Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams

Rishi Sharma and Ray Hilborn

Abstract: We assembled data on coho salmon (*Oncorhynchus kisutch*) from 14 streams in western Washington, including annual smolt counts and annual escapement, either as absolute counts or as an index. We also compiled data on large woody debris (number·km^{-1} of stream), road densities in the watersheds (km road·km^{-2}), gradient of the streams (%), valley slope adjacent to the stream (%), drainage area in the watershed (km^2), and pool, pond, and lake areas (m^2·km^{-1}). We explored the relationships between habitat variables and two measures of coho production, the maximum production of smolts in the stream (capacity) and the maximum smolts/spawner (productivity). Using the 11 streams with pool and pond counts, we found that pool and pond densities served as good predictors of smolt density (r^2 = 0.85 for pools and 0.68 for ponds, independently). Pools produced 0.39 smolts·m^{-2} and ponds produced 0.07 smolts·m^{-2} in the multiple regression fit, accounting for 92% of the residual error. We also found that lower valley slopes, lower road densities, and lower stream gradients were correlated with higher smolt density.

Résumé : Nous avons rassemblé des données sur le Saumon coho (*Oncorhynchus kisutch*) de 14 cours d'eau du Washington occidental, entre autres des recensements annuels de saumoneaux et des échappées annuelles, tant en valeurs absolues qu'en indices relatifs. Nous avons aussi compilé des informations sur la présence de débris ligneux de grande taille (nombre·km^{-1} de cours d'eau), sur la densité des routes dans le bassin versant (km route·km^{-2}), la pente du cours d'eau (%), la pente de la vallée adjacente au cours d'eau (%), la surface de drainage dans le bassin versant (km^2), ainsi que la surface des profonds, des étangs et des lacs (m^2·km^{-1}). Nous avons alors exploré la relation entre les variables de l'habitat et deux mesures de production des saumons, la production maximale de saumoneaux dans le cours d'eau (capacité) et le maximum de saumoneaux par géniteur (productivité). Dans les 11 cours d'eau pour lesquels nous avions des données sur les profonds et les étangs, les densités des profonds et des étangs se sont avérées être de bonnes variables prédictives de la densité des saumoneaux (r^2 = 0,85 pour les profonds et 0,68 pour les étangs, indépendamment). Une régression multiple qui explique 92% de l'erreur résiduelle indique que les profonds produisent 0,39 saumoneau·m^{-2} et les étangs 0,07 saumoneau·m^{-2}. Les valeurs plus faibles de pentes des vallées, de densités des routes et de pentes des cours d'eau sont liées aux densités de saumoneaux plus élevées.

[Traduit par la Rédaction]

Introduction

The decline in salmon in the Pacific Northwest is ascribed to a combination of factors including habitat loss and degradation, overharvesting, hatchery practices, and changes in marine conditions (NRC 1996; Weitkamp et al. 1995; Bisson et al. 1997). As society seeks to rebuild these populations, we must make choices among alternative efforts in reducing harvesting, changing hatchery practice, and modifying or preserving habitat. Without quantitative relationships describing the impact of these factors on salmon production, such choices cannot be made rationally. Despite the vast amount of work on the impact of habitat on salmonids, there are surprisingly few relationships established between easily measurable habitat variables and the ability of habitat to produce salmon on a watershed scale. Moreover, there have been few attempts to link land uses to changes in habitat or salmon production.

Bradford et al. (1997) assembled data on 106 coho salmon (*Oncorhynchus kisutsch*) streams where smolt counts were available (through mark–recapture methods). The habitat variables assembled in their database were stream length, watershed area, stream gradient, valley slope, and geographical latitude. However, the only habitat variables that explained variation in smolt production were stream length and geographic latitude. Nickelson et al. (1992*a*, 1992*b*) described empirical relationships for 18 Oregon streams between different habitat types and the density of overwintering juvenile coho found in those habitats. Their work suggests that pool and pond areas should be good predictors of smolt production in coho systems as they provide

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Table 1. Smolt trap counts.

Location	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
Bear Creek				571	604	439	508	816	801	251
Courtney Creek				1 147	1 130	1 034	1 436	1 165	1 507	1 039
Lost Creek					3 633	1 936	4 743	1 587	3 026	1 949
Wildcat Creek					5 941	2 158	4 193	3 763	5 540	2 964
Snow Creek				5 201	9 156	9 090	8 344	7 048	7 700	1 871
Little Tahuya Creek				5 560	9 772	3 748	9 042	9 615	7 278	10 228
Mission Creek							19 023	15 218	18 716	17 011
Mill Creek		33 020	23 241	15 788	22 191	9 036	20 138	24 103	33 048	35 088
Big Beef Creek	20 374	39 954	37 054	18 600	47 300	20 755	40 076	24 596	26 724	36 646
Little Pilchuk Creek	22 640	35 588	35 846	32 575	13 009	22 397	36 292	26 680	25 739	24 098
Bingham Creek								31 806	33 464	43 945
Harris Creek					23 632	11 824	30 035	34 951	17 062	29 025
Deschutes River					60 275	65 776	131 261	64 757	65 518	101 901
S.F. Skykomish River			291 991	358 104	281 624	298 736	215 788	228 603	226 633	191 692

Note: Data as per Chuck Baranski (1989, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501-1051) and Mindy

a buffer in the overwintering of the juvenile coho salmon and are therefore causally related to smolt abundance in a stream. Other studies have also simply measured the abundance of juvenile fish per unit area of different types of habitat (Quinn and Peterson 1996; Holtby and Scrivener 1989; Chapman 1966) but not the actual production of juveniles as measured by downstream migration.

