Physical constraints on trout (*Oncorhynchus* spp.) distribution in the Cascade Mountains: a comparison of logged and unlogged streams

Joshua J. Latterell, Robert J. Naiman, Brian R. Fransen, and Peter A. Bisson

Abstract: The upstream extent of coastal cutthroat (*Oncorhynchus clarki clarki*) and rainbow (*Oncorhynchus mykiss*) trout distribution in logged and unlogged streams of the western Cascade Mountains appears to be primarily constrained by steep channel gradient and sparse pool habitat. Narrow or intermittent wetted channels are also important constraints in logged drainages. The upstream extent of trout distribution appears to be resilient to the combined impacts of historic and current forest management activities, in the absence of impassable road culverts. The probability of trout presence decreased with channel gradient and increased with pool abundance in both logged and unlogged streams, as indicated by logistic regression analysis of physical stream attributes flanking the trout distribution limit in 37 logged and 21 unlogged streams. Reductions in wetted channel width reduced the likelihood of trout presence in logged streams. Logistic regression models fit to data from logged drainages generated accurate predictions of trout presence or absence when applied to data from unlogged drainages. The pervasive extent of native trout in the channel networks of the Cascade Mountains emphasizes the ecological importance of small streams in watershed planning.

Résumé : La distance en amont à laquelle s'étend la répartition des truites fardées côtières (*Oncorhynchus clarki clarki*) et des truites arc-en-ciel (*Oncorhynchus mykiss*) dans des cours d'eau soumis ou non à la coupe forestière dans la chaîne des Cascades de l'ouest semble être limitée principalement par des chenaux à forte pente et la pénurie d'habitats de profonds. Des chenaux étroits ou immergés de façon intermittente sont aussi des contraintes importantes dans les bassins de drainage exploités. S'il n'y a pas de ponceaux de route impossibles à traverser, l'étendue de la répartition des truites semble résiliente aux impacts combinés des activités de la gestion forestière actuelles et passées. La probabilité de la présence de la truite décroît en fonction de la pente du chenal et augmente avec l'abondance des profonds, tant dans les cours d'eau exploités que dans ceux qui ne le sont pas; c'est ce que révèle une analyse de régression logistique des caractéristiques physiques des cours d'eau en fonction des limites de répartition de la truite dans 37 cours d'eau exploités et 21 qui ne le sont pas. Une diminution de la largeur mouillée du chenal réduit la probabilité de la présence de la truite dans les cours d'eau exploités. Des modèles de régression logistique ajustés aux données provenant de cours d'eau exploités prédisent avec précision la présence ou l'absence des truites lorsqu'on les applique aux données provenant des cours d'eau non exploités. L'étendue remarquable de la répartition de la truite indigène dans les réseaux hydrographiques de la chaîne des Cascades met en relief l'importance écologique des petits ruisseaux dans la planification de la gestion des bassins versants.

[Traduit par la Rédaction]

Introduction

Characterization of habitat features controlling the distribution and abundance of vulnerable fish populations is necessary for effective management of human activities in forested montane watersheds of the Pacific Coastal ecoregion. Despite abundant literature describing the conditions associated with productive trout habitat, the physical conditions associated with the upstream boundary of trout distribution remains poorly known. Similarly, logging-related alterations to physical and biological stream characteristics have been well documented, yet little information exists regarding whether these changes have influenced trout distribution.

Trout distribution has become a key management concern in Washington State because current management regulations restrict certain logging activities along streams where fish are present more than where fish are absent. Trout distribution (i.e., coastal cutthroat (*Oncorhynchus clarki clarki*)

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and rainbow (*Oncorhynchus mykiss*) trout) is of particular interest because these species typically persist farther upstream than any other fish species in the Cascade Mountains (McPhail 1967; Wydoski and Whitney 1979). Predictive models for mapping trout distribution across landscapes are under development in British Columbia (Porter et al. 2000) and Washington State. Within these efforts, most trout distribution data were collected from streams within commercial forestlands. As a result, uncertainty about whether logging and other related forest management activity have altered the historic boundaries of trout distribution has become an important management concern.

Trout distribution reflects the pattern of colonization and persistence by populations well adapted to modern climatic, biotic, hydrologic, and geomorphic conditions (Nelson et al. 1992). The physical and biotic factors that shape distribution patterns may vary in type and importance over time and space. For example, regional distribution patterns of trout populations near Puget Sound likely reflect the extent of glaciation, arrangement of remnant populations, topography, climate, and dispersal ability (McPhail and Lindsey 1986). Within individual river basins, trout distribution may further reflect variation in temperature (Roper et al. 1994), channel size (Hartman and Gill 1968; Platts 1979) and gradient (Bozek and Hubert 1992; Kruse et al. 1997), species interactions (Fausch et al. 1994), habitat patch size (Reiman and McIntyre 1995), and migratory behavior (Trotter 1989). Within streams and among reaches, dispersal barriers (Nelson et al. 1992; Kruse et al. 1997), catastrophic disturbances (e.g., debris torrents), and spatial variation in factors limiting persistence (e.g., interspecific competition, refugia, nutrient availability, prey abundance, or spawning and rearing habitat) may further regulate trout distribution.

