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Geomorphic and Anthropogenic Influences on Fish and Amphibians in Pacific Northwest Coastal Streams

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Abstract.—Physical habitat degradation has been implicated as a major contributor to the historic decline of salmonids in Pacific Northwest streams. Native aquatic vertebrate assemblages in the Oregon and Washington Coast Range consist primarily of coldwater salmonids, cottids, and amphibians. This region has a dynamic natural disturbance regime, in which mass failures, debris torrents, fire, and tree-fall are driven by weather but are subject to human alteration. The major land uses in the region are logging, dairy farming, and roads, but there is disagreement concerning the effects of those activities on habitat and fish assemblages. To evaluate those effects, we examined associations among physical and chemical habitat, land use, geomorphology, and aquatic vertebrate assemblage data from a regional survey. In general, those data showed that most variation in aquatic vertebrate assemblage composition and habitat characteristics is predetermined by drainage area, channel slope, and basin lithology. To reveal anthropogenic influences, we first modeled the dominant geomorphic influences on aquatic biotic assemblages and physical habitat in the region. Once those geomorphic controls were factored out, associations with human activities were clarified. Streambed instability and excess fines were associated with riparian disturbance and road density, as was a vertebrate assemblage index of biotic integrity (IBI). Low stream IBI values, reflecting lower abundances of salmonids and other sediment-intolerant and coldwater fish and amphibian taxa, were associated with excess streambed fines, bed instability, higher water temperature, higher dissolved nutrient concentrations, and lack of deep pools and cover complexity. Anthropogenic effects were more pronounced in streams draining erodible sedimentary bedrock than in those draining more resistant volcanic terrain. Our findings suggest that the condition of fish and amphibian assemblages in Coast Range streams would be improved by reducing watershed activities that exacerbate erosion and mass-wasting of sediment; protecting and restoring multilayered structure and large, old trees in riparian zones; and managing landscapes so that large wood is delivered along with sediment in both natural and anthropogenic mass-wasting events. These three measures are likely to increase relative bed stability and decrease excess fines by decreasing sediment inputs and increasing energy-dissipating roughness from in-channel large wood and deep residual pools. Reducing sediment supply and transport to sustainable rates should also ensure adequate future supplies of sediment. In addition, these measures would provide more shade, bankside cover, pool volume, colder water, and more complex habitat structure.

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INTRODUCTION

The forested Oregon and Washington Coast Range ecoregion has a cool, wet temperate climate (Omernik and Gallant 1986), with a dynamic natural disturbance regime in which landslides, debris torrents, wildfire and wind-driven tree-fall are important in shaping the landscape and its streams (Dietrich and Dunne 1978; Benda et al. 1998, 2003; Bisson et al. 2003). These disturbances are essential for forming and maintaining complex and productive habitat for biota in the region (Reeves et al. 1995). Native aquatic vertebrates in wadeable streams of this ecoregion consist largely of coldwater fish and amphibian assemblages that are species-depauperate compared with those in many parts of the United States. Common species include resident and anadromous salmonids and lampreys, sculpins, minnows, and amphibians (Herger and Hayslip 2000; Hughes et al. 2004). Stream habitat degradation has been implicated as a major factor contributing to the historic decline of salmonids and the integrity of the food webs supporting them in the Pacific Northwest (Nehlsen et al. 1991). Land disturbances and native vegetation removal increase sediment delivery rates from natural processes in stream catchments (Waters 1995; Jones et al. 2001). Human land uses in the Coast Range consist primarily of silviculture, dairy farming, and roads. These activities can increase erosion rates and sediment supply to streams above those in the absence of human activities (Beschta 1978; Reid et al. 1981; Waters 1995; May 2002). In riparian areas, these activities reduce the effectiveness of riparian corridors in trapping sediment and stabilizing long-term sediment storage in streambanks and valley bottoms (Gregory et al. 1991).

The landscape setting, however, is an influential context underlying human effects in this region (Figure 1). Geoclimatic factors and landscape position exert strong controls on the vigor of geologic weathering, sediment delivery, transport and deposition processes, and on the flow and morphology of streams (Leopold et al. 1964). Furthermore, landscape characteristics, including topography and geology, constrain the types of land and water management activities that are possible and profitable. Finally, many of these same landscape characteristics can exacerbate or ameliorate the degree to which human activities alter the sediment and water delivery processes that in turn influence substrate size, stability, and channel form. It is not surprising, then, that researchers have reported that stream ecosystems in the Coast Range ecoregion vary in their sensitivity to human disturbances, depending upon stream drainage area, channel slopes, and basin geology (e.g., Beschta et al. 1995; Spence et al. 1996).

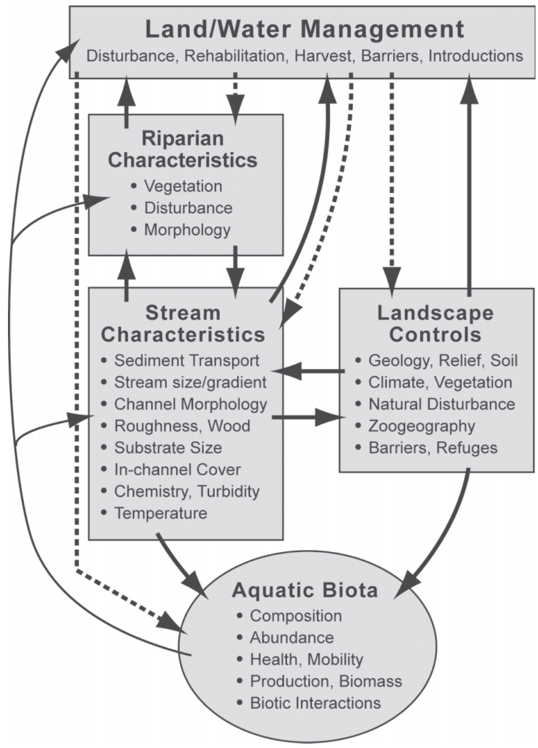

Figure 1. Conceptual diagram of natural and anthropogenic influences on aquatic biota and the physical–chemical habitat supporting it. Solid and dashed arrows represent natural and anthropogenic influences, respectively.

There is considerable debate concerning the effects of human activities on habitat and aquatic vertebrate assemblages in the Coast Range ecoregion, but increased sedimentation of streambeds has been identified as a likely cause of impairment (Nehlsen et al. 1991; Waters 1995; Spence et al. 1996). The recent experimental work of Suttle et al. (2004) demonstrated mechanisms through which bedded fine sediments reduce juvenile salmonid growth and survival, and earlier research (e.g., Chapman 1988) demonstrated mechanisms by which fine sediments reduced survival of embryos and emerging salmon fry. However, much of the uncertainty in demonstrating anthropogenic causes of sediment effects on stream biota on a regional scale stems from the fact that human land-use activities covary with strong geomorphic gradients that control aquatic biota through their influence on sediment supply, transport, and channel morphology.

Our objective was to evaluate geomorphic and anthropogenic influences on aquatic vertebrates in this region, separating the most important of these influences to the full extent possible with our survey data. To do so, we examined associations among physical and chemical habitat, land use, geomorphology, and biotic assemblages.

METHODS

Sampling Design

Aquatic vertebrate assemblage composition, chemical and physical habitat, and riparian vegetation structure were measured in a survey of the Coast Range ecoregion conducted by the Oregon Department of Environmental Quality and the Washington Department of Ecology in cooperation with the U.S. Environmental Protection Agency (Herger and Hayslip 2000). Stream sample reaches were selected as a probability sample using the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) sampling protocols (Stevens and Olsen 1999; Herlihy et al. 2000). The sample (Figure 2) is representative of the population of 23,700 km of first- through third-

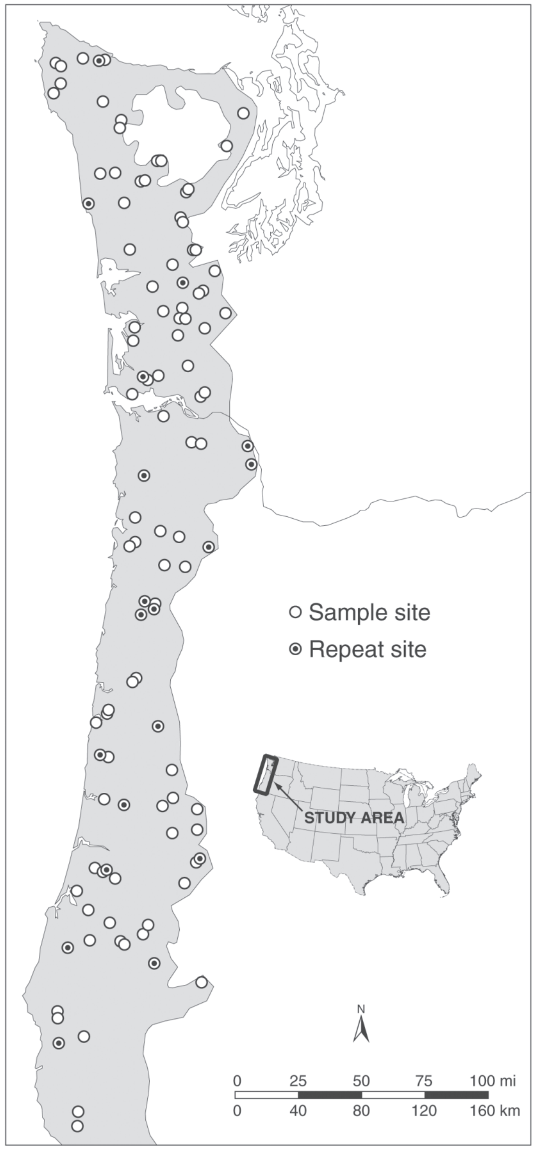

Figure 2. Locations of Coast Range sample sites in Oregon and Washington.

order streams (Strahler 1957) delineated on 1:100,000-scale U.S. Geologic Survey topographic maps of the region. The survey included one or more visits to 104 stream reaches in Oregon ($n = 57$) and Washington ($n = 47$), during the summer low-flow seasons of 1994 and 1995. To evaluate measurement and short-term temporal variability during the sample season, 19 sample reaches were revisited in the same season, and the 57 Oregon sites were revisited in the summer of 1996 following a 50-year storm. Sample lengths were 40 times their summer season wetted width, but no less than 150 m (Lazorchak et al. 1998)

Aquatic Vertebrates

Stream fish and amphibians were sampled by one-pass electrofishing over the entire length of each sample reach (Lazorchak et al. 1998), a level of effort that Reynolds et al. (2003) found adequate for collecting all but the rarest species in upland and lowland wadeable streams in Western Oregon. Field crews used Smith-Root backpack electrofishers set at pulsed DC, 300 volt-amperes, 900–1,100 V, and a frequency of 60–70 Hz. A crew of two to three persons typically fished the reach in 1–3 h. Taxa were identified in the field, and specimens were vouchered at the Oregon State University Ichthyology Museum. The concepts and procedures for calculating an IBI for aquatic vertebrate assemblages (including fish and amphibians) in these streams were described by Hughes et al. (2004). Their IBI contains eight assemblage metrics: percent alien species, percent coolwater species, percent anadromous species, percent coldwater species, number of size-classes, number of tolerant individuals, number of native coldwater species, and number of native coldwater individuals. The last three IBI metrics were scaled for watershed area, a procedure that adjusts for the expectation of greater taxa richness in larger streams. Because of the relationships among gradient, elevation and catchment area in this region, this procedure also eliminated most of the dependence of taxa richness on stream gradient and elevation among our sample sites (Hughes et al. 2004).

