed the stream, we assumed a value of $0.001 \text{ m} \cdot \text{m}^{-1}$.

Latitude.—The latitude of each stream (defined as the midpoint of the watershed) was obtained from topographic maps and relevant gazetteers (USGS 1981, 1983).

Discharge.—For our analyses, we sought estimates of mean annual discharge, minimum monthly mean discharge, and maximum monthly mean discharge. For larger British Columbia streams, these values were usually obtained from gauging station summaries (Environment Canada 1991). Discharge data for gauged U.S. streams were found in USGS (1993). Discharge data were sometimes available in the original reports of coho salmon smolt abundances.

For streams without gauging stations, we estimated the discharge from regression equations calculated from data for nearby gauged streams. Discharge data were collected for several streams with gauging stations in a similar biogeoclimatic zone, and a regression of discharge on drainage area was calculated after both variables were log-transformed. Separate regressions were calculated for the minimum and the maximum monthly mean discharges and the mean annual discharge. These regression equations were then used to predict discharge values of ungauged streams from their drainage areas.

Discharge variables were correlated with each other and with stream length. To reduce these correlations, we calculated relative discharge extremes by dividing the monthly minimum and maximum discharges by the mean annual discharge. The new variables provide a measure of the severity of low flow or flood extremes for the river. We also calculated water yield (mean annual

discharge/drainage area) as an index of the flow in the river relative to its size. The new variables were only weakly correlated with stream length (Table 1).

Data Analysis

We used simple and multiple regression to search for predictors of mean smolt abundance. Because of the potential for a type I error resulting from conducting several analyses, attention was paid only to the factors that were significant with $P < 0.01$. All variables were $\log_e$ -transformed because variability in smolt abundance increased with the mean. For each stream, the number of years of data was used as a weight in the analysis (Neter and Wasserman 1974).

We compared the shape of the frequency distribution of annual estimates of smolt yield from each stream to the normal distribution using the Shapiro-Wilks test of normality as implemented by SAS (SAS Institute 1988). We also tested whether the distribution could be described by a lognormal distribution by first using the $\log_e$ transformation on smolt abundances. Only systems having 10 or more years of data were used in this analysis.

Results

Mean Smolt Production

Mean coho salmon smolt abundance was strongly correlated with stream length (Figure 1), and the slope of the regression of $\log_e(\text{smolts})$ on $\log_e(\text{stream length})$ was not different from 1 ($F = 0.1$; $df = 1, 84$; $P = 0.71$). The slope of 1 means that the number of smolts produced per unit of stream length was constant and independent of stream size. Therefore, subsequent analyses were

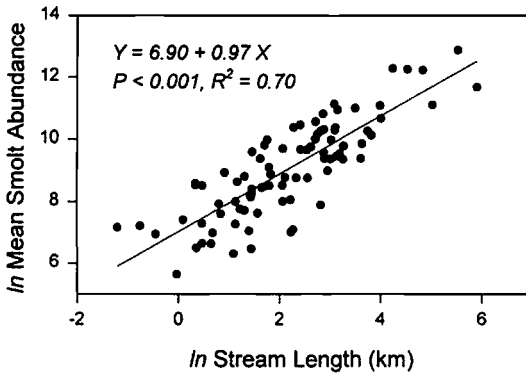


FIGURE 1.—Relation of mean coho salmon smolt abundance (Y) to stream length (X) for 83 streams and rivers (double $\log_e$ plot).

conducted with production rates (i.e., smolts/km of stream). Of the habitat variables, smolt production rate was only correlated with latitude (Table 2).

Examination of the plot of smolt production as a function of latitude indicated smolt production was lowest and least variable at the edges of the latitudinal range, and highest and most variable in the middle latitudes (Figure 2). Because these data were not suitable for standard parametric regression analysis, we summarized this pattern in two ways that gave similar results. First, we used the nonparametric probability density technique described by Rice (1993) to estimate median and interquartile ranges for smolt production rates at 2° intervals from 45 to 53°N latitude. The square root of the number of years of data contributing to each data point was used as a weight in this analysis (Table 3). Second, we divided, post hoc, the data into latitude ranges, and calculated the mean and standard deviation of smolt production rates (Table 4). Data were $\log_e$ -transformed because the variance was proportional to the mean. There were differences in the $\log_e$ (production rates) among these categories (analysis of variance: $F = 12.2$; $df = 3, 82$; $P < 0.0001$), streams

TABLE 2.—Bivariate correlations between coho salmon smolt production rates and the habitat variables listed in Table 1. For each pair, r is listed above P ; $N = 83$.

Correlate	$\log_e$ (gradient)	$\log_e$ (valley slope)	$\log_e$ (latitude)	$\log_e$ (min-flow)	$\log_e$ (max-flow)	$\log_e$ (yield)
$\log_e$ (smolts/km)	0.16	-0.20	0.38	-0.26	0.10	-0.09
	0.14	0.07	<0.001	0.02	0.34	0.42

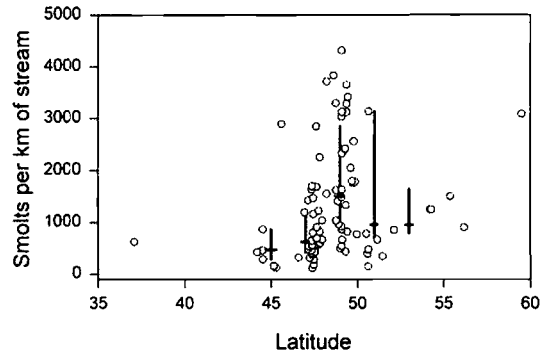


FIGURE 2.—Coho salmon smolt production rates plotted by stream latitude. Vertical lines indicate interquartile ranges estimated by the probability density method of Rice (1993); horizontal bars are medians.

located between 48 and 50°N being the most productive (Table 4).

