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Modelling of landscape variables at multiple extents to predict fine sediments and suitable habitat for *Tubifex tubifex* in a stream system

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SUMMARY

1. Aggregations of fine sediments are a suitable proxy for the presence and abundance of *Tubifex tubifex*, one of the obligate hosts in the parasitic life cycle that causes salmonid whirling disease (*Myxobolus cerebralis*).
2. To determine and evaluate practical approaches to predict fine sediments (<2 mm diameter) that could support *Tubifex* spp. aggregations, we measured habitat features in a catchment with field measures and metrics derived from digital data sets and geospatial tools at three different spatial extents (m^2) within a hierarchical structure.
3. We used linear mixed models to test plausible candidate models that best explained the presence of fine sediments measured in stream surveys with metrics from several spatial extents.
4. The percent slow water habitat measured at the finest extent provided the best model to predict the likely presence of fine sediments. The most influential models to predict fine sediments using landscape metrics measured at broader extents included variables that measure the percentage land cover in conifer or agriculture, specifically, decreases in conifer cover and increases in agriculture.
5. The overall best-fitting model of the presence of fine sediments in a stream reach combined variables measured and operating at different spatial extents.
6. Landscape features modelled within a hierarchical framework may be useful tools to evaluate and prioritise areas with fine sediments that may be at risk of infection by *Myxobolus cerebralis*.

Keywords: benthos, ecosystem, erosion/sedimentation/landuse, fish, geospatial, parasites/pathogens, physical habitat modelling

Introduction

Tubifex tubifex Müller (Annelida: Oligochaeta: Tubificidae) is a tubificid oligochaete found in a variety of aquatic habitat types (Brinkhurst, 1996). *Tubifex tubifex* is one of the obligate hosts in the life cycle of *Myxobolus cerebralis* Höfer (Myxozoa: Myxosporea: Myxobolidae), the causative agent of salmonid whirling disease. This European fish parasite was inadvertently introduced to North America within regions of susceptible and native fish hosts. Inside *T. tubifex*, *M. cerebralis* emerges from spores and attaches to the lining of the worm intestine (Brinkhurst, 1996). After approximately 90 days, the parasite develops into the triactinomyxon (TAM) stage and is egested from the worm into the water column.

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TAMs released into the water infect susceptible salmonid hosts by penetrating the epithelial cells. The parasite migrates through peripheral nerves ultimately ending in the spinal cord and cranial region (Hedrick & El-Matbouli, 2002). With no natural immunity to the parasite, many fish populations in western North America have been negatively affected (Bartholomew & Reno, 2002; Krueger *et al.*, 2006). Since the fish hosts are several, and the obligate invertebrate host is only *T. tubifex*, predicting the likely habitat for the oligochaete host may be a preferred way to determine areas of highest risk for infection within catchments (Hiner & Moffitt, 2002; Schisler & Bergersen, 2002; Krueger *et al.*, 2006).

Tubificid oligochaetes occur in many aquatic benthic habitats (Reynoldson, 1987); however, substrate is believed to be a primary factor influencing the abundance and distribution of *T. tubifex* (Lazim & Learner, 1987). Fine substrates are favoured by *T. tubifex* and are common in stream habitats that have been incised and widened. Such areas often have reduced riparian shade and tend to support higher stream temperatures and lower oxygen concentrations and these conditions favour *T. tubifex* over other invertebrate species (Schisler & Bergersen, 2002). Broad-scale landscape features have been associated with sediment depositions at local levels (Allan, Erickson & Fay, 1997) and could therefore influence the likelihood of *T. tubifex* presence. Stream habitat variables such as surface slope and sediment proportions that predict the presence of *T. tubifex* have been shown to vary with spatial extent (Anlauf & Moffitt, 2008). A synergism among measures taken at several spatial scales may be useful in predicting *T. tubifex.* Further, although direct influence of some variables may not always be discernable, the impact of certain habitat features can be viewed through intermediate pathways.

Other researchers have predicted the likely distribution of the fish parasite *M. cerebralis* using habitat variables measured within a catchment (Isaak & Hubert, 1999; Hiner & Moffitt, 2002). The variation in prevalence and the severity of infection from the parasite are reliant on the interactions between the pathogen, its hosts and the environment (Reno, 1998). The features of the physical environment are probably the least defined components of the *M. cerebralis* life cycle, and the benefits of understanding those gradients will aid in the management of affected populations and ecosystems as a whole (Hedrick, 1998; Zendt & Bergersen, 2000; Anlauf & Moffitt, 2008).