Some studies have also been done on reach-specific sites to estimate smolt outmigrants. Letselle et al. (1996) and Reeves et al. (1989) suggest reach-specific characteristics to estimate overall smolt production. The limiting factors analysis and the EDT (ecosystem diagnosis and treatment) approach both use reach-specific habitat characteristics by life stage of juvenile salmon to determine smolt abundance for a stream. Beechie et al. (1994) tested the Reeves et al. (1989) methodology on the Skagit River in western Washington and found it to be reasonably accurate on different levels of resolution (both reach-specific and river-basin-specific). However, on a watershed level, few studies have tried analyzing what may be the important habitat variables that relate to smolt abundance, and a more simplified data-driven approach is examined in this paper. The cross-sectional analysis across different streams in a watershed examined here could help in understanding the common variables that correlate to smolt abundance and in determining the important stream characteristics related to higher abundance in large watersheds.

Other studies have shown how systems change in relation to human impacts. Jones and Grant (1996) showed that long-term changes have occurred in stream flows associated with clearcutting and road construction. Jones and Grant (1996) demonstrated that peak discharges increased in some streams because of changes both in flow routing as a result of road construction and in water balance as a result of clearcutting and forest succession. Tripp and Poulin (1986) and Quinn and Peterson (1994) have shown a decrease in egg–fry survival because of increased peak flows. In addition, Everest et al. (1987) points out that sedimentation caused by erosion and landslides (indirectly linked to road density) is also a major cause of reduction in freshwater habitats essential for juvenile salmon. Urbanization also leads to increased road density as well as loss of habitat resulting from ditching, diking, and draining (Sherwood et al. 1990; Beechie et al. 1994). Road density is the only land-use variable related to smolt abundance in our analysis and may serve as an indicator of these effects.

The purpose of this study is to combine the approachs of Bradford et al. (1997) and Nickelson et al. (1992*a*, 1992*b*); we will explore systems for which total smolt counts are available and relate the smolt abundance to habitat and watershed variables. This paper explores simpler habitat–smolt relationships so that predictions can be made at a regional scale provided that sufficient spawners come back to a particular system. This would provide a quantitative measure to evaluate stream habitat modifications and their consequence on overall smolt abundance on a regional scale. The end products of our analysis are quantitative relationships between different stream habitat characteristics, different watershed characteristics, and smolt abundance and the uncertainties surrounding these estimates.

Materials and methods

Smolt and adult data

We assembled data on available smolt counts from different streams across Washington State. Study streams had long time-series of annual smolt counts, normally via weirs or scoop traps. Stream locations are shown in Fig. 1.

All smolts are progeny of spawners two years previously (Table 1). For some streams, an estimate of total female spawners was available (Table 2), usually from counts of redds (the observed redds in surveyed areas are expanded to the entire system based on expansion factors for the particular system), whereas on other streams, only peak index counts of the number of fish per mile were available.

Stream- and watershed-specific variables

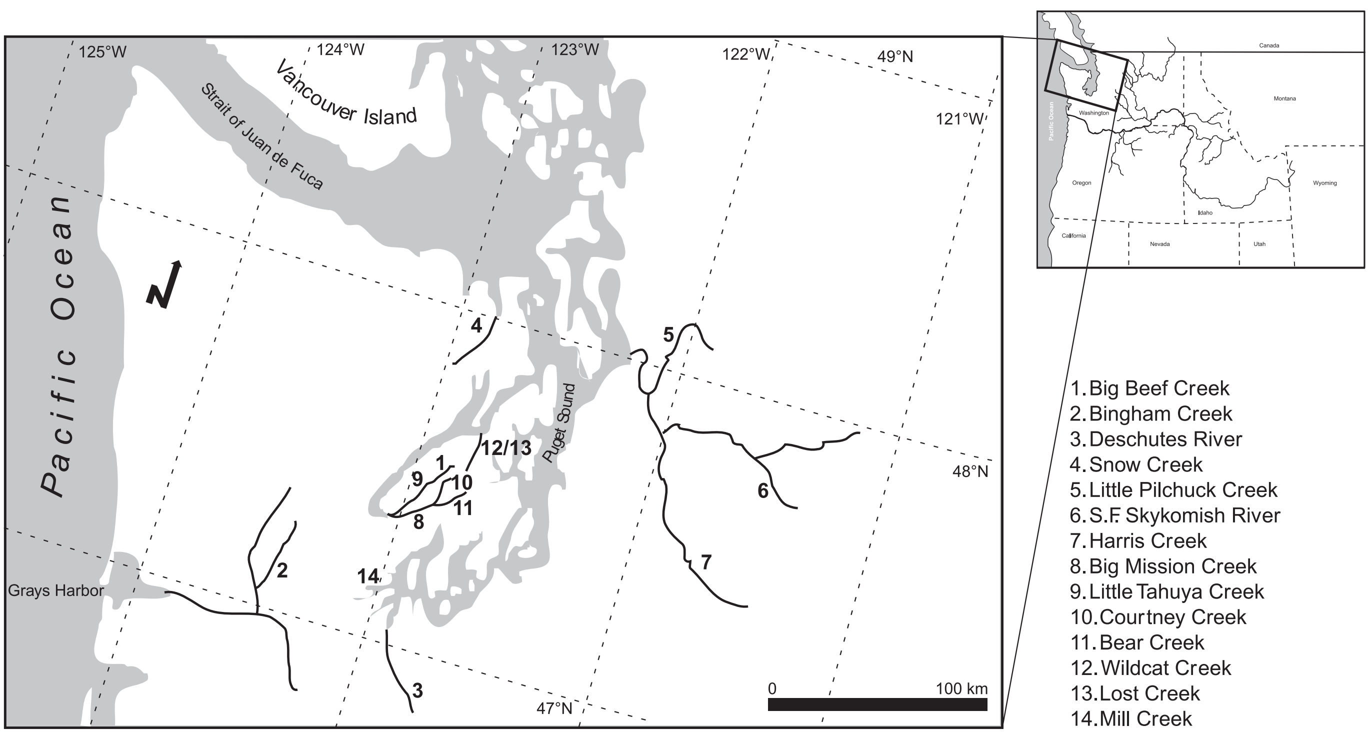
The independent variables used in this analysis were organized into three specific categories: (*i*) stream-specific attributes such as pool areas, pond areas, woody debris, stream length, and stream gradient, (*ii*) watershed-specific variables (drainage area and valley slope), and (*iii*) land-use variables for which road density serves as an index.