The resilience of trout distribution to forest management activities is difficult to predict because of the wide array of responses exhibited by salmonids to logging-related alterations. Logging influences on salmonid abundance appear to vary according to differences in stream size and the degree to which riparian forest and channel characteristics are modified (Murphy et al. 1986). Potential consequences of contemporary forest management on trout distribution likely depend on the historical harvest practices and the nature of distribution constraints in effect before human disturbance. For example, the historic practice of clearing large woody debris (LWD; diameter ≥10 cm and length ≥2 m) from streams may have diminished fish populations in cleared stream reaches (Dolloff 1986). Without LWD to retain sediments and scour pools, channels that previously exhibited forced step–pool morphology may have reverted to a plane-bed or bedrock morphology that provides meager "lateral habitat" for trout (Moore and Gregory 1988). Conversely, trout access to headwater stream reaches may actually have been enhanced where management activities removed log jams that obstructed upstream migration (Narver 1971). Likewise, patterns of increased salmonid production after riparian logging have been observed in the Cascade Mountains (Murphy and Hall 1981; Bisson and Sedell 1984), largely as a result of increased autotrophic food pathways. In streams in which bioenergetic demands constrained trout distribution, increased production after logging might facilitate range extension. However, salmonid production may decline shortly after logging, as sunlight is shaded out by dense second-growth canopies (Murphy et al. 1986) and riparian supplies of LWD are exhausted. In streams in which modest or intermittent flows constrain trout distribution, logging-related hydrologic alterations such as increased summer low flows and extension of the open channel (Hicks et al. 1991; Ziemer and Lisle 1998) may enable fish to invade previously inaccessible habitat, at least for a short time. However, as cleared lands revegetate, summer stream flows may actually drop below prelogging levels (Hicks et al. 1991). Debris torrents, which may increase in frequency with forest management (Swanson et al. 1987), can decimate trout populations and dramatically alter channel morphology, though impacted channels appear to be swiftly recolonized (Lamberti et al. 1991).

We sought to determine whether the upstream distribution limits of resident trout occur under similar abiotic conditions in logged and unlogged montane headwater streams draining forested watersheds of the western Cascade Mountains, specifically, have forest management activities enhanced or exacerbated the physical conditions under which trout occur? For example, if steep channel gradients constrain trout distribution, are trout in unlogged watersheds able to invade and persist in steeper streams relative to trout in logged watersheds? We undertook this study to provide a basis for future decision-making in the management of forestry in this region. The objectives of our study were (*i*) to identify the physical constraints and stream characteristics at the upstream limits of trout distribution and (*ii*) to determine whether forest management activities have altered constraints on trout distribution and, consequently, the historic upstream boundaries of trout distribution.

Materials and methods

Study area

The western Cascade Mountain range is located within the northern mainland mountain subregion of the Pacific Coastal ecoregion (Fig. 1), where summers are typically cool and dry and winters are temperate and exceptionally wet (average annual precipitation ranges from 100 to 350 cm). Our study focused on first- and second-order channels that occur within colluvial, bedrock, and small alluvial valleys (Montgomery and Buffington 1998) across a broad range of channel widths (0.5–15 m), gradients (0.1%–50% slope), basin elevations (300–1200 m), and drainage areas (5–1200 ha). Channel substrates are patchy but generally consist of gravels and cobbles. Aquatic vertebrate communities in headwater streams were dominated by coastal cutthroat and rainbow trout, riffle and torrent sculpin (*Cottus gulosus* and *Cottus rhotheus*, respectively), Pacific giant salamander (*Dicamptodon tenebrosus*), and tailed frogs (*Ascaphus truei*). Natural disturbances strongly shape headwater stream ecology and structural characteristics. Rapid snowmelt or "rain-on-snow" events drive peak stream flows in the spring and early summer. Headwater stream channels may run dry before fall rains or be sustained throughout the summer by late-melting snow, depending on elevation (Ziemer and Lisle 1998). Swift flood surges laden with woody debris, alluvium, and soil (debris flows) occasionally restructure channel morphology and riparian forest structure (Swanson et al.

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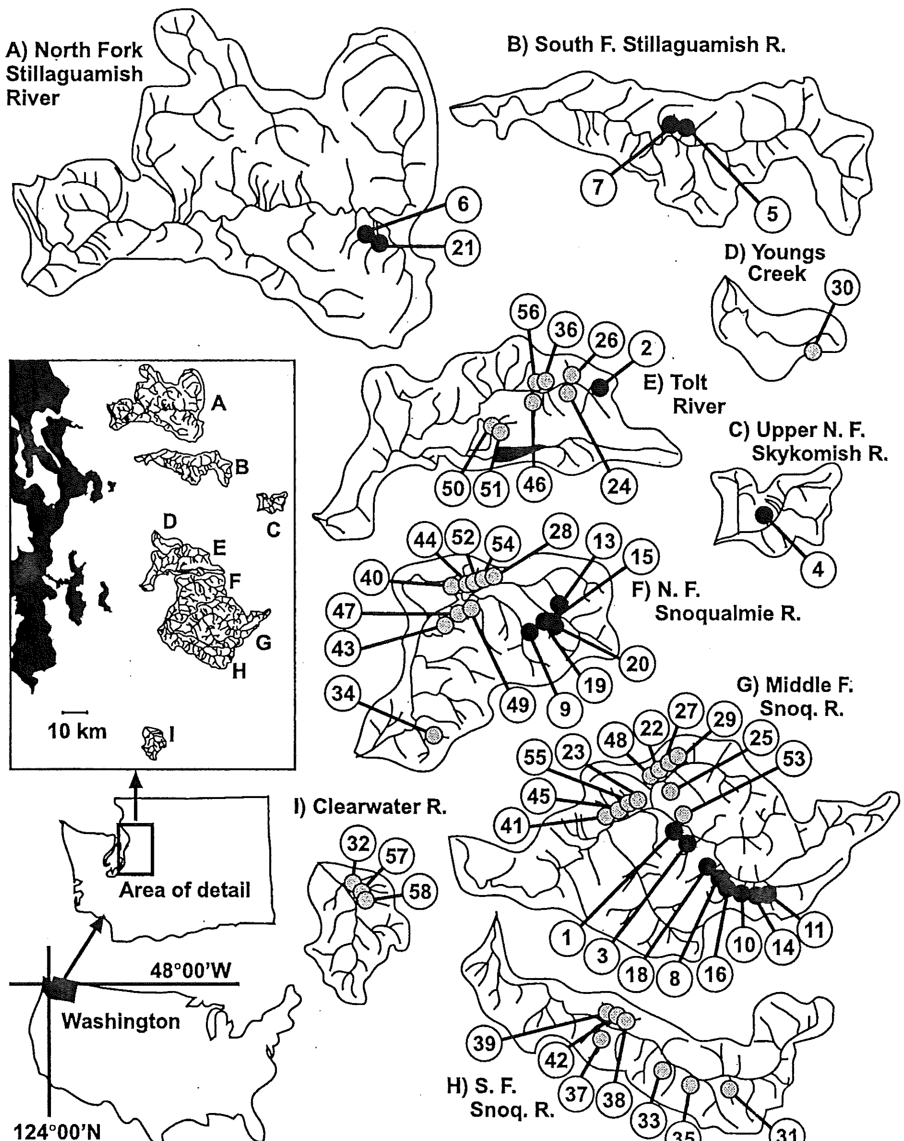
Fig. 1. Map of study sites in the Cascade Mountains, Washington. Spatial juxtaposition of subbasins (i.e., A–I) is illustrated in the "Area of detail". Locations of numbered study sites are indicated by circles on the enlarged subbasin diagrams. Solid circles indicate unlogged sites and shaded circles indicate logged sites.