Combining variables measured or estimated at large spatial scales (landscape) with variables measured or estimated at finer, local scales (stream reach) in modelling instream habitat provides a further opportunity to reveal controlling mechanisms (Allan & Johnson, 1997). The relationship between *T. tubifex* and fine substrates has been documented (Lazim & Learner, 1987; Kaeser & Sharpe, 2006; Anlauf & Moffitt, 2008). Our study, therefore, pursued ways to predict and understand variables that influenced the quantity of fine sediments (particle size <2 mm diameter), as a surrogate for *T. tubifex* populations. We developed and tested habitat models to predict the quantity of fine sediments in streams using habitat features measured at multiple spatial extents: 500-m, 2000-m and the entire extent of the upstream segment (total length; hereafter referred to as the TL) above the start of each stream reach where fine sediments were measured. Our objectives were to compare model results when landscape characteristics of the same resolution were summarised at three spatial extents, and to determine whether the incorporation of both local and landscape habitat characteristics improved predictive models.

Methods

Study area

We conducted this study in the Pahsimeroi River drainage basin, a tributary of the Salmon River, located in eastern Idaho, U.S.A., between the Lost River and Lemhi mountain ranges (Fig. 1). The Pahsimeroi valley drains approximately 2175 km^2 with elevations ranging from 1413 to 3846 m and average annual flows in the mainstem Pahsimeroi River during the study period ranging from 6.091 m^3 s^{-1} in 2001 to 4.717 m^3 s^{-1} in 2004. Like many areas of the western intermountain region, the Pahsimeroi River is influenced by local land-use practices including irrigated agriculture and livestock grazing (Bureau of Land Management, 1999; Colvin & Moffitt, 2008). Land cover and vegetation are comprised mostly of sagebrush steppe, grassland communities in the valley and conifer communities in upland mountain drainages (Fig. 1). The Pahsim-

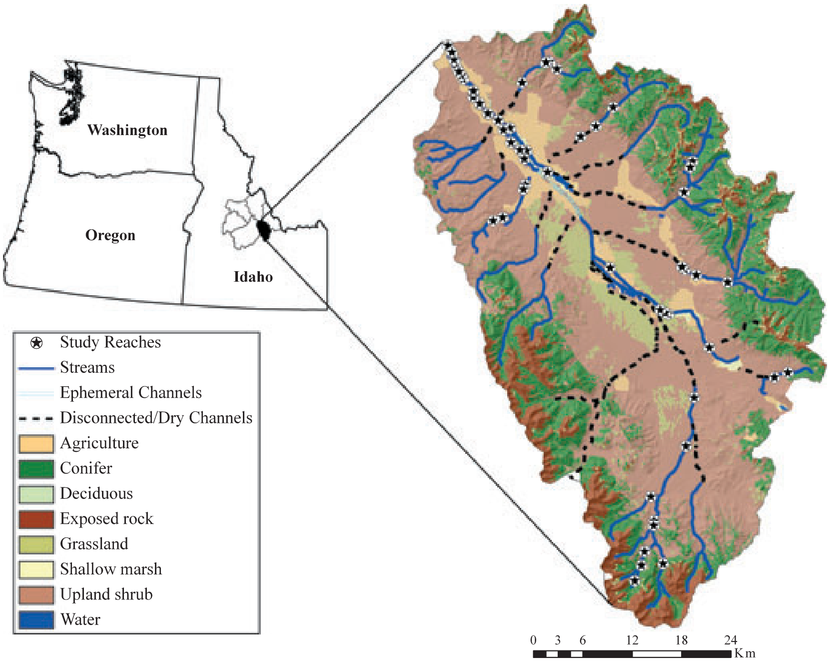

Fig. 1 Major land cover types represented in the Pahsimeroi River drainage (Idaho GAP Analysis 1999) and sample site locations (n = 56).

eroi catchment has been selected as high priority for restoration to enhance populations of threatened and endangered salmonids (Shumar, Reaney & Herron, 2001; National Oceanographic and Atmospheric Administration, 2004).

The underlying geology of the subbasin varies; much of the valley and adjacent mountain ranges are composed of metamorphosed gneiss and schist, with both sedimentary (limestone and dolomite) and volcanic (fine grained basalt) rock deposits (Young & Harenberg, 1973; Alt & Hyndman, 1989). Glacial, alluvial and fluvial deposits blanket the valley floor, and the principal aquifer in the valley is contained in the alluvium (Young & Harenberg, 1973). The mainstem Pahsimeroi River consists of three distinct sections disconnected due predominantly to subsurface flow. The upper and middle sections of the Pahsimeroi River are disconnected year-round while the middle and lower Pahsimeroi River sections have an intermittent connection during certain times of the year. The tributaries in the drainage basin exit confined canyon corridors and enter extensive alluvial deposits. Due to the highly porous nature of the coarse alluvium, the majority of the streams within the subbasin exhibit large percolation losses. As a result, the majority of these tributaries contribute little to the surficial flow of the Pahsimeroi River (Bureau of Land Management, 1999; Colvin & Moffitt, 2008). Additionally, much of the water from these channels is diverted to irrigation canals as the streams enter the large alluvial fans. The water that feeds the baseflow of the mainstem is derived primarily from subsurface flow and emerges as springs in the Pahsimeroi valley (Young & Harenberg, 1973; Colvin & Moffitt, 2008).