The three categories are not mutually exclusive. The stream attributes are often related to the watershed and land-use variables. However, this categorization may suggest some likely independent

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
755	667	112	636	992			538	413	138
1 451	1 415	238	1 483	1 460			1 755	1 234	1 041
2 496	1 213								
5 317	3 598								
6 947	10 113	641	6 296	6 915	448	4 300	4 787		
11 027	4 448	1 357	2 735	7 761			5 943	3 873	3 117
15 770	7 318	7 091	14 528	13 906			18 261	13 010	15 548
33 920	21 175	26 902	18 418	28 230					
25 446	23 637	10 872	24 614	16 437	19 427	22 563	18 720	13 071	18 431
24 916	34 808	33 373	36 723	20 467					
30 939	25 205	22 233	15 742	29 041	23 712	27 639			
35 039	25 970	24 289	26 218	22 773					
64 452	99 241	91 057	54 397	117 087	133 066	11 248	57 204		
184 584									

Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346, fide Lestelle et al. 1993.

Fig. 1. Map of western Washington, U.S.A., showing the respective study sites.



predictors to relate to the abundance of coho smolts by system (basin-wide approach).

Table 3 shows the various stream attributes. Most of the stream-specific variables (gradient, valley slope, drainage area, and stream length) used in the analyses were obtained from Bradford et al. (1997). Specific stream characteristics such as woody debris and pool, pond, and lake areas were obtained from Baranski (1989) and from independent surveys conducted by the Point No Point Treaty Council (Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346, personal communication).

Road density was obtained from a geographic information system database (Lunetta et al. 1997) at a Washington area unit (WAU) scale. This scale is typically 40–200 km^2 in resolution and encompasses areas larger than some of the stream watersheds analyzed here. Because the resolution of these WAUs is extremely large, we actually overlap multiple watersheds in our stream database, and hence the same road density is used for some of the streams in this analysis. The purpose of analyzing this relationship was to determine if any surrogate measure for land use (road density serves as an index for intensity of land use) could be related to smolt abundance on a watershed level.

Spawner–recruit analysis

Where we had both spawner and smolt counts, we fit the data to a spawner–recruit model incorporating habitat constraints (described by Moussali and Hilborn (1986)):

$$(1) \qquad S_t = \frac{E_{t-2}}{\dfrac{1}{p} + \dfrac{1}{c} E_{t-2}}$$

Table 2. Escapement data.

Location	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Female escapement counts																	
Snow Creek	187	522	288	166	328			253	179	22	240	340	7	49	56		
Big Beef Creek	1018	654	295	1 108	499	411	465	277	883	227	1053	514	283	368	188	283	517
Bingham Creek					355	1268	946	543	2869	914	1445	963	5895	1905			
Deschutes River		2784	905	3 104	1 135	1599	3669	1946	1871	2609	2069	5185	3188	473	1340		
S.F. Skykomish River	6000	9000	9887	14 671	12 389	7725	3255	2688	1747								
Peak index counts																	
Bear Creek		1.8	22	20	56	26	6	2	32	24	14	48	6	36	14	20	
Courtney Creek		7.3	71.3	30	23.9	15	12.5	6.2	10	13.8	30	35	3.8	25	7.5	7.5	
Little Tahuya Creek		33	103	30	112	24	176	11	48	29	95	110	10	27	12	51	
Mission Creek	11.9	60	27.3	12.5	186.7	12.1	23	23.9	80	30.5	53.3	40	5.8	23.2	20.5	16.8	

Note: Data as per Bill Tweit, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501-1051, fide Lestelle et al. 1993).

Table 3. Stream specific habitat attributes, watershed attributes, and road density.