Frequency Distribution of Smolt Abundance

The frequency distribution of annual estimates of smolt abundance more frequently followed a normal distribution than the skewed lognormal form. Of 24 data sets with 10 or more years of data, 9 were not different from either normal or lognormal distributions and 2 were different from both ($P < 0.05$). In the 13 cases that were significant for only one distribution, 11 were different from the lognormal and 2 were different from the normal distribution. This difference in proportions was significant (McNemar test, Sokal and Rohlf 1995: $\chi^2 = 7.1$, $df = 1$, $P < 0.01$). Because 20 of 24 cases were not distinguishable from the normal distribution, we concluded that this distribution was suitable for summarizing annual variation in abundance.

Annual Variation in Smolt Production

Annual variation in the number of smolts produced from each stream was strongly correlated

TABLE 3.—Summary statistics of coho salmon smolt production rates (smolts/km of stream) estimated by the nonparametric density estimation procedure of Rice (1993), by latitude, showing the median and the interquartile and 5, 95% ranges.

Latitude (°N)	Median	Percentile ranges			
		25	75	5	95
45	457	291	868	124	2,849
47	642	419	1,198	161	2,259
49	1,476	823	2,849	435	3,650
51	924	664	3,129	186	3,286
53	902	787	1,642	345	3,286

TABLE 4.—Mean and SD of $\log_e$ -transformed coho salmon smolt production rates, summarized by latitude ranges, with back-transformed estimates of the mode [$\exp(\bar{x})$] and the 5 and 95% percentile points for the distributions, calculated as $\exp(\bar{x} \pm 1.645 \text{ SD})$. Mean for the log-normal distribution is $\exp(\bar{x} + \frac{1}{2}\sigma^2)$ (Beauchamp and Olson 1973).

Latitude range ($^{\circ}\text{N}$)	N	Mean	SD	Mode	5, 95%
<46	7	6.128	1.072	459	79, 2,677
46–48	33	6.546	0.713	696	216, 2,249
48–50	33	7.417	0.655	1,664	568, 4,883
>50	13	6.734	0.862	841	203, 3,474

with average smolt abundance (Figure 3). If the slope of this regression were 2, then variability would follow a constant coefficient of variation (CV) model. However, the slope was slightly less than 2 ($F = 7.5$; $df = 1, 58$; $P < 0.01$), which means that smolt abundance was proportionately less variable in more productive systems. The median CV ($100 \cdot \text{SD}/\text{mean}$) for all streams, for either smolt numbers or smolt density, was 37% (interquartile range, 26–48%). Annual variation in smolt production was not correlated with any of the habitat variables in multiple regressions that included mean smolt abundance (all $P > 0.10$).

Smolt Size and Age

For streams north of 48°N , where variation in smolt age was observed, we found a positive relation between age and latitude (data $\log_e$ -transformed, $r = 0.71$, $P < 0.001$, $N = 36$; Figure 4). Neither smolt density (smolts/km of stream) or the other habitat variables were significant in multiple regressions that included latitude (all $P > 0.05$).

The analysis of smolt size was complicated by the observation that in streams with poor growing

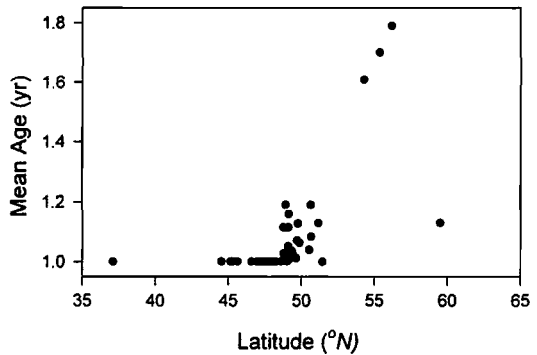


FIGURE 4.—Relation of mean coho salmon smolt age to stream latitude.

conditions, coho salmon juveniles may stay an extra year or more, which will tend to increase mean smolt size when averaged over all ages. Therefore, we restricted our analysis to the length of age-1 smolts as a measure of growing conditions in the first year of freshwater residence. This analysis might also be biased because in streams where 2- or 3-year-old smolts are produced, there is a tendency for the largest individuals to migrate after the first year (Holtby 1988; Irvine and Ward 1989), and the average size of migrating age-1 smolts will be an overestimate of the average growing conditions for all juveniles in their first year. Therefore, we conducted two analyses, the first with all age-1 smolt data and the second with a subset of streams in which fewer than 5% of smolts were older than age-1. The latter analysis was relatively unbiased by the interaction between smolt size and smolt age.

Longer streams tended to produce larger age-1 smolts (Figure 5). Of the other habitat variables, only valley slope was significant in multiple regressions that included stream length: length, mm

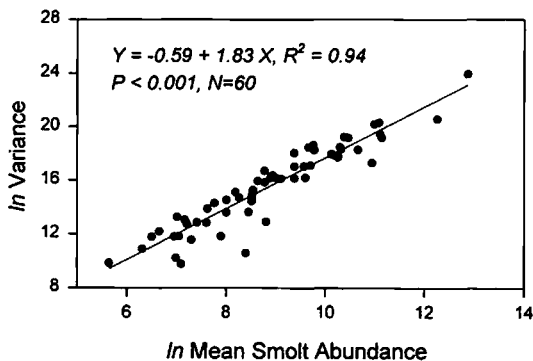


FIGURE 3.—Relation of interannual variance (Y) to mean coho salmon smolt abundance (double $\log_e$ plot).