Study stream reaches

To estimate and measure instream characteristics, we created points in a geospatial (GIS) along a 1 : 24 000 scale stream coverage. Each point became the start of a potential study reach site and had associated with it a site number and northing and easting UTM coordinates. We then parsed the drainage into six strata based on stream slopes derived from a 10-m digital elevation model, and used a stratified random sampling design to select study reach sites from each slope stratum. The reach slope strata (percent slope) were defined as follows: I = 0–0.5%; II = >0.5–1.0%; III = >1.0–1.5%; IV = >1.5–2.0%; V = >2.0–4.0% and VI = >4.0–6.0%. We selected sixty 100-m stream reaches for instream surveys. The number of reaches surveyed by strata were: 17, 15, 5, 9, 10 and 4, for stratum I, II, III, IV, V and VI respectively. The intensity of sampling within each stratum was based on the proportionate distribution of gradients throughout the drainage. We measured and evaluated the aquatic habitat during late May–September 2003 using field methods described in Anlauf & Moffitt (2008).

Habitat variables

Instream habitat characteristics were measured within specific habitat units defined and characterised by similar morphological and hydrological features, i.e. pools or riffles (Bisson *et al*., 1982; Frissell *et al*., 1986; Hawkins *et al*., 1993), and summarised within 100-m stream reaches. The 100-m reach served as our local or finest spatial extent. We obtained an empirical estimate of fine sediments based on visual observation of the percent distribution of streambed area, relative to the total habitat area, consisting of sediments <2 mm in diameter (Hausle & Coble, 1976; Everest *et al*., 1987). We obtained an average value for each reach and this value became our response variable. We selected three habitat variables as our local scale predictors, each of which was measured in the field and summarised within the 100 m reach: width-depth ratio, percent slow water habitat and percent slope (Table 1). These variables were chosen given their perceived influence over fine sediments and because they are commonly measured and summarised in stream habitat surveys.

Geospatial habitat data were derived from existing data sources (Table 1) and measured within a 100-m stream buffer on either side of the stream at three stream segment lengths: 500-m, 2000-m and the entire extent of the upstream segment (TL) above the start of each stream reach where fine sediments were measured (Fig. 2). Geospatial data summarised within this buffered stream segment include land cover/use and geology variables, total upstream length and stream slope (Table 1).

Table 1 Description of reach (instream) and landscape (GIS-derived) habitat data used in analyses. Reach habitat was summarised for a 100-m reach. Landscape habitat was calculated within a 100-m buffer along both sides of specified stream segments. Percent fine sediments was the dependent variable in all analyses

Habitat variable	Description of measure	Data source
Instream		
Percent fine sediments	Proportion of stream bed area classified as sediments <2 mm	Measured in field
Percent reach slope	Average stream slope calculated for a 100-m reach length	Gradient generated in each grid cell from a USGS 10-m DEM
Percent slow habitat	Proportion of total habitat area classified as pools or glides	Measured in field
Width : depth ratio	Ratio of wetted width and average depth along transects	Measured in field
GIS-derived		
Percent agriculture	Area classified as agriculture (row crops, irrigated pasture and low intensity urban)	Derived from land cover/use layer (Idaho GAP Analysis 1999); (http://www.wildlife.uidaho.edu/idgap/index.html)
Percent conifer cover	Area classified as forest; includes subalpine fir, Douglas fir, Subalpine pine, mixed subalpine forests	The land cover variables were combined into like groupings based on similar flora types listed in the metadata
Percent shrub/forb cover	Area classified as rangeland (warm mesic shrubs, curlleaf mountain mahogany, salt desert shrub, mountain big sagebrush, low sagebrush, basin WY sagebrush, mountain low sagebrush, graminoid-forb riparian and shrub riparian)	
Percent surficial deposits	Area classified quaternary surficial deposits; includes continental deposit rock type or alluvium fill (unconsolidated deposits of cobble, gravel, sand, silt, clay)	Idaho Geological Survey; (http://www.idahogeology.org)
Upstream length	Total channel length upstream of 100 m reach	1 : 24 000 digitised stream layer from USGS topographic maps
Percent stream slope	Average stream slope calculated upstream of 100 m reach	Gradient generated in each grid cell from a USGS 10 m DEM