Chemical and Physical Habitat

Water temperature was measured upon arriving at the stream in the morning. A 4-L grab-sample and two 60-mL syringes of stream water were collected midstream at each sample reach (Lazorchak et al. 1998). The syringes were sealed with Luer-lock valves to prevent gas exchange. All samples were iced and sent to the analytical laboratory within 24 h. Syringe samples were analyzed for pH and dissolved inorganic carbon (DIC), and the 4 l sample was split into aliquots and preserved within 48–72 h of collection. Detailed information on the analytical procedures is published by USEPA (1987). In brief, Fe, Mn, and base cations were determined by atomic absorption, anions (SO_4^{2-}, NO_3^-, Cl^-) by ion chromatography, dissolved organic carbon (DOC) by a carbon analyzer, total N and P by persulfate oxidation and colorimetry, electrical conductivity by standard methods, and turbidity by nephelometry.

Physical habitat data were collected from longitudinal profiles and from 11 cross-sectional transects evenly spaced along the sampled stream reach (Kaufmann and Robison 1998). Maximum (thalweg) depth was measured at 100 evenly spaced points along the stream reach (150 points for streams less than 2.5 m wide). The location and amount of woody debris, and habitat unit classification (e.g., riffle, pool) were recorded while measuring the thalweg. Data collected along transects included channel dimensions (width, depth, bank angle), systematic "pebble counts," channel gradient, bearing (for calculating sinuosity), areal cover of fish concealment features (e.g., brush, undercut banks, large wood), riparian vegetation cover and structure, and the occurrence and proximity of riparian human disturbances (e.g., roads, buildings, stumps, agriculture). See Kaufmann et al. (1999) for calculations of reach-scale summary metrics from field data, including mean channel dimensions, residual pool depth, geometric mean substrate diameter, wood volume, bed shear stress, relative bed stability (RBS), riparian vegetation cover and complexity, and proximity-weighted indices of riparian human disturbances. Contributing drainage areas were delineated and measured on 1:24,000-scale U.S. Geological Survey topographic maps using geographical informational systems techniques.

Disturbance Indices

We calculated a composite riparian condition index (RCond) from the reach summary data describing the cover and structure of riparian vegetation and a proximity-weighted tally of streamside human activities. RCond was defined as follows:

$$RCond = \{(XCL)(XCMGW)[1/(1+W1\_HALL)]\}^{(1/3)}$$

The index increases with decreases in streamside human activities (W1_HALL), and increases in large-diameter tree cover (XCL) and riparian vegetation complexity (XCMGW, the sum of woody vegetation cover in the tree, shrub, and ground cover layers). The riparian measures contributing to this index are detailed by Kaufmann et al. (1999).

We used digital road data (TIGER 1990) as a surrogate measure of catchment disturbance. The TIGER data were compared with updated forest road data and found adequate for our purposes. We scaled catchment road density (Rd_DenKM) by the highest value we observed among our sample reach catchments (6 km/km^2) and combined it with RCond to define an index of watershed + riparian condition as

$$WRCond = [1/(1+(Rd\_DenKM/6))]\ RCond$$

Anthropogenic Sedimentation

To reveal the influence of anthropogenic sedimentation on biota, we needed measures of streambed particle size and the percentage of silt-size particles that reasonably scaled these stream characteristics by their major natural controls. Because stream power for transporting progressively larger sediment particles increases in direct proportion to the product of flow depth and slope, steep streams tend to have coarser substrates than similar size streams on gentle slopes. Similarly, the larger of two streams flowing at the same slope will tend to have coarser substrate, because its deeper flow has more power to scour and transport fine substrates downstream (Leopold et al. 1964; Morisawa 1968). Many researchers have scaled observed stream reach or riffle substrate size (e.g., median diameter D_{50}, or geometric mean diameter D_{gm}) by the calculated mobile, or "critical" substrate diameter (D_{cbf}) in the stream channel. The scaled median streambed particle size is expressed as relative bed stability (RBS), calculated as the ratio $D_{50}/D_{cbf;}$ (Dingman 1984; Gordon et al. 1992), where D_{50} is based on systematic streambed particle sampling ("pebble counts") and D_{cbf} is based on the estimated streambed shear stress at bank-full flows. Kaufmann et al. (1999) modified the calculation of D_{cbf} to incorporate large wood and pools, which can greatly reduce shear stress in complex natural streams. They formulated both D_{gm} and D_{cbf} so that RBS could be estimated from physical habitat data obtained from large-scale regional ecological surveys. In interpreting RBS on a regional scale, they argued that, over time, streams adjust sediment transport to match supply from natural weathering and delivery mechanisms driven by the natural disturbance regime, so that RBS in appropriately stratified regional reference sites should tend towards a range characteristic of the climate, lithology, and natural disturbance regime. Earlier researchers demonstrated reductions in D_{50} relative to D_{cbf} as a result of increases in sediment supply containing a mix of particle sizes, and had investigated the processes causing these reductions (Lisle 1982; Dietrich et al. 1989; Buffington 1998). We hypothesized that large positive (armoring) or negative (fining) deviations from this size were anthropogenic if they were associated with measures of human disturbances and not other natural gradients, and could be explained by these plausible mechanisms. In streams with low RBS, bed materials are easily moved by floods smaller than bank-full, so may be rapidly transported downstream. The persistence of fine surficial streambed particles is made possible under these circumstances by high rates of sediment supply (including fines) that continue to replenish the streambed.

We used log-transformed relative bed stability (LRBS) as an independent variable in regression analyses to interpret the likely influence of anthropogenic alteration of bed sediment size on aquatic vertebrate assemblages. However, percentages of fine particles might be elevated to levels that are potentially deleterious to biota in some streams without substantially affecting the central tendency of substrate diameter or the general stability of the streambed. As an alternate estimate of excess fine sediments in these streams, we also calculated the deviation of surficial fine sediments (<0.06 mm) from a regression on D_{cbf} (a function of streambed shear stress). We previously applied this approach to Appalachian streams to assess the effects of land use on aquatic macroinvertebrates (Bryce et al. 1999) and the percentage of sand and silt in streambeds (USEPA 2000).

Data Analysis

We took an analytical approach conceptually different from covariance structure analysis (Riseng et al. 2006; Zorn and Wiley 2006; both this volume) or multiple linear regression (Burnett et al. 2006, this volume). Our approach was similar to covariance structure analysis (CSA) in that it includes some intention in attributing portions of variance to one predictor or another when they covary. Like CSA, our approach was motivated by the desire to describe likely functional relationships among controls and responses and to reduce ambiguity in the interpretation of multiple linear regression (MLR) when colinearity among predictor variables was substantial. Similar to the "normalization" approaches described by Wiley et al. (2002) and Baker et al. (2005), we intentionally asserted some dominant functional relationships between natural forcing functions and their responses, based on deterministic modeling of relationships that can be confidently theorized. Specifically, we scaled stream bed particle size data by bed shear stress as described by Kaufmann et al. (1999) and we examined aquatic vertebrate assemblages after transforming species-abundance data into an index of biotic integrity (IBI; Hughes et al. 2004). We then employed correlation analysis and sequentially withheld certain categories of data in MLR to examine the relationships between anthropogenic disturbances and aquatic biota in the Coast Range, particularly aiming to clarify the influence of anthropogenic sedimentation. This approach was warranted because we have considerable confidence in modeling expected aquatic vertebrate taxa richness and substrate size in streams, and because the magnitude of deviation from those expectations can be reasonably attributed to human activities. Our analytical strategy followed seven steps:

1) We assembled a database of potential explanatory variables (Table 1), including landscape variables that could act as natural controls on aquatic vertebrate assemblages, human disturbance (stressor) variables, and in-stream measures of habitat volume, hydraulic energy, substrate size composition, channel complexity, cover, temperature, ionic strength, and nutrients. We eliminated many variables that showed no appreciable or biologically relevant variation in the region (e.g., pH), or that were highly correlated or redundant with other variables in the data set (e.g., sum of base cations was redundant with ANC).

2) We divided potential explanatory variables into three groups: landscape variables that are relatively unaffected by human activities in this region, landscape and riparian variables that are measures of human disturbance or are reasonable surrogates of human disturbance, and instream measures of physical and chemical habitat, most of which are subject to direct or indirect alteration by humans (Table 1).

3) We used univariate correlation (Spearman rank order correlation, SAS 2004) to explore associations between IBI and potential controlling variables to determine which variables were probably *not* important in explaining regional

Table 1. Variables used in multiple linear regression and correlation analysis

Variable code	Definition
Response variable	
IBI	Index of biotic integrity based on stream fish and amphibians (Hughes et al. 2004)
Landscape setting:	
LAreaKM	Log_{10}(drainage area—km^2)
LS	Log_{10} (mean % slope of sample reach)
Elev	Elevation at sample reach (m)
LQsp	Log_{10} (areal discharge at summer sample time ($m^3 s^{-1} km^{-2}$))
LITH	Basin lithology (0 = Volcanic, 1 = Sedimentary)
Human distub./condition:	
Rd_DenKM	Basin road density from TIGER data (km/km^2)
W1_HALL	Proximity weighted tally of riparian/streamside disturbances
RCond (see text)	Riparian condition: veg. cover, structure, and human disturbances
WRCond (see text)	Watershed + riparian condition index
RDxRCond	Interaction of Rd_DenKM and RCond
RDx(1-RCond)	Interaction of Rd_DenKM and (1-RCond)
In-channel habitat ——— Water quality:	
TEMPSTRM	Stream water temperature at time of sampling (°C)
LNTL	Log_{10} (total nitrogen μg/L as N) in stream water
LPTL	Log_{10} (total phosphorus μg/L as P) in stream water
CONDUCT	Electrical conductivity (μS/cm) of stream water
In-channel habitat ——— Physical habitat:	
RP100	Mean residual depth at thalweg (m)
RPGT75	Number of pools with residual depth ≥ 0.75m in reach
SDD	Std deviation of depth at thalweg (m)
LV1W_msq	Log_{10}(large wood volume [m^3 wood/m^2 bank-full channel])
XFC_BRS	Proportion areal cover of in-channel brush and small woody debris
XFC_UCB	Proportion areal cover of undercut banks
%BDRK	Bedrock (percent of streambed area)
EX_FN (see text)	Excess % streambed silt (deviation % < 0.06 mm diameter)
LRBS (see text)	Log_{10} of relative bed stability = $Log_{10}(D_{gm}/D_{cbf})$
Used in correlations only:	
XCMGW	Mean riparian tree + shrub + ground woody cover (%)
%FN	Streambed fines (% < 0.6 mm diameter)
%SAFN	Streambed sand + fines (% < 2 mm diameter)
D_{gm}	Streambed particle geometric mean diameter (mm)

IBI variation and to describe similar covarying patterns of association. These associations were the basis for stratifying sample sites into classes with apparently similar major controls on assemblages and physical-chemical habitat. As a result of these analyses, we stratified by catchment lithology (sedimentary and volcanic) and by catchment area (large ≥15 km^2, and small <15 km^2).

4) Where possible and supported by plausible mechanisms, we scaled the in-channel predictor variables most strongly associated with IBI to factor out natural geomorphic controls, redefining variables to be interpreted as anthropogenic deviations from natural expectations (Wiley et al. 2002; Baker et al. 2005). Geometric mean streambed particle diameter was scaled by critical diameter to define relative bed stability

(RBS, log transformed as LRBS), and percent bed surface silt (%FN) was scaled by critical diameter to define excess percent silt (EX_FN).

5) We carried out three rounds of MLR analysis on each strata, first modeling IBI based on instream physical and chemical variables and natural landscape controls; second, on natural landscape controls and measures of human land use measured at catchment and local riparian scales (riparian measures at catchment scale were not available); and third, on variables from all categories in Table 1.