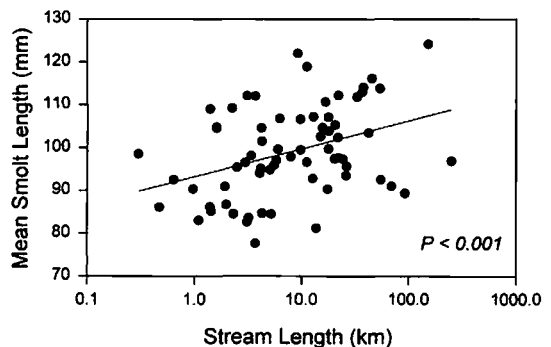


FIGURE 5.—Relation of mean length of age-1 coho salmon smolts to the length of stream.

$= 82.4 + 3.9 \cdot \log_e(\text{stream length, km}) - 3.3 \cdot \log_e(\text{valley slope})$; $R^2 = 0.44$, $P < 0.001$. The negative coefficient for valley slope indicates larger smolts are produced by rivers in gentler terrain. Mean smolt length was not related to smolt density ($r = 0.04$, $P = 0.73$). Results were very similar when the subset of streams that produced almost exclusively age-1 smolts were used.

Discussion

Factors Influencing Mean Smolt Abundance

We found that coho salmon smolt abundance was mostly correlated with stream length, suggesting that in a very general sense smolt production is likely limited by the availability of physical habitat. A combination of other factors such as rearing habitat quality, spawning habitat, spawner abundance, and invertebrate production probably all contribute to the remaining variation in abundance.

We found the abundance of smolts per length of stream channel was independent of total stream length. Baranski (1989), Holtby et al. (1990), and Marshall and Britton (1990), each using smaller data sets, found the coefficient of the regression of abundance on stream length was greater than 1, perhaps because they included fewer large rivers in their analyses than we did. Other models for predicting smolt production have used wetted area rather than stream length (Symons 1979; Reeves et al. 1989; Kennedy and Crozier 1993). These models may be best suited to small streams, where the whole width of the stream is suitable for rearing juveniles. Mundie (1969) distinguished habitat use between large and small rivers; in large systems, coho salmon fry are confined to slack water habitats in the margins of streams, whereas they find suitable habitat across the widths of small streams. Hartman (1965) and Lister and Genoe (1970) also found juvenile coho salmon were confined to the margins of larger rivers, where they used log jams or overhanging banks. In some cases, much of the productivity may originate from tributaries rather than from the main stem (Beechie et al. 1994). Indeed, if stream area were the variable limiting production of coho salmon smolts irrespective of stream size, then the exponent of the log-log regression of smolt production on stream length would be greater than the value of 1 we found, because area should increase exponentially with stream length. Thus, across the range of stream sizes considered here, stream length appears to be the most appropriate general measure of habitat abundance.

We were unable to improve the precision of predictions of smolt abundance by using other habitat variables coupled with stream length. Hubert and Kozel (1993) found that many stream features used by juvenile coho salmon (e.g., deep pools, undercut banks, and woody debris) are correlated with channel gradient or stream discharge, which led us to hypothesize that these variables might serve as surrogates for instream habitat features. Baranski (1989) found a correlation between coho salmon smolt production and gradient for 10 Washington streams, and Brown et al. (1989) noted that catches of coho salmon juveniles were inversely related to stream gradient at the sampling site in a study of 23 coastal streams. Fish abundance and channel gradient are also correlated for other salmonid species (Chisholm and Hubert 1986; Kozel et al. 1989). However, in our analysis, neither gradient nor discharge variables were significant predictors of smolt yield. The analysis of gradient was probably weakened because we had to average gradient over the total length of the stream that was inhabited by coho salmon, whereas the actual distribution of juveniles may be restricted to specific reaches of the river, perhaps near the spawning grounds or in areas of preferred habitat (Hartman 1965). Further, the sign of the correlation between habitat features and gradient or discharge varies with the type of feature; for example, the occurrence of log dams, dammed pools, and pools with woody cover are all positively related to stream gradient, but occurrences of deep pools and lateral pools are negatively related to gradient (Hubert and Kozel 1993). All of these features have been shown to be important for juvenile coho salmon (Hartman 1965; McMahon and Hartman 1989; Nickelson et al. 1992). A more direct inventory of habitat features from aerial photographs or streamside surveys (including an assessment of human impacts on the landscape) might be more successful at improving the precision of predictions of smolt abundance.

Our flow variables were not correlated with coho salmon smolt yield. In coastal coho salmon streams, the greatest discharge usually occurs in winter months, when it is due to rainstorms (e.g., Chapman 1962). Inverse correlations between flood severity and the abundance of smolts the following spring have been observed (Knight 1980), and the importance of winter flows for overwinter survival has been noted (Mason 1976; Tschaplinski and Hartman 1983; McMahon and Hartman 1989). Low flow during midsummer has also been implicated as the limiting factor in some

studies of coho salmon production (Neave 1949; Wickett 1951; Chapman 1962; Mathews and Olson 1980), although others have found weak or non-existent relationships between summer flow and smolt or adult abundance (Smoker 1955; Knight 1980; Scarnecchia 1981), possibly because limiting factors and variation in mortality later in the year masked the role of the summer period. Correlations between mean annual flow and coho salmon production have been documented (Smoker 1955; Scarnecchia 1981; Anderson and Wilen 1985), suggesting that annual discharge can integrate rearing conditions over the whole year. Thus, although the exact mechanism may vary, it seems annual variation in flow can affect coho salmon production in streams. However, our analysis suggests that the long-term average discharge regime of a stream does not produce a detectable impact on the average production of coho salmon smolts.