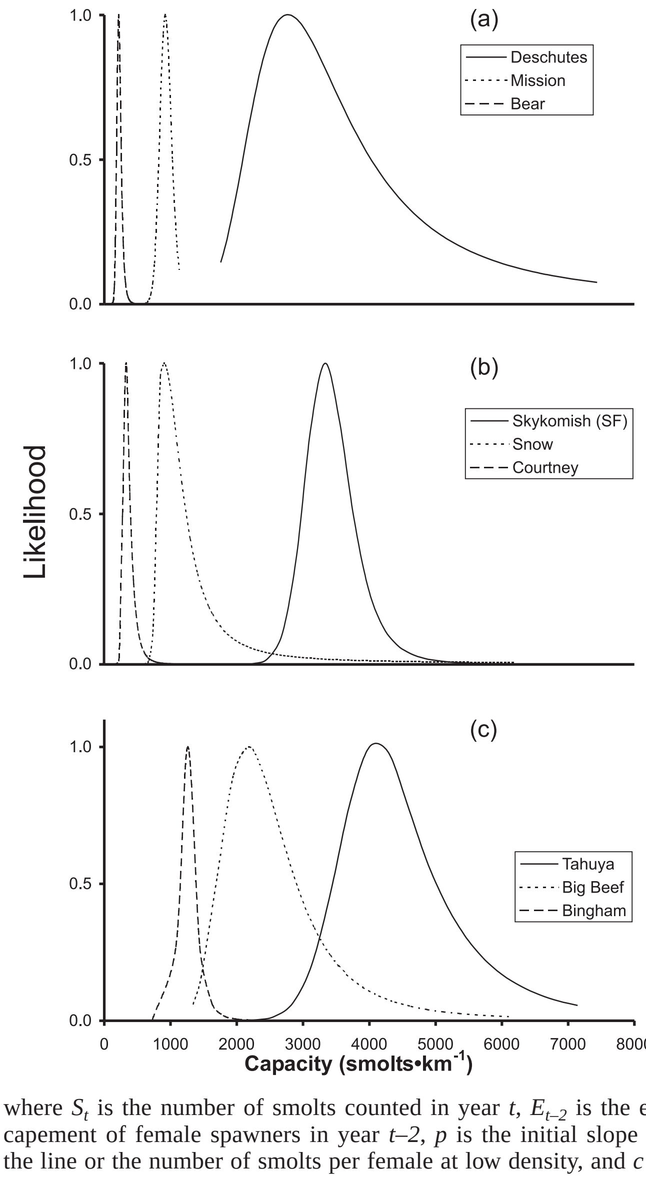
Names	Length (km)[a]	Drainage area (km^2)[a]	Gradient (%)	Valley slope (%)	Pool area (m^2)[b]	Total area (m^2)[b]	Pool length (m)[b]	Pond area (m^2)[b]	Lake length (m)[b]	Lake area (m^2)[b]	Road density (km·km^{-2})[c]	Actual count (LWD)[d]	Proportion sampled	LWD count extrapolated
Bear Creek	2.36	31.2	0.03	0.22	2 511	5 593	0	0	0	0	2.58	na	na	na
Courtney Creek	4	13	0	0	5 959	10 866	0	0	0	0	3	467	0.39	1 197
Lost Creek	3	19	0	0	5 125	9 178	0	0	0	0	3	na	na	na
Wildcat Creek	6.72	27.5	0.02	0.29	10 189	18 248	0	0	0	0	2.83	na	na	na
Snow Creek	8.8	30.8	0.027	0.25	21 227	56 806	0	0	750	24 000	2.44	573	1	573
Little Tahuya Creek	1.39	0.87	0.02	0.09	9 788	12 038	2 030	28 103	0	0	2.58	304	0.48	629
Mission Creek	15.15	75.1	0.01	0.18	36 727	74 812	0	0	0	0	2.58	887	0.49	1 810
Mill Creek	16.51	184	0.003	0.09	78 618	118 118	2 150	38 640	2 100	838 072	2.86	na	na	na
Big Beef Creek	16.4	35.7	0.01	0.25	45 920	71 165	3 028	23 178	953	776 710	2.83	624	0.175	3 570
Little Pilchuk Creek	9.74	79.3	0.01	0.03	26 414	28 726	7 789	312 892	610	30 500	2.3	na	na	na
Bingham Creek	22.2	90.7	0.01	0.13	na	na	na	na	na	na	2.68	na	na	na
Harris Creek	11.61	80.3	0.01	0.11	27 486	37 007	2 355	102 057	0	0	2.2	na	na	na
Deschutes River	54	414	0.003	0.1	na	na	na	na	na	na	3.9	2 119	0.22	9 455
S.F. Skykomish River	92.4	932	0.009	0.127	na	na	na	na	na	na	0.48	na	na	na

Note: na, not available.
[a]Bradford et al. (1997).
[b]Baranski (1989), fide Lestelle et al. (1993), Point No Point Treaty (Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346).
[c]EPA, Western Washington Watershed screening data, Lunetta et al. (1997).
[d]LWD = large woody debris; TFW Reports, R. Mackintosh, North West Indian Fish Commission, 6730 Martin Way E, Olympia, WA 98516; Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346).

Table 4. Parameter estimates of productivity and capacity with confidence intervals (CI) using the Beverton–Holt equation.

Locations	Productivity, smolts·female^{-1} (95% CI)	Capacity, smolts·km^{-1} (95% CI)
Big Beef Creek	146 (100–600)	2156 (1340–3659)
Snow Creek	71 (52–106)	910 (739–1818)
Bingham Creek	na (na)	1236 (112–1351)
Deschutes River	51 (35–83)	2745 (1852–5926)
S.F. Skykomish River	247 (130–850)	3352 (2706–4058)
Bear Creek	na (na)	218 (165–297)
Mission Creek	na (na)	915 (766–1109)
Little Tahuya Creek	na (na)	4145 (3022–6259)
Courtney Creek	na (na)	323 (258–499)

Fig. 2. Profiles indicating the capacities (smolts·km^{-1}) of the various streams.



where S_t is the number of smolts counted in year t, E_{t-2} is the escapement of female spawners in year $t-2$, p is the initial slope of the line or the number of smolts per female at low density, and c is the maximum number of smolts that can be produced by the stream. For streams for which counts of female spawners and subsequent smolts were available, we used the method of maximum likelihood (Hilborn and Mangel 1997) to estimate the parameters p and c.

We predicted the smolt count from the spawning numbers as a function of eq. 1 and values of p and c assuming that the observations are log-normally distributed. The log-normal assumption is usually deemed appropriate for these relationships because of the multiplicative nature of survival between egg deposition and smolt counts (Hilborn and Walters 1992). The likelihood of observing S_t smolts given the predicted value is

$$(2)\qquad L(S_t|p,c) = \frac{1}{\sqrt{2\pi\sigma^2}}\frac{1}{(S_t)}\exp\left[-\frac{(\ln(S_t)-\ln(\hat{S}_t))^2}{2\sigma^2}\right]$$

where $\hat{S}_t$ is the predicted number of smolts from eq. 1 given p, c, and E. The total likelihood is simply the product of each of these over all t where data are available.

The method of likelihood profile (Hilborn and Mangel 1997) was used to calculate confidence intervals (CI) for p and c. We could estimate both p and c for streams for which absolute spawner counts were available (five streams). For the remaining four streams with only index spawning counts, the units of p were not interpretable because the absolute number of female spawners on the system was unknown, but c could be estimated.