1987). Autochthonous production in small headwater streams is typically low (Naiman and Sedell 1979), limited by low nutrient availability, cold temperatures, and dense riparian canopies (Murphy et al. 1981) of western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*).

Study design

A paired-reach sampling design was used to assess the influence of physical habitat attributes on the likelihood of trout presence and absence in 58 separate low-order streams (Fig. 1). Streams draining lakes, ponds, or hanging valleys were excluded because many have been artificially populated with hatchery-raised trout or exotic species. Field surveys were conducted in 1999 and 2000 between the late-spring snowmelt runoff and summer low-flow periods (May–September). Detailed habitat inventories were conducted in two contiguous 100-m sections immediately upstream and downstream of the upper distribution limit (i.e., the last trout observed).

Sites from both unlogged ($N = 21$) and logged ($N = 37$) drainages were surveyed to determine whether the likelihood of trout presence and absence in streams of similar physical character differed between drainages managed for timber production and protected drainages representative of pre-logging conditions. Most of the drainage area upstream from unlogged sites remained in native late-seral forest, whereas most trees had been harvested at least once in logged sites. At logged sites, riparian forests had been clearcut once or twice in the past, though contemporary harvests left intact streamside forest buffers. Time elapsed since last harvest ranged widely across logged sites, from <2 years (e.g., recently harvested) to ~50 years (e.g., second growth). Gen-

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erally, a suite of forest management activities occurred at logged sites, most notably road construction and culvert installation.

Data collection

A single electrofishing pass was used to locate the upstream limit of trout distribution. Sampling was initiated in a trout-bearing stream reach and progressed upstream until one of the following minimum criteria was met: (*i*) no trout were encountered for 400 m, despite rigorous searching, (*ii*) the channel was dry for over 200 m, or (*iii*) upstream channel slope consistently exceeded 30%. Sampling often continued beyond the point where these minimum criteria were met whenever the surveyor's confidence in the identified distribution limit was in doubt.

Habitat characteristics, including (*a*) mean channel gradient, (*b*) bankfull and wetted channel width, (*c*) pool characteristics, (*d*) LWD abundance, and (*e*) canopy closure, were measured in 100-m (slope distance) stream reaches immediately upstream and downstream from the trout distribution limit. Channel gradient (% slope) was measured incrementally over segments of uniform gradient but variable length, using a clinometer. Horizontal distance and elevation gain were calculated for each segment. Mean channel gradient for each 100-m section was calculated by dividing the total elevation gain by the total horizontal distance over all individually measured segments. Wetted (WW) and bankfull channel widths (BFW), as indicated by bank shape and perennial vegetation, were measured with a fiberglass tape to the nearest 0.1 m at transects spaced 20 m apart perpendicular to flow and were averaged for each section. To improve survey consistency across streams of different sizes, slow-water habitats were only considered pools if minimum criteria were met. Residual pool depth had to meet or exceed 0.1 m, whereas minimum pool area was scaled to BFW. Specifically, only pools ≥ 0.5 m^2 in area (as per visual estimation) were counted where mean BFW was 0–2.5 m. Likewise, the minimum pool area was 1, 2, and 3 m^2 where BFW was 2.5–5, 5–10, and 10–15 m, respectively (adapted from 1994 Timber–Fish–Wildlife Ambient Monitoring Program Manual, Northwest Indian Fisheries Commission, 6730 Martin Way East, Olympia, WA 98506, U.S.A.). Pools that met these criteria were tallied and measured for residual depth (Lisle 1987) in all streams. Features contributing to pool formation were recorded for each pool. Pieces of LWD intruding into the wetted channel were tallied for each section at every site. The general condition of riparian and surrounding forests was qualitatively assessed (e.g., young, pole, mature, and old), according to tree stem diameter and vertical complexity of the stand. A spherical densiometer was used to estimate canopy closure (%) at each transect. A digital altimeter was used to determine the elevation at each distribution limit. The geographic location of each distribution limit was recorded on 1 : 24 000 topographic maps and transferred into a geographic information system (GIS). Drainage area at each distribution limit was estimated with ArcInfo™ 8.0 (ESRI, Inc., 380 New York St., Redlands, CA 92373-8100) from 10-m digital elevation models derived by the University of Washington Puget Sound Regional Synthesis Model (PRISM) working group.

Data analysis

Logistic regression was used to model the likelihood of trout presence in a 100-m stream reach as a function of physical stream attributes in all sites combined (i.e., full combined model, A), logged sites (i.e., full logged model, B), and unlogged sites (i.e., full unlogged model, C). Models were fitted without interactions, as recommended by Neter et al. (1996), to permit the interpretation of $\exp(\beta_a)$ as the odds ratio. All analyses were performed with SPSS 10.0.5 (SPSS Inc. 1989–1999). Logistic regression provided a probabilistic prediction of trout presence and was well suited for this application because the dependent variable was binomial (trout presence or absence). Further, this technique does not assume normality, equal variances, or a linear response (Tabachnick and Fidell 1996). The form of the fitted multiple logistic regression model or response function is

$$(1) \qquad \pi = e^{\beta' X}/(1 + e^{\beta' X})$$

where π is the estimated probability of trout presence, and $\beta' X$ is the linear model, which is

