Pattern detection in stream networks: quantifying spatial variability in fish distribution

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Abstract

Biological and physical properties of rivers and streams are inherently difficult to sample and visualize at the resolution and extent necessary to detect fine-scale distributional patterns over large areas. Satellite imagery and broad-scale fish survey methods are effective for quantifying spatial variability in biological and physical variables over a range of scales in marine environments but are often too coarse in resolution to address conservation needs in inland fisheries management. We present methods for sampling and analyzing multiscale, spatially continuous patterns of stream fishes and physical habitat in small- to medium-size watersheds (500–1000 hectares). Geospatial tools, including geographic information system (GIS) software such as ArcInfo dynamic segmentation and ArcScene 3D analyst modules, were used to display complex biological and physical datasets. These tools also provided spatial referencing information (e.g. Cartesian and route-measure coordinates) necessary for
conducting geostatistical analyses of spatial patterns (empirical semivariograms and wavelet analysis) in linear stream networks. Graphical depiction of fish distribution along a one-dimensional longitudinal profile and throughout the stream network (superimposed on a 10-metre digital elevation model) provided the spatial context necessary for describing and interpreting the relationship between landscape pattern and the distribution of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in western Oregon, U.S.A. The distribution of coastal cutthroat trout was highly autocorrelated and exhibited a spherical semivariogram with a defined nugget, sill, and range. Wavelet analysis of the main-stem longitudinal profile revealed periodicity in trout distribution at three nested spatial scales corresponding ostensibly to landscape disturbances and the spacing of tributary junctions.

**Key words**

coastal cutthroat trout, dynamic segmentation, empirical semivariogram, fish distribution, network, *Oncorhynchus clarki clarki*, pattern detection, spatial variability, wavelet analysis.

1. **Introduction**

Pattern detection is an important process in science because it provides the raw material from which research questions arise and hypotheses are developed. Increasing our ability to detect patterns in natural ecosystems not only helps us evaluate current models of ecological understanding, but also enables us to discover new patterns (Lawton, 1996). In fisheries and aquatic sciences, it is important to develop new approaches that maximize pattern detection in three dimensions, rather than the typical one- or two-dimensional graphical representations of rivers and large water bodies (Kracker, 1999). Because ecological phenomena are contingent on the spatial scale and context of observation, it is also necessary to collect data over a broad extent and at as fine a resolution as possible so that our ability to detect patterns across multiple scales is maximized (Schneider, 2001).

Stream fishes are inherently difficult to sample at the resolution and extent necessary to detect fine-scale distributional patterns over large areas. Satellite imagery and broad-scale fish survey methods used in large lakes and marine environments are often too coarse in resolution to address conservation needs in inland fisheries management. In fact, current methods for monitoring trends in freshwater fish populations may not be sufficient for detecting impacts and implementing corrective
actions before sensitive taxa are reduced to low population levels (Ham and Pearsons, 2000). The coastal cutthroat trout (Oncorhynchus clarki clarki), which occurs in watersheds of the Pacific Northwest (U.S.A.) from southern Alaska to northern California (Trotter, 1989), is one of several species of native salmonids for which changes in population abundance are particularly difficult to detect. Compared to other species in the same genus (e.g. rainbow trout, O. mykiss, coho, O. kisutch and chinook salmon, O. tshawytscha), relatively little is known about the habitat requirements of coastal cutthroat trout. This lack of information on the factors influencing the distribution and abundance of the species is unfortunate because several studies have shown that cutthroat trout are very susceptible to pressure from recreational angling (Gresswell and Harding, 1997) and habitat degradation resulting from timber harvesting (Reeves et al. 1997).