The relationship between stream and watershed variables and smolt abundance

We used a linear regression between smolt output and habitat variables to examine the relationship between smolt abundance and habitat characteristics:

$$(3)\qquad P_s = \alpha + \beta V_{i,s} + \varepsilon_s$$

where P_s is smolts·km^{-1} in stream s, $V_{i,s}$ is the independent stream or watershed variable (pool density, pond density, road density, etc.) in stream s, α is a constant, β is the slope parameter of the variable ($V_{i,s}$), and ε is the normal additive error.

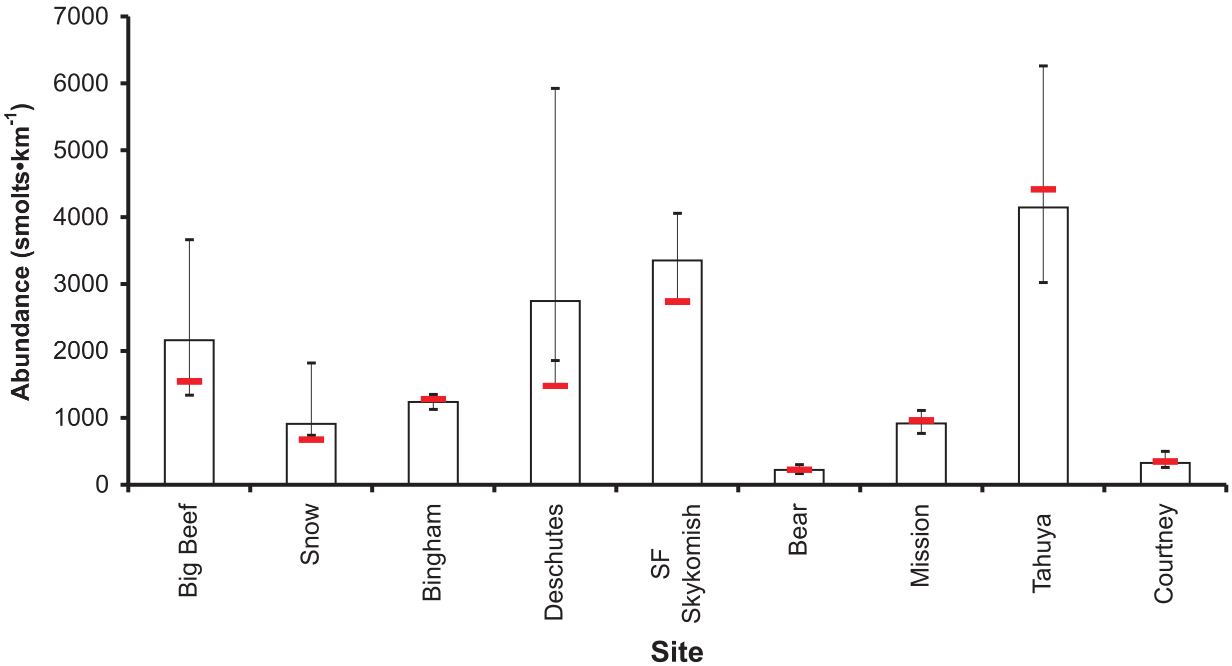
We used the normal likelihood to find the best estimates of our parameters:

$$(4)\qquad L(P_s|\alpha,\beta) = \frac{1}{\sqrt{2\pi\sigma^2}}\exp\left[-\frac{((P_s)-(\hat{P}_s))^2}{2\sigma^2}\right]$$

Likelihood profiles were generated on the slope parameter using eq. 4. We know that on a reach scale, the habitat variables (pool density, pond density, and large woody debris (LWD)) are positively correlated with smolt abundance, and for the pool and pond densities, we expect that the slope parameter will be significant. However, we do not know how the watershed variables or the index of land use will correlate with smolt abundance. We performed analyses with each variable independently as some of the stream habitat and watershed variables are highly correlated.

Rather than look at a traditional approach of statistical inference, i.e., significance or nonsignificance of a particular variable

Fig. 3. Comparisons of the mean smolt abundances to the capacities for the nine streams where spawner and smolt data were available. The histogram represents the capacity, the thin line indicates the confidence bounds on the capacity estimate, and the solid bar on the line indicates the observed mean of the data for a particular stream.



(the value of the β parameter in eq. 3), we performed a likelihood profile analysis on each independent variable (Hilborn 1997).

Results

Spawner–recruit analysis results

We obtained estimates of productivity and capacity (Table 4). Productivity varied from 50 smolts per female on Deschutes River to 246 smolts per female on Skykomish River. We could not estimate the Bingham Creek productivity because of the very poor fit to the curvilinear shape of eq. 2. The likelihood profiles for the capacity parameters (Fig. 2) are rescaled with the highest likelihood of a specified capacity for that particular stream. Capacities measured as smolts·km^{-1} varied considerably and the stream with the highest smolts·km^{-1} was Little Tahuya Creek (4145 smolts·km^{-1}) in Hood Canal, and the lowest was Bear Creek (218 smolts·km^{-1}).

Ideally, p and c obtained from the spawner–recruit data could be correlated with the stream and watershed variables. However, because we had only five streams with absolute female escapement data, we instead analyzed correlations between habitat variables and the average number of smolts produced from each stream, increasing our sample size to 14 streams for some of our watershed variables. Average smolt abundance compared fairly well with the capacities obtained from our analysis (described above) (Fig. 3). In almost all cases, the observed mean of the data lies within the 95% confidence bounds of the parameter estimate (other than Deschutes River and Snow Creek).