6) Local influences on IBI were interpreted from the first round of MLR, human stressors from round two, and likely mechanisms of anthropogenic effects from round three. Natural landscape variables were available in all three rounds of MLR, allowing us to factor out or interpret remaining unscaled natural variation in the IBI.

7) The MLR predictor variable selection procedure was stepwise (forward-backward), including and retaining only variables with $p < 0.15$ (SAS 2004), and confirming best-model selection by examining all possible MLR models with less than or equal the number of resultant predictor variables. Only three of the predictor variables actually selected in the various MLR models using these variable selection criteria had $p > 0.05$, and most had $p < 0.01$. All final models were significant at $p < 0.01$; most at $p < 0.0001$. To avoid overfitting (overparameterization), we attempted to build models with fewer than $n/(5–10)$ predictor variables, where n is the number of sample sites in a particular modeled stratum. To further avoid overfitting, we also constrained the number of predictor variables so that the root mean square error (RMSE) of the regression model was generally larger than 7.0, which was the RMSE reported by Hughes et al. (2004) for same-stream repeat measurements of IBI. The RMSE reported by Hughes et al. is equivalent to the pooled standard deviation of site revisits (Kaufmann et al. 1999), representing a practical limit of a MLR model to associate variation of IBI in sites across the region with ancillary site data (Kaufmann et al. 1999). A regression model with RMSE substantially less than the RMSE for measurement variation would be suspected of overfitting.

RESULTS

Coast Range Stream Characteristics

The Coast Range survey yielded a sample of wadeable small to medium size, dilute, coldwater streams diverse in slope, bed substrate size, large dead wood loadings, canopy cover, and riparian vegetation structural complexity (Table 2). Areal discharge (discharge per unit drainage area), elevation, and channel slope tended to be higher, and water temperature and various measures of human disturbance tended to be lower, in streams draining volcanic basins. Though stream temperatures at the time of summer sampling ranged from 7.3°C to 25.3°C, only one site had a temperature in excess of 18°, and only several had temperatures less than 10°. There were no distinct temperature classes of streams, and most of the summertime stream temperature variation was associated with stream size, elevation, areal discharge, canopy cover and human disturbances. The survey captured 38 aquatic vertebrate species, but typically there were only 3–5 species in a given sample reach. Common or cosmopolitan aquatic vertebrates species included three salmonids, five cottids, two cyprinids, one petromyzontid, and four amphibians (Table 3). Tailed frog and coast range sculpin were the only two species that were strongly associated with volcanic lithology, whereas cutthroat trout, rainbow trout, torrent sculpin, riffle sculpin, and Pacific giant salamander were not strongly associated with either lithology. Red-legged frog, speckled dace, rough-skinned newt, redside shiner, prickly sculpin, and threespine stickleback were 3–4 times as likely to be found in streams draining sedimentary basins as in volcanic.

The IBI, summarizing the deviation of fish and amphibian taxa richness and composition

Table 2. Sample distributions of selected basin, channel, and riparian characteristics of 104 Coast Range stream reaches.

Variable	Overall median (range)	Sedimentary sites median (range)	Volcanic sites median (range)
Drainage area (km^2)	14 (0.09–160)	15 (0.09–160)	14 (0.41–119)
Discharge at summer sample time (m^3s^{-1})	0.067 (0–2.12)	0.033 (0–2.12)	0.013 (0.0003–1.16)
Areal discharge at summer sample time ($m^3s^{-1}km^{-2}$)	0.0033 (0–0.047)	0.0025 (0–0.047)	0.0095 (0.0002–0.020)
Elevation at sample reach (m)	121 (3–673)	105 (3–622)	251 (43–673)
Mean slope of reach water surface (%)	1.2 (0.08–22)	1.1 (0.08–9.4)	2.0 (0.40–22)
Mean wetted width (m)	5.6 (0–23)	4.9 (0–23)	6.1 (1.6–23)
Mean depth at thalweg (m)	0.36 (0–1.4)	0.35 (0–1.40)	0.41 (0.06–0.93)
Mean residual depth at thalweg (m)	0.17 (0.01–0.74)	0.17 (0.02–0.72)	0.15 (0.01–0.38)
Mean canopy cover–mid-channel (densiometer %)	78 (13–100)	78 (13–100)	76 (19–100)
Mean riparian tree + shrub + ground woody cover (%)	100 (1.7–181)	102 (1.7–181)	95 (37–181)
Mean riparian tree canopy cover (%)	40 (0.8–89)	34 (0.8–89)	44 (11–81)
Mean riparian tree canopy cover—trees > 0.3 m dbh (%)	22 (0–67)	22 (0–67)	24 (0.4–67)
Riparian human disturb.—(Prox-wt'd. obs per plot)	1.2 (0–5.2)	1.2 (0–5.2)	0.43 (0–2.6)
Road density in basin (km/km^2)	1.6 (0–5.9)	1.6 (0–5.9)	1.5 (0–3.5)
Large wood vol. (m^3 wood / m^2 bank-full channel area)	0.022 (0–1.9)	.023 (0–1.9)	0.017 (0.0006–0.57)
Substrate fines (% < 0.6 mm diameter)	7 (0–100)	18 (0–100)	0 (0–32)
Substrate sand + fines (% < 2 mm diameter)	29 (0–100)	38 (0–100)	9.1 (0–58)
Substrate % bedrock	3.6 (0–69)	1.8 (0–60)	5.2 (0–69)
Substrate D_{gm}—geom mean diameter (mm)	10 (0.008–1,040)	3.8 (0.008–1,040)	57 (0.75–950)
LRBS = Log_{10} of relative bed stability = $\log(D_{gm}/D_{cbf})$	–0.67 (–4.1– +1.23)	–1.1 (–4.1–+1.23)	–0.26 (–1.50–+1.06)
Conductivity (μS/cm)	77 (29–493)	77 (29–493)	76 (45–139)
Water temp. at summer sample time (degrees C)	13 (7–25)	14 (7–25)	12 (7–14)
pH	7.2 (5.5–8.1)	7.2 (5.5–8.1)	7.2 (6.4–7.8)
Acid neutralizing capacity (μeq/L)	498 (79–1,680)	440 (79–1,680)	579 (240–1,180)
Dissolved organic carbon (mg/L)	1.6 (0.5–13)	2.8 (0.5–13)	1.0 (0.5–1.9)
Dissolved oxygen (mg/L)	9.6 (1–12)	9.3 (1–11)	10 (8.6–12)
Chloride (μeq/L)	116 (0.8–2,820)	124 (0.8–2,820)	85 (20–240)
Total nitrogen (μg/L as N)	260 (38–3,200)	316 (60–3,200)	158 (38–1,200)
Total phosphorus (μg/L as P)	20 (5–580)	30 (5–580)	10 (5–50)
Turbidity (NTU)	2.0 (0.5–178)	3.0 (0.5–178)	1.0 (0.5–6.0)

Table 3. The 19 most cosmopolitan fish and amphibian species found in wadeable Coast Range streams. Note species with apparent affinity for sedimentary[a] versus volcanic[b] lithology or their correlates.

Common name	Genus-species	% of sample reaches			Mean
		Overall	Sed.	Volc.	Count/site
Cutthroat trout	*Oncorhynchus clarkii*	61	65	52	23
Rainbow trout	*O. mykiss*	55	52	62	62
Reticulate sculpin[a]	*Cottus perplexus*	49	58	28	63
Coho salmon[a]	*O. kisutch*	48	52	38	38
Pacific lamprey[a]	*Lampetra tridentata*	46	52	31	15
Torrent sculpin	*C. rhotheus*	24	25	24	65
Pacific giant salamander	*Dicamptodon tenebrosus*	24	28	17	10
Riffle sculpin	*C. gulosus*	20	22	17	68
Red-legged frog[a]	*Rana aurora*	18	23	07	4
Speckled dace[a]	*Rhinichthys osculus*	17	22	07	36
Rough-skinned newt[a]	*Taricha granulosa*	17	20	07	11
Tailed frog[b]	*Ascaphus truei*	16	09	34	14
Redside shiner[a]	*Richardsonius balteatus*	12	16	03	36
Coastrange sculpin[b]	*C. aleuticus*	12	09	21	32
Prickly sculpin	*C. asper*	12	16	03	24
Threespine stickleback[a]	*Gasterosteus aculeatus*	09	12	03	13

compared with reference values, ranged from 13 to 94 (interquartile range = 43–66) in the whole region. Low values were more prevalent in streams draining sedimentary versus volcanic terrain (Figure 3A). Streams with low disturbance (high riparian condition, high watershed + riparian condition, and low catchment road densities) were found in both lithologies, but high anthropogenic disturbance was more common in sedimentary terrain (Figures 3B, C, D). Human activities on the gentler, more biologically productive sedimentary terrain began earlier, and have been more intensive and widespread than those on the steeper, less productive volcanic terrain.

Pattern of IBI Association with Individual Landscape, Disturbance, and Habitat Variables

Scaling the index of biotic integrity metrics by catchment area and using percentage metrics virtually eliminated correlations with catchment area, as well as stream slope, elevation and bed shear stress (Hughes et al. 2004). Consequently, we did not show IBI correlations with those variables in Table 4, but did make them available to MLR models. Considering the natural landscape control variables, IBI was negatively associated with catchment lithology regionally and within both catchment size strata, indicating a pattern of lower IBI values in streams draining sedimentary lithology. Lithology was represented by LITH, an indicator variable with values of 0 for volcanic and 1 for sedimentary rock. In this region, volcanic rock is more resistant to weathering than the softer sedimentary sandstones and siltstones (Pater et al. 1998). In addition, IBI was positively associated with low-flow areal discharge, LQsp, which gives a rough indication of groundwater contribution to low flow. LQsp tended to be higher in volcanic streams, and was also positively correlated with LRBS ($r = 0.42$, $p < 0.0001$) and negatively correlated with W1_HALL ($r = -0.40$, $p < 0.0001$), the measure of local riparian disturbances across the region (Table 2). (The negative correlation between LQsp and W1_HALL was strongest in small volcanic streams, with $r = -0.70$, $p = 0.002$).