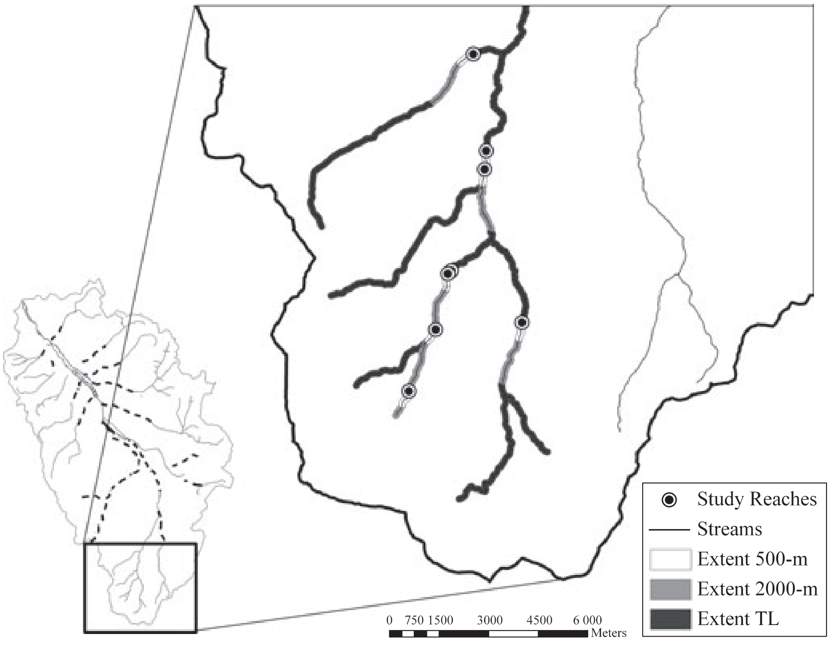

Fig. 2 Stream buffers at the 500-m, 2000-m and TL extents from which geospatial landscape data were derived and subsequently used in modelling in the Pahsimeroi River drainage basin.

The extent of upstream length within the drainage was calculated as a surrogate for catchment area. We used this variable in habitat models because the nature of flow discontinuity in the Pahsimeroi River drainage prohibited an accurate use of the traditional catchment approach for understanding hydraulic connections in the system (Colvin & Moffitt, 2008). Upstream length expressed the total upstream distance from a study reach including all adjacent tributaries theoretically contributing to total stream flow. Total upstream length was a relative metric corresponding to the total upstream wetted habitat present. When calculating this metric, we excluded stream segments that were dry or disconnected due to ephemeral flow. To validate the use of this metric as a surrogate for catchment area, the correlation between upstream total length and catchment area was assessed for a subset of sites. Pearson correlation coefficients were determined for data from a subset of catchments that could be accurately delineated in the Pahsimeroi River drainage ($n = 8$; $r = 0.980$).

Statistical analysis

Linear models were fit with the procedure PROC MIXED in SAS (SAS Institute Inc., 2000) using the local reach and geospatial landscape variables chosen and theorised to influence the quantity of fine sediments estimated within aquatic habitats. The percent of fine sediments measured within a reach was modelled as the response variable on continuous measures of stream habitat at the local extent (100-m reach) and landscape habitat at three broader spatial extents (500-m, 2000-m and TL). Combined multiple-scale models, including variables at both the local and landscape extents, were then developed using variables that appeared in the best approximating models from the preceding analyses. To meet normality assumptions, an arc sine square root transformation was applied to the fine sediment response. To ensure assumptions of independence were not violated, multiple landscape extents (500-m, 2000-m and TL) were not included in the same model as the variables estimated within the buffers at these extents overlapped (Fig. 2).

Model development, fitting and selection

We first evaluated single-variable models at each of the spatial extents. Multi-variable models were then evaluated at each extent using combinations of variables that appeared in the best single-variable models. A condition index was evaluated for the set of variables in each of the models to identify those with high collinearity (Belsley, Kuh & Welsch, 1982). Those models with a condition index <10 were retained. Multiple-extent models were then developed using the predictors that appeared in the best reach and landscape models. When developing multi-variable candidate models, a maximum of two predictor variables were included in each model (with exception to the global model) due to the instability associated with overfitting or over-parameterising (Burnham & Anderson, 2002).