$$(2) \qquad \beta' X = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_a X_a$$

where β_0 is the regression constant, β_a denote regression coefficients, and X_a denote independent predictor variables. As indicated above, logistic regression calculates the probability of success (i.e., trout presence, $\pi \geq 0.50$) over the probability of failure (i.e., trout absence, $\pi < 0.50$), which results in an estimated odds ratio, $\exp(\beta_a)$. The effect of increasing one predictor variable X_a by a single unit on the odds of trout presence is estimated by multiplying the probability of trout presence by $\exp(\beta_a)$, assuming that all other predictor variables are held constant (Neter et al. 1996). Stream attributes that differed between reaches upstream and downstream of the trout distribution limit ($p \leq 0.05$, Wilcoxon signed ranks tests) or between logged and unlogged sites ($p \leq 0.05$, Mann–Whitney U tests) were eligible for inclusion in the logistic regression models. Attributes with strong multicollinearity ($|r_S| \geq 0.50$) were excluded to improve the descriptive and predictive ability of the models (Neter et al. 1996). The Wald statistic was used to evaluate the statistical significance of the influence of each stream attribute on the likelihood of trout occurrence. Log-likelihood tests were used to determine which variables could be removed from the model. Chi-square goodness-of-fit (i.e., model χ^2) tests were used to determine whether the set of stream attributes was significantly related to the likelihood of trout presence. The probability of trout presence for each stream section was predicted from stream attributes and compared with the observed trout occurrence to assess model performance.

A simple model using channel gradient as the only predictor variable was also fit to the entire data set (i.e., combined gradient model, A_G) and separately to data from logged (i.e., logged gradient model, B_G) and unlogged sites (i.e., unlogged gradient model, C_G) to determine whether the likelihood of trout presence could be accurately predicted from channel gradient alone, as observed for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) (Kruse et al. 1997). Accurate predictive tools based on gradient alone have strong management utility, because channel gradient is easily approximated from topographic maps or digital eleva-

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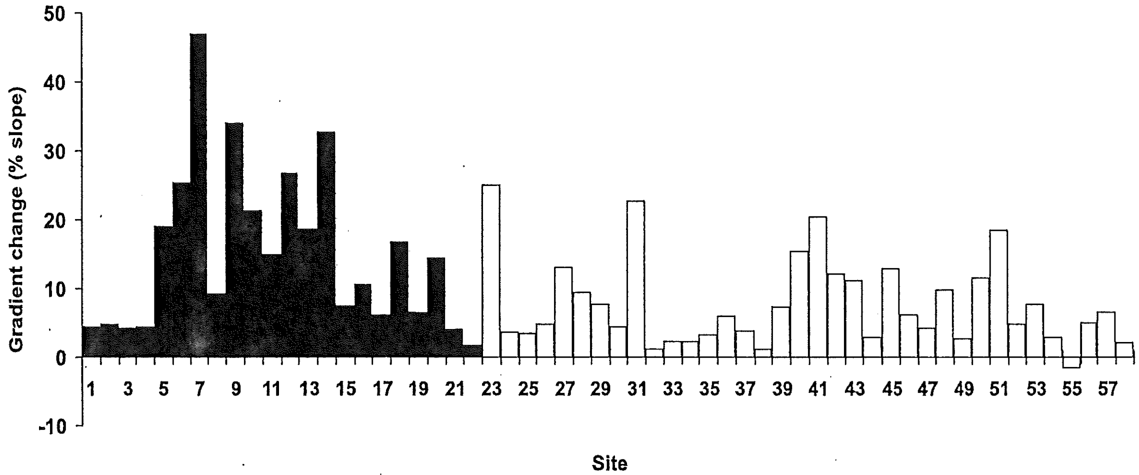
Fig. 2. Change in channel gradient encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.

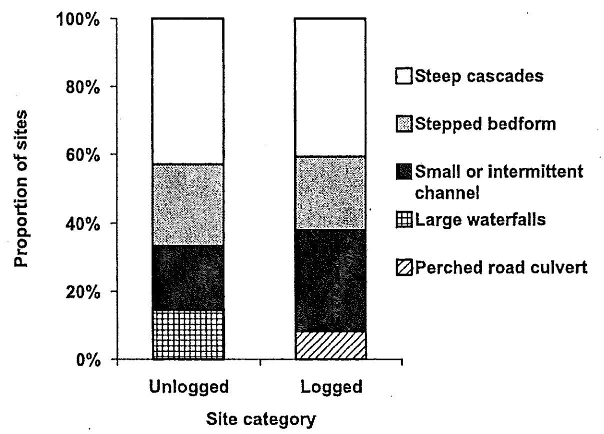


tion models and because stream characteristics, such as pool spacing and depth and channel width, are often related to channel gradient, as mediated by LWD (Montgomery and Buffington 1998).

Separate multiple logistic regression models (B, B_G, C, and C_G) were fitted to data from logged sites and unlogged sites and cross-validated to determine whether logging and related forest management activity have altered historic upstream boundaries of trout distribution. Comparison of the models indicates whether similar abiotic factors determine upstream distribution limits in logged and unlogged streams selected for study, though we cannot discern whether these models have general applicability to other watersheds in the region. The preferred method for validation of regression models is through the collection of new data from other watersheds in the region, though this was not feasible. In the absence of new data collected from other watersheds in the region, cross-validation is useful in evaluating the reasonableness and predictive ability of the selected model (Neter et al. 1996), in this case, the performance of a model based on data from logged streams when applied to unlogged streams is of primary interest.

In cross-validation, data sets from logged sites and unlogged sites were used alternately as "model-building" and "validation" sets (Neter et al. 1996). Models were applied to validation data sets (i.e., full logged model B vs. unlogged sites data set and full unlogged model C vs. logged sites data set). The probability of trout presence for each stream section was predicted from habitat features in the validation data set and compared with the observed trout presence. Cohen's kappa (K) values (Cohen 1960) were used to interpret the classification results of each logistic model, as recommended by Titus and Mosher (1984). The K statistic indicates whether model predictions are significantly better than random classifications; it expressed the proportion of sites correctly classified by the model after removing the effect of correct classification by chance. When $K = 0$, no improvement over chance was provided by the logistic regression model, whereas $K = 1$ only when all cases are correctly classified. When K is much lower than the observed correct classification rate, the observed classification rate and, subsequently, group predictability are overstated. The statistical significance of kappa values were assessed with the z statistic, as recommended by Titus and Mosher (1984).