Coastal cutthroat trout are widespread in western Oregon and are the dominant salmonid in headwater streams of the Coast Range and Cascades mountains. The species exhibits a complex life history with non-migratory, potamodromous and anadromous forms that are integrated genetically but still poorly understood in terms of gene flow among populations (Wenburg and Bentzen, 2001). The importance of small, headwater streams as rearing habitat for non-migratory and migratory populations suggests that patterns of land management practices could have a significant impact on the long-term viability of cutthroat trout populations in coastal watersheds (Rosenfeld et al. 2002). Unfortunately, specific information on the distribution and abundance of coastal cutthroat trout with respect to landscape patterns is limited (Hooton, 1997). Spatially explicit data on trout distribution in individual watersheds are needed to identify trout population responses to habitat alteration (caused by, e.g., road construction, timber harvesting, and riparian modifications) at intermediate spatial and temporal scales where managers are most capable of effecting change (Fausch et al. 2002).

We present methods for sampling and analyzing multiscale, spatially continuous distribution patterns of coastal cutthroat trout in small- to medium-sized mountain watersheds (500–1000 hectares [ha]). Our objective was to quantify the distribution of coastal cutthroat trout at a resolution and extent previously unmatched in the study of stream fishes. We hypothesized that the spatial structure of coastal cutthroat trout distribution can be quantified with geostatistical modeling, and that intensive, spatially continuous sampling is necessary for detecting complex, context-dependent associations between trout abundance and landscape patterns at multiple spatial scales. Specifically, we were interested in (1) developing geospatial methods for visualizing landscape pattern and fish distribution, (2) quantifying spatial variation in fish
abundance in stream networks, and (3) identifying potential influences of forest and watershed management practices on coastal cutthroat trout distribution over a range of spatial scales.

2. Methods

2.1 Study area

This study was conducted as part of an on-going research program evaluating the effects of landscape pattern on the distribution of coastal cutthroat trout in headwater streams (Gresswell et al. in press). Over the period 1998–2001, spatially continuous data were collected on coastal cutthroat trout abundance and physical stream habitat in watersheds throughout western Oregon, totaling 230 linear kilometers (km) of surveyed stream (Map 1). Camp Creek, a tributary to the Umpqua River, serves as a temporal reference watershed for the study and has been sampled annually from 1998 through 2003. Although data are still being processed in the other study watersheds, Camp Creek provides a model for methods development and hypothesis testing.

Upper Camp Creek is a third-order watershed (2200 ha) located in the Coast Range mountains of western Oregon (Map 1). The watershed ranges in elevation from 170 metres (m) to 780 m. It is vegetated with mixed conifer forest on the upslope (Douglas-fir, *Pseudotsuga menziesii*; western red cedar, *Thuja plicata*; and western hemlock, *Tsuga heterophylla*) and broadleaf communities in the riparian corridor (red alder, *Alnus rubra*; vine maple, *Acer circinatum*; and bigleaf maple, *Acer macrophyllum*). The combination of steep topography, high rainfall (130 centimetres/year), and sedimentary geology makes Camp Creek, like other headwater basins in the Coast Range mountains, prone to disturbances such as debris flows and landslides. Timber harvesting has occurred in approximately 50% of the basin since the 1940s, but currently the watershed is designated as a late-successional forest reserve aimed at preserving and promoting the reestablishment of old-growth conifers (FEMAT, 1993). At the downstream boundary of the study area, a four-metre-high barrier waterfall blocks the upstream migration of anadromous salmonids and effectively isolates the headwater fish community, which consists of non-migratory coastal cutthroat trout and one species of sculpin (*Cottus perplexus*).

2.2 Field surveys of physical habitat and fish distribution

Stream segments were identified for survey based on the potential extent of coastal cutthroat trout distribution, which was determined from a
database of trout distribution and the locations of barriers to upstream movement (Gresswell et al. in press). After stream segments were identified for survey, a census of stream segment characteristics (valley floor type, channel constraint, riparian vegetation), reach morphology (Montgomery and Buffington, 1997) and channel unit type (e.g. pool, riffle-rapid, cascade: Bisson et al., 1982) was completed. Physical variables including habitat-unit size (e.g. length, depth, and width), substrate size class, channel type, valley segment type and woody debris accumulations were recorded for all habitat units. Visual estimates of channel-unit length and width were corrected for observer bias with a subset of verified field measurements (Hankin and Reeves, 1988). To facilitate georeferencing of surveyed segments in a geographic information system (GIS), the locations of tributary junctions and road crossings were noted on 1:24,000-scale topographic maps and cross-referenced with the habitat census data.