For all models developed at each spatial extent (100-m, 500-m, 2000-m and TL), we concluded that the predictive capabilities were effective if the global model fit the data based on the r-square and root mean square error (RMSE) values. To select the most plausible model(s), Akaike Information Criteria (AIC) were used. We used the small sample approximation, $AIC_{c,}$ because the sample size to predictor ratio was 18. We considered models with ΔAIC values less than or equal to three as competing models. The relative plausibility of each model was then obtained based on the weight of evidence (Akaike weights, w_i) relative to the best approximating model (Burnham & Anderson, 2002; Littell *et al.*, 2006).

To incorporate probable spatial dependence occurring within the dataset, each reach on the same stream was assigned to a unique group and the degree of spatial dependence was modelled within each group. We examined the residuals of each global model at each of the four spatial extents within each group to evaluate the degree of spatial dependence. We assessed three different covariance structures and used AIC_c to select the best fit. The autoregressive (AR) covariance structure, which considers sites closer together to be likely more correlated to one another than sites that are further apart, provided the best fit, based on the AIC_c values (Table 2). We therefore defined this structure for all subsequent analyses.

Table 2 Covariance structure models evaluated for analysis of spatial dependence

Scale	Covariance structure	AIC_c	ΔAIC_c	w_i
500-m	Autoregressive	−262.0	0.0	0.877
	None	−257.5	4.5	0.092
	Spatial spherical	−255.3	6.7	0.030
2000-m	Autoregressive	−264.2	0.0	0.648
	None	−262.4	1.8	0.263
	Spatial spherical	−260.2	4.0	0.087
Total Length	Autoregressive	−271.4	0.0	0.801
	None	−268.0	3.4	0.146
	Spatial spherical	−265.9	5.5	0.051

Results

Fine sediment characterisation

The percent of fine sediments across all the stream reaches surveyed ranged from 0.10% to 100%. The highest mean percentage (±SD) was within stratum I (31.8 ± 22.4%) followed by stratum II (24.8 ± 18.9%) and lowest for slope stratum IV (4.1 ± 3.6%). At the finest spatial extent (100-m), the percentage of fine sediments decreased with increasing reach slope and increasing percent of slow habitat. At broader spatial extents, a strong relationship was also observed between the percentage of fine sediments and agriculture, conifer cover, surficial deposits and the average stream slope (Table 3). These relationships are reported in Table 3 for the TL extents only; similar relationships were observed at the 500-m and 2000-m spatial extents, although diminished slightly in magnitude.

Model fitting and selection of plausible models

At the finest spatial extent (100-m), the global model including all three habitat variables adequately described the data ($r^2 = 0.507$, RMSE = 0.015). Six candidate models were then evaluated, and the best model predicting the percentage of fine sediments included slow habitat ($w_i = 0.999$) (Tables 4 & 5).

Global models to predict fine sediments using geospatial habitat variables measured at the three coarse spatial extents adequately described the data for the 500-m ($r^2 = 0.466$, RMSE = 0.016), 2000-m ($r^2 = 0.498$, RMSE = 0.015) and TL ($r^2 = 0.609$, RMSE = 0.013) scales. At each of the three extents, we found the best approximating single variable models predicting the percentage of fine sediments to include agriculture. Using AIC_c criteria, we found a competing model, including conifer cover, at the 2000-m extent. At the TL extent, two competing models included conifer cover or stream slope. None of the multi-variable models evaluated appeared as competing models when compared to the single variable models using AIC_c (Tables 3 & 5).

Multiple-extent models

Multiple-extent models were developed using the variables that appeared in the best models at each of

Table 3 Pearson correlation coefficients (r) among habitat variables measured at each spatial extent (100-m reach, TL)

	Fine sediments	Slow habitat	Reach slope	Width : depth ratio	Agriculture	Conifer cover	Surficial deposits	Shrub lands	Stream slope
Fine sediments		0.658	−0.467	0.172	**0.751**	**−0.708**	0.620	−0.405	**−0.749**
Slow habitat	0.658		−0.353	0.069	0.569	−0.503	0.467	−0.352	−0.498
Reach slope	−0.467	−0.353		−0.089	−0.577	0.566	−0.640	0.291	**0.751**
Width : depth ratio	0.172	0.069	−0.089		0.314	−0.361	0.237	−0.041	−0.298
Agriculture	**0.751**	0.569	−0.577	0.314		**−0.889**	**0.714**	−0.638	**−0.909**
Conifer cover	**−0.708**	−0.503	0.566	−0.361	**−0.889**		**−0.716**	0.226	**0.864**
Surficial deposits	0.620	0.467	−0.640	0.237	**0.714**	**−0.716**		−0.365	**−0.715**
Shrub lands	−0.405	−0.352	0.291	−0.041	−0.638	0.226	−0.365		0.500
Stream slope	**−0.749**	−0.498	**0.751**	−0.298	**−0.909**	**0.864**	**−0.715**	0.500	

Bold values indicate $r \geq 0.7$ or $r \leq -0.7$, $n = 56$.

the four spatial extents. Two models produced plausible predictions at each of the three coarsest extents. Each of the models included slow habitat measured at the 100-m extent and conifer cover and agriculture measured at the 500-m, conifer cover and agriculture measured at the 2000-m, and conifer cover, agriculture, and stream slope measured at the TL extent. When we combined all models across all extents, four models were considered competing models, each of which included habitat variables estimated at the reach extent and/or the TL extent (Table 6). Models including variables estimated at the 500-m and 2000-m extents were excluded based on $\mathrm{AIC_c}$ values (Tables 5 & 6).