Linear model analysis

Some of the habitat variables were highly correlated, and therefore an analysis was done with each watershed and stream habitat variable independently (Fig. 4), recognizing that the correlation between habitat variables may explain the correlation between those variables and smolt abundance. Among all variables examined, the best correlation with smolt density was obtained from pool density (r^2 = 0.85). The likelihood profile of β (Fig. 5) is explained in some meaningful modification of watershed attribute for each parameter. These figures contain far more information than either a point estimate of the slope or a traditional p value. For instance, we can observe that stream gradient, valley slope, pool and pond densities, and LWD are correlated with smolt abundance. The biological significance can be judged by examining the x-axis, in each case relating the amount of additional smolt abundance to be expected by an increase in the habitat variable. Figure 5 illustrates the uncertainty of the fit and how likely we are to see a particular effect as compared with other hypothesized effects. A standard frequentist method would provide the slope parameter and confidence bounds (this, however, gives you no information on the distribution of probability within that interval). In contrast, the likelihood profile (Fig. 5) shows us the uncertainty around the point estimate and how likely some value may be with respect to another slope value. Therefore, in the case of our analysis, other variables that may not be statistically significant, such as gradient, valley slope, LWD, and road density, still show an effect on smolt abundance (Fig. 5). These profiles illustrate the possible effects of different independent variables on our predicted variable and also illustrate the uncertainty around the best fit.

Smolt abundance declines with increasing gradient and valley slope (Fig. 4). The likelihood profiles of these variables (Fig. 5) also indicate a likely reduction in smolt abundance as higher-gradient tributaries are examined. The results suggest a 400 smolts·km^{-1} increase per 1% decrease

Fig. 4. Best fits for the response variable (smolts·km^{-1}) with separate predictor variables: (*a*) gradient; (*b*) valley slope; (*c*) pool density; (*d*) pond density; (*e*) large woody debris (LWD) density; (*f*) drainage density; (*g*) road density; and (*h*) lake density.

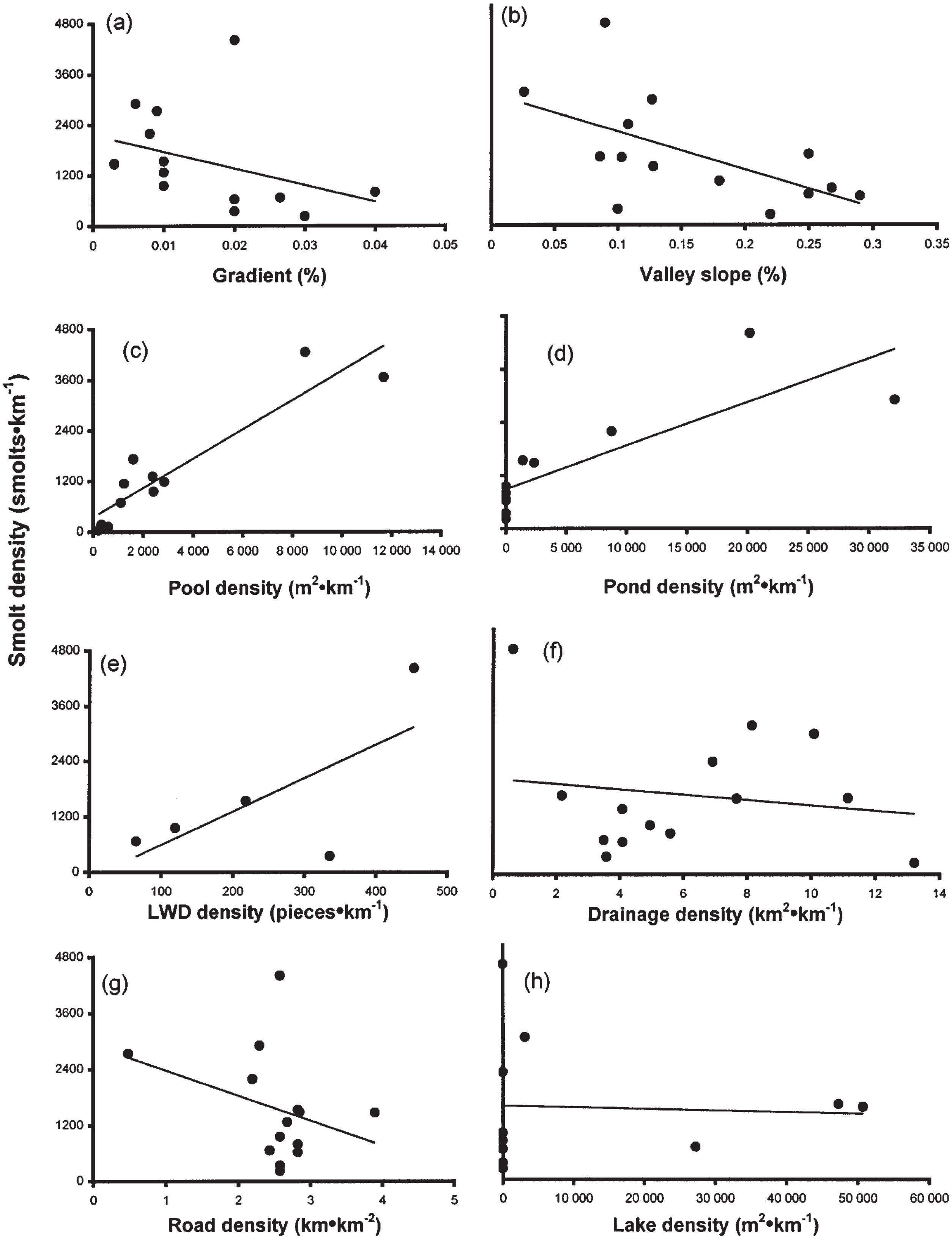
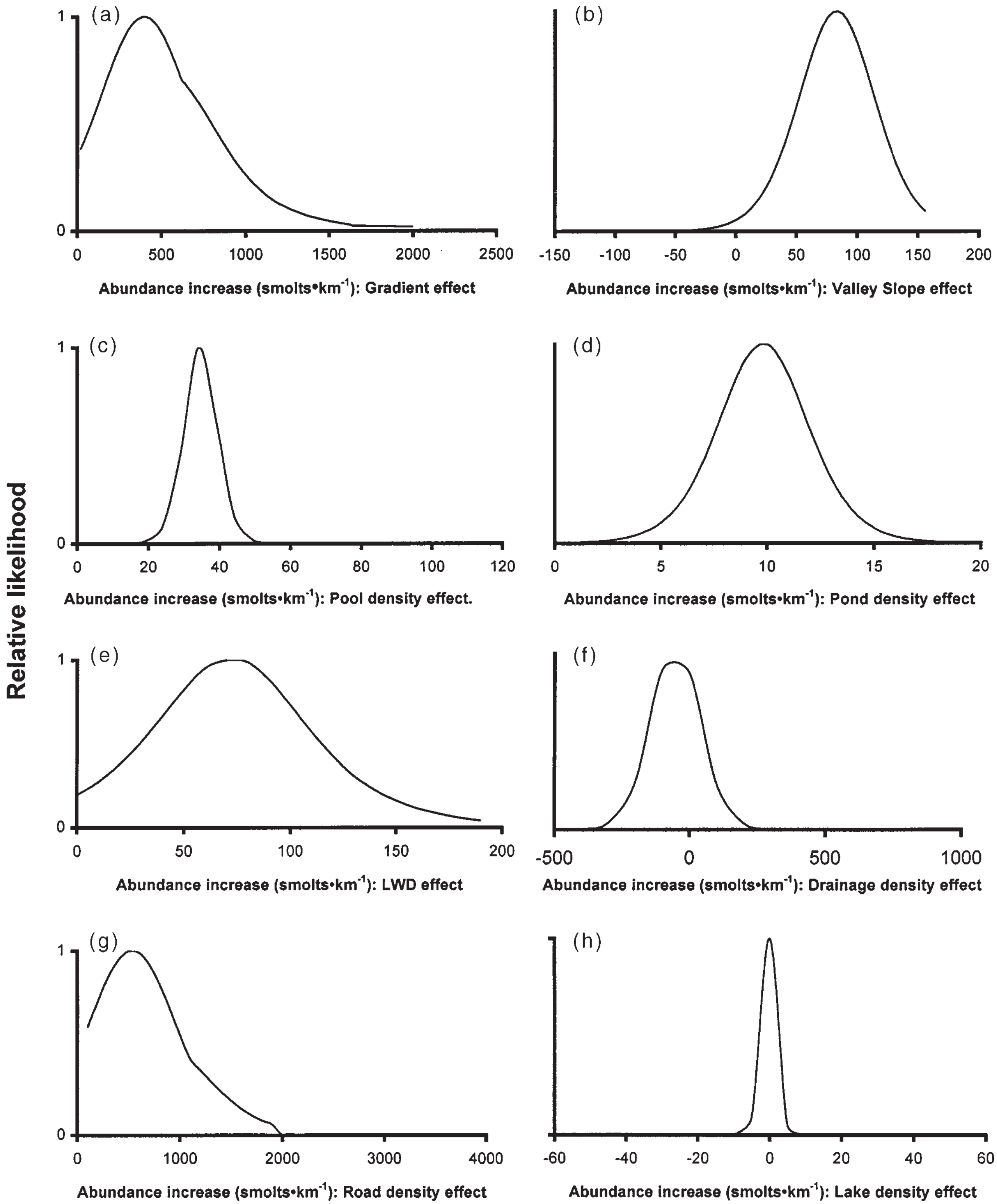