In the whole region, IBI was positively correlated with WRCond and RCond, indicators of basin and riparian condition, and negatively related to Rd_DenKM and W1_HALL, indicators

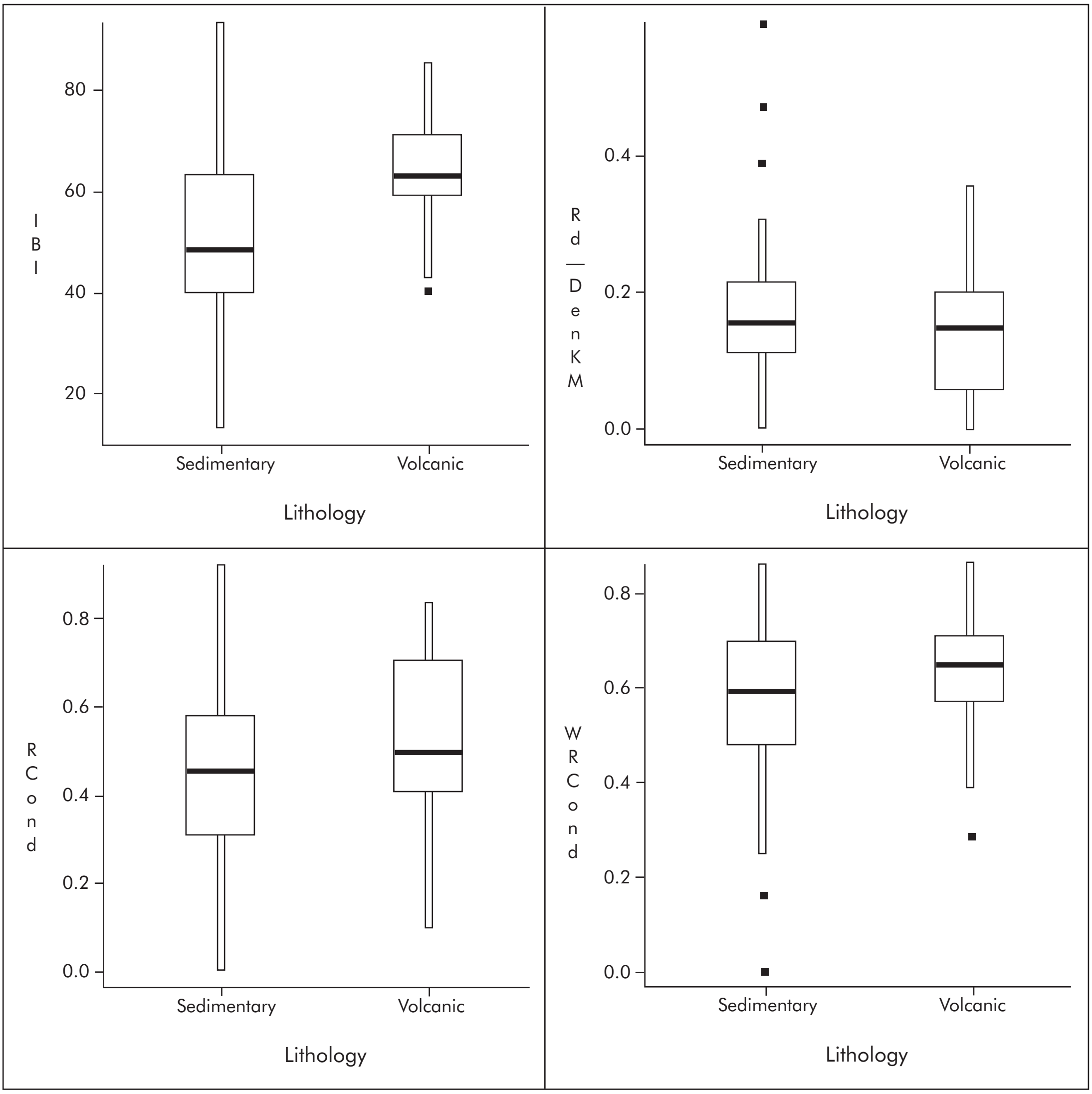

Figure 3. Ecological condition of Pacific Northwest Coast Range streams, and indicators of human disturbance versus watershed lithology: (a) index of biotic integrity of stream fish and amphibians (IBI), (b) catchment road density (Rd_DenKM), (c) riparian condition (RCond), and (d) watershed+riparian condition (WRCond). Boxes depict medians and quartiles; whiskers denote ranges; points are outliers deviating more than 2 SD from the mean.

of basin and riparian disturbance (Table 4). Correlations with these measures of human disturbance tended to be higher within the smaller streams and the volcanic lithology strata. However, the negative association between IBI and the product (interaction) of basin road density and riparian disturbances reveals IBI declined with human disturbance in each lithology, but generally IBI was lower and more variable in sedimentary streams (Figure 4).

In the region overall, the strongest associations between IBI and in-channel physical-chemical habitat were with measures of streambed particle size (Table 4), represented by the percentage of silt (%FN) and the index of median particle size deviation from reference

Table 4. Spearman rank-order correlations (r) of fish/amphibian stream IBI with potential controlling variables in Coast Range streams (bold denotes r-values $\geq$ 0.40; asterisk denotes Bonferroni-corrected p < 0.05). Drainage area strata were small = 0.09–<15 km^2 and large= 15–160 km^2.

	Whole	Drainage area		Lithology		Sedimentary		Volcanic	
	region	Large	Small	Sedi.	Volc.	Large	Small	Large	Small
Variables	(n = 98)	(n = 48)	(n = 50)	(n = 69)	(n = 29)	(n = 35)	(n = 34)	(n = 13)	(n = 16)
%FN	**–0.67***	**–0.56***	**–0.73***	**–0.55***	**–0.40**	**–0.47**	**–0.58***	–0.09	**–0.53**
%BDRK	0.28	0.12	**0.46***	**0.40***	**–0.44**	0.24	**0.55***	**–0.52**	**–0.40**
LRBS	**0.58***	**0.48***	**0.71***	**0.53***	0.11	**0.43**	**0.62***	–0.13	0.21
EX_FN	–0.28	–0.08	**–0.43***	–0.39*	–0.30	–0.27	**–0.44**	–0.29	**–0.43**
RPGT75	0.16	0.26	0.08	0.18	–0.05	0.33	–0.04	–0.34	0.18
LV1W_msq	–0.12	0.06	–0.25	–0.14	–0.08	0.04	–0.24	**0.45**	**–0.43**
XFC_UCB	**–0.42***	**–0.48***	–0.37	–0.37*	–0.08	**–0.52***	–0.22	0.15	–0.21
XFC_BRS	**–0.40***	–0.36	**–0.41**	–0.33	–0.19	**–0.41**	–0.23	0.32	**–0.55**
LNTL	–0.34*	**–0.41**	–0.32	–0.21	–0.26	**–0.47**	0.00	0.07	**–0.58**
LPTL	**–0.47***	**–0.43***	**–0.50***	–0.32	–0.13	–0.35	–0.29	**0.44**	**–0.40**
TEMPSTRM	–0.30*	–0.39	–0.24	–0.15	–0.33	–0.36	0.04	0.02	**–0.44**
CONDUCT	–0.04	–0.08	–0.03	–0.18	**0.45**	–0.22	–0.16	**0.53**	**0.42**
RCond	0.31*	0.33	0.29	0.30	0.12	0.38	0.19	0.39	–0.02
W1_Hall	–0.39*	–0.35	**–0.43**	–0.28	**–0.41**	–0.32	–0.28	–0.06	**–0.63**
XCMGW	0.15	0.27	0.07	0.22	–0.08	**0.40**	0.06	0.35	–0.36
Rd_DenKM	–0.35*	0.02	**–0.54***	–0.25	**–0.72***	0.15	**–0.51***	**–0.73***	**–0.70***
WRCond	0.34*	0.30	0.35	0.29	0.32	0.32	0.24	**0.55**	0.15
LQsp	**0.47***	0.35	**0.56***	**0.41***	0.19	0.29	**0.51**	–0.21	0.37
Elev	0.32	0.38	0.31	0.18	0.19	0.31	0.11	0.10	0.07
LITH	**–0.42***	**–0.42***	**–0.42***	na	na	na	na	na	na

conditions (LRBS). These correlations were stronger in small streams than in large ones, and stronger in sedimentary than in volcanic lithology. Correlation of IBI with LRBS was low in the volcanic strata, where bedrock and excess silt were both negatively correlated with IBI (explaining in part the lack of association with LRBS, which increases with %BDRK and decreases with EX_FN). In contrast, IBI showed strong positive correlation with %BDRK and strong negative correlation with EX_FN, and therefore strong positive correlation with LRBS, in small sedimentary streams.

IBI was negatively associated with streamwater phosphorus and nitrogen concentrations, undercut banks, and brush cover in the whole region. This pattern was true of all strata except large volcanic streams, where correlations with these variables were weaker or reversed. Total phosphorus was uncorrelated with catchment area or road density, but was negatively correlated (Spearman $r = –0.43$, $p < 0.0001$) with local riparian condition (RCond). These phosphorus correlations were consistent with dominant anthropogenic sources, or anthropogenic mobilization of natural sources. IBI also showed a weak to moderate negative correlation with water temperature in the entire region and all strata, with the strongest correlation in small volcanic streams ($r = –0.44$, $p > 0.05$).

Regression Modeling of IBI from Landscape, Disturbance, and Habitat Variables

Whole region.—The best MLR model predicting IBI from in-channel physical-chemical habitat variables and landscape controls was dominated by a strong positive association with relative bed stability (LRBS), our inverse indicator of anthropogenic sedimentation (Table 5A). It included a moderately strong positive association with areal discharge, and moderate amounts of variance explained by elevation (positive term)

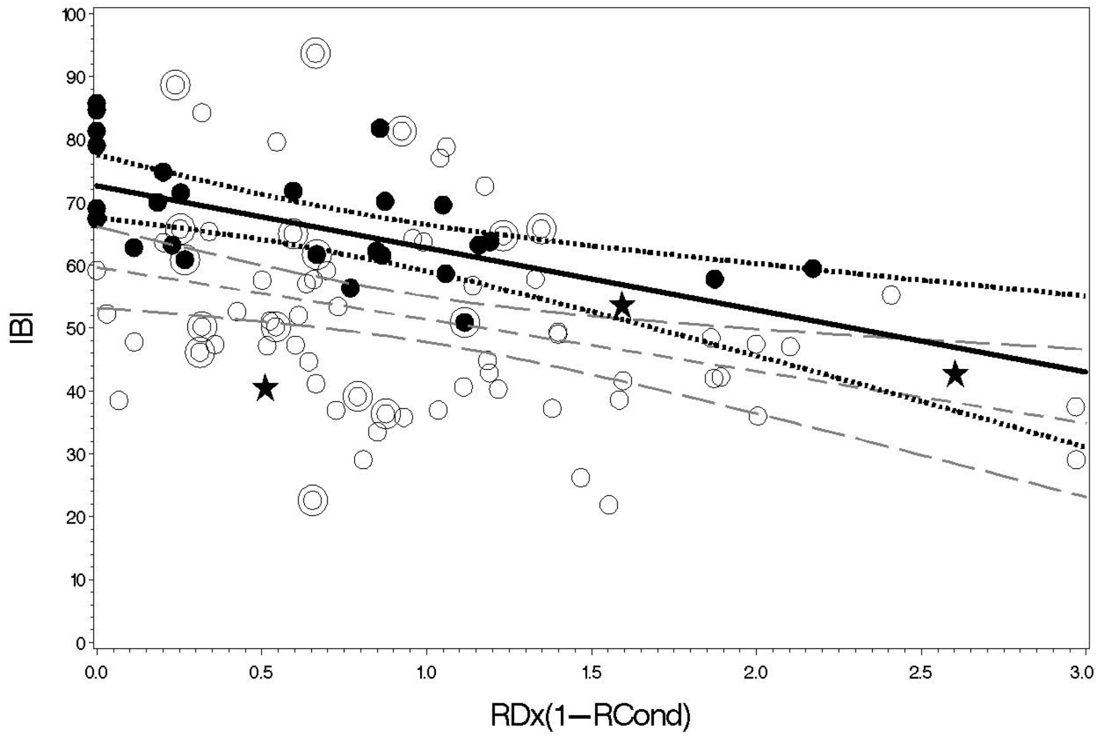

Figure 4. Stream reach IBI versus the interaction between watershed and riparian disturbance, represented by RDx(1-RCond). Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock, and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The regression line and its 95% confidence limits about the mean are shown separately for volcanic reaches: (IBI= 72.6 – 9.84 RDx(1-RCond), with R^2 = 0.37, RMSE = 9.0, and $p < 0.0005$) and sedimentary reaches: (IBI= 59.7 – 8.27 RDx(1-RCond), with R^2 = 0.12, RMSE = 14.9, and $p < 0.0039$).

and the areal percent of undercut banks (negative). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the model R^2 declined slightly, but the terms were similar—the LRBS term in the first model was replaced by the interaction of basin and riparian disturbances and the indicator variable for lithology (Table 5B). When all three types of variables were available as potential predictors, the resultant best model was the same as the first model, but included a negative term for the interaction between basin and riparian disturbance (Table 5C).

