American Fisheries Society Symposium 48:457–471, 2006

A Spatially Explicit Approach for Evaluating Relationships among Coastal Cutthroat Trout, Habitat, and Disturbance in Small Oregon Streams

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Abstract.—Small stream systems are complex networks that form a physicochemical template governing the persistence of aquatic species such as coastal cutthroat trout *Oncorhynchus clarkii clarkii*. To gain new insight into these interactions, we initiated an integrated program of landscape-scale sampling that is focused on fine- and broad-scale relationships among upslope landscape characteristics, physical stream habitat, and the spatial patterns of cutthroat trout abundance. Our sample of 40 catchments (500–1,000 ha) represented approximately 15% of the 269 barrier-isolated catchments in western Oregon that support populations of cutthroat trout. Because data were collected in a spatially contiguous manner throughout each catchment, it was possible to collect biological and geographic information necessary to assess the spatial structure of cutthroat trout abundance. Results underscore the influence of the physical habitat template at a variety of spatial scales. For example, cutthroat trout move throughout the accessible portions of small streams. Some cutthroat trout congregate in areas of suitable habitat and form local populations that may exhibit unique genetic attributes. At times, some cutthroat trout move into larger downstream portions of the network where they may contribute to the genetic character of anadromous or local potamodromous assemblages. Results underscore the advantages of viewing habitats that are critical to the fitness and persistence of cutthroat trout populations as matrices of physical sites that are linked by movement. It is apparent that human activities that impede movement among suitable habitat patches can have unanticipated consequences for metapopulations of cutthroat trout and may ultimately affect their persistence.

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INTRODUCTION

Two basic questions in aquatic ecology relate to how aquatic systems are organized in space and how they change in time. In a more general sense, interest in the relationship between organisms and their habitats undoubtedly dates to the earliest hunter/gathers. Although the questions are simple (e.g., what influences the distribution and abundance of animals), the answers are extremely complex because they represent the integration of environmental heterogeneity and the adaptation of organisms to that habitat template (Southwood 1977; Healey and Prince 1995).

The spatial and temporal dynamics of landscapes increase habitat complexity (Frissell et al. 1986; Pickett and Cadenasso 1995) and complicate the study and interpretation of habitat–fish relationships at multiple scales (Turner et al. 1989; Frissell et al. 1997). Interactions among physical, chemical, and biological characteristics of terrestrial, riparian, and aquatic systems further obfuscate understanding of habitat–fish relationships, especially at broad spatial scales. Frissell et al. (1986) developed a hierarchical method for classifying stream systems in the context of the catchments of which they are a part, and this type of integrated multiscale approach is widely accepted as a means of understanding the influence of disturbance and land management in catchments (Imhof et al. 1996).

Habitat studies for aquatic ecosystems most often have been conducted at the local scale (Imhof et al. 1996), which seems inappropriate for organisms, such as salmonids, that require a variety of habitats depending on season or life stage (Northcote 1997). Furthermore, research has often focused on the relationship between physical habitat and anadromous salmonids (Nickelson et al. 1992; Reeves et al. 1995), but strong inferences are difficult to develop because anadromous fish spend much of their lives in the ocean where they are affected by an array of environmental variables that are not accounted for, including commercial harvest (Hicks et al. 1991) and fluctuating ocean conditions (Pearcy 1992). In contrast, potamodromous coastal cutthroat trout *Oncorhynchus clarkii clarkii* live in freshwater their entire lives. Thus, they are likely to be more tightly linked to changes in terrestrial habitats than anadromous fishes, but much less effort has been expended to describe these linkages.

Interactions between terrestrial and aquatic systems are especially relevant in small streams that often are inhabited by cutthroat trout. These stream channels can represent more than 70% of the cumulative channel length in mountainous catchments of the Pacific Northwest (Benda et al. 1992). In addition, small streams are often directly affected by natural and anthropogenic disturbance (Gomi et al. 2002; May and Gresswell 2004). Fortunately, in small stream systems it may be possible to quantify the spatial and temporal extent of these processes and their influence on the spatial patterns of cutthroat trout abundance.

We describe a research approach developed for small western Oregon streams. Our goals were to investigate (1) patterns of cutthroat trout abundance in small streams, (2) habitat quality and quantity in these systems and how it influences patterns of cutthroat trout abundance, and (3) how relationships between habitat and cutthroat trout abundance change through space and time in response to natural and anthropogenic disturbance (Figure 1). These goals were integrated into a program of landscape-scale catchment sampling to investigate the fine- and broad-scale relationships among upslope landscape characteristics, stream physical habitat, and the abundance of cutthroat trout. We present a general overview of our research with associated strengths and weaknesses and a summary of results to date.

METHODS

Geographical and Ecological Context

The historic range of coastal cutthroat trout extended from Humboldt Bay, California to Prince William Sound, Alaska. The subspecies exhibits

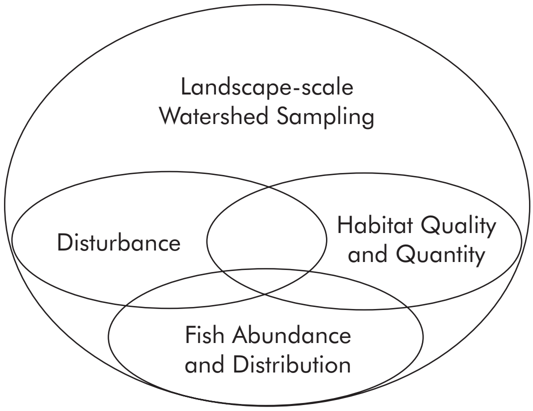

Figure 1. Conceptual framework for assessing interrelationships among habitat quality and quantity, coastal cutthroat abundance and distribution, and natural and anthropogenic disturbance. Relationships among fish, habitat, and disturbance are captured by landscape-scale catchment sampling.

a diverse array of life histories, including anadromous, amphidromous, potamodromous, and nonmigratory forms (Trotter 1989). Recent range-wide declines in abundance and distribution have raised concerns about the persistence of the subspecies, especially the anadromous form (Nehlsen et al. 1991; Hall et al. 1997), and petitions have been submitted to list coastal cutthroat trout under the Endangered Species Act.