Fig. 3. General features of reaches immediately upstream from the trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) distribution limit at unlogged and logged sites.



Results

Stream attributes of the upstream distribution limit

The upstream limit of trout distribution was frequently associated with a sharp increase in channel gradient (Fig. 2). Steep cascades, stepped-bed channel profiles, or waterfalls appeared to restrict upstream dispersal in a majority of logged (62.2%) and unlogged sites (81.0%) (Fig. 3). Channel gradient was significantly greater in stream reaches where trout were absent in both unlogged and logged sites ($p < 0.01$; Wilcoxon signed ranks test) (Table 1). Mean channel gradients in the downstream reaches of unlogged and logged sites averaged 9.1% but ranged from 1% to 22% overall. Trout were consistently absent from channels where gradient exceeded 22%, despite intensive surveys in channels up to 53% gradient. The mean channel gradient of reaches where trout were absent was greater ($p < 0.01$) in unlogged sites, as

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Table 1. Key stream habitat characteristics for 100-m stream reaches immediately upstream (U) and downstream (D) of the upstream limit of trout distribution in unlogged and logged sites and all sites combined.

		Unlogged			Logged			Combined		
Stream characteristic	Statistic	U		D	U		D	U		D
Channel gradient (%)	Mean (SE)	25.0* (2.6)	>	9.1 (1.0)	16.7* (1.2)	>	9.1 (0.8)	19.7 (1.3)	>	
	Range	7–53		3–21	6–37		1–22	6–53		1–22
Bankfull width (m)	Mean (SE)	6.4 (0.6)	=	5.7 (0.7)	5.4 (0.5)	=	5.5 (0.5)	5.7 (0.4)	=	5.5 (0.4)
	Range	2–13		2–16	2–16		2–16	2–16		2–16
Wetted width (m)	Mean (SE)	3.8* (0.5)	=	3.5 (0.5)	2.2* (0.3)	<	2.8 (0.2)	2.8 (0.3)	=	3.1 (0.2)
	Range	0–8		1–11	0–6		1–6	0–8		1–11
No. pools·100 m^{-1}	Mean (SE)	13.1 (1.8)	<	17.1 (1.8)	12.2 (1.6)	<	15.5 (1.5)	12.5 (1.2)	<	16.1 (0.2)
	Range	0–28		2–30	0–31		0–33	0–31		0–33
Residual pool depth (cm)	Mean (SE)	24.9 (3.3)	=	30.2 (6.6)	26.2 (2.8)	=	25.7 (1.8)	25.7 (2.1)	=	27.3 (2.7)
	Range	10–77		12–158	11–89		12–54	10–89		10–158
LWD·100 m^{-1}	Mean (SE)	41.9 (5.6)	=	42.1 (6.1)	48.8 (5.7)	=	40.2 (4.6)	46.3 (4.1)	=	40.9 (3.6)
	Range	0–85		9–139	5–159		0–106	0–159		0–159
Gravel substrate (%)	Mean (SE)	14.9* (2.8)	<	25.6 (3.8)	28.3* (4.2)	=	26.5 (2.8)	22.4 (2.8)	=	26.1 (2.2)
	Range	0–40		7–73	0–84		0–63	0–84		0–84
Canopy closure (%)	Mean (SE)	73.3 (6.0)	=	72.6 (5.4)	70.2 (4.3)	=	71.3 (4.4)	71.3 (3.5)	=	71.8 (3.4)
	Range	4–100		12–100	17–100		18–100	4–100		12–100

Note: Asterisks (*) indicate where significant differences ($p \le 0.05$, Mann–Whitney U test) exist between unlogged and logged sites (e.g., unlogged U vs. logged U). Differences ($p \le 0.05$, Wilcoxon signed ranks test) between U and D sections are indicated with "<" or ">" according to the direction of the differences or by "=" if no difference was detected. SE, standard error; LWD, large woody debris.

indicated by Mann–Whitney *U* tests (Table 1). Gradient immediately upstream of the limit of trout distribution in unlogged sites averaged 25.0% vs. 16.7% in logged sites. Waterfalls were associated with the upstream trout distribution limit in 3 of 21 (14.3%) unlogged sites (Fig. 3).

The limit of trout distribution was typically associated with declines in pool abundance in both unlogged and logged sites (Fig. 4). Pool abundance was significantly lower in stream reaches where trout were absent ($p < 0.01$, Wilcoxon signed ranks tests; Table 1), though few of these were completely devoid of pools (i.e., four logged sites and one unlogged site). Trout were found in reaches without pools at only one site. Pool abundance averaged 16·100 m^{-1} in downstream reaches and 13·100 m^{-1} in upstream reaches, most of which were formed by scour around boulders and woody debris. Pool abundance was similar in unlogged and logged sites, as indicated by Mann–Whitney *U* tests (Table 1). In several streams, isolated pools bounded by dry streambed comprised the only habitat available at the upstream limit of trout distribution; trout crowded into these pools at high densities (i.e., >5 individuals·m^{-2}).

Channel constrictions or subsurface flows were associated with the upstream limit of trout distribution more frequently in logged sites than in unlogged sites (Fig. 3). The wetted width of upstream reaches was usually narrower than that of the downstream reaches in logged sites (Fig. 5). In contrast, wetted channel width did not differ between upstream and downstream reaches in unlogged sites (Table 1). Mean wetted widths of upstream reaches were significantly narrower ($p \le 0.01$) in logged sites than in unlogged sites (Table 1). Wetted channel widths in downstream sections of unlogged and logged sites were indistinguishable ($p > 0.05$). Trout were found in isolated pools upstream from the initiation point of perennial streamflow at three sites, but never where the mean wetted channel width averaged less than 0.3 m·100 m^{-1}. In unlogged sites, substrates were significantly coarser in upstream reaches, though the relative proportion of substrate classes was strongly correlated with channel gradient.