The abundance of coho salmon smolts per kilometer of stream channel was greatest in the center of the species' latitudinal range and decreased towards the extremes. This pattern has been observed for many other species (Gaston 1990). Godfrey (1965) noted that adult coho salmon abundance was lower at the edges of the range and our analysis shows the variation in adult abundance is in part due to clinal variation in the productivity during the freshwater stage of the life cycle. However, this conclusion should be considered preliminary, because we found fewer data from streams at the extremes of the species' range than in the central British Columbia-Washington region. Although the causes of lower abundances at the extremes of the range are unknown, a short growing season and harsh conditions in the north and high midsummer water temperatures in the south have been suggested (Sandercock 1991).

Variability in Coho Salmon Smolt Production

We found that the annual variation in coho salmon smolt abundance for individual streams was more likely to be normally distributed rather than to show the skewed distribution (usually modelled by the lognormal function) often found for fish and other populations (Hennemuth et al. 1980; Myers and Pepin 1990; Fogarty 1993). The lognormal distribution is usually thought to be generated when survival over a life history stage results from randomly and independently varying survival over a sequence of shorter stanzas (Peterson 1981). The more symmetric distribution we observed could occur if density-dependent mortality occurs relatively late in the freshwater pe-

riod, which could truncate the occasional occurrence of very high densities caused by high seeding rates or good survival during the first part of the freshwater stage.

The capacity of streams to produce coho salmon smolts should not be thought of as constant. Although habitat likely limits production, we found the annual variation in smolt abundance was substantial ($CV = 37\%$). Correlations of coho salmon abundance with interannual variation in streamflows at different times of the year (Neave 1949; Smoker 1955; Scarnecchia 1981) support the notion that the carrying capacity is related to the abundance of suitable habitats at critical times, and that annual variation in flow will affect the availability of these habitats. Longer-term variation in habitat capacity will occur when extreme flows modify the morphology of the stream. In addition to annual changes in the carrying capacity of the stream, variation in abundance will be caused by density-independent mortality both before and after the compensatory period. Finally, some of variability in our data is due to measurement error, especially for larger systems that are sampled with index traps rather than with weirs. Estimation error can also exist when weirs are used, because they are not always fish proof and they can be washed away during high flows.

The magnitude of natural variation in coho salmon smolt production needs to be kept in mind during the design of monitoring programs for estimating the effects of habitat change or enhancement activities on production. Simple sample size calculations show that using a one-sided *t*-test to detect a 50% increase in mean abundance after habitat enhancement ($\alpha = 0.05$) will require at least 5 years of before-and-after monitoring. When more sophisticated statistical designs are used (e.g., Carpenter 1990), estimates of variability summarized here can be used for sample size and power calculations.

Smolt Size and Age

The correlation between mean smolt age and latitude we describe agrees with the descriptive summaries of Drucker (1972) and Sandercock (1991). Presumably it is due to the shorter growing season in northern rivers, which prevents juveniles from reaching sufficient size for smolting after their first year (Holtby 1988). However, among streams that produced 95% or more age-1 fish, we found no relation between smolt size and latitude. Thus, on this more restricted geographic range, local factors have a greater influence on growth

than latitude (Sandercock 1991). Smolt size was not related to smolt density. This is perhaps not surprising, because smolt abundance is often unrelated to the abundance of juveniles during the previous summer, when density-dependent growth can occur (Holtby and Scrivener 1989).

Larger smolts were produced by longer streams in broader floodplains. In our database, steeper streams generally flow out of mountainous areas, whereas longer, low-gradient streams are found in lowlands or coastal plains. It is likely that the low-gradient streams have higher water temperatures and a longer growing season than high-gradient streams, and they also have more off-channel habitat, all of which can result in larger smolts (Peterson 1982; Holtby 1988).

Prediction of Coho Salmon Smolt Yields

Despite our attempts to incorporate habitat features, stream length remains the most useful predictor of mean smolt abundance at the overview or regional level. The use of latitude-specific smolt production rates can make a slight improvement to the precision of predictions. Nonetheless, the confidence limits around a prediction of smolt yield for a single stream are very wide, and even the interquartile ranges can vary by a factor of 2 (Table 3). The utility of this approach is improved somewhat if the production from a group of streams is desired. For example, for a combined estimate from $n = 10$ streams, the standard error of the estimate ($SD/\sqrt{n}$) would be about $\pm 30\%$ of the mean (data from Table 4). This level of precision is likely suitable for overview studies; however, site-specific, data-intensive habitat models will be required for evaluating coho production for individual streams. Reeves et al. (1989), Nickelson et al. (1992), and Beechie et al. (1994) provided examples of the detailed approach, although the precision of their methods is only beginning to be evaluated.

The limited utility of habitat measures for predicting smolt abundance may also be related to the complex pattern of movements that have been observed in some populations. In small coastal streams, fry have been observed to travel through estuary or nearshore regions to nearby streams to rear (e.g., Mason 1976). In larger systems, movement has been observed among tributary streams and the main stem, especially just before winter (Scarlett and Cederholm 1984). These movements mean that a proportion of the smolts produced each year from a stream may have spent a significant amount of time rearing in other habitats. Thus any

relation between habitat features and the average abundance of smolts from that stream may be weakened by the presence of individuals originating elsewhere.