Potamodromous and nonmigratory forms are relatively abundant in small stream systems, but little is known about factors influencing the spatial patterns of abundance of the subspecies in these areas. We focused on catchments above barriers inhibiting upstream migration, where there are no confounding effects from the presence of anadromous salmonids. We hypothesized that it would be easier to identify and interpret the interactions among terrestrial and aquatic components of isolated catchments because coastal cutthroat trout in these systems are directly linked to the freshwater habitat and the surrounding drainage throughout their lives. In addition, coastal cutthroat trout may be much more vulnerable to disturbance in small isolated streams, and information concerning the effects of land management activities (e.g., timber harvest, aggregate mining, and associated road construction and maintenance) is scarce for these systems.

Sampling Design

Two spatial scales were particularly important for this study. The first concerns the large-scale variation across western Oregon using catchments as analytical units and the influence of geologic, geomorphic, and climatic factors on natural and anthropogenic disturbance regimes. The second spatial scale of interest focused on channel units, geomorphic reaches, and stream segments as analytical units to investigate variation within catchments. Although there is a substantial amount of information at the channel unit (10–100 m), and in some cases the stream-segment level (100–1,000 m), the effects of natural disturbance and land-management activities at the catchment scale are poorly understood. Because consequences of anthropogenic and natural disturbance vary substantially within a catchment, managing catchments as systems may be critical for the persistence of many aquatic organisms.

In order to make inferences about coastal cutthroat trout across western Oregon, we defined the sample unit as an entire catchment. To capture the spatial context of the population of catchments, the sample was extended across all of the known barrier-isolated Oregon catchments west of the Cascade Range divide where coastal cutthroat trout was the only salmonid ($N = 269$; Gresswell et al. 2004). We used standard sampling procedures to subsequently select study catchments from the group of known populations (Scheaffer et al. 1990). Because physiographic province and geology were expected to influence cutthroat trout-habitat relationships across western Oregon, the above-barrier catchments were grouped by ecoregion: (Coast Range, Klamath Mountains, and Cascades; Pater et al. 1998) and erosion-potential class (resistant or weak rock types; Gresswell et al. 2004). A sample of 40 catchments was selected in proportion to the number of isolated catchments with coastal cutthroat populations occurring in each of the six strata (Figure 2). A sample size of 40 catchments represents approximately 15% of the population of barrier-isolated catchments with cutthroat trout in western Oregon, and we assumed that it would be feasible to complete the sample within a period of 3 years.

We sampled during low-discharge periods from June through September. To sample 40 catchments in 3 years, it was necessary to limit

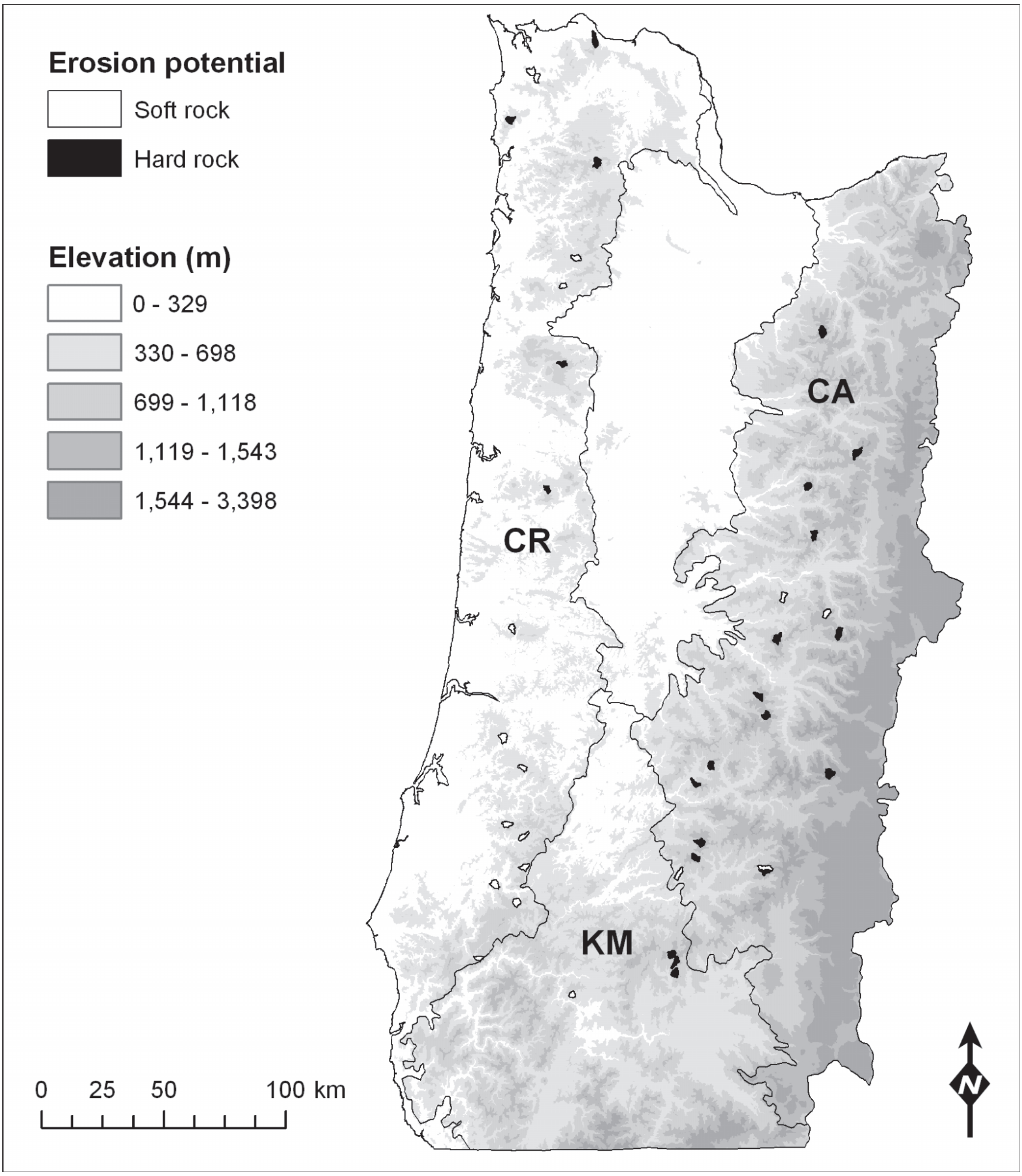

Figure 2. Locations of 40 catchments selected from 269 barrier-isolated coastal cutthroat populations in western Oregon. Catchments were grouped by ecoregion (Coast Range [CR], Klamath Mountains [KM], and Cascades [CA]) and erosion potential (resistant rock types and weak rock types); sample catchments were subsequently selected from each of the six strata.