All three whole-region models explained about half the regional variance in IBI. Not surprisingly, the RMSE's of these models (11.6–12.5 IBI units) did not suggest that they were overfit, as they were considerably larger than the RMSE of repeat sampling (7.0) reported by Hughes et al. (2004). We suspected that other undefined variables may have accounted for patterned variation across the region, or that disturbance processes were not homogeneous in various classes of streams in the region. Therefore, we subsequently modeled small and large sedimentary streams and volcanic streams as separate strata to describe possibly different patterns of association of IBI with explanatory variables. The small sample size of the volcanic lithology stratum (29) precluded substratification by basin size; as regression models with more than one or two predictor variables would not be advisable for

Table 5. Results of multiple linear regression predicting IBI in all Coast Range wadeable streams.

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = *f* (in-channel physical-chemical habitat and landscape controls):						
Intercept	+74.7	5.25	–	–	–	<0.0001
LRBS	+5.72	1.28	0.335	0.335	0.335	<0.0001
LQsp	+6.13	2.08	0.246	0.098	0.433	0.0043
Elev	+0.025	0.009	0.106	0.040	0.474	0.0185
X_UCB	–58.0	29.48	0.159	0.024	0.498	0.0527
Summary of fit: total df = 85 RMSE = 12.2 Prob > F < 0.0001						
b) IBI = *f* (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+80.22	5.52	–	–	–	<0.0001
RDx(1-RCond)	–8.60	2.04	0.201	0.201	0.201	<0.0001
LQsp	+6.78	2.13	0.198	0.133	0.334	0.0020
Elev	+0.0235	0.0103	0.097	0.071	0.404	0.0243
LITH	–5.67	3.41	0.172	0.019	0.423	0.1004
Summary of fit: total df = 88 RMSE = 12.5 Prob > F < 0.0001						
c) IBI = *f* (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+76.45	5.16	–	–	–	<0.0001
LRBS	+3.92	1.35	0.296	0.296	0.296	0.0047
LQsp	+5.22	2.04	0.209	0.095	0.391	0.0124
RDx(1-RCond)	–6.30	2.03	0.205	0.054	0.444	0.0026
Elev	+0.026	0.009	0.094	0.046	0.491	0.0046
X_UCB	–62.81	28.37	0.170	0.030	0.521	0.0297
Summary of fit: total df = 84 RMSE = 11.6 Prob > F < 0.0001						

the resultant substrata, each containing about half of the sample sites.

Streams draining small catchments with sedimentary lithology.—When we considered in-channel physical-chemical habitat and natural landscape variables (no human disturbance variables) as potential predictors, LRBS dominated the model (partial $R^2 = 0.52$) and, combined with %BDRK, these two variables alone explained almost 60% of the variance in IBI (Table 6A). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the model R^2 declined greatly (0.27), and only the negative basin-riparian interaction term RDx(1-RCond) was significant (Table 6B). When we included all three types of variables as potential predictors, MLR yielded a strong three variable model ($R^2 = 0.74$) in which the interaction of road density and riparian condition replaced LRBS, and a strong positive term remained for %BDRK (Table 6C). As did the first model (Table 6A), this model also included a positive term for areal discharge. The model RMSEs (10.2–16.4) were well above 7.0, so did not suggest overfitting.

Streams draining large catchments with sedimentary lithology.—As observed for small streams in sedimentary lithology, a positive association with LRBS was the major term in the best model built from in-channel physical-chemical habitat and natural landscape variables alone (Table 7A). Additional moderate negative association with water temperature, moderate positive association with the frequency of deep residual pools, and weak association with elevation yielded a final model explaining 61% of the regional variance of IBI in large streams draining sedimentary lithology. When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables (Table

Table 6. Results of multiple linear regression predicting IBI in Coast Range wadeable streams with sedimentary lithology and drainage areas less than 15 km^2.

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = *f* (in-channel physical-chemical habitat and landscape controls):						
Intercept	+78.77	9.72	–	–	–	<0.0001
LRBS	+6.60	3.25	0.518	0.518	0.518	0.0542
%BDRK	+0.96	0.37	0.415	0.064	0.582	0.0168
LQsp	+8.06	3.69	0.187	0.072	0.654	0.0393
Summary of fit: total df = 26 RMSE = 12.4 Prob > F < 0.0001						
b) IBI = *f* (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+62.65	5.10	–	–	–	<0.0001
RDx(1-RCond)	–11.4	3.87	0.268	0.268	0.268	0.0068
Summary of fit: total df = 25 RMSE = 16.4 Prob > F = 0.0068						
c) IBI = *f* (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+78.74	8.60	–	–	–	<0.0001
%BDRK	+1.65	0.24	0.429	0.429	0.429	<0.0001
RDxRCond	–11.83	2.94	0.064	0.182	0.611	0.0006
LQsp*	+9.98	3.03	0.106	0.129	0.740	0.0033
Summary of fit: total df = 25 RMSE = 10.2 Prob > F < 0.0001						

*LQsp replaced LRBS in Stepwise MLR (LRBS was first entry with Partial R^2 = 0.45 and P = 0.0002).

7B), the R^2 of the best model was considerably reduced (0.40). About half of the explained variance was attributed to the interaction of catchment disturbance and riparian condition (positive term), and the other half to the combination of areal discharge and elevation (both positive terms). When all three types of variables were available as potential predictors, the resultant best model was identical to that without the human disturbance variables, suggesting that the first model was not missing habitat variables correlated with human disturbances (compare Tables 7C and 7A). The model RMSE of 9.4 IBI units for the most complex model in this stratum was greater than the RMSE of sampling variability (7.0), giving no suggestion of overfitting.

Streams draining catchments with volcanic lithology.—When we considered only in-channel physical-chemical habitat and natural landscape variables as potential predictors, volcanic streams differed from the sedimentary streams in having excess silt (EX_FN), rather than LRBS, as the first predictor variable. Additional moderate associations with conductivity and areal discharge (both positive), and percent bedrock (negative) produced a best model explaining 60% of the variance in IBI across streams draining volcanic lithology in the region (Table 8A). When basin and riparian human disturbance variables were substituted for physical-chemical habitat variables, the best model was dominated by a strong negative association with catchment road density, with a minor positive term for areal discharge (Table 8B). When all three types of variables were available as potential predictors, the resultant best model was identical to the first model but with an additional strong negative association with catchment road density (compare Tables 8A and 8C). Road density explained 47% of the IBI variance, reducing the partial R^2 values of all the other predictor variables from the levels they had contributed to explaining IBI variation in the absence of road density. The RMSE values of the two more complex models were 6.3 and 5.8 IBI units (Tables 8A and 8C). Even though the tests for inclusion of all predictor variables (P-values

Table 7. Results of multiple linear regression predicting IBI in Coast Range wadeable streams with sedimentary lithology and drainage areas ≥ 15 km².

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = *f* (in-channel physical-chemical habitat and landscape controls):						
Intercept	+73.1	10.38	–	–	–	<0.0001
LRBS	+5.88	1.51	0.232	0.232	0.232	0.0005
TEMPSTRM	–2.02	0.63	0.141	0.171	0.403	0.0034
RPGT75	+4.68	1.31	0.120	0.139	0.542	0.0012
Elev	+0.039	0.017	0.122	0.070	0.612	0.0295
Summary of fit: total df = 33 RMSE = 9.4 Prob > F < 0.0001						
b) IBI = *f* (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+57.33	8.93	–	–	–	<0.0001
RDxRCond	+11.2	5.8	0.190	0.190	0.190	0.0628
LQsp	+7.50	2.72	0.121	0.088	0.278	0.0097
Elev	+0.053	0.021	0.124	0.119	0.397	0.0190
Summary of fit: total df = 34 RMSE = 11.4 Prob > F = 0.0012						
c) IBI = *f* (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+73.1	10.38	–	–	–	<0.0001
LRBS	+5.88	1.51	0.232	0.232	0.232	0.0005
TEMPSTRM	–2.02	0.63	0.141	0.171	0.403	0.0034
RPGT75	+4.68	1.31	0.120	0.139	0.542	0.0012
Elev	+0.039	0.017	0.122	0.070	0.612	0.0295
Summary of fit: total df = 33 RMSE = 9.4 Prob > F < 0.0001						

Table 8. Results of multiple linear regression predicting IBI in Coast Range wadeable streams with volcanic lithology.

Variable	Estimate	Std. error	Indep. R^2	Partial R^2	Model R^2	Prob > F
a) IBI = *f* (in-channel physical-chemical habitat and landscape controls):						
Intercept	+76.33	6.95	–	–	–	<0.0001
EX_FN	–0.944	0.202	0.284	0.284	0.284	0.0001
CONDUCT	+0.185	0.0423	0.220	0.175	0.459	0.0002
LQsp	+11.07	2.90	0.131	0.136	0.595	0.0009
%BDRK	–0.300	0.0836	0.069	0.145	0.604	0.0016
Summary of fit: Total df = 27 RMSE = 6.3 Prob > F < 0.0001						
b) IBI = *f* (basin-riparian anthropogenic influences and landscape controls):						
Intercept	+88.84	7.95	–	–	–	<0.0001
Rd_DenKM	–6.60	1.44	0.474	0.474	0.474	0.0001
LQsp	+6.44	3.76	0.131	0.055	0.530	0.0987
Summary of fit: Total df = 27 RMSE = 8.1 Prob > F < 0.0001						
c) IBI = *f* (physical-chemical habitat, landscape controls, basin-riparian anthropogenic influences):						
Intercept	+79.84	6.66	–	–	–	<0.0001
Rd_DenKM	–2.77	1.28	0.474	0.474	0.474	0.0420
EX_FN	–0.743	0.209	0.284	0.071	0.546	0.0018
CONDUCT	+0.146	0.043	0.220	0.060	0.606	0.0027
LQsp	+9.47	2.79	0.131	0.082	0.689	0.0026
%BDRK	–0.254	0.081	0.069	0.097	0.786	0.0046
Summary of fit: Total df = 27 RMSE = 5.8 Prob > F < 0.0001						

= 0.0001–0.0420) and the final models themselves ($p < 0.0001$) were highly significant, the model RMSE values were lower than the RMSE of repeat measurement variance (7.0), and the ratio of parameters to sample size was 5–7, suggesting marginal overfitting. We therefore suggest interpreting the minor contributors to these models in the volcanic stratum with caution.