Map 1. Study area in western Oregon, USA. Camp Creek is one of 41 watersheds surveyed to assess landscape pattern and the distribution of coastal cutthroat trout.
Fish sampling was conducted to obtain detailed information on fish distribution. The relative abundance of young-of-year and adult (≥ 1 year) coastal cutthroat trout in all pools and cascades was assessed with single-pass electrofishing (Jones and Stockwell, 1995). To identify the upstream extent of coastal cutthroat trout distribution, tributaries and the main-stem segment were sampled for 50–300 m (approximately 10–40 individual pool sample units) beyond the point at which no more fish were detected. All fish were identified and the coastal cutthroat trout were measured (fork length to ±1 millimetre [mm]) and weighed (±0.1 grams [g]). Scale samples were collected from five to ten fish in each 10-mm length category for age determination. The complete survey of physical habitat and fish distribution in Camp Creek was completed in eight non-consecutive days (11–25 August 2001). The field crew required to survey 11 km of stream included 14 biology technicians: two groups of two or three technicians each working simultaneously to conduct physical habitat surveys, and two or three groups of three to five technicians each sampling fish.

2.3 Data processing and GIS

Prior to incorporation in a GIS, stream survey and fish abundance data were entered in a relational database composed of hierarchically-linked basin, segment, reach, and unit tables in Microsoft Access. Visual estimates of channel-unit length and width were corrected for observer bias by applying a linear correction factor derived from comparisons of estimated versus measured channel dimensions (Hankin and Reeves, 1988). Dynamic-segmentation methodology (ESRI, 2001) was used to georeference the stream survey data to the stream network and to construct a spatially explicit, relational database for each watershed (Radko, 1997; Jones et al. 2001). Landmarks such as bridge crossings and tributary junctions were used to calibrate the digital stream length to the actual surveyed stream length. Consecutively numbered habitat units and associated attributes, including unit dimensions, woody debris, substrate, and fish numbers, were then joined to the calibrated stream network by establishing a dynamic link between the Microsoft Access database and ArcGIS (ESRI, 2001).

A three-dimensional map of landscape terrain was generated with 10-m digital elevation model (DEM) and the ArcScene 3D analyst module of ArcGIS. Overlays of fish abundance and stream habitat data on the three-dimensional terrain provided a means of assessing patterns of fish abundance and channel morphology in a landscape context. The abundances of trout at each sample point (pool or cascade) were extruded vertically in ArcScene to produce a graphical representation of fish distribution throughout the stream network. To view and record
animations of landscape patterns and the spatial distribution of trout from different angles, we used the MapAnimator 3D extension for ArcGIS.

2.4 Geostatistical analysis

Proximity in the linear stream network was defined as the distance between points along the stream path, or the network distance. To model spatial dependence in coastal cutthroat trout distribution, we used network distance rather than the Euclidean distance typically applied in geostatistical analysis of two-dimensional surfaces (Rossi et al. 1992). A square distance matrix of all possible network distances separating the 609 units sampled in Camp Creek was calculated in Arc/Info with ArcPlot commands netcover, stops, and nodedistance (ESRI, 1996). A spatial weights matrix was created that contained the network distances between 370,881 sample-unit pairs. An empirical semivariogram was computed by calculating half the average squared difference between points in each distance class interval (20 m) and plotting this value versus the mean separation distance between sample points, or lag (Legendre and Fortin, 1989; Palmer, 2002). The number of distance pairs used to calculate semivariance at each distance class interval ranged from 731 to 961. A spherical model was fitted to the resulting empirical semivariogram in S-PLUS statistical software to obtain parameter estimates for the variogram range and sill (S-PLUS 2002). The spatial module of S-PLUS calculated the spherical model using a local minimizer for smooth non-linear functions subject to bounded parameters (L. M. Ganio, Oregon State University, unpublished data).