Discussion

The processes that structure and influence aquatic ecosystems are complex; stream systems are hierarchical, relying on landscape habitat that operates at multiple spatial extents. Aquatic systems also have a longitudinal dependence, with each successive habitat influenced by the preceding habitats (Hawkins *et al.*, 1993; Wiens, 2002). When predicting species assemblages at broader spatial extents, the communities observed may be governed by large-scale hydrological and geological patterns (Richards *et al.*, 1997; Bis, Zdanowicz & Zalewski, 2000; Sponseller, Benfield & Valett, 2001). In contrast, studies at local, finer spatial extents can often show significant variability and emphasise the importance of biological and physical factors operating on a finer scale (Allan & Johnson, 1997). Quantifying the importance of these two perspectives can only be accomplished when datasets include both landscape and site-based habitat factors (Allan & Johnson, 1997). Poff (1997) suggested that the functional relationships that exist between species and certain habitat features can be organised hierarchically and defined at differing spatial scales.

It seems intuitive that we found the proportion of slow water habitat measured at the finest spatial extent to be the best predictor of fine sediments. However, evaluations of catchments on a reach-by-

Table 4 Candidate linear mixed models posed to explain percent of fine sediments. Global models and single variable models were posed at each scale. At the landscape extent, models were evaluated at each spatial scale for a total of 21 landscape scale models. At the multi-scale level, a total of 12 multiple scale models were evaluated

- Reach (100-m)
  - Slow habitat + Reach slope + Width : depth ratio (global)
  - Slow habitat
  - Reach slope
  - Slow habitat + Percent reach slope
  - Slow habitat + Width : depth ratio
  - Reach slope + Width : depth ratio
- Landscape-GIS derived (500-m, 2000-m, TL)
  - Stream slope + Upstream length + Surficial deposits + Agriculture + Shrub/Forb cover + Conifer cover (global)
  - Conifer cover
  - Agriculture
  - Shrub/forb cover
  - Surficial deposits
  - Stream slope
  - Upstream length
- Multi-scale (reach (100-m) and most significant variables from each single extent landscape models)
  - Slow habitat + Agriculture + Conifer cover + Stream slope (global)
  - Slow habitat + Agriculture
  - Slow habitat + Conifer cover
  - Slow habitat + Stream slope

Table 5 Best approximating and competing linear mixed models explaining the percent fine sediment in at each extent; 100-m reach, 500-m, 2000-m, TL and multiple extent ($n = 56$). ΔAIC_c and w_i values are pertinent to models within each extent only

Extent	Model	r^2	RMSE	AIC_c	ΔAIC_c	w_i
Single extent						
100-m	Slow habitat	0.433	0.016	−306.3	0.00	0.999
500-m	Agriculture	0.391	0.016	−293.3	0.00	0.932
2000-m	Agriculture	0.417	0.016	−290.5	0.00	0.572
2000-m	Conifer	0.311	0.017	−289.8	0.07	0.403
TL	Agriculture	0.565	0.014	−299.5	0.00	0.543
TL	Conifer cover	0.501	0.015	−298.0	1.5	0.256
TL	Stream slope	0.561	0.014	−297.3	2.2	0.181
Multiple extents						
100-m and 500-m	Slow habitat + Conifer cover	0.509	0.015	−303.2	0.00	0.598
	Slow habitat + Agriculture	0.417	0.014	−302.4	0.80	0.417
100-m and 2000-m	Slow habitat + Agriculture	0.538	0.014	−303.4	0.00	0.514
	Slow habitat + Conifer cover	0.577	0.014	−302.9	0.50	0.400
100-m and TL	Slow habitat + Conifer cover	0.623	0.013	−309.2	0.00	0.500
	Slow habitat + Agriculture	0.643	0.012	−307.6	1.6	0.418
	Slow habitat + Stream slope	0.669	0.012	−307.4	1.8	0.378

