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RESEARCH ARTICLE

Does the scale of our observational window affect our conclusions about correlations between endangered salmon populations and their habitat?

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Abstract Differences in the strength of species-habitat relationships across scales provide insights into the mechanisms that drive these relationships and guidance for designing in situ monitoring programs, conservation efforts and mechanistic studies. The scale of our observation can also impact the strength of perceived relationships between animals and habitat conditions. We examined the relationship between geographic information system (GIS)-based landscape data and Endangered Species Act-listed anadromous Pacific salmon (*Oncorhynchus* spp.) populations in three subbasins of the Columbia River basin, USA. We characterized the landscape data and ran our models at three spatial scales: local (stream reach), intermediate (6th field hydrologic units directly in contact with a given reach) and catchment (entire drainage basin). We addressed three questions about the effect of scale on relationships between salmon and GIS representations of landscape conditions: (1) at which scale does each predictor best correlate with salmon redd density, (2) at which scale is overall model fit maximized, and (3) how does a mixed-scale model compare with single scale models (mixed-scale meaning models that contain variables characterized at different spatial scales)? We developed mixed models to identify relationships between redd density and candidate explanatory variables at each of these spatial scales. Predictor variables had the strongest relationships with redd density when they were summarized over the catchment scale. Meanwhile strong models could be developed using landscape variables summarized at only the local scale. Model performance did not improve when we used suites of potential predictors summarized over multiple scales. Relationships between species abundance and land use or intrinsic habitat suitability detected at one scale cannot necessarily be extrapolated to other scales. Therefore, habitat restoration efforts should take place in the context of conditions found in the associated watershed or landscape.

Keywords Multiple spatial scales · Spatial extent · Habitat · Pacific salmon · Land use · Spatial analysis · Restoration · Conservation

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Introduction

Organisms experience and interact with their environment over a variety of scales. Physiological processes operate at the cellular scale, foraging activities occur over a larger spatial domain and the factors governing the environment itself operate over still larger scales. The importance of scale to ecology is well documented in the literature (Wiens 1989; Levin 1992; Rastetter et al. 2003; Urban 2005) and the number of studies that have explored this important ecological paradigm has increased dramatically over the past few decades (Schneider 2001).

Scale and scaling

There are many definitions of the word "scale" in the scientific literature (Jenerette and Wu 2000; Schneider 2001), which is often a function of the discipline in question. However, it behooves ecologists to embrace multiple definitions of the term scale (Jenerette and Wu 2000). Jenerette and Wu (2000) described two "types" of scale: geographic and operational [as originally described by Lam and Quattrochi (1992)]. Geographic scale refers to the extant, scope, or general size of a map or study area, while operational scale refers to the geographic scale at which a given process operates. Observational scale is a third type of scale that adds yet another level of complexity to how we view ecological processes. The principles of scale are certainly not limited to space. While we seek to quantify how processes operating at various spatial scales affect the ecology of organisms, we must be astutely aware of how the scale of our observation affects our conclusions about how organisms interact with their environments (Wiley et al. 1997). Phenomena that we observe at a given location are the result of multiple factors, operating over a hierarchy of scales (Poff 1997). Finally, there is the concept of scaling, whereby one tries to extrapolate information gathered at a local scale to a larger area or for multiple species. Scaling is essential to both ecologists and managers alike in that ecologists seek to understand how processes observed locally operate broadly, and managers often make decisions that affect entire ecosystems (Urban 2005). Therefore, understanding the significance of scale, both from the perspective of our observation window, and how an organism experiences its environment is critical if we seek to identify spatial patterns of communities. Unfortunately, it could be argued that ecologists cannot adequately predict or even identify factors operating across various scales that drive observed spatial distributions of flora and fauna (see Resetarits 2005). This difficulty arises, in part, from the fact that we often know little about an organism's perception of scale when they make habitat selection decisions (Resetarits 2005). It is also critical for the management of endangered organisms, especially those with migratory behavior, in that local solutions must be selected within the context of conditions in the surrounding landscape. Therefore, there is utility in identifying scaling relationships beyond academic endeavors. Resource managers are confronted with trying to make decisions that affect a large geographic area, but are forced to do so using information that was gathered over a small area.