IBI, Bed Stability, and Disturbance Relationships

In contrast to the plot of IBI versus human disturbance (Figure 4), a plot of IBI versus LRBS (Figure 5) shows no clear distinction in the response to disturbance between lithologies, except that both IBI and LRBS were higher in volcanic streams. The contrasting relationship of IBI to %BDRK is also illustrated in Figure 5, where all volcanic sites with more than 25% bedrock or EX_FN greater than 5% have lower than expected IBI values, given their LRBS. However, the relationship of LRBS to the product (interaction) of basin road density and riparian disturbances (Figure 6) reveals LRBS declined with human disturbance in each lithology, with lower values for sedimentary streams, just as was observed for IBI in Figure 4. Most of the least disturbed streams (by this measure) had LRBS ± 0.5, and LRBS generally declined more steeply in sedimentary streams (more erodible lithology) than in volcanic streams (more resistant to erosion

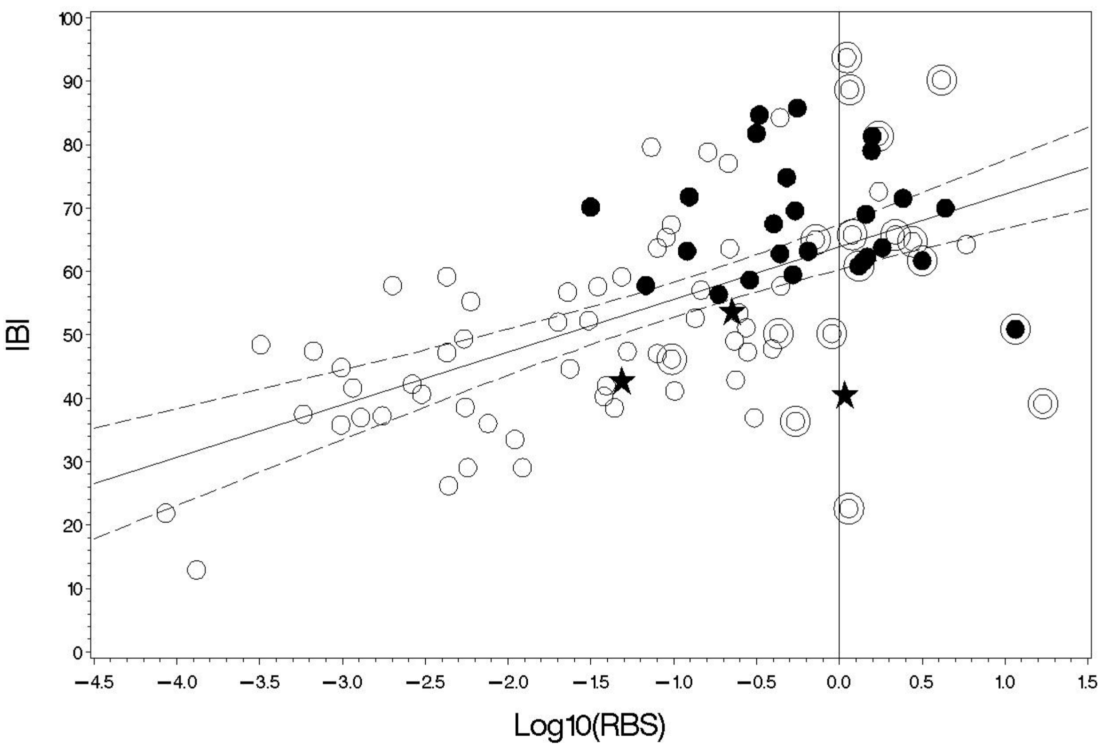

Figure 5. Stream reach IBI versus $\log_{10}$ of relative bed stability at bank-full flows (RBS). Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The vertical line originating at 0.0 is the value of RBS indicating $D_{gm} = D_{cbf}$. Regression lines and their 95% confidence limits about the mean were calculated for all sample reaches (IBI = 63.85 + 8.28 x LogRBS), with $R^2 = 0.35$, RMSE = 13.6, and $p < 0.0001$. The regression without circled and starred points is IBI = 67.39 + 9.95 x LogRBS, with $R^2 = 0.49$, RMSE = 11.5, and $p < 0.0001$.

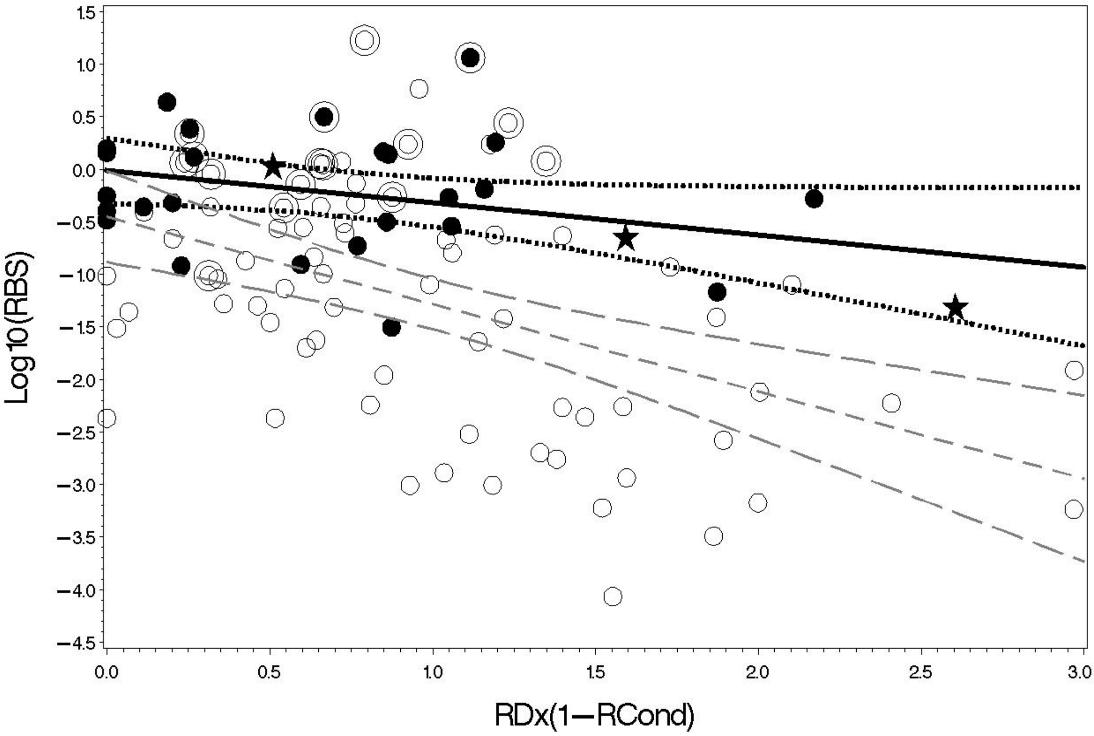

Figure 6. Log_{10} of stream reach relative bed stability (RBS) versus the interaction between watershed and riparian disturbances, represented by RDx(1-RCond). Open circles denote sedimentary catchments; black dots and stars are volcanic catchments. Circled black dots and double circles denote reaches with bed surface greater than 25% bedrock, and black stars are volcanic reaches with more than 5% excess silt (EX_FN). The regression line and its 95% confidence limits about the mean are shown separately for volcanic reaches (LRBS = 0.015 – 0.305 RDx(1-RCond), with $R^2 = 0.13$, RMSE = 0.57, and $p < 0.0586$) and sedimentary reaches (LRBS = –0.451 – 0.831 RDx(1-RCond), with $R^2 = 0.22$, RMSE = 1.03, and $p < 0.0001$).

and weathering). Streams with more than 25% bedrock were associated with moderate levels of basin-riparian disturbance. LRBS, in the formulation by Kaufmann et al. (1999), increases with bedrock exposure. Therefore, variation in the response of IBI to LRBS increases when bedrock is present, because the apparent response of IBI to bedrock can be positive or negative according to the geomorphic setting of a stream.

LQsp, the log transformed ratio of summer low flow discharge divided by drainage area, appeared as a moderate to minor predictor of IBI in many of the models in various strata, always as a positive term, and frequently along with positive elevation, negative temperature, or positive stream water electrical conductivity terms. LQsp was not related to the date of sampling during the summer low flow period ($r = 0.09$, $p = 0.39$). We cautiously interpret it to be a measure of the groundwater contribution to base flow. However, its expected regional association with lower water temperatures ($r = –0.41$, $p < 0.0001$) was not evident within each lithology stratum, nor was it correlated with conductivity ($r = –0.11$, $p = 0.32$). It was generally higher in volcanic than in sedimentary lithology (Table 2) because of its fractured nature and greater permeability (Hicks 1989). Even though rainfall and runoff are probably higher in volcanic drainages because they tend to include higher elevations, LQsp was not correlated with elevation overall ($r = 0.014$, $p = 0.18$) or within separate lithologies. Interestingly, LQsp was negatively correlated with riparian disturbances ($r = -0.40$, $p < 0.0001$), particularly in volcanic lithology ($r = -0.60$, $p = 0.0006$). This association might be explained by anthropogenic augmentation of winter runoff. Higher runoff per unit precipitation would reduce groundwater recharge, and therefore reduce summer base flow, when precipitation is sparse. This possible anthropogenic connection is highly conjectural at this time, but merits further investigation.

The final general pattern evident in the MLR models was the contrasting role of bedrock between the two lithologies. Bedrock influenced IBI positively in streams draining sedimentary lithology but negatively in volcanic streams. In sedimentary streams, bedrock was commonly observed as a major component together with high percentages of sand and silt in low gradient streams where boulders, cobbles, and coarse gravel were relatively uncommon. This pattern is consistent with relatively rapid weathering of sandstone and siltstone to loose sand and silt. In many fine bedded streams, bedrock may be a positive influence on structural complexity, as it can form deep pools, particularly where large woody debris is sparse or too small to be stable or hydraulically influential (Kaufmann 1987). In volcanic streams, large proportions of bedrock were found in the steepest and coarsest-bedded streams, and its presence may be an indicator of past catastrophic scouring by debris torrents (Swanson and Dyrness 1975; Kaufmann 1987), naturally occurring phenomena with spatial and temporal frequency augmented by human activities.

DISCUSSION

Few studies in the Pacific Northwest have been designed to address specific relationships between changes in habitat attributes and structure of fish assemblages (Bisson et al. 1992; Spence et al. 1996); even fewer (e.g., Herger et al. 2003; Hughes et al. 2004) have addressed such questions on a regional scale. Although not specifically designed to investigate the influence of habitat on aquatic vertebrate assemblages, the statistical survey data we analyzed allowed a regionally representative description of these assemblages in the population of 23,700 km of wadeable first- through third-order Coast Range streams. Further, because of the ancillary physical, chemical, and landscape data collected at the same locations, we were able to examine the strength and character of associations between biotic assemblages and potential causes and influences. Though such data do not demonstrate cause, they provide weight-of-evidence concerning the dominance of processes and influences in the region.

Although the strongest single predictors of IBI were raw measures of percent fine streambed particles, we did not include these in the variables available to MLR because a substantial proportion of their regional variance was associated with channel slope and stream size. The strongest predictor variables in MLR models built from in channel physical-chemical data and natural landscape controls for the whole region and all substrata were indicators of anthropogenic sedimentation, calculated by scaling substrate size by bed shear stress (which incorporates slope and stream size). In the whole region and in both stream size classes draining sedimentary lithology, the scaled substrate size measure was LRBS (which we interpret here as an inverse indicator of anthropogenic sedimentation). In volcanic lithology, LRBS was not a good predictor of IBI. Instead, the scaled substrate size measure EX_FN was the best in-channel predictor, with percent bedrock as an additional negative term. Because bedrock and silt influence LRBS in opposite directions, the utility of LRBS as a predictor of IBI was "neutralized" in volcanic streams. These results also suggest that, in the naturally coarser-bedded volcanic streams, general fining of streambeds was less deleterious than accumulation of small amounts of silt that do not substantially affect the mean substrate diameter (as we usually measure it). Weathering of basalt in this region generally proceeds from boulders to gravel, then to silt, without generating much sand. This pattern is in contrast to the weathering of sandstones, which degrade quickly from bedrock and boulders to abundant silt, sand and fine gravel with less in the gravel and cobble size fraction.

When human disturbances and natural landscape controls were presented to MLR, road density alone, riparian condition (RCond), or the interaction of road density with riparian disturbance, {RDx(1-RCond)} were the major predictors of IBI in the whole region or in any single stratum. When in-channel variables were presented at the same time as human disturbances and landscape controls, road density or its riparian interactions either replaced or were replaced by an indicator of anthropogenic sedimentation (LRBS as inverse indicator in sedimentary lithology and EX_FN in volcanics). This pattern was due to the covariance among IBI, sedimentation indices, and human disturbances.