Other habitat characteristics, including bankfull width, residual pool depth, number of LWD, and canopy closure, did not differ among upstream and downstream sections or between unlogged and logged sites. Drainage area, elevation, and mean annual precipitation at the distribution limit varied widely but did not differ significantly between unlogged and logged sites. Drainage area at the upstream limit of distribution averaged 130 ha across all sites and ranged from 2 to 517 ha. Elevation at the upstream limit of trout distribution ranged from 279 to 962 m. Forest stands were classified as young, pole, and mature in 18.9, 73.0, and 8.1%, respectively, of logged sites. Stands were classified as young, pole, mature, and old in 9.5, 14.3, 23.8, and 52.4%, respectively, of the unlogged sites.

Relationship between trout presence and physical stream attributes

The likelihood of trout presence declined with increasing channel gradient, decreased pool abundance, and decreased wetted channel width across all sites combined (Table 2), though trout presence was not related to wetted channel width in unlogged sites. Other variables were either not significantly related to trout presence and absence or were ex-

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Fig. 4. Change in pool frequency (per 100 m) encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.

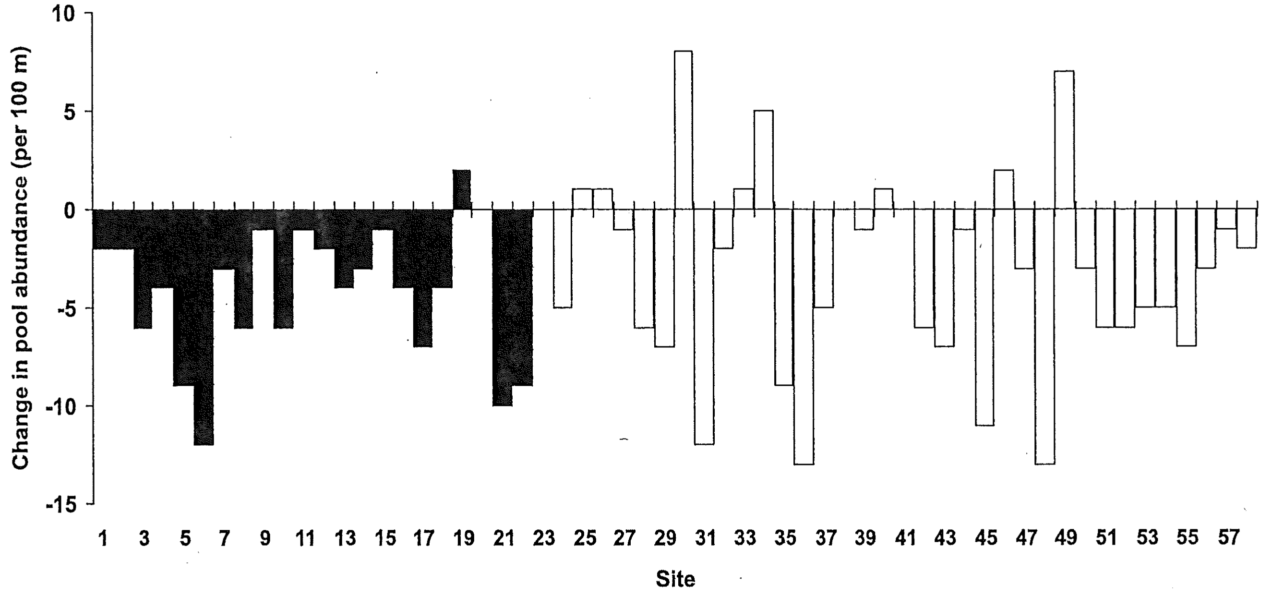
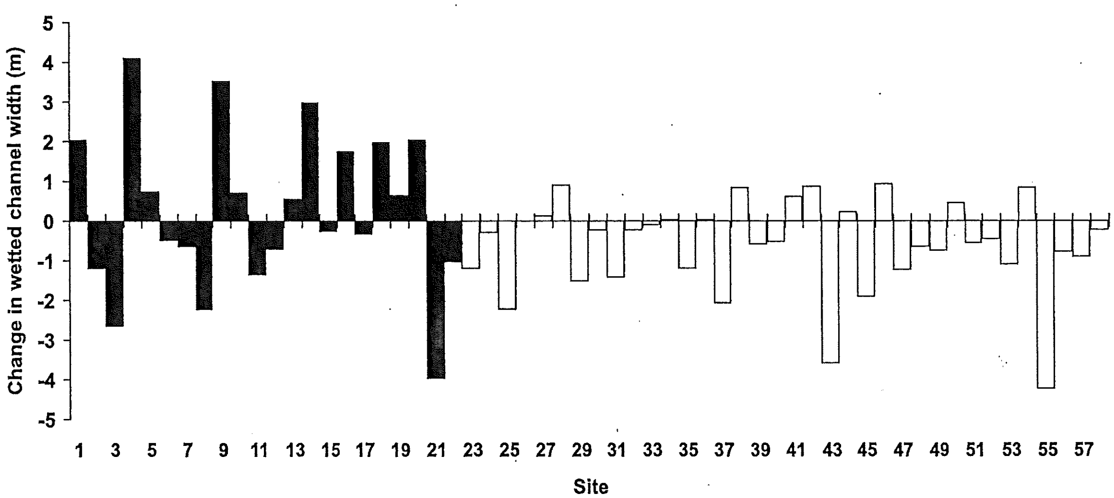


Fig. 5. Change in wetted channel width encountered by trout (*Oncorhynchus clarki clarki* and *Oncorhynchus mykiss*) at the upstream limit of distribution at unlogged (solid bars) and logged (open bars) sites.