Fig. 5. Likelihood profiles of quantitative changes in smolt density as the result of increasing or decreasing some predictor variables (the *x*-axis shows the expected increase or decrease in abundance (smolts·km^{-1}) with change in the predictor variable): (*a*) gradient, the increase in abundance per percent decrease in gradient; (*b*) valley slope, the increase in abundance per percent decrease in valley slope; (*c*) pool density, the increase in abundance per increase in pool area by 100 m^2·km^{-1}; (*d*) pond density, the increase in abundance per increase in pond area by 100 m^2·km^{-1}; (*e*) large woody debris (LWD) density, the increase in abundance per 10 additional pieces of LWD·km^{-1} of stream; (*f*) drainage density, the increase in abundance per increase in drainage area by 1 km^2·km^{-1} of stream length; (*g*) road density, increase in abundance per decrease in road density by 1 km·km^{-2} in the watershed; and (*h*) lake density, the increase in abundance per increase in lake area by 100 m^2·km^{-1}.



in gradient and an 84 smolts·km^{-1} increase per 1% decrease in valley slope. This result is not surprising as coho salmon tend to spawn and rear in lower-gradient tributaries (Bisson et al. 1988).

Although there were very few streams with LWD data, the results were interesting and suggested an additional 7 smolts·km^{-1} (Fig. 5) for every additional LWD·km^{-1}. We can observe that the profile for LWD is the flattest, thus illustrating the uncertainty surrounding additional pieces of LWD and the hypothesized effect that one would expect to observe on streams with higher LWD concentration. Road density had a negative correlation with smolt abundance, but this was largely due to the outlying points in the data set. The results suggest a decrease of 500 smolts·km^{-1} for each 1 km·km^{-2} increase in road density. However, no effect is about half as likely as observing the above-stated effect. These profiles illustrate the uncertainty in the estimate of β and the possible distribution of effects likely to be observed on streams in this particular watershed.

The watershed variable drainage density and the stream-habitat variable lake density show no correlation with smolt abundance, whereas road density is negatively correlated with smolt abundance. Drainage density and lake density slopes are centered on zero (Fig. 5). This suggests that perhaps these variables are not really important for coho juvenile survival. Even though some juvenile coho use lakes to rear, it appears that these variables in the systems studied did not show any significant relationships.