In summary, because of the many factors that have been documented to affect coho salmon smolt production and because different factors may be important in different streams at different times, there are likely no general predictive models that will yield precise estimates of smolt production potential. Managers requiring precise estimates will still have to make more detailed habitat measurements; with enough data, region-specific models can be developed (e.g., Reeves et al. 1989). Nonetheless, the current exercise has served to review the available data, and has generated predictive tools suitable at the regional or large watershed level. With additional information on fecundity and egg-smolt survival (Bradford 1995), it is possible to use these tools to convert predicted smolt yields to escapement targets (e.g., Beidler et al. 1980) when more detailed information is lacking.

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Appendix 1: Smolt Data

TABLE A1.1.—Smolt data for streams and rivers in Alaska, British Columbia, California, Oregon, and Washington. Mean length is the length of age-1 smolts; *N* is the number of years of data.

Stream	Smolt abundance		N	Mean age (year)	Mean length (mm)	Source
	Mean	SD				
Alaska						
Porcupine Creek	4,694	915	4	1.80	84.5	Thedinga and Koski (1984)
Sashin Creek	1,654	621	10	1.70	83.0	Crone and Bond (1976)
Situk River	213,000		1	1.17	91.0	Thedinga et al. (1994)
British Columbia						
Antigonish Creek	2,784		1		109.2	Finnegan (1991)
Barrett Creek	5,006		1	1.02	104.8	Fedorenko and Cook (1982)
Bible Camp side channel ^a	3,634		1	1.06	90.0	Argue et al. (1979)
Black Creek	59,065	24,314	10	1.06	111.8	Clark and Irvine (1989); Fielden et al. (1989); Labelle (1990); Bocking et al. (1991); Nass et al. (1993)
Bonsall Creek	15,820		1	1.01	118.9	Patterson et al. (1979)
Campbell River	18,954		1	1.00	114.1	Schubert (1983)
Capilano River	56,410	5,749	2			Marshall and Britton (1990)
Carnation Creek	2,996	905	20	1.19	82.7	Andersen and Scrivener (1992)
Cheakamus River	38,667		1			Marshall and Britton (1990)
Chef Creek above fence 2 ^b	9,362	2,345	4			Marshall and Britton (1990)
Chef Creek between fences ^b	5,172	644	3			Marshall and Britton (1990)
Chef Creek total system	14,708	3,305	3			Marshall and Britton (1990)
Coghlan Creek	11,787	3,222	7	1.01	94.9	Schubert (1982); Schubert and Kalnin (1990); Farwell et al. (1991a, 1991b, 1992); Kalnin and Schubert (1991)
Cowichan and Koksilah rivers	1,527,750	172,181	2	1.04	95.5	Armstrong and Argue (1977); Argue et al. (1979)
Cowichan River	203,425		1			Lister et al. (1971)
Cowichan side channel ^a	2,458	940	2	1.06	81.0	Argue et al. (1979)
Devereux Creek	11,945		1	1.13	103.9	Fielden et al. (1985)
Fifteen Mile Creek	1,049	367	2	1.16	92.5	Fedorenko and Cook (1982)
French Creek	29,471	10,364	5	1.03	97.6	Fielden et al. (1989); Labelle (1990); Bocking et al. (1991); Nass et al. (1993)
Hooknose Creek	4,987	1,618	10			Hunter (1959)
Hopedale Creek	7,554	3,590	3	1.05	95.5	Fedorenko and Cook (1982)
Hunt's Creek	5,110	2,086	12	1.03	86.2	Lister and Walker (1966); Paine et al. (1975); Sandercock and Minaker (1975)
Kelvin Creek	18,134		1	1.11	95.9	Argue et al. (1979)
Keogh River	71,062	15,706	11	1.08	99.2	de Hrussovczy-Wirth (1979); Irvine and Ward (1989); Ward (unpublished) ^c
Keogh River west	776	447	2	1.19		Irvine and Ward (1989)
Lachmach River	17,203	11,144	5	1.61	81.2	Finnegan et al. (1990); Finnegan (1991); Davies (1991a, 1991b); Davies et al. (1992)
Little Qualicum River	11,483		1	1.04	93.5	Lister et al. (1979)
Little Stawamus River	6,659	639	2	1.07	77.7	Argue and Armstrong (1977)
Mamquam Channel ^a	4,401	2,846	3			Sheng et al. (1990)
McTaggart Creek	3,165		1	1.00	122.0	Matthew and Stewart (1985)
Meighn Creek	5,634	2,917	3	1.13	83.7	Argue and Armstrong (1977)
Miller Creek and Pond	5,369		1	1.00	109.0	Patterson et al. (1979)
Misty Inlet Creek	764		1		90.9	Irvine and Ward (1989)
Misty Outlet Creek	647		1			Irvine and Ward (1989)
Nile Creek	4,973	1,381	9			Wickett (1951)
Pastuch Creek	4,446	199	2	1.03	84.7	Argue et al. (1979)
Post Creek	1,087	166	2	1.11	86.7	Fedorenko and Cook (1982)
Qualicum River main stem	32,040	15,123	12	1.02	99.5	Lister and Walker (1966); Paine et al. (1975); Sandercock and Minaker (1975); Fraser et al. (1983)
Qualicum River system ^b	34,807	14,659	15	1.02	96.6	Lister and Walker (1966); Paine et al. (1975); Sandercock and Minaker (1975); Fraser et al. (1983)
Quinsam River	42,388	9,353	5		92.5	Reinhardt and MacKinnon (1979); Blackmun et al. (1985)
Rust Creek	1,295	690	3	1.04	98.6	Fedorenko and Cook (1982)

TABLE A1.1.—Continued.