the amount of time to 3 d for sampling an individual catchment. Pilot studies suggested that to meet time constraints for the field portion of the project, it would be necessary to limit the maximum drainage area of sample catchments to approximately 1,000 ha. In cases where a barrier-isolated catchment exceeded 1,000 ha, the area above each tributary junction (moving progressively farther upstream) was estimated until at least one subcatchment less than 1,000 ha was identified and that upstream subcatchment was sampled. If two or more subcatchments (500–1,000 ha) occurred above a tributary junction, one was randomly selected for sampling.

Because each catchment was surveyed only once, we selected an additional catchment to serve as an interannual temporal reference. Camp Creek (Umpqua River drainage) was sampled annually 1998–2004. Camp Creek also was used as the study site for within-catchment assessments of cutthroat trout movement and genetic structure.

Field Surveys of Physical Habitat and Cutthroat Trout

Prior to initial surveys, the channel network of each catchment was divided into stream segments (Frissell et al. 1986; Moore et al. 1997) using existing databases, topographic and geologic maps, aerial photographs, and field reconnaissance to identify tributary junctions (tributaries contributing ≥ 15% of mainstem flow) and geologic barriers to fish movement (waterfalls > 2 m). In the field, each segment was divided into geomorphic reach types (beaver complex, cascade, step-pool, plane-bed, pool-riffle, dune-ripple, colluvial, or bedrock channel) based on substrate, gradient, bed morphology, and pool spacing (Montgomery and Buffington 1997); minimum reach length was 10 active channel widths. Subsequently, channel-unit types (pool, riffle-rapid, cascade, and vertical step) were classified in each reach according to criteria developed by Bisson et al. (1982). Physical variables including channel-unit size (e.g., length, maximum depth, and width), substrate size-class (bedrock, boulder, cobble, gravel, sand, and silt; Moore et al. 1997), valley segment type (broad and narrow; Moore et al. 1997), channel type (constrained and unconstrained; Moore et al. 1997), and woody debris accumulations (i.e., ≥5 pieces, ≥15 cm in diameter and 3 m in length; classified in 10-piece aggregations; Moore et al. 1997) were recorded for all channel units.

Following physical habitat assessment, we estimated relative abundance of cutthroat trout ≥ 70 mm in all pools and cascades using single-pass electrofishing (Bateman et al. 2005). To identify the upstream extent of cutthroat trout distribution, the main-stem segment and tributaries were electrofished for 50–300 m (approximately 10–40 individual pool sample units) beyond the point at which no more cutthroat trout were detected. All captured cutthroat trout were anesthetized with clove oil to reduce handling stress (Taylor and Roberts 1999), measured (fork length; ±1 mm), and weighed (±0.1 g). Scale samples (23–254 per catchment) were collected from up to 10 cutthroat trout in each 10-mm length category for age determination.

Repeated sampling of Camp Creek provided the means to examine both within- and among-year changes in physical habitat and cutthroat trout abundance patterns (Hendricks 2002). In Camp Creek, tagged and marked individuals (753 tagged with a passive integrated transponder [PIT] and 5,322 fin-clipped) were monitored bimonthly from June 1999 to August 2000. To increase the probability of relocating individual cutthroat trout, each survey included all channel-units from the waterfall at the downstream terminus of the study area to the end of fish distribution in the main stem and tributaries. To further increase temporal resolution, locations of 35 radio-tagged cutthroat trout were recorded 3–5 d each week, January–June 2000. Emigration out of the catchment was estimated with a rotating fish trap.

Genetic Diversity

Caudal-fin tissue was collected from up to 100 cutthroat trout from each catchment to assess genetic diversity. Tissue collections were distributed spatially within a catchment by sampling up to 10 fish in 10-mm size-classes from each stream segment until 100 samples were obtained or the end of fish distribution was reached. If end of fish distribution was reached before 100 samples were obtained, we assumed that a large percentage of the population was sampled (Bateman et al. 2005), and therefore, the range of genetic variation in the population was represented. Fin tissue was preserved in a buffer solution (100 mM trisHCl pH8, 100 mM EDTA pH8, 10 mM NaCl, 0.5% (w/v) SDS) or a desiccant (anhydrous sulfide crystals) prior to genetic analysis (Guy 2004). Seven microsatellite loci in three multiplexed sets were chosen after screening for reliable PCR amplification, ease of scoring, and polymorphism (Guy 2004).

Additional tissue samples were collected in Camp Creek to assess cutthroat trout population structure within a small stream network and to evaluate the effects of fish passage barriers on coastal cutthroat trout genetic variation (Wofford et al. 2005). Genetic sampling occurred at 10 sites in the Camp Creek watershed. Prior to sampling, the catchment was surveyed to identify barriers to cutthroat trout passage. Genetic sampling sections were bounded by tributary junctions or fish-passage barriers, except in the upper portion of the main stem where two additional sections were added because no tributaries or passage barriers occurred in a relatively extensive section of stream. Sample collection proceeded as noted above except that tissue was collected from all cutthroat trout captured in six sections where abundance was low. Sample processing was conducted in the manner described above (Wofford et al. 2005).