To evaluate the hierarchical spatial structure in the longitudinal distribution of coastal cutthroat trout, the wavelet power function was calculated relative to distance upstream along the main-stem channel of Camp Creek. Wavelet analysis is a statistical technique used to explore spatial structure as a function of scale and position along a one-dimensional transect. The principal advantage of wavelet analysis over the semivariogram is that the dominant scales of variation can be directly related to position along the transect, making it possible to identify potential environmental factors that influence spatial structure in the modeled variable (Bradshaw and Spies, 1992). Bradshaw and Spies (1992) found that the Gaussian wavelet model was most appropriate for data that are characterized by sequential peaks and troughs. Fish distribution data in Camp Creek fitted this description and were modeled accordingly with Interactive Wavelet Analysis software provided by Torrence and Compo (1998). The process of wavelet analysis involved a moving window of a specific size and shape (i.e. the ‘wavelet’ which in this case approximated the shape of a Gaussian curve) that proceeded along the data transect. As the moving window detected patterns in the
data with a like size and shape, the value of the wavelet power function increased. To evaluate spatial structure at multiple scales, many runs were performed, each with an increasingly larger window size. Detailed mathematical descriptions of wavelet analysis and explanations of its application in ecology can be found in Bradshaw and Spies (1992) and Csillag and Kabos (2002).

3. Results

3.1 Visualizing pattern in three-dimensional networks

Three-dimensional visualization and animation techniques were highly effective for evaluating landscape pattern and the spatial distribution of coastal cutthroat trout at multiple spatial scales (Map 2). Analysis of spatial heterogeneity in fish distribution in a network context was essential for formulating hypotheses about fish–habitat relationships that are context and scale dependent. Fish distribution was less heterogeneous in the tributaries than in the main stem of Camp Creek; however, there was no apparent longitudinal trend in the variation or abundance of trout in the main stem. Visual comparison of historic debris flow locations with fish distribution along the main stem indicated the potential for associations between trout abundance patterns and large-scale landscape features. Analysis of fish distribution in a landscape context was particularly useful for developing hypotheses and identifying appropriate methods for quantitative analysis. For example, the distribution of coastal cutthroat trout was patchy at fine and coarse scales, indicating that the data were spatially autocorrelated and would require geostatistical analysis prior to statistical modeling to account for spatial dependence. Pools with similar morphology (e.g. width, depth, and substrate composition) often contained different numbers of trout depending on the location of the habitat unit within the basin.

3.2 Spatial variability in fish distribution

Spatially continuous sampling of stream habitat and fish abundance throughout the network revealed a high degree of spatial variation that was difficult to evaluate through visual analysis alone. Fine-scale variation in fish distribution masked patterns at larger scales; thus, more sophisticated approaches were required to quantify underlying data structure. For example, geostatistical analysis was necessary to quantify spatial structure in the distribution of coastal cutthroat trout and identify the range of distances over which trout abundance was autocorrelated.
The distribution of coastal cutthroat trout in Camp Creek was strongly autocorrelated as a function of separation distance and fitted a spherical theoretical variogram model with a range, sill, and nugget of 950 m, 6.8 m, and 3.0 m, respectively (Figure 1). The sill is the horizontal asymptote of the variogram, the range is the separation distance beyond which any two sample points may be considered spatially independent, and the nugget is the y-intercept. In Camp Creek, coastal cutthroat trout abundance was spatially autocorrelated at distances less than 950 m. The predictable spatial variance structure in the distribution of coastal cutthroat trout in Camp Creek was important for two reasons: (1) it suggested underlying processes that may be unique to the physical template of the watershed, and (2) it allowed the effects of spatial dependence to be included in more complex, spatially explicit statistical models.
To evaluate the hierarchical patterns in the main-stem channel, the wavelet power function was plotted relative to distance upstream and the period, or spatial scale of variation (Figures 2a and 2b). Coastal cutthroat trout exhibited periodicity at three nested spatial scales: fine (less than 500 m), intermediate (500–2000 m) and large (more than 2000 m). Fine-scale variation in trout abundance was associated with changes in channel gradient and the distribution of pools and riffles at the reach scale. Intermediate-scale patterns approximated the spatial extent of stream segments separating tributary junctions and geomorphic constraints to fish movement. Large-scale patterns in fish distribution identified in wavelet analysis were related to the interaction of processes at fine and intermediate scales and to the overall geomorphic pattern of the stream network (Figure 2b).
4. Discussion