Stream	Smolt abundance		N	Mean age (year)	Mean length (mm)	Source
	Mean	SD				
Ryder Creek	3,590	1,923	3	1.05	95.2	Fedorenko and Cook (1982)
Salmon River main stem	17,582	9,268	7	1.01	95.7	Schubert (1982); Schubert and Kalnin (1990); Farwell et al. (1991a, 1991b, 1992); Kalnin and Schubert (1991)
Salmon River system ^b	29,369	11,927	7	1.01	95.3	Schubert (1982); Schubert and Kalnin (1990); Farwell et al. (1991a, 1991b, 1992); Kalnin and Schubert (1991)
Salwein Creek	8,955	3,169	4	1.03	99.7	Fedorenko and Cook (1982); Schubert (1984)
Street Creek	1,479	326	3	1.04	104.6	Fedorenko and Cook (1982)
Tenderfoot Creek and Pond	7,923	2,546	3	1.09	84.9	Argue and Armstrong (1977)
Trent River	16,255	5,210	6	1.01	97.9	Fielden et al. (1989); Labelle (1990); Bocking et al. (1991); Nass et al. (1993)
Upper Keogh River	6,486	2,762	4	1.04		Irvine and Ward (1989)
Upper Paradise channel ^a	4,752	2,266	7			Sheng et al. (1990)
Worth Creek channel ^a	262	311	6			Sheng et al. (1990)
California						
Waddell Creek	6,445	4,266	4			Shapovalov and Taft (1954)
Oregon						
Deer Creek	2,014	617	15		84.5	Chapman (1965); Hall and Lantz (1969); Knight (1980)
Fish Creek	2,689	373	3		110.7	Everest et al. (1988)
Flynn Creek	667	366	14		85.2	Chapman (1965); Hall and Lantz (1969); Knight (1980)
Gnat Creek	2,048	1,041	5			Willis (1962)
Needle Branch Creek	283	138	14		90.3	Chapman (1965); Hall and Lantz (1969); Knight (1980)
Sand Creek	1,207	133	3		106.7	Sumner (1953)
Spring Creek	1,360	583	10		86.1	Skeetsick (1970)
Washington						
Bear Creek	552	233	10		96.5	Lenzi (1983); Baranski (1989)
Big Beef Creek	30,072	9,530	12		107.1	Baranski (1989)
Big Rock Creek	3,464		1		104.6	Lenzi (1983)
Bingham Creek	31,806		1		112.2	Seiler et al. (1984)
Carpenter Creek	21,435		1		105.3	Lenzi (1983)
Christmas Creek	1,110	762	10			QDNR (1993)
Clearwater River	67,971	16,769	4		124.1	Seiler et al. (1984); QDNR (1993)
Coulter Creek	13,771		1		97.4	Blankenship and Tivel (1980)
Courtney Creek	1,156	369	10		94.0	Lenzi (1987); Baranski (1989)
Creamer Slough ^a	628		1		109.0	King and Young (1986)
Deschutes River	64,675	25,825	6		113.8	Seiler et al. (1981, 1984)
Goldsborough Creek	11,792	5,025	2		113.0	Blankenship and Tivel (1980)
Griffin Creek	49,858		1		90.3	Blankenship and Tivel (1980)
Harris Creek	25,772	7,718	9		104.7	Lenzi (1987); Baranski (1989)
Hurst Creek	5,050	1,807	12		110.8	QDNR (1993)
Kelsey Slough ^a	504	431	2		115.9	King and Young (1985, 1986)
Little Bear Creek	15,629	10,296	2		92.8	Blankenship and Tivel (1980)
Little Pilchuck Creek	28,307	7,069	13		103.5	Lenzi (1985, 1987); Baranski (1989)
Little Tahuya Creek	7,208	3,266	10		106.8	Lenzi (1985, 1987); Baranski (1989)
Lost Creek	2,355	1,278	9		98.2	Lenzi (1985, 1987); Baranski (1989)
Maple Glen Slough ^a	326		1		109.4	King and Young (1985, 1986)
Mill Creek	24,809	7,997	12		116.1	Lenzi (1987); Baranski (1989)
Minter Creek	28,456	7,337	11			Salo and Bayliff (1958)
Mission Creek	14,307	5,048	7		99.8	Lenzi (1987); Baranski (1989)
Mud Creek	24,591		1		112.1	QDNR (1993)
North Creek	11,701	8,310	2		97.4	Blankenship and Tivel (1980)
Schafer Park Slough ^a	420	69	2		120.1	King and Young (1985, 1986)
Schafer Slough tributary ^a	584		1		122.9	King and Young (1985, 1986)
Shale Creek	3,000	1,439	11		108.3	QDNR (1993)
Sherwood Creek	12,695		1			Blankenship and Tivel (1980)
Skookum Creek	6,380		1		107.2	Blankenship and Tivel (1980)
Snahapish Creek	8,038	3,274	13		114.0	QDNR (1993)
South Fork Skykomish River	208,758	29,278	5		89.4	Seiler et al. (1981, 1984)

TABLE A1.1.—Continued.