Analysis of Spatial Structure

The spatial patterns of cutthroat trout abundance in channel networks were evaluated with geostatistical techniques. Variograms were used to indicate the degree of spatial autocorrelation among samples. For 22 catchments where a spherical variogram model was applicable, the range (i.e., the distance over which observations were autocorrelated) was used to determine the dominant scale of variation (i.e., patch size) in the spatially referenced data (Rossi et al. 1992). Initial variogram analysis was limited to the mainstem channels of four streams. To rigorously quantify spatial structure in cutthroat trout abundance throughout the channel network of a catchment, it was necessary to (1) develop an automated method of determining the network distance (distance along the stream channel) between all sampled points (Torgersen et al. 2004), and (2) create a software routine to perform network variogram analyses in a commercially available statistical application (Ganio et al. 2005).

RESULTS AND INTERPRETATION

Spatial Patterns of Abundance

Because all pools and cascades were sampled in each catchment, it was possible to develop a spatially explicit representation of cutthroat trout abundance in the channel network (Figure 3). Visual examination revealed that cutthroat trout abundance was not uniform within individual catchments, and some stream sections had greater numbers than others. In fact, in many catchments, abundance patterns were highly structured, and the number of cutthroat trout in individual channel units was more similar to neighboring units than those farther away. Conversely, patterns of abundance varied substantially among catchments.

By incorporating supporting data layers, it was possible to build hypotheses concerning the physical processes and structures that may influence patterns of cutthroat trout abundance. Drainage patterns of the fish-bearing portion of the channel network also varied, but dendritic (one or more tributaries) and simple (no tributaries) patterns were the two most common groups. Although a myriad of physical factors and processes can influence the patterns of cutthroat trout abundance in channel networks, bedrock lithology was the dominant factor among those we examined. For example, a greater proportion of complex, dendritic patterns were found in the Coast Range ecoregion (87%) where sedimentary bedrock was common, but simple patterns were more common in the Cascades ecoregion (13%), where the bedrock lithology was predominantly basalt (Guy 004). Kaufmann and Hughes (2006, this volume) found that anthropogenic disturbances were higher and fish assemblage condition was lower in stream sections with sedimentary bedrock when compared to equivalent sections with volcanic geology.

Initial variogram analysis conducted along the main-stem channels of four streams showed spatial autocorrelation in cutthroat trout abundance; however, visual examination of cutthroat trout abundance patterns suggested that spatial structuring was occurring throughout the channel network (Figure 3). Results of network variogram analyses revealed a number of different spatial structures and scales of variation as indicated by the shapes of the variograms. Patterns of cutthroat trout abundance in the 40 sampled catchments ranged from completely random to highly structured (gradients, patches, and nested patches; Ettema and Wardle 2002; C. E. Torgersen and R. E. Gresswell, unpublished data). The dominant scale of variation (i.e., patch size) in cutthroat trout abundance was assessed for 22 catchments that fit the spherical model, and 75% of the variation in patch size was explained by rock stability (Figure 4). Resistant rock types (basalt, granite, and hard sedimentary) subject to narrow, shallow debris flows were associated with shorter spatial scales of variation in cutthroat trout distribution than weaker rock types. Weak rock types (pyroclastics, tuff, schists, and soft sedimentary) had gentle slopes formed by wide, deep earthflows and were associated with longer spatial scales of variation in cutthroat trout distribution. Other physical catchment characteristics, including the average distance between tributary junctions and the maximum pathway distance (maximum distance separating any two points in the distribution of cutthroat trout) in the network, were also positively associated with the dominant scale of variation in cutthroat trout abundance, but not correlated with each other ($r = 0.41$, $P > 0.05$) (Torgersen and Gresswell, unpublished data).

Physical factors influencing the spatial extent of stream occupied by cutthroat trout (number of kilometers occupied by cutthroat trout upstream of the starting point) are of particular interest to fisheries managers. Previous research on coastal cutthroat trout distribution in small streams has not had the advantage of spatially contiguous data, so the task of developing predictive models has been challenging (Latterell et al. 2003). Data from 40 catchments in western Oregon enabled analyses to relate patterns of cutthroat trout relative abundance to three landscape variables derived from remote sensing imagery and geographical information system (GIS) data layers. We used information derived from field surveys of cutthroat trout distribution in the channel network to develop statistical models that predicted the spatial extent of cutthroat trout distribution as a proportion of catchment size. The spatial extent of cutthroat trout distribution was negatively correlated with mean stream slope ($r = -0.65$, $P < 0.01$) and positively correlated with mean annual precipitation (Daymet 2004) ($r = 0.50$, $P < 0.01$) and forest vegetation type ($r = 0.51$, $P < 0.01$) (Cohen et al. 2002; Torgersen and Gresswell, unpublished data). The total abundance of cutthroat trout in the study catchments as a proportion of watershed area was much more difficult to predict than spatial extent and was not significantly associated ($r = 0.10$, $P = 0.52$) with forest vegetation type.

Temporal Patterns and Movement

Cutthroat trout moved frequently in Camp Creek, but distances were short. Habitat-unit-scale (2–95 m) movement was common throughout the year, and reach-scale (66–734 m) and segment-scale (229–3,479 m) movements were more common during the late winter and