reach approach are often not feasible. When the catchment was examined using spatial extents greater than the 100-m study reach, we found that measures of landscape cover and land use were important factors influencing the prediction of fine sediments. Our best models, based on variables derived from a GIS, were those that used explanatory variables of vegetation cover (conifer), land use (agriculture) and stream slope. Considering the processes occurring within a catchment, the TL extent appeared to be important for predicting fine sediments. In this study, we used the TL extent as a proxy for catchment area. Catchment area and habitat characterised at this scale have been shown to be important predictors of instream habitat by placing the habitat within the context of the stream network (Allan & Johnson, 1997; Richards *et al*., 1997; Feist *et al*., 2003; Allan, 2004). Additionally, this scale is often the extent at which instream data are summarised when prioritising restoration efforts and salmon recovery (Nehlson, 1997).

The inherent functional and causative relationships present among features and linkages measured at local and landscape scales have been emphasised in recent studies (Richards, Johnson & Host, 1996; Richards *et al*., 1997; Davies, Norris & Thomas, 2000; Wang, Seelbach & Hughes, 2006; Hutchens *et al*., 2009). A primary objective of our study was to improve predictions of whirling disease risk using multi-scale metrics to understand habitat. Identification of habitat factors influential in *T. tubifex* and *M. cerebralis* proliferation has been addressed previously (Hiner & Moffitt, 2002; Bartholomew *et al*., 2005; Kaeser & Sharpe, 2006; Kaeser, Rasmussen & Sharpe, 2006), but our novel contribution identified landscape and GIS-derived habitat features that influence these local instream habitat conditions for *T. tubifex*. We were interested in predicting fine sediments, due to their direct influence on aggregations of *Tubifex* spp, and implications in the ecology of *Myxobolus cerebralis* (Anlauf & Moffitt, 2008). Identification of variables

Table 6 Candidate linear mixed models describing the percent of fine sediments selected in overall best set of multiple extent models including reach (100-m), 500-m, 2000-m, TL

Extent	Model parameter estimate ± SE	r^2	RMSE	AIC_c	ΔAIC_c	w_i
100-m, TL	Slow habitat + Conifer cover (0.031 ± 0.006) (−0.029 ± 0.008)	0.623	0.013	−309.2	0.0	0.440
100-m, TL	Slow habitat + Agriculture (0.031 ± 0.007) (0.024 ± 0.006)	0.643	0.012	−307.6	1.6	0.197
100-m, TL	Slow habitat + Stream slope (0.032 ± 0.006) (−0.005 ± 0.001)	0.669	0.012	−307.4	1.8	0.178
100-m	Slow habitat (0.037 ± 0.006)	0.433	0.016	−306.3	2.9	0.103

that specifically promote local increases in fine sediments in stream habitats in addition to determining the most appropriate scale at which to draw inference are invaluable within the context of whirling disease research and management.

The proportion of slow habitats, a local scale habitat variable, occurred repeatedly in the set of best models. Slow water habitats (pools) and fast water habitats (riffles) represent distinctly different ecological habitats with notably different biota inhabiting them. Biota display variations in taxonomic composition, morphology and physiological traits (Hawkins *et al.*, 1993). At the reach scale, slow water habitats can often predict the presence of obligate depositional taxa (Richards *et al.*, 1997) since they accumulate fine sediments and exhibit a positive relationship to burrowing invertebrates. Pools are critical for sediment storage and release to downstream habitats. Depending on the pool geometry within a system, sediment transport and transient sediment storage will vary with gradient, flow structure and interval, and specific bed topography (Rathburn & Wohl, 2003). To understand sediment dynamics more specifically within a stream system, an understanding of the major contributors of sediment is necessary. Further, employing the use of numerical models to evaluate sediment mobility and storage given sediment influxes would further elucidate how sedimentation patterns influence proximal habitats and the aquatic biota inhabitants (Rathburn & Wohl, 2003). Slow water habitats, along with other features measured instream, can be placed in the context of processes occurring at larger scales thereby mediating the distribution of certain stream invertebrates through the control over local habitats (Richards *et al.*, 1997).

Land cover/land use variables appeared repeatedly and consistently across spatial extents, emphasising their importance. Further, models that simultaneously included reach and landscape predictors were better than landscape models alone. Townsend *et al.* (2003) found that the best prediction of local stream invertebrate diversity was made when variables from multiple scales were modelled together. In our study, agriculture and forest cover occurred more frequently in the competing models at multiple scales. Stream habitat quality and biotic integrity have been found to be negatively correlated with agriculture or urbanisation and positively correlated with the presence of forest cover (Potter, Cubbage & Schaberg, 2005; Walters, Roy & Leigh, 2009). Agricultural land use is frequently associated with increased sedimentation in stream channels, often altering the invertebrate communities present within the stream (Allan *et al.*, 1997). Bed substrate characteristics have been shown to be strongly influenced by land cover patterns at the scales that extended the entire length of the stream (Sponseller *et al.*, 2001). Permanent streamside vegetation has also been found to explain variation in the percentage of fines and erosion (Richards *et al.*, 1996) as well as the variability in benthic invertebrate biotic index scores (Potter *et al.*, 2005). Forest cover, which is frequently negatively associated with degraded stream conditions, was among the most critical habitat factors. These results testify to the modifying influence that lateral connections can have on both sediment delivery and erosional processes.