Reporting on results of the same survey data we examined in this chapter, Herger et al. (2003) found weak correlations between aquatic vertebrate composition and human disturbances at the landscape and local scales, reporting that assemblages were primarily structured by natural physical and biogeographical gradients. They suggested scaling assemblage metrics and combining them further into an IBI to more clearly reveal the impacts of human activities on streams in the region. Hughes et al. (2004) developed an IBI for the Coast Range ecoregion that confirmed those expectations. For the region as a whole, they found that the IBI, which includes a set of eight aquatic vertebrate assemblage characteristics, was negatively related to riparian disturbances and basin road density. Within the channel, they found a relatively strong positive association of IBI with LRBS, an inverse measure of excess fine sediments that we found to be negatively associated with the anthropogenic disturbances (Figure 6). Hughes et al. (2004) reported that the IBI was significantly (negatively) correlated with a number of different estimates of anthropogenic disturbance, with IBI scores significantly higher in minimally disturbed reference sites than in randomly-selected sites. Increases in the percentages of coolwater fish and amphibian species, nonnative species, and tolerant individuals were also associated with human disturbances. Conversely, declines in the proportions of coldwater fish and amphibian species, the number of size- (age-) classes, and the species richness and numeric abundance of native coldwater species were also associated with human disturbance.

Hughes et al. (2004) did not examine the relationships of their IBI to possible controls within the different stream sizes or lithologies that we address in this chapter. However, our results for the region as a whole, examining habitat and landscape associations with the same IBI, are very similar to their reported positive correlations of IBI with local reach-scale bed stability, instream cover, and the cover and structural complexity of riparian vegetation. We also agree with their findings that IBI was negatively correlated with local reach-scale fine sediment and riparian human disturbances, and with catchment road density. Their findings and ours are consistent with those of Reeves et al. (1993), who showed reduced diversity in juvenile anadromous salmonid assemblages in selected Oregon Coast Range basins with high levels of timber harvest and road construction.

Some studies in the Pacific Northwest have shown higher salmonid and salamander density and biomass in streams subject to clear-cutting than in old-growth reaches and attributed these differences to higher primary productivity (Murphy et al. 1981; Hawkins et al. 1983). Although these studies also reported increases in macroinvertebrate diversity, they did not report findings on age structure or diversity of the entire aquatic vertebrate assemblage. Other studies (Bisson and Sedell 1984; Bisson et al. 1992) report similar increases in salmonid biomass and abundance with logging disturbances, but also reported that streams subjected to logging and channel cleaning lacked age-class diversity, consistent with our results and those of Reeves et al. (1993).

Our analysis of factors controlling IBI scores extended beyond that of Hughes et al. (2004) by strengthening the weight-of-evidence supporting anthropogenic effects (particularly from sediment) and by examining differences in potential controls as a function of stream basin size and lithology. Streambed particle size and channel morphology are influenced strongly by catchment geology (Hack 1973). Volcanic rock (generally basalt), relatively hard and resistant to weathering, underlies the steeper terrain of this region (Pater et al. 1998). Though the underlying rock is resistant to erosion, and delivery of sediment to streams by surface erosion is minor, this steep terrain is subject to infrequent, but catastrophic mass-failures (shallow, rapid landslides) that can deliver large amounts of sediment and wood to streams (Swanson and Dyrness 1975; Dietrich and Dunne 1978). These events sometimes trigger debris torrents that can scour parts of the stream network to bedrock, while depositing large amounts of debris downstream. By contrast, much of the less steep terrain in the region is underlain with softer, more erodible sedimentary rock, which generates more fine sediment (sand, silt, clay), than does volcanic rock. The modes of delivery are similar in sedimentary catchments (Benda et al. 1998, 2003), though slower-moving, deep-seated earth flows and rotational failures sustain large inputs of fine sediments over longer periods of time (Swanston 1991). The stream margins and valley bottoms in sedimentary terrain are large sediment reservoirs held intact by the roots of streamside vegetation. As a result, and in contrast with streams in volcanic terrain in this region, activities that damage riparian vegetation in sedimentary basins result in larger chronic inputs of fine sediment.

Kaufmann and Larsen (unpublished) reported that streams draining soft sedimentary lithology showed greater apparent sedimentation response to disturbance than did those draining basins underlain by hard basalt (volcanic). Furthermore, they showed that RBS was likely to be lower in smaller and lower gradient streams than in larger or higher gradient streams subject to apparently equal levels of anthropogenic stress. Kaufmann and Larsen (unpublished) reported stronger negative correlations between land disturbance and the numerator (substrate mean diameter) of the RBS ratio than with its denominator (critical diameter). They argued that this pattern strongly suggested that land use has augmented sediment supplies and increased streambed fine sediments in Coast Range wadeable streams.

Generally, we found higher IBI scores in volcanic than in sedimentary terrain, but this resulted from greater landscape disturbance and greater sedimentation response to that disturbance in streams draining sedimentary lithology. We observed high IBI values in minimally disturbed streams in both lithologies, making it unlikely that there is an inherent difference in biotic integrity as measured by the highest IBI scores. The generally lower IBI values in streams of sedimentary lithology likely resulted because there are more disturbed basins and streams in the more productive sedimentary lithology. We found that IBI in streams draining steep catchments of volcanic lithology were more negatively associated with catchment disturbances than with riparian disturbances (Table 4). However, the negative association of IBI with riparian disturbance (W1_Hall) in volcanic catchments was stronger in smaller streams than in larger ones (Table 4). In sedimentary basins, by contrast, the negative association of IBI was stronger with catchment disturbance in small streams than large streams, but its negative association with riparian disturbance was stronger in large streams.

Kaufmann and Larsen (unpublished) and Scott (2002) reported, respectively, higher correlation of RBS and percent substrate less than 2 mm with riparian disturbance in streams of sedimentary lithology, but higher correlation with catchment disturbances (road density) in streams of volcanic lithology. These are the same patterns that we observed between IBI and disturbance in the two lithologies. The authors attributed this pattern to the likelihood that sediment supply entering streams by mass failures in the typically steep, constrained, V-shaped valleys of volcanic watersheds would show greater response to road disturbances in steep areas remote from the channel. Their findings are supported by Reid et al. (1981) and Furniss et al. (1991), who concluded that mass-wasting from forest roads was the largest contributor of sediment to streams in forest lands of this region. In milder sloping sedimentary terrain where valleys are wider and streams are less constrained, Scott (2002) and Kaufmann and Larsen (unpublished) expected that most sediment supplies originated from banks and riparian zones. Delivery processes in these streams might be more similar to those in a lowland Wisconsin drainage described by Trimble (1999), where riparian vegetation removal and disturbances increased sediment delivery from channel movement, bank cutting, and incision. Our finding that IBI was negatively associated with excess silt or positively associated with relative bed stability in these lithologies may explain why IBI associations with basin and riparian disturbances also differ depending on catchment lithology.

Beyond the major negative association of IBI with disturbance-related sedimentation that was present in both lithologies and generally across the range of stream sizes, we found differing habitat-biota associations in the two lithologies. In small sedimentary streams, bedrock provides stable substrate in streambeds dominated by silt and sand, and may also form pools. The negative association between IBI and the percent of the stream bed composed of bedrock in volcanic streams may reflect a response to the overabundance of stable substrate in channels severely scoured due to natural or anthropogenic debris torrents (Swanson and Dyrness 1975; Kaufmann 1987). However, Kaufmann (1987) and Reeves et al. (1993) reported that bedrock exposure was also typical of streams draining volcanic basins with old growth forest. In both cases, these conditions indicate a low sediment supply rate relative to transport capacity, or a stream adjustment to prolonged increases in stream power sufficient to mobilize finer substrates (i.e., past bed instability, or low past RBS). Kaufmann and Larsen (unpublished) reported that low RBS in Coast Range volcanic streams was associated both with an increase in fine sediments, as well as an increase in streambed shear stress, and that both are associated with catchment roads and riparian disturbances. Elevated shear stress (from hydrologic alteration or channel simplification) without an increase in sediment supply is likely to lead, eventually, to bedrock exposure. Other in-channel factors associated with IBI in volcanic streams (higher conductivity, lower temperature, shading, abundant instream large wood) are consistent with channel conditions that foster high salmonid densities in the region (Spence et al. 1996). The lack of a strong relationship of IBI with pool depth in volcanic streams is perplexing. FEMAT (1993), for example, cited studies that documented substantial decreases in the number of large deep pools in river systems west of the Cascade Mountains. However, these decreases could be attributed to the loss of large wood and boulders as pool-forming structures (Lisle 1982), filling of pools with sediment (Lisle and Hilton 1992), and loss of sinuosity in stream channels, all of which are consistent with augmented sediment supplies and lowering of RBS, which is a strong predictor of IBI.

Index of biotic integrity was negatively associated with indicators of anthropogenic disturbance (roads and degraded riparian vegetation), their effects on sediment supply (excess fine sediments, bed and bank instability, turbidity), and other effects related to these factors (lack of deep residual pools, higher temperatures, higher nutrients, bedrock exposure). These findings agree with the scientific understanding concerning salmonid habitat requirements and limiting factors, as well as their relationship to human disturbances in streams that are the focus of coho salmon research and management in the region (Reiser and Bjornn 1979; Spence et al. 1996)

Key Findings

We demonstrated four key aspects about Coast Range streams. First, scaling abundance and richness IBI metrics by stream size aided interpretation of human effects by removing systematic natural variability (Hughes et al. 2004). Second, scaling substrate size by bank-full shear stress, as employed by Kaufmann et al. (1999) and USEPA (2000) to assess anthropogenic streambed fining, removed natural variability in substrate data and facilitated our detecting the effects of anthropogenic sedimentation on aquatic vertebrates. Third, lower IBI values, reflecting low richness and abundance of salmonids, tailed frogs and other coldwater and sediment-intolerant taxa, were associated with higher catchment road density and riparian disturbances, and in turn with lower RBS, higher excess fine sediment, reduced frequency of deep residual pools, higher water temperature and dissolved nutrient concentrations, and reductions in cover complexity. Fourth, anthropogenic effects were more pronounced in streams draining erodible sedimentary bedrock than in those draining more resistant volcanic terrain. We advise ecologists seeking to understand the effects of anthropogenic disturbance on stream systems to first evaluate the influences of natural gradients or differences in stream size, stream power, geology, and other natural drivers on their candidate disturbance indicators. The indicators can then be calibrated to remove consistent natural variation, improve predictions, and reduce the data scatter common in ecological dose–response relationships.

Management Implications

Natural disturbances are a major influence on habitat and biota in Coast Range streams (Reeves et al. 1995). Episodic landslides, fire, and other natural disturbances contribute a wide range of sediment sizes to stream channels. When large wood is delivered along with sediment, it stabilizes steam bed gravels and fine sediments, aiding the development of spatially and hydraulically complex habitat for stream biota. In this region, human activities have augmented natural rates of sediment supply to streams. Conversely, human influences have reduced the present and potential future supplies of large wood to these streams. Consequently, streams currently exhibit highly mobile beds with excess fine sediments and simplified morphology. This trend is likely to lead to more bedrock channels where slopes are high and increased fine sediments in lower gradient channels downstream. The beneficial effects of natural disturbances will lessen over time if rates of sediment and large wood transport (or decay) exceed their rates of replacement from upland and riparian areas within stream catchments.