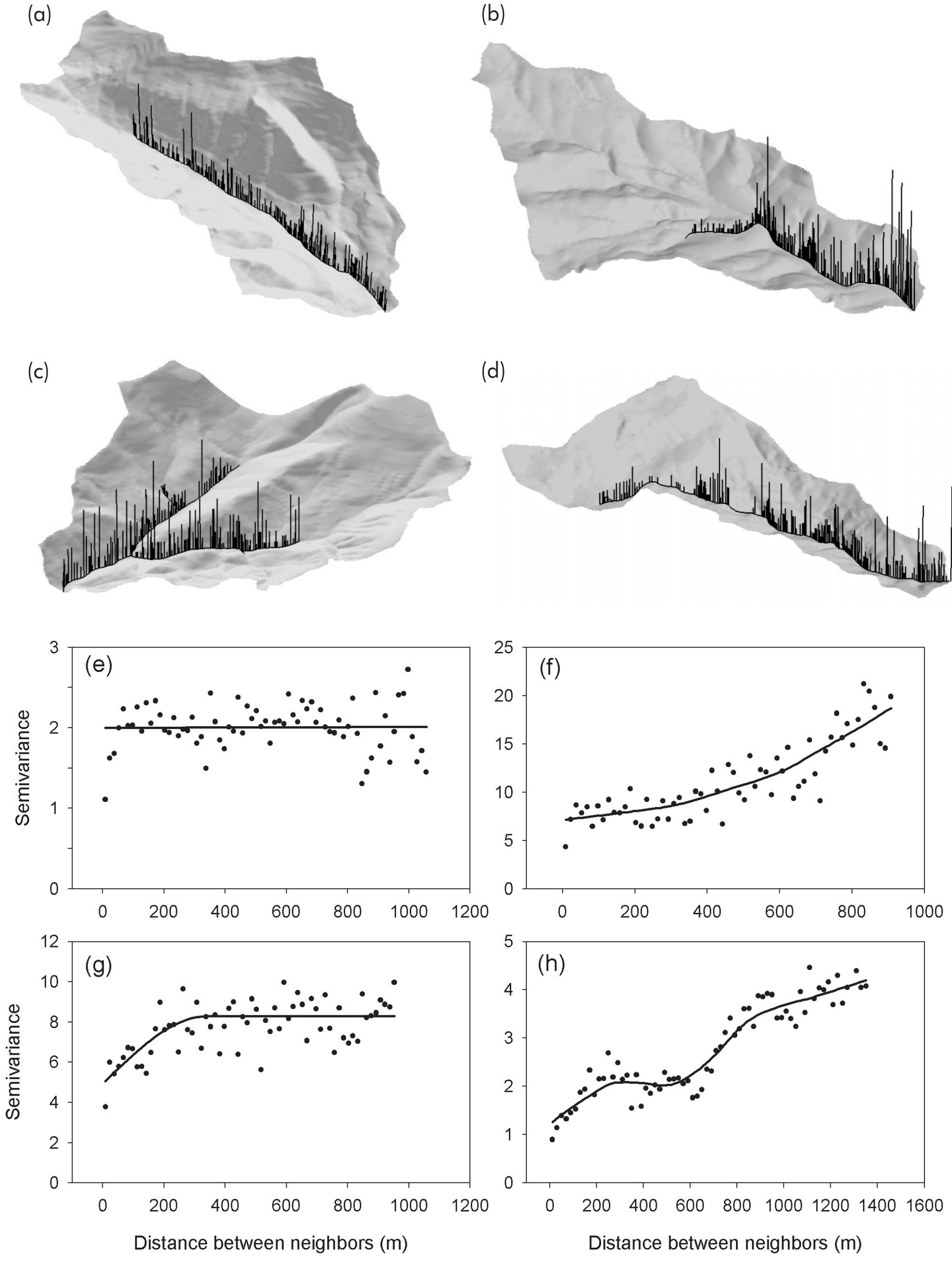

Figure 3. Spatial variation in the distribution and relative abundance of coastal cutthroat trout (length ≥ 70 mm) in four small streams in western Oregon. Vertical bars in three-dimensional representations of Hardy Creek (a), East Fork Laying Creek (b), Rock Creek (c), and Miller Creek (d) indicate the relative abundance of cutthroat trout sampled in pool and cascade habitats with single-pass electrofishing. Paired three-dimensional representations and semivariograms of cutthroat trout counts illustrate different patterns of spatial autocorrelation: (a, e) no spatial structure, (b, f) large-scale heterogeneity with a pronounced trend or gradient, (c, g) small-scale heterogeneity with distinct patches, and (d, h) nested heterogeneity at two different scales (Ettema and Wardle 2002).

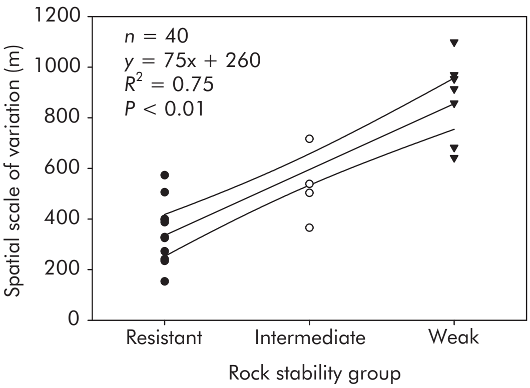

Figure 4. Relationship between the dominant spatial scale of variation in coastal cutthroat trout counts and rock stability in headwater basins of western Oregon.

spring (Hendricks 2002). Movements over greater distances were associated with annual spring spawning events; the least movement occurred when discharge was at a minimum in October. About 80% of PIT-tagged cutthroat trout occupied pool habitats from June through October, but from December through March, when discharge was high and water temperatures were low, pools were used almost exclusively. Only 63 cutthroat trout (<1% of those tagged and marked) were captured in the downstream trap between February and June (Hendricks 2002).

Using a kernel density estimator (Silverman 1986) to quantify spatial variation in fish counts, we identified several interannual patterns of cutthroat trout relative abundance in Camp Creek (Figure 5). Although it is apparent that abundance varies substantially among years, some areas in Camp Creek consistently exhibit high relative abundance of cutthroat trout (Figure 5). Concomitantly, some areas exhibited consistently low numbers of cutthroat trout. Similar interannual patterns of abundance have been noted in another small stream in the Umpqua River drainage that has been monitored annually since 2001 (Gresswell, unpublished data). Efforts to identify habitat characteristics related to areas of consistently high and low relative abundance are ongoing.