Stream	Smolt abundance		N	Mean age (year)	Mean length (mm)	Source
	Mean	SD				
Stillaguamish River	388,243	158,665	2	96.9	Seiler et al. (1984)	
Tiger Creek	21,530		1	97.1	Lenzi (1983)	
Union River	22,109		1	102.6	Blankenship and Tivel (1980)	
Upper Chehalis River	116,643		1		Brix and Seiler (1977)	
Wagley Creek	2,246		1	112.0	Lenzi (1983)	
Wildcat Creek	3,873	1,553	9	101.5	Lenzi (1987); Baranski (1989)	

^a Sidechannels and sloughs were not used in the analysis.^b Estimates for these streams were not used in the analysis.^c B. R. Ward, University of British Columbia.

Appendix 2: Habitat Data

TABLE A2.1.—Habitat data for the streams in Appendix 1. Discharges are the mean annual discharge and the minimum and maximum monthly mean discharges.

Stream	Latitude (°N)	Length (km)	Drainage area (km ²)	Gradient (m·m ⁻¹)	Valley slope (m·m ⁻¹)	Discharge (m ³ ·s ⁻¹)		
						Mean	Minimum	Maximum
Alaska								
Porcupine Creek	56°11'	5.2						
Sashin Creek	55°23'	1.10	10.0	0.0030	0.261	0.935	0.086	2.94
Situk River	59°27'	69.4						
British Columbia								
Antigonish Creek	54°14'	2.23	10.8	0.045	0.131	1.53	0.565	2.20
Barrett Creek	49°07'	1.60	0.37	0.004	0.001	0.007	0.000	0.031
Bible Camp side channel	48°47'	1.21		0.000	0.000			
Black Creek	49°52'	33.00	72.8	0.030	0.028	3.73	0.286	7.27
Bonsall Creek	48°53'	11.20	13.0	0.008	0.062	0.550	0.080	1.07
Campbell River	49°02'	37.80	63.7	0.002	0.043	2.35	0.464	3.88
Capilano River	49°18'	23.30	197	0.010	0.030	20.2	4.27	28.2
Carnation Creek	48°56'	3.10	10.1	0.020	0.220	0.840	0.120	1.72
Cheakamus River	49°48'	15.10	1,010	0.040	0.280	31.5	16.0	83.3
Chef Creek above fence 2	49°27'	3.48		0.020	0.043			
Chef Creek between fences	49°27'	0.82		0.000	0.001			
Chef Creek total system	49°27'	4.30	26.4	0.020	0.043	1.10	0.080	2.51
Coghlan Creek	49°07'	5.05	14.2	0.040	0.115	0.428	0.040	0.946
Cowichan River	48°46'	124.96	544	0.003	0.093	39.4	5.79	82.9
Cowichan side channel	48°46'	0.82		0.000	0.001			
Devereux Creek	51°10'	17.98	74.0	0.020	0.185	6.43	1.99	8.83
Fifteen Mile Creek	49°07'	0.64	2.0	0.031	0.038	0.047	0.002	0.150
French Creek	49°21'	22.09	58.3	0.010	0.086	2.86	0.217	5.76
Hooknose Creek	52°08'	5.83	14.7	0.040	0.140	1.93	0.690	2.74
Hopedale Creek	49°06'	2.49	0.93	0.002	0.001	0.020	0.000	0.073
Hunt's Creek, Qualicum system	49°23'	1.40	17.6	0.020	0.204	0.678	0.049	1.65
Kelvin Creek	48°45'	5.50	59.0	0.010	0.152	2.90	0.220	5.84
Keogh River total system	50°40'	21.80	129	0.010	0.094	9.85	2.36	16.7
Keogh River, upper	50°39'	8.24	24.3	0.007	0.244	2.38	0.492	3.82
Keogh River, west tributary	50°32'	1.61	15.9	0.015	0.053	1.66	0.330	2.63
Lachmach River	54°17'	13.75	41.2	0.020	0.215	4.16	1.35	5.78
Little Qualicum River	49°20'	26.00	237	0.014	0.154	11.8	2.05	22.2
Little Stawamus River	49°42'	3.70	3.1	0.024	0.106	0.195	0.121	0.319
Mamquam Channel	49°44'	0.36		0.000	0.001			
McTaggart Creek	51°27'	9.17	21.0	0.010	0.177	0.355	0.049	1.38
Meighn Creek	49°45'	3.20	2.6	0.030	0.063	0.162	0.103	0.27
Miller Creek and Pond	48°37'	1.40	1.1	0.016	0.048	0.025	0.002	0.093
Misty Inlet Creek	50°36'	1.92	11.8	0.010	0.026	1.29	0.249	2.02
Misty Outlet Creek	50°37'	4.24	14.3	0.007	0.025	1.51	0.298	2.39
Nile Creek	49°25'	6.04	15.0	0.030	0.180	1.01	0.200	1.90
Pastuch Creek	48°47'	4.28	5.7	0.014	0.063	0.175	0.012	0.506
Post Creek	49°06'	1.98	27.0	0.031	0.081	0.888	0.115	1.73
Qualicum River main stem	49°23'	9.75	130	0.010	0.137	6.63	0.620	13.1

TABLE A2.1.—Continued.