Discussion

Although low adult spawner abundance in river systems in Puget Sound is being blamed for the lower cohort abundance in corresponding years (time series observed in the 1980s and early 1990s), the data suggest otherwise. It has been shown that the average smolt abundance on most of these streams lies within the confidence bounds (95% CI) for the capacity of smolt abundance estimated in these streams through standard likelihood estimation techniques. Hence, the streams appear not to be spawner limited (other than Deschutes River and Snow Creek) but may instead be limited by some other factor.

Nickelson et al. (1992*a*) emphasized that pool and pond areas were the limiting factors to smolt abundance in seeded streams in Oregon. In addition, he computed the capacity of fry in different types of pool habitat (Nickelson et al. 1992*b*). However, we did not have the pool habitat broken down further into Nickelson's subcategories by season. Nickelson's results show that on average the number of smolts is about 0.4 smolts·m^{-2} of pool area over the year and 1.8 smolts·m^{-2} of pond area over the year. Our results from a multiple regression analysis using pool and pond densities, which explained 92% of the residual error, were 0.4 smolts·m^{-2} of pool area and 0.07 smolts·m^{-2} of pond area (correlation between pool and pond densities was high, however, with $r = 0.47$) in summer. Unfortunately, we did not have stream data that would compare with Nickelson's results for the entire year as done in Oregon, and therefore, the ponds' true effect might be underestimated. Both studies, however, obtain very similar values for the effect of pool areas on smolt abundance. A possible reason for this difference in pond effects may be due to the fact that Nickelson's studies were conducted on Oregon coastal streams with a steeper gradient. These streams are extremely vulnerable to high flow events in winter, and side-channel habitat (side-channel ponds) is extremely important in these coastal streams. This may not be the case for Puget Sound streams, which are somewhat protected from extremely high flow events by the Olympic mountains located to the west of Puget Sound.

The streams in Washington do not appear to be spawning limited as the average smolt abundance on these streams lies within the 95% CI of the capacity. However, the capacity does vary and a clear correlation between average smolt abundance and summer pool density has been established. For most of the summer stream and watershed variables analyzed, the summer pool areas had the strongest correlation with the smolt abundance. This implies that summer pool area is one of the limiting factors of smolt abundance on western Washington streams. Ponds typically provide refuge during high winter flows, and the low value of smolts produced per pond area in our analysis suggests that these habitats are less important than summer pools for the watersheds studied. However, because we did not have stream data for the entire year, this effect may be underestimated. Both pools and ponds are, however, complexly intertwined as side channel ponds are extremely important for overwintering (Nickelson et al. 1992*a*).

The major weakness of our study is the correlation between habitat factors. Pool density, pond density, and LWD·km^{-1} are all highly correlated, and one cannot simply say that increasing any one of these would increase smolt production by itself. Despite this autocorrelation, it is known that pools by themselves are just one part of the overall determinant of coho abundance. Pools with habitat structure in the form of LWD generally contain far more coho than pools without this form of cover and shelter. LWD appearing elsewhere in the channel, i.e., nonstructural LWD not in association with pools, may have little or no role in influencing fish numbers. This study was not conducted at the scale of resolution to separate out the contribution of LWD; however, the point that pool habitat is the prime and proximal determinant of juvenile coho salmon abundance can still be made. Studies such as that of Bisson et al. (1988) show similar findings.

In addition, low gradient areas tend to have more coho juveniles present because they have more pools than steeper cascades and low valley slope normally provides abundant side-channel rearing areas such as ponds. Nickelson et al. (1992*a*, 1992*b*) and Beechie and Sibley (1997) have shown similar results on a stream-specific basis.

This analysis allows us to calculate the possible increase in smolt production resulting from different forms of habitat modification. However, this is subject to the limitation that we assume the streams are not spawning-stock limited, and all other factors are comparable with those of the streams in the data sets used.

This method could provide valuable insight into which areas to target for habitat restoration by showing us where habitat restoration activities are likely to have the greatest effect on smolt abundance at the watershed level. We can observe that where pool areas can be increased substantially, coho salmon smolt abundance is likely to increase. This activity is most feasible on lower-gradient and valley slope systems. Thus, effects of in-stream habitat modification on smolt abundance could be hypothesized and, after post-treatment experiments, evaluated with this benchmark.

A complete computational framework for evaluating the benefits of habitat improvement will need to include spawning stock availability and factors beyond habitat limitation on rearing capacity (e.g., Beechie et al. (1994) and Reeves et al. (1989)). Nickelson and Lawson (1998) also take this approach a step further by looking at population viability. However, the simpler approach shown here could serve as a tool for formulating pretreatment hypotheses on watersheds where such data are not available. In addition, data such as pool and pond densities could be collected fairly easily on a watershed level and, using this simple regression model, could help in understanding the limiting factors of freshwater rearing. We could also use this simplified approach to estimate juvenile abundance in the particular streams of a region. In today's realm of endangered species, this is a useful tool in understanding the limitations of habitat and how it might relate to juvenile abundance of salmon.

Bradford et al. (1997) found that smolt abundance was best explained by stream length and latitude. We have moved beyond Bradford's analysis by looking at smolt abundance per kilometre of stream and found that a number of habitat factors are related to smolt abundance. By looking only within Puget Sound, we may have eliminated some of the variability that Bradford found in his geographically broader analysis. Although there should be little surprise that the habitat factors such as pool and pond area are related to smolt abundance, this study is the first to relate downstream smolt counts to watershed and stream attributes averaged across small watersheds.

In conclusion, this approach could be a valuable tool for habitat restoration planning as well as for estimating likely increases in juvenile salmon abundance (for this case, in western Washington and Hood Canal streams). This technique could provide insight into the likely effects that various habitat-enhancement measures may have on the particular stream in that watershed or basin.

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