Genetic Structure

Genetic differentiation among 27 isolated populations of cutthroat trout in this study was high (mean Fst = 0.33), but intrapopulation genetic diversity determined by microsatellite analysis (mean number of alleles per locus = 5, mean He = 0.60) was only moderate (Guy 2004). When all populations were combined, there was evidence of genetic isolation by geographic distance, but isolation by distance was not observed if populations were compared by ecoregion. Differences in genetic diversity between the Coast Range ecoregion (mean alleles = 47) and the Cascade Mountains ecoregion (mean alleles = 30) were statistically significantly ($P = 0.02$), and Guy (2004) suggested that this pattern was related to the interactions of drift, gene flow, and the physical environments of the two ecoregions. Topological stream channel complexity (ratio of summed tributary lengths to the main stem length) and connectivity (number of vertical steps > 1 m divided by the mean step height) were greater in the Coast Range (0.54 and 27.7, respectively) than the Cascade Mountains (0.1 and 18.7, respectively), and differences were statistically significant ($P = 0.00$ and $P = 0.02$ for complexity and connectivity, respectively). Results suggested that genetic patterns in the Coast Range were more strongly influenced by gene flow than in the Cascade Mountains, where drift appeared to be the dominant factor influencing genetic diversity (Guy 2004).

At the catchment spatial scale, Wofford et al. (2005) found that dispersal barriers strongly influenced coastal cutthroat trout genetic structure among sample locations in Camp Creek, and barriers were associated with reduced genetic diversity and increased genetic differentiation. In Camp Creek, cutthroat trout exhibit many small, partially independent populations that are directly influenced by genetic drift. For example, mean gene diversity was 0.50 within populations, and mean allelic richness was 3.96. Gene diversity and allelic richness decreased with increasing distance upstream and above barriers to

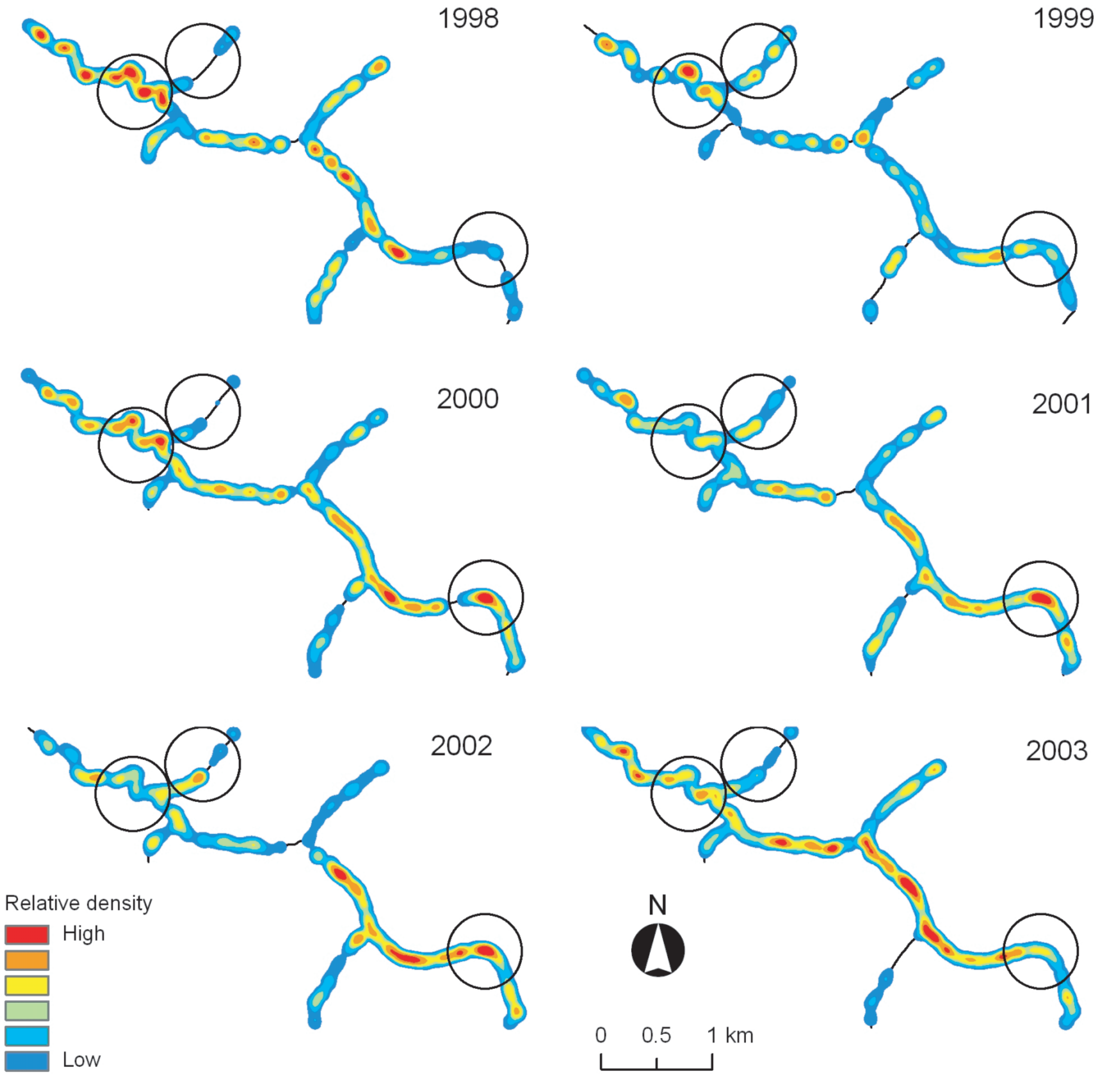

Figure 5. Interannual variation in the summer distribution of coastal cutthroat trout in Camp Creek (1998–2003). The relative density (fish/m²) of trout was estimated using a kernel density function. Circles provide a spatial reference for comparing patterns among years.

movement. Tributaries that were connected with the main stem usually had relatively high levels of allelic richness and gene diversity, but samples obtained upstream of barriers to gene flow exhibited low values for both measures of diversity. Wofford et al. (2005) hypothesized that increased habitat fragmentation in small streams may result in genetic and demographic isolation that leads to reduced genetic diversity of cutthroat trout populations and compromises long-term population persistence.