Increasing the resolution and extent of sampling revealed unexpected patterns in the distribution and abundance of coastal cutthroat trout in a headwater stream. Although it is generally recognized that ecological
data are spatially autocorrelated (Legendre and Fortin, 1989) we did not anticipate that the relationship could be modeled so precisely, or that including the network topology in the analysis would be so important for quantifying spatial variability in fish distribution. Spatial analysis of stream networks is still relatively uncommon due to the difficulty of calculating a matrix of network distances and to the lack of commercially available software that can perform such calculations in a single geostatistical package. However, the benefits of applying a network approach in fisheries and aquatic sciences are rapidly becoming more apparent (Little et al. 1997; Gardner et al. 2003).

The primary objectives of this study were to develop geospatial methods for visualizing landscape pattern and fish distribution and to quantify spatial variation in fish abundance in stream networks. However, the ultimate goal of the research program is to identify influences of forest and watershed management practices on the distribution of coastal cutthroat trout distribution. The geospatial and statistical methods developed in this study provide the means to perceive the influences of landscape pattern on the distribution of coastal cutthroat trout at multiple spatial scales within reaches (10^2 m), segments (10^3 m) and throughout entire stream networks (10^4 m). With the ability to quantify spatial variability in fish distribution in the semivariogram, empirical models can be developed that incorporate spatial dependence and thereby provide a more accurate representation of fish–habitat relationships (Hobert et al. 1997). Moreover, the parameters of the semivariogram (the range and sill) can be compared among basins to evaluate the relationship between landscape pattern and spatial heterogeneity in coastal cutthroat trout distribution. Wavelet analysis also has potential for detecting complex patterns in fish distribution, but this method is a relatively new tool in ecological analysis and will need to be adapted for detecting spatial patterns in a stream network as opposed to a single stream channel.

The methods presented in this study represent the first steps towards developing a quantitative approach to assessing the effects of landscape pattern on fish distribution. Thus, the next challenge is to build predictive models that will be capable of testing hypotheses about associations and causal relationships between stream fishes and their environment.

Given the complexity of natural and anthropogenic patterns on the landscape, it is unlikely that investigation at any single spatial scale will be effective for detecting associations between fish abundance and land-use practices. Thus, a more spatially continuous approach to sampling stream fishes provides the flexibility to detect patterns over a range of scales (Fausch et al. 2002). Landscape patterns in the Pacific
Northwest region, U.S.A. have been influenced by both natural and anthropogenic disturbances that have created a patchwork of young and old conifer forests interlaced with ribbons of deciduous riparian corridors (Garman et al. 1999). Because coastal cutthroat trout in headwater streams are dependent on the presence and structure of large woody debris to provide cover from dramatic flood events (Harvey, 1998; Connolly and Hall, 1999) it is probable that patterns in fish abundance will reflect the mosaic structure of anthropogenic influences and the natural physiographic template. However, detecting differences in the spatial pattern of fish abundance with respect to landscape structure may be difficult with existing site-based methods for sampling stream fishes. Until recently, traditional sampling methods in stream fish ecology have been too coarse to detect spatial patterns and associations in fish distribution and, therefore, may be inappropriate for evaluating human impacts on complex ecosystems (Ham and Pearsons, 2000). The continued development and testing of alternative sampling approaches for assessing spatial patterns in fish distribution such as single-pass electrofishing (Jones and Stockwell, 1995; Kruse et al. 1998) and snorkeling (Mullner et al. 1998; Roni and Fayram, 2000) will be important for increasing our understanding of stream fishes and evaluating human impacts in aquatic ecosystems (Angermeier and Smogor, 1995).

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