Intermediate factors or drivers

Although land cover/land use variables appeared predominantly in this study, they of course are highly correlated with other relatively immutable landscape features such as stream slope, elevation and geology. These static features exert direct influence over land cover, and land use is highly influenced by these geomorphic characteristics. Specifically, land use can often mask the importance of surficial geology. At intermediate scales, geology and climate can set physical limits for subsequent scales and stream hydrology and riparian vegetation, influenced by climate and geology contribute to the differences seen at these finer resolutions (Malmquist, 2002). The addition of surficial geology can therefore often account for more variation than inclusion of land use properties alone (Allan & Johnson, 1997). The catchment characteristics of the soil porosity (a product of surficial geologies), gradient, elevation and climatic regimes, will influence the variation in location and prevalence of particular land use practices and land cover types. The configuration and composition of these natural features often influences the suitability and thereby presence of agricultural land uses (Allan, 2004).

Although surficial deposits did not appear in any of the plausible models, geology and groundwater movement in the Pahsimeroi system are important features. In the Pahsimeroi River, baseflow of the mainstem is derived primarily from subsurface flow and emerges as springs in the Pahsimeroi valley. Because of this highly groundwater-governed baseflow, the Pahsimeroi has a fairly stable flow. The sediments in the lower reaches are rarely disturbed or reworked providing a secure environment for many depositional invertebrate taxa to thrive. The geology of a region gives an indication of the erodibility of the underlying geologic material, groundwater-surface water exchange, groundwater chemistry and streambed composition (Gordon, McMahon & Finlayson, 1992). Because of this dynamic situation and the relatively coarse categorisation of geology in this study, the lack of prominence of this variable in our models seems understandable. Further differentiating between surficial geology formations may have emphasised the value of this variable.

Conclusions and management implications

Our study provides insight for managers and other researchers regarding ways to use multi-scale metrics and models in a hierarchical fashion to generate estimates of specific habitat characteristics. Our work builds on that of others such as Harig & Fausch (2002) who commented that large-scale variables can be used as coarse filters in predictive studies to detect differences in local habitats where needed. Geospatial techniques such as those used in this study can be employed to reduce the dependence on costly fine scale studies. Spatial analysis using GIS technologies and remote sensing are becoming powerful tools for restoration planning and site selection (Mollot & Bilby, 2007; Jorgensen *et al.*, 2009). We used these tools to supplement invaluable field data collection.

Managers can use GIS-derived metrics to help prioritise areas of high risk or those best for restoration in a tiered approach (Walters *et al.*, 2009). With a multi-scale approach, important factors affecting the hierarchy of habitat relationships can be appropriately weighted (Hutchens *et al.*, 2009). Because regional processes influence local stream habitat conditions, this is a plausible approach to further understanding of stream structure and communities. The application of the models for predicting areas of highest likelihood of *T. tubifex*, and consequently of *M. cerebralis* risk, in our study could be validated in drainage basins throughout the intermountain west. Digitally available land use characteristics are readily available. The environmental gradients we observed exist within most drainage basins. The Pahsimeroi River is less affected by the urban interface and more directly influenced by the prevalence of agriculture directly adjacent to the lowland riverine system (Colvin & Moffitt, 2008). Although the specific composition and configuration of surficial geology within a drainage basin will vary, understanding how these feature correlate to land cover/use, in addition to how these relationships will affect the distribution of sediments, will further facilitate the transferable nature of this model approach.

The presence and distribution of fine sediments within stream habitats is natural and is a reflection of both local habitat structure as well as adjacent riparian composition and upslope processes. Because of the nature of stream systems, persistent sediment delivery within the cycle of variable annual flow events, and persistent sediment deposition within slow water, low gradient habitats is natural. The conversion of floodplains to agriculture lands and the elimination of riparian buffer zones have and will continue to exacerbate potentially excessive amounts of fine sediments that not only harbour the intermediate host for the *M. cerebralis* parasite, but also provide little value to spawning and rearing salmonids. The relative abundance of fine sediments within these systems can be managed through the use of erosion control measures and maintenance of riparian buffers.

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