DISCUSSION

Although thorough examination of the data collected in this research program has only begun, it is evident that the approach has several strengths that differentiate it from previous attempts to quantify relationships between physical habitat and the pattern of cutthroat trout abundance. First, using a probability-based process to sample catchments provided a known scope of inference (Stevens and Olsen 1999), and we are not aware of any other study that has combined this spatial extent with the intensity of sampling within each of the sample catchments. The use of probability-based sampling in itself is not unique, and there are examples of both broad landscape scale and fine instream scale studies (Johnson and Gage 1997; Paulsen et al. 1998; Larsen et al. 2004); however, using the catchment as the sample unit and measuring variables at each level of the spatial hierarchy within each catchment is unparalleled. Our sample of 40 catchments represents approximately 15% of the 269 barrier-isolated catchments that support populations of coastal cutthroat trout in western Oregon. Furthermore, because the samples were selected in proportion to their occurrence in six strata based on geographic location and erosion potential, it is possible to investigate the influence of these broad-scale factors on the observed catchment-scale relationships.

A second major contribution of this research is related to the collection of spatially contiguous data throughout each of the catchments (Fausch et al. 2002). This approach provided the biological and geographic information to examine the spatial structure of cutthroat trout abundance in all 40 study catchments. Several recent studies have employed spatially contiguous sampling in stream systems (Labbe and Fausch 2000; Fausch et al. 2002; Torgersen et al. 2006, this volume), but none of these studies has combined the spatial extent and fine-scale detail to examine spatial structure of cutthroat trout abundance with geostatistical techniques in stream networks (Torgersen et al. 2004; Ganio et al. 2005). Our results underscore the influence of the physical habitat template on the spatial pattern of cutthroat trout abundance at a variety of spatial scales. Moreover, through repeated sampling within individual catchments, it is possible to evaluate how the pattern of relative abundance changes through time, and thereby identify those areas, and characteristics of those areas, that more frequently support higher numbers of cutthroat trout and those that consistently support lower numbers of cutthroat trout.

By examining a wide variety of biological traits it was possible to develop what may be the most thorough and spatially explicit picture of life history organization of any fish taxon to date. Data collected in this survey of catchments across western Oregon have already yielded new insights into patterns of relative abundance, movement, and genetic structure of cutthroat trout populations that are isolated above migration barriers. Ongoing studies are further evaluating the effects of physical landscape and catchment-scale features on patterns of cutthroat trout abundance and relationships with age structure and growth of isolated populations of the subspecies. Related studies have examined intra-annual variation of food availability and diet in relation to riparian vegetation (Romero et al. 2005), and the influence of wood and sediment distribution on the geomorphology of small streams in the Oregon Coast Range (May and Gresswell 2003a, 2003b, 2004).

Finally, variation in cutthroat trout abundance patterns among catchments reflects diverse environments and selective factors, such as geology, geomorphology, climate, and land-management history. These results underscore the advantages of viewing physical habitat as a matrix of physical sites critical to the fitness and persistence of cutthroat trout populations that are linked by movement (Kocik and Ferreri 1998). Consequently, human activities that impede movement among habitat patches can have lasting consequences for local cutthroat trout populations and assemblages and may ultimately affect persistence (Labbe and Fausch 2000; Kruse et al. 2001; Harig and Fausch 2002).

Although we are not advocating use of the methodological approach discussed in this paper for all research on cutthroat trout–habitat relationships, it does have distinct advantages. The relationships we identified with this methodology provide information needed to develop hypotheses that can be evaluated further using alternate statistical and experimental designs. Our methods also present the means to "scale up" from the local scale (individual channel units) to regional scale (ecoregions). The approach does have disadvantages, however. For example the effort, time, and expense required to collect these data are not trivial, and in many cases may be cost prohibitive. Furthermore, contiguous sampling may not be practical for long-term monitoring applications over large regions (Pacific Northwest). Numerous sampling protocols have been developed to meet this objective (Hankin and Reeves 1988; Hughes et al. 2000; Larsen et al. 2004). Such monitoring methods can be used to attain accurate and precise estimates of central tendency and expanded approximations for a variety of biotic and physical variables, but it is less certain that these data are appropriate for investigating the underlying ecological relationships that determine distribution and abundance of biota in a catchment. Without thorough understanding of these critical relationships, however, we suggest that it is difficult to identify the linkages between natural and anthropogenic disturbance on physical habitat and the resulting consequences for cutthroat trout and other aquatic biota. The sampling strategies described in this paper provide an alternative approach for assessing relationships between salmonid distribution and physical habitat that opens the door for continued methods development and innovation in the near future.

ACKNOWLEDGMENTS

We thank numerous individuals that assisted with field work from 1998 through 2002, especially J. Dhundale, T. Dietrich, K. Hood, S. Lampson, D. Leer, C. Lorion, C. Oyler, and N. Romero. L. M. Ganio developed software routines used for semivariogram analyses; M. Banks supported genetic analyses, providing both facilities and counseling; and D. Hockman-Wert provided GIS support. Preliminary drafts of the manuscript were reviewed by G. Larson, R. Jachowski, K. Burnett, J. Ebersole, and D. Zaroban, and their insightful comments were integrated into the final manuscript. This project was produced through the Cooperative Forest Ecosystem Research Program, with funding provided by the USGS Forest and Rangeland Ecosystem Science Center and the Oregon Department of Forestry.

REFERENCES

Bateman, D. S., R. E. Gresswell, and C. E. Torgersen. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. Journal of Freshwater Ecology 20:335–345.

Benda, L., T. J. Beechie, R. C. Wissmar, and A. Johnson. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river catchment, Washington State, USA. Canadian Journal of Fisheries and Aquatic Sciences 79:1246–1256.

Bisson, P. A., J. L. Nielsen, R. A. Palmasono, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62–73 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Cohen, W. B., T. A. Spies, R. J. Alig, D. R. Oetter, T. K. Maiersperger, and M. Fiorella. 2002. Characterizing 23 years (1972–1995) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5:122–137.

Daymet. 2004. Daily surface weather and climatalogical summaries. Daymet U.S. Data Center, University of Montana, Numerical Terradynamic Simulation Group (NTSG). Available: http://www.daymet.org/climateSummary.jsp (June 2003).