If attaining or approaching the biotic integrity of fish and amphibian assemblages in wadeable streams throughout the Coast Range ecoregion are desired outcomes, our findings suggest the following habitat management and restoration goals. First, reduce watershed activities that exacerbate erosion and mass-wasting (e.g., landslides and other hillslope failures). Second, protect and rehabilitate riparian zone vegetation, fostering the development of multilayered structure and large, old trees. Third, manage landscapes so that large wood is delivered along with coarse and fine sediments in both natural and anthropogenic mass-wasting events. These three measures would likely increase relative bed stability and decrease excess fines by decreasing sediment inputs and increasing energy-dissipating roughness from in-channel large wood and deep residual pools. Reducing sediment supply and transport to sustainable rates should also ensure adequate future supplies of sediment. In addition, these measures would provide more shade, bankside cover, pool volume, colder water, and more complex habitat structure.

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REFERENCES

Baker, E. A., K. E. Wehrly, P. W. Seelbach, L. Wang, M. J. Wiley, and T. Simon. 2005. A multimetric assessment of stream condition in the Northern Lakes and Forests ecoregion using spatially explicit statistical modeling and regional normalization. Transactions of the American Fisheries Society. 134: 697–710.

Benda, L., D. Miller, P. Bigelow, and K. Andras. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management 178:105–119.

Benda, L. E., D. J. Miller, T. Dunne, G. H. Reeves, and J. K. Agee. 1998. Dynamic landscape systems. Pages 261–288 *in* R. J. Naiman and R. E. Bilby, editors. River ecology and management: lessons from the Pacific Coastal ecoregion. Springer-Verlag, New York.

Beschta, R. L. 1978. Long-term patterns of sediment production following road construction and logging in the Oregon coast range. Water Resources Research 14:1011–1016.

Beschta, R. L., J. R. Boyle, C. C. Chambers, W. P. Gibson, S. V. Gregory, J. Grizzel, J. C. Hagar, J. L. Li, W. C. McComb, T. W. Parzybok. M. L. Reiter, G. H. Taylor, and J. E. Warila. 1995. Cumulative effects of forest practices in Oregon. Prepared for the Oregon Department of Forestry, Oregon State University, Corvallis.

Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. Pages 121–129 *in* W. R. Meehan, T. R. Merrell, Jr., and T. A. Henley, editors. Fish and wildlife relationships in old-growth forests: proceedings of a symposium. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Bisson, P. A., T. A. Quinn, G. H. Reeves, and S. V. Gregory. 1992. Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest river systems. Pages 189–232 *in* R. J. Naiman, editor. Watershed management: balancing sustainability and environmental change. Springer-Verlag, New York.

Bisson, P. A., B. E. Rieman, C. Luce, P. G. Hessburg, D. C. Lee, J. L. Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178: 213–229.

Bryce, S. A., D. P. Larsen, R. M. Hughes, and P. R. Kaufmann. 1999. Assessing relative risks to aquatic ecosystems: a mid-Appalachian case study. Journal of the American Water Resources Association 35:23–36.

Buffington, J. M. 1998. The use of streambed texture to interpret physical and biological conditions at watershed, reach, and sub-reach scales. Doctoral dissertation. University of Washington, Seattle.

Burnett, K. M., G. H. Reeves, S. E. Clarke, and K. R. Christiansen. 2006. Comparing riparian and catchment influences on stream habitat in a forested, montane landscape. Pages 175–197 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitat and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds on large salmonids. Transactions of the American Fisheries Society 117:1–21.

Dietrich, W. E., and T. Dunne. 1978. Sediment budget for a small catchment in mountainous terrain. Zeitschrift für Geomorphologie, Supplementbande 29:191–206.

Dietrich, W. E., J. W. Kirchner, H. Ikeda, and F. Iseya. 1989. Sediment supply and the development of the coarse surface layer in gravel bed rivers. Nature (London) 340:215–217.

Dingman, S. L. 1984. Fluvial hydrology. W. H. Freeman, New York.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. U.S. Government Printing Office, Report 1993-793-071, Washington, D.C.

Furniss, M. J., T. D. Roelofs, and C. S. Yee. 1991. Road construction and maintenance. Pages 297–324 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology, an introduction for ecologists. Wiley, New York.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Hack, J. T. 1973. Stream profile analysis and stream-gradient index. United States Geological Survey Journal of Research 1:421–429, Denver.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173–1185.

Herger, L. G., and G. Hayslip. 2000. Ecological condition of streams in the Coast Range Ecoregion of Oregon and Washington. U.S. Environmental Protection Agency, EPA/910/R-00/002, Seattle.

Herger, L. G., A. Weiss, S. Augustine, and G. Hayslip. 2003. Modeling fish distributions in the Pacific Northwest Coast Range using EMAP data. U.S. Environmental Protection Agency, EPA /910/R-03/000, Seattle.

Herlihy, A. T., D. P. Larsen, S. G. Paulsen, N. S. Urquhart, and B. J. Rosenbaum. 2000. Designing a spatially balanced, randomized site selection process for regional stream surveys: the EMAP mid-Atlantic pilot study. Environmental Monitoring and Assessment 63:95–113.

Hicks, B. 1989. The influences of geology and timber harvest on channel morphology and salmonid populations in Oregon. Doctoral dissertation. Oregon State University, Corvallis.

Hughes, R. M., S. Howlin, and P. R. Kaufmann. 2004. A biointegrity index for coldwater streams of western Oregon and Washington. Transactions of the American Fisheries Society 133:1497–1515.

Jones, K. B., A. C. Neale, M. S. Nash, R. D. Van Remortel, J. D. Wickham, K. H. Ritters, and R. V. O'Neill. 2001. Predicting nutrient and sediment loadings to streams from landscape metrics: a multiple watershed study from the United States mid-Atlantic region. Landscape Ecology 16: 301–312.

Kaufmann, P. R. 1987. Channel morphology and hydraulic characteristics of torrent-impacted forest streams in the Oregon Coast Range, U.S.A. Doctoral dissertation. Oregon State University, Corvallis.

Kaufmann, P. R., and E. G. Robison. 1998. Physical habitat characterization. Pages 77–118 *in* J. M. Lazorchak, D. J. Klemm, and D. V. Peck, editors. Environmental Monitoring and Assessment Program—Surface Waters: field operations and methods for measuring the ecological condition of wadeable streams. U.S. Environmental Protection Agency, EPA/620/R-94/004F, Washington, D.C. Available: http://www.epa.gov/emap/html/pubs/docs/groupdocs/ surfwatr/field/ws_abs.html (August 2004).

Kaufmann, P. R., P. Levine, E. G. Robison, C. Seeliger, and D. V. Peck. 1999. Quantifying physical habitat in wadeable streams. U.S. Environmental Protection Agency, EPA/620/R-99/003, Washington, D.C. Available: http://www.epa.gov/emap/ html/pubs/docs/groupdocs/surfwatr/field/ws_abs.html (August 2004).

Lazorchak, J. M., D. J. Klemm, and D. V. Peck, editors. 1998. Environmental Monitoring and Assessment Program—Surface Waters: field operations and methods for measuring the ecological condition of wadeable streams. U.S. Environmental Protection Agency, EPA/620/R-94/004F, Washington, D.C. Available: http://www.epa.gov/emap/html/pubs/docs/groupdocs/surfwatr/field/ws_abs.html (August 2004).

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.

Lisle, T. E. 1982. Effects of aggradation and degradation on riffle-pool morphology in natural gravel channels, northwestern California. Water Resources Research 18:1643–1651.

Lisle, T. E., and S. Hilton. 1992. The volume of fine sediment in pools: an index of sediment supply in gravel-bed streams. Water Research Bulletin 28: 371–383.

May, C. L. 2002. Debris flows through different forest age classes in the central Oregon Coast Range. Journal of the American Water Resources Association 38:1097–1113.

Morisawa, M. 1968. Streams, their dynamics and morphology. McGraw-Hill, New York.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the North American Wildlife Conference 110:469–478.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Omernik, J. M., and A. L. Gallant. 1986. Ecoregions of the Pacific Northwest. U.S. Environmental Protection Agency, EPA/600/3/77-105, Corvallis, Oregon.

Pater, D. E., S. A. Bryce, T. D. Thorson, J. Kagan, C. Chappell, J. M. Omernik, S. H. Azevedo, and A. J. Woods. 1998. Ecoregions of western Washington and Oregon. U.S. Geological Survey, Reston, Virginia.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 224–349 *in* J. Nielsen, editor. Evolution and the aquatic ecosystem. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Reeves, G. H., F. H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. Transactions of the American Fisheries Society 122:309–317.

Reid, L. M., T. Dunne, and C. J. Cederholm. 1981. Application of sediment budget studies to the evaluation of logging road impact. Journal of Hydrology 20:49–62.

Reiser, D. W., and T. C. Bjornn. 1979. Influence of forest and rangeland management on anadromous fish habitat in western North America, 1. Habitat requirements of anadromous salmonids. U.S. Forest Service, General Technical Report PNW-96, Portland, Oregon.

Reynolds, L., A. T. Herlihy, P. R. Kaufmann, S. V. Gregory, and R. M. Hughes. 2003. Electrofishing effort requirements for assessing species richness and biotic integrity in western Oregon streams. North American Journal of Fisheries Management 23:450–461.

Riseng, C. M., M. J. Wiley, R. J. Stevenson, T. G. Zorn, and P. W. Seelbach. 2006. Comparison of coarse versus fine scale sampling on statistical modeling of landscape effects and assessment of fish assemblages of the Muskegon River, Michigan. Pages 555–575 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitat and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

SAS (Statistical Applications Software). 2004. SAS for Windows, Release 9.1. Statistical Applications Software (SAS) Institute, Cary, North Carolina.

Scott, L. 2002. Relationships among in-stream physical habitat, land use, and geology in small coastal streams of northern Oregon. M.S. thesis. Oregon State University, Corvallis.

Spence, B. C., G. A. Lomnicky, R M Hughes, and R. P. Novitzki. 1996. An ecosystem approach to salmonid conservation. National Marine Fisheries Service, Report TR-4501–96-6057, Portland, Oregon.

Stevens, D. L., Jr., and A. R. Olsen. 1999. Spatially restricted surveys over time for aquatic resources. Journal of Agricultural, Biological, and Environmental Statistics 4:415–428.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913–920.

Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969–974.

Swanston, D. N. 1991. Natural processes. Pages 139–179 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitat. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Swanson, F. J., and C. T. Dyrness. 1975. Impact of clearcutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. Geology 3:293–396.

TIGER. 1990. Modified topologically integrated geographic encoding and referencing system. Available: http://www.census.gov/geo/www/tiger (March 2005).

Trimble, S. W. 1999. Decreased rates of alluvial sediment storage in the Coon Creek basin, Wisconsin, 1975–93. Science 285:1244–1246.

USEPA (U.S. Environmental Protection Agency). 1987. Handbook of methods for acid deposition studies: laboratory analysis for surface water chemistry. U.S. Environmental Protection Agency, EPA 600/4–87/026, Washington, D.C.

USEPA (U.S. Environmental Protection Agency). 2000. Mid-Atlantic Highlands streams assessment. U.S. Environmental Protection Agency, EPA/903/R-00/015, Philadelphia.

Waters, T. F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society, Monograph 7, Bethesda, Maryland.

Wiley, M. J., P. W. Seelbach, K. E. Wehrly, and J. S. Martin. 2002. Regional ecological normalization using linear models: a meta-method for scaling stream assessment indicators. Pages 201–224 *in* T. P. Simon, editor. Biological response signatures: patterns in biological integrity for assessment of freshwater aquatic assemblages. CRC Press, Boca Raton, Florida.

Zorn, T. G., and M. J. Wiley. 2006. Influence of landscape characteristics on local habitat and fish biomass in streams of Michigan's Lower Peninsula. Pages 375–393 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitat and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.