cluded because of strong multicollinearity ($r_S \geq 0.50$). Chi-square goodness-of-fit tests indicated that the logistic response function was appropriate for all models. The full combined model (A) fitted to all sites correctly classified trout presence or absence in 100 of 116 (86.2%) stream reaches. Fifty-two of 58 stream reaches (89.7%) were correctly classified as trout bearing, and 48 of 58 stream reaches (82.8%) were correctly classified as devoid of trout. The chance-corrected classification rate (K = 72.4% ± 12, 95% confidence interval (CI)) was significantly better ($p < 0.01$) than would be expected resulting from chance alone. Assuming other variables were held constant, model A indicated that a 1% increase in channel gradient (e.g., 11% to 12%) reduced the odds of trout presence by 29%–32%. Likewise, the presence of one additional pool per 100-m stream section, assuming other predictor variables were held constant, increased the odds of trout presence by 12%–18%. Increasing wetted channel width by 1 m increased the odds of trout presence by 182%, assuming other predictor variables were held constant. The combined gradient model (A_G) correctly classified trout presence or absence in 84 of 116 (72.4%) stream reaches, overall. The chance-corrected classification rate (K = 44.8% ± 17, 95% CI) indicated that this model correctly classified more stream reaches than would be expected resulting from chance alone ($p < 0.01$).

Autocorrelations were observed among each factor included in the logistic regression models, but factors were retained if we considered them to represent unique mechanistic controls on trout distribution so long as $|r_S|$ did not exceed 0.50. Channel gradient was correlated with wetted channel width in both upstream ($r_S = 0.33$, $p < 0.05$) and downstream ($r_S = 0.45$, $p < 0.05$) sections but was only correlated with pool

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Table 2. Logistic regression analysis results for models of the relationship between the likelihood of trout presence and physical stream attributes, based on data from all sites combined, logged sites, and unlogged sites, and the associated change in odds of fish presence resulting from a one-unit increase in the stream attribute, controlling for other attributes.

Data set	N	Model	Variables	b (SE)	p	Exp(b) (95% CI)	Change in odds (%)
Combined	116	A	Constant	0.961 (0.719)	0.18		
			Gradient	−0.335 (0.065)	<0.01	0.715 (0.630–0.812)	−29.5
			Wetted width	0.560 (0.197)	0.01	1.750 (1.189–2.576)	+75.0
			Pool abundance	0.114 (0.036)	<0.01	1.121 (1.045–1.203)	+12.1
		A_G	Constant	2.765 (0.559)	<0.01		
			Gradient	−0.209 (0.041)	<0.01	0.812 (0.746–0.880)	−18.8
Logged	74	B	Constant	0.553 (0.927)	0.55		
			Channel gradient	−0.389 (0.092)	<0.01	0.678 (0.566–0.811)	−32.2
			Wetted width	1.037 (0.315)	<0.01	2.820 (1.520–5.232)	+182.0
			Pool abundance	0.096 (0.044)	0.03	1.101 (1.010–1.200)	+10.1
		B_G	Constant	2.397 (0.659)	<0.01		
			Channel gradient	−0.192 (0.050)	<0.01	0.825 (0.748–0.910)	−17.5
Unlogged	42	C	Constant	2.264 (1.232)	0.07		
			Channel gradient	−0.340 (0.104)	<0.01	0.712 (0.581–0.873)	−28.8
			Pool abundance	0.168 (0.076)	0.03	1.183 (1.020–1.374)	+18.3
		C_G	Constant	3.619 (1.073)	<0.01		
			Channel gradient	−0.244 (0.074)	<0.01	0.783 (0.677–0.906)	−21.7

Note: SE, standard error; CI, confidence interval.

abundance in downstream sections ($r_S = 0.47$, $p < 0.05$). Wetted channel width and pool abundance were correlated in upstream sections alone ($r_S = 0.28$, $p < 0.05$), whereas wetted channel width and residual pool depth were correlated in upstream ($r_S = 0.38$, $p < 0.05$) and downstream ($r_S = 0.46$, $p < 0.05$) sections.

Comparison of trout distribution in logged and unlogged streams

Separate models fitted to logged (B, B_G) and unlogged (C, C_G) sites performed fairly well when applied to validation data sets; each model correctly predicted trout presence or absence in over 70% of the stream sections in the validation sets (Table 3). Kappa values were relatively high (43–71%; Table 3), indicating that each model correctly predicted trout presence and absence in a much greater proportion of the stream reaches than would be expected from chance alone. However, all K values were slightly lower than the observed correct classification rate, which suggests that uncorrected model performance may have been slightly overstated. The probability of trout presence declined with increasing channel gradient and decreasing pool abundance at both logged and unlogged sites, though wetted channel width was only related to trout presence at logged sites. The full unlogged model (C) predicted trout presence where trout were actually absent in 14 of 37 (38%) logged stream reaches, whereas the full logged model (B) predicted trout presence where trout were actually absent for only 4 of 21 (19.0%) unlogged stream reaches. The full logged model (B) correctly predicted trout presence and absence in slightly more of the unlogged stream reaches than the logged gradient model (B_G). The models based on unlogged sites (C, C_G) were equally successful, overall, in predicting trout presence and absence in logged stream reaches.

Discussion

Physical constraints on trout distribution

Our results indicate that the upstream boundaries of coastal cutthroat and rainbow trout distribution in low-order streams of the western Cascade Mountains near Puget Sound are influenced by steep channel gradient, the availability of pool habitat, and small stream size. Although this study examined only 58 streams, we believe that these factors have strong effects on the extent of trout distribution in many headwater streams of the Cascade Mountains. The probability of trout presence significantly decreased in steeper channels but increased with increasing stream size and pool abundance. The influence of channel gradient appeared to overwhelm the effects of either pool abundance or wetted width, though autocorrelation among channel gradient, pool abundance, and wetted channel width precludes inferences on the relative importance of each factor. Trout readily accessed channels with up to a 22% gradient and commonly occurred where channel gradient exceeded 10%. Similar ranges have been reported for Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*; Dunham et al. 1999) and bull trout (*Salvelinus confluentus*; Watson and Hillman 1997). Based on our results, trout were more likely to be present in steep channels when pool habitat was plentiful. Pools probably facilitated trout access and persistence in steep channels by providing

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Table 3. Proportion of stream reaches where trout presence was correctly classified in cross-validation tests (i.e., models B and B_G were used to classify unlogged stream reaches, and models C and C_G were used to classify logged stream reaches).