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology and Evolution 17:177–183.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. 1997. A resource in crisis: changing the measure of salmon management. Pages 411–444 *in* D. J. Stouder, P. A. Bisson, and R. J.

Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a catchment context. Environmental Management 10:199–214.

Ganio, L. M., C. E. Torgersen, and R. E. Gresswell. 2005. A geostatistical approach for describing spatial pattern in stream networks. Frontiers in Ecology and the Environment 3:138–144.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Headwater and channel networks: understanding processes and downstream linkages of headwater systems. BioScience 52:905–916.

Gresswell, R. E., D. S. Bateman, G. W. Lienkaemper, and T. J. Guy. 2004. Geospatial techniques for developing a sampling frame of watersheds across a region. Pages 517–530 *in* T. Nishida, P. J. Kailola, and C. E. Hollingworth, editors. GIS/spatial analyses in fishery and aquatic sciences (Volume 2). Fishery-Aquatic GIS Research Group, Saitama, Japan.

Guy, T. J. 2004. Landscape-scale evaluation of genetic structure among barrier-isolated populations of coastal cutthroat trout, *Oncorhynchus clarki clarki.* M.S. thesis. Oregon State University, Corvallis.

Hall, J. D., P. A. Bisson, and R. E. Gresswell. 1997. Searun cutthroat trout: biology, management, and future conservation. American Fisheries Society, Oregon Chapter, Corvallis, Oregon.

Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.

Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12:535–551.

Healey, M. C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. Pages 176–184 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Hendricks, S. R. 2002. Seasonal changes in distribution of coastal cutthroat trout in an isolated watershed. M.S. thesis. Oregon State University, Corvallis.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483–518 *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.

Hughes, R. M., S. G. Paulsen, and J. L. Stoddard. 2000. EMAP-Surface Waters: a multiassemblage, probability survey of ecological integrity in the U.S.A. Hydrobiologia 423:429–443.

Imhof, J. G., J. Fitzgibbon, and W. K. Annable. 1996. A hierarchical evaluation system for characterizing catchment ecosystems for fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):312–326.

Johnson, L. B., and S. H. Gage. 1997. Landscape approaches to the analysis of aquatic ecosystems. Freshwater Biology 37:113–132.

Kaufmann, P. R., and R. M. Hughes. 2006. Geomorphic and anthropogenic influences on fish and amphibians in Pacific Northwest coastal streams. Pages 429–455 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Kocik, J. F., and C. P. Ferreri. 1998. Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):191–200.

Kruse, C. G., W. A. Hubert., and F. J. Rahel. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. Northwest Science 75:1–11.

Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Larsen, D. P., P. R. Kaufmann, T. M. Kincaid, and N. S. Urquhart. 2004. Detecting persistent change in the habitat of salmon-bearing streams in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 61:283–291.

Latterell, J. J., R. J. Naiman, B. R. Fransen, and P. A. Bisson. 2003. Physical constraints on trout (*Oncorhynchus* spp.) distribution in the Cascade Mountains: a comparison of logged and unlogged streams. Canadian Journal of Fisheries and Aquatic Sciences 60:1007–1017.

May, C. L., and R. E. Gresswell. 2003a. Processes and rates of sediment and wood accumulation in headwater streams of the Oregon coast range, USA. Earth Surface Processes and Landforms 28: 409–494.

May, C. L., and R. E. Gresswell. 2003b. Large wood recruitment and redistribution in headwater streams in the southern Oregon coast range, U.S.A. Canadian Journal of Forest Research 33: 1352–1362.

May, C. L., and R. E. Gresswell. 2004. Spatial and temporal patterns of debris flow deposition in the Oregon coast range, USA. Geomorphology 57: 135–149.

Montgomery, D. R., and J. B. Buffington. 1997. Channel-reach morphology in mountain drainage catchments. Geographic Society of America Bulletin 109:596–611.

Moore, K. M. S., K. K. Jones, and J. M. Dambacher. 1997. Methods for stream habitat surveys. Oregon Department of Fish and Wildlife, Information Report 97–4, Portland.

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.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

Northcote, T. G. 1997. Potamodromy in Salmonidae - living and moving in the fast lane. North American Journal of Fisheries Management 17:1029–1045.

Pater, D. E., S. A. Bryce, T. D. Thorson, J. Kagan, C. Chectaresppell, J. M. Omernik, S. H. Azevedo, and A. J. Woods. 1998. Ecoregions of Western Washington and Oregon. U.S. Geological Survey, scale 1: 350:000, Reston, Virginia.

Paulsen, S., R. M. Hughes, and D. P. Larsen. 1998. Critical elements in describing and understanding our nation's aquatic resources. Journal of the American Water Resources Association 34: 995–1005.

Pearcy, W. G. 1992. Ocean ecology of north Pacific salmonids. University of Washington Press, Seattle.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269:331–334.

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 334–349 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Romero, N., R. E. Gresswell, and J. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797–1807.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62:277–314.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1990. Elementary survey sampling. PWS-Kent Publishing Company, Boston.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, New York.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

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

Taylor, P. W., and S. D. Roberts. 1999. Clove oil: an alternative anaesthetic for aquaculture. North American Journal of Aquaculture 61:150–155.

Torgersen, C. E., C. V. Baxter, H. W. Li, and B. A. McIntosh. 2006. Landscape influences on longitudinal patterns of river fishes: spatially continuous analysis of fish–habitat relationships. Pages 473–492 in R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Torgersen, C. E., R. E. Gresswell, and D. S. Bateman. 2004. Pattern detection in stream networks: Quantifying spatial variability in fish distribution. Pages 405–420 *in* T. Nishida, P. J. Kailola, and C. E. Hollingworth, editors. GIS/spatial analyses in fishery and aquatic sciences (volume 2). Fishery-Aquatic GIS Research Group, Saitama, Japan.

Trotter, P. C. 1989. Coastal cutthroat trout: a life history compendium. Transactions of the American Fisheries Society 118:463–473.

Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: theory development and testing. Landscape Ecology 3:245–252.

Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Factors influencing within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628–637.