Stream	Latitude (°N)	Length (km)	Drainage area (km ²)	Gradient (m·m ⁻¹)	Valley slope (m·m ⁻¹)	Discharge (m ³ ·s ⁻¹)		
						Mean	Minimum	Maximum
Qualicum River system	49°23'	11.15	148	0.010	0.145	7.30		14.7
Quinsam River	49°59'	54.88	209	0.010	0.055	8.49		17.1
Rust Creek	49°06'	0.30	0.09	0.000	0.001	0.001	1.95	0.008
Ryder Creek	49°06'	4.14	13.0	0.030	0.090	0.388	2.20	0.872
Salmon River main stem	49°08'	26.23	49.0	0.002	0.108	1.44	0.000	3.04
Salmon River system	49°08'	31.28	85.0	0.003	0.326	3.57	0.035	8.57
Salween Creek	49°06'	6.00	2.6	0.001	0.001	0.063	0.240	0.192
Street Creek	49°06'	1.60	5.0	0.003	0.001	0.131	1.43	0.355
Tenderfoot Creek and Pond	49°55'	0.61	0.46	0.025	0.000	0.026	0.003	0.052
Trent River	49°38'	7.92	72.0	0.020	0.239	3.68	0.007	7.19
Upper Paradise channel	49°50'	0.42		0.000	0.001		0.020	
Worth Creek channel	49°11'	0.15		0.000	0.001		0.282	
California								
Waddell Creek	37°06'	10.30	61.3	0.011	0.148	0.604	0.011	0.922
Oregon								
Deer Creek	44°32'	2.32	3.04	0.018	0.274	0.174	0.014	0.542
Fish Creek	45°09'	16.70	171	0.008	0.286	11.03	2.11	17.8
Flynn Creek	44°31'	1.43	2.02	0.025	0.199	0.115	0.010	0.357
Gnat Creek	46°12'	4.8						
Needle Branch Creek	44°31'	0.97	0.75	0.014	0.353	0.043	0.004	0.130
Sand Creek	45°17'	9.70	39.5	0.006	0.043	2.28	0.163	7.35
Spring Creek	45°37'	0.47	1.79	0.049	0.186	0.102	0.009	0.316
Washington								
Bear Creek	47°29'	2.36	31.2	0.030	0.217	0.764	0.236	1.33
Big Beef Creek	47°39'	16.40	35.7	0.010	0.250	5.41	0.970	13.5
Big Rock Creek	47°49'	4.20	16.0	0.025	0.016	0.925	0.274	1.64
Bingham Creek	47°09'	22.20	90.7	0.010	0.128	5.20	1.09	11.4
Carpenter Creek	47°58'	20.60	90.0	0.007	0.040	5.17	1.09	11.3
Christmas Creek	47°39'	9.30	20.5	0.004	0.260	1.18	0.334	2.17
Clearwater River	47°33'	151.7	396	0.005	0.115	22.59	3.53	59.2
Coulter Creek	47°24'	24.20	97.9	0.011	0.071	5.62	1.16	12.4
Courtney Creek	47°28'	3.57	12.8	0.023	0.098	0.740	0.230	1.28
Creamer Slough	47°06'	0.50		0.000	0.001			
Deschutes River	46°57'	54.00	414	0.003	0.103	23.61	3.66	62.2
Goldsbrough Creek	47°13'	37.00	84.7	0.006	0.034	4.86	1.03	10.6
Griffin Creek	47°37'	17.50	42.2	0.003	0.300	2.43	0.594	4.85
Harris Creek	47°21'	11.61	80.3	0.008	0.108	4.61	0.991	9.95
Hurst Creek	47°34'	7.8	15.1	0.008	0.191	0.873	0.262	1.54
Kelsey Slough	47°06'	0.32		0.000	0.000			
Little Bear Creek	47°46'	12.70	10.9	0.006	0.084	0.633	0.203	1.07
Little Pilchuck Creek	47°59'	9.74	79.3	0.006	0.026	4.55	0.981	9.81
Little Tahuya Creek	47°27'	1.39	0.87	0.015	0.088	0.051	0.027	0.064
Lost Creek	47°39'	3.38	18.9	0.040	0.268	1.09	0.313	1.98
Maple Glen Slough	47°06'	0.40		0.000	0.001			
Mill Creek	47°12'	16.51	184	0.003	0.086	10.52	1.92	25.1
Minter Creek	47°22'	16.70	35.5	0.011	0.098	2.05	0.518	3.99
Mission Creek	47°26'	15.15	75.1	0.010	0.176	4.31	0.940	9.24
Mud Creek	47°34'	3.1	16.4	0.008	0.121	0.948	0.280	1.69
North Creek	47°46'	20.30	65.5	0.006	0.076	3.76	0.843	7.93
Schafer Park Slough	47°06'	0.52		0.000	0.001			
Schafer Slough Tributary	47°06'	0.08		0.000	0.001			
Shale Creek	47°38'	7.9	15.2	0.006	0.180	0.878	0.263	1.55
Sherwood Creek	47°23'	22.70	166.5	0.004	0.121	9.42	1.75	22.2
Skookum Creek	47°09'	12.90	92.5	0.004	0.092	5.31	1.11	11.7
Snahapish Creek	47°39'	19.2	48.1	0.003	0.174	2.77	0.659	5.62
South Fork Skykomish River	47°50'	92.40	932	0.009	0.127	53.0	6.98	154
Stillaguamish River	48°14'	249.80	2,011	0.003	0.076	100	11.6	315
Tiger Creek	48°14'	5.79	16.6	0.009	0.123	0.957	0.282	1.71
Union River	47°27'	15.01	91.9	0.016	0.100	5.28	1.10	11.6
Upper Chehalis River	46°35'	363.90	2,318	0.001	0.029	79.3	8.10	293
Wagley Creek	47°51'	3.70	6.29	0.011	0.025	0.365	0.131	0.579
Wildcat Creek	47°39'	6.72	27.5	0.020	0.287	1.58	0.422	3.00