		Unlogged stream reaches		Logged stream reaches	
		Model B	Model B_G	Model C	Model C_G
Trout present	Predicted	19	18	30	31
	Actual	21	21	37	37
	Correct	0.905	0.857	0.811	0.838
Trout absent	Predicted	17	17	23	22
	Actual	21	21	37	37
	Correct	0.810	0.810	0.622	0.595
Overall	Correct	0.857	0.833	0.716	0.716
Chance-corrected	Kappa (95% CI)	0.714 (0.22)	0.666 (0.23)	0.432 (0.20)	0.432 (0.21)
	p	<0.01	<0.01	<0.01	<0.01

Note: CI, confidence interval.

launching areas for leaping barriers (Adams et al. 2000) and refugia from predation and thermal extremes during summer low flows (Bisson et al. 1988). Stream size has been identified as a driving factor in the presence and abundance of stream salmonids (e.g., coastal cutthroat trout) elsewhere in the ecoregion (Rosenfeld et al. 2000). Our data indicate that trout were less likely to occur as the wetted channel became negligible or intermittent, though our observations indicate that the extreme margins of trout distribution may extend beyond the point at which streams exhibit seasonal intermittency. Other variables examined in this study did not appear to be important constraints on the upstream trout distribution limits in the streams that we examined.

The stability of the upstream limit of trout distribution over space and time remains ripe for future research. Stream salmonids may exhibit extensive, complex patterns of movement, though the mechanisms determining the frequency and extent of movement remain poorly understood (Gowan et al. 1994). The steep, narrow stream reaches that epitomize the upstream distribution limit of trout may be volatile and heterogeneous over time. Assuming that at least a small number of individuals in a trout population exhibit extensive movements (see Gowan and Fausch 1996), we speculate that fluctuations in upstream distribution limits, in concert with variation in habitat suitability and accessibility, are likely.

Influence of logging on trout distribution

Although logging and related activities may influence the structural and biotic attributes of headwater streams (Murphy and Hall 1981; Bisson and Sedell 1984; Gregory et al. 1987), the combined impacts of historic and current forest management activity within low-order streams of the Cascade Mountains near Puget Sound do not appear to have altered the conditions under which the upper boundary of trout distribution occurs. Trout presence and absence in unlogged streams was predicted with a high degree of accuracy by the logistic regression model based on stream attributes near the distribution limit of trout in logged streams. However, though geomorphic habitat characteristics were similar between unlogged and previously logged streams in the downstream section where trout were present, the gradient and wetted channel width upstream from the upper distribution limit were greater, on average, in unlogged sites. Observed differences in stream attributes above the upper distribution limit may have been caused by rather abrupt increases in channel gradient at some unlogged sites in watersheds with steep valley walls. Trout appear to inhabit streams with similar attributes in logged and unlogged sites but are unlikely to access and persist in streams once channel gradient, pool abundance, or wetted channel widths exceed certain thresholds. The high degree of success exhibited by cross-validation of the full logged model (B) on the unlogged data set suggests that these thresholds occur at similar levels in logged and unlogged sites.

Logging and related activities may alter key factors that regulate small-scale channel gradient, or bed slope, such as sediment supply, transport capacity, and the vegetation within and adjacent to the channel (Montgomery and Buffington 1998). Increased discharge may trigger channel incision, whereas aggradation may occur in streams with exhausted transport capacity. Channel gradient at the reach scale (e.g., ≥100 m) may be relatively resilient to logging-related impacts because it is largely controlled by large-scale processes such as tectonic uplift and erosion of the landscape over geologic time (Montgomery and Buffington 1998).

In conclusion, habitat-based models are valuable tools for estimating upstream distribution limits of trout, particularly in areas where intrusive field surveys are unadvisable, such as those inhabited by threatened or endangered fish populations. Our results indicate that easily measured channel features can be used to accurately predict the incidence of trout in streams during late spring and summer. Because the extent of trout distribution throughout entire river basins may be governed by factors operating at other spatial scales (see Huryn and Wallace 1987), our models should be used in conjunction with detailed surveys of large waterfalls or other known barriers when predicting the upstream extent of trout distribution. Application of our models in regions with fundamentally different hydrologic, erosional, or tectonic processes is not advised because relationships between trout distribution and channel morphology probably differ among watersheds in different biogeographic or geomorphic provinces (Nelson et al. 1992; Montgomery and Buffington 1998; Hicks and Hall 2003).

Our investigation considered the influence of major physical factors on patterns of reach-scale trout distribution, but

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patterns at larger scales (e.g., segment, valley, and watershed) may also reflect biotic processes. The ability of trout to invade and persist in steep streams may also be regulated, in part, by biotic factors such as predation or intraspecific competition for food and refugia. Further investigations are warranted for a more comprehensive understanding of the factors responsible for patterns of trout distribution within and among streams.

Our results highlight the prevalence and resiliency of native trout in very small, steep streams of forested mountain watersheds in the Cascade Mountains. Historically, small headwater streams of the Pacific Coastal ecoregion have received little protection from land-management actions because it was incorrectly believed that they contained few or no fish, despite their broader ecological significance. Only recently have headwater streams benefited from increased protection from potentially damaging land-use practices. Population characteristics of stream-resident trout in the Pacific Coastal ecoregion remain poorly known. The distribution patterns of stream-dwelling trout appear relatively resilient to anthropogenic and natural disturbances. However, connectivity between trout populations in small, headwater streams may be necessary for the long-term maintenance of genetic (and presumably adaptive) diversity (Latterell 2001) and to permit recolonization following stochastic extinctions of local populations resulting from natural metapopulation dynamics. Reducing or eliminating unnatural barriers to upstream dispersal (such as suspended culverts) is needed to ensure that the natural distribution potential and patterns of gene flow in trout populations is fully realized.

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