Riverscapes and hierarchy

Riverine ecosystems present unique challenges when trying to study the influence of scale. Complex stream networks embedded within a three-dimensional matrix of landscapes presents a challenge to ecologists trying to understand how scaling affects the ecology of these systems. Much attention has been paid to the hierarchical arrangement of temporally dynamic riverine ecosystems, with their complex catchments nested within larger landscapes, all containing rich biota (Frissell et al. 1986). As such, riverine ecosystems are often referred to as 'riverscapes' (Ward 1998; Fausch et al. 2002; Wiens 2002; Allan 2004), the riverine equivalent to terrestrial landscapes. Hierarchy theory states that what we observe within our sampling point quadrat is really the product of many other factors operating over successive larger extents (Allen and Starr 1982; Poff 1997). Climate interacts with geology and topography to form river basin and river network features, which in turn drives geomorphological processes. These processes control habitat structure and disturbance regimes, which ultimately control the content and structure of aquatic and riparian habitats we see on the ground (Montgomery 1999). However, components found lower in this hierarchy or continuum can influence the higher order drivers. For example, riparian conditions can drive recruitment of coarse organic matter, including woody and herbaceous debris, which affects sediment aggradation/degradation patterns from bank erosion or upstream processes, e.g., landslides (Frissell et al. 1986; Martin and Benda 2001). These local shifts in sedimentation patterns can affect geomorphology, resulting in feedback between these two components in the hierarchy. Further, interactions throughout the aforementioned hierarchy are sensitive to anthropogenic influences (e.g., land use patterns) that may occur locally but affect large areas (Montgomery 1999). Successful models have incorporated this hierarchical framework by including variables operating at multiple scales (Olden et al. 2006). However, attempts to extrapolate from field studies on species-specific habitat preferences to species distributions across regions have been problematic (Fausch et al. 2002; Wiens et al. 2002). The difficulty is likely related to the fact that local habitat conditions upon which aquatic species depend are, in turn, controlled by the patterns of land use, land cover, climate and geology that operate over broad spatial extents (Frissell et al. 1986; Imhof et al. 1996; Richards et al. 1996; Davies et al. 2000). Even relationships between landscape characteristics of interest may vary with the scale of observation. For example, a particular geology type may be highly correlated with agriculture in the riparian area but barely correlated with agriculture over the entire catchment. Analyses across multiple scales are therefore essential for untangling relationships between the river and its corresponding landscape.

Studies examining a wide variety of aquatic species at multiple life-stages have noted that relationships between habitat and abundance can depend on the extent over which the habitat is measured (Morley and Karr 2002; Snyder et al. 2003; Wang et al. 2003; Torgersen and Close 2004; Boys and Thoms 2006; Moerke and Lamberti 2006; Johnson et al. 2007). A series of three analyses conducted in the Pacific Northwest used coarse-grained geographic information system (GIS) representations of landscape conditions to predict Pacific salmon (*Oncorhynchus* spp.) distributions over whole watersheds (Pess et al. 2002; Feist et al. 2003; Steel et al. 2004). Among these three studies, only Feist et al. (2003) investigated the importance of scale in defining the potential habitat predictors of salmon distribution. In this paper, we expand on the work of Feist et al. (2003) by exploring the importance of scale in multiple subbasins and in more than one species. We also employ more rigorous statistical methods for testing our hypotheses. We use a similar methodology (to the aforementioned papers) to analyze relationships between habitat condition, quantified at three spatial scales, and the population performance of Pacific salmon over time. Doing so provides insights into the scale-specific relationships between habitat condition and the habitat associations of anadromous Pacific salmon that may have implications for the distribution of other aquatic species. Given the migratory life history of anadromous salmonids, their fitness is affected by habitats outside the catchments in which they spawn and rear. This pattern differs from resident fish species, which spend their entire lives within a given catchment. We argue that the steelhead and stream-type Chinook salmon described in the aforementioned papers and in this paper are reasonable proxies for scale-specific relationships between habitat and population performance because they rear for 1 year, or more, within their natal streams before migrating out to sea (Gilbert 1912; Everest and Chapman 1972; Howell et al. 1985; Myers et al. 1998; Quinn 2005). The total time that a given individual spends in freshwater, from the egg to outmigrating smolt, can reach 2 years, or more. Therefore, they are intimately tied to their riverine habitats during the freshwater phase of their life history, more so than other anadromous salmonids that spend far less time in their freshwater habitats (e.g., pink (*O. gorbuscha*) and chum (*O. keta*) salmon). Further, the freshwater life history stages of steelhead and stream-type Chinook salmon are critical to subsequent stages, since they cannot outmigrate to marine environments until they have reached a minimum size and condition (Quinn 2005). Therefore, the types and quality of habitats they occupy during their lengthy freshwater stages are essential to their survival.

The aim of this study was to address three questions: (1) at which scale does each potential GIS based landscape predictor variable have the strongest relationship with salmon performance; (2) at which scale is overall model fit maximized; and (3) how does a multi-scale model compare with single scale models? Multi-scale models contain GIS based landscape predictor variables measured at different scales (local, intermediate or catchment) within a given model. In contrast, single-scale models contain GIS based landscape predictor variables measured at one scale only (local, intermediate or catchment). By examining the question of scale in these three different ways, we minimized any biases that may have resulted from exploring the question one variable at a time versus by using all possible variables in a multiple regression context. Our analyses are unique in that we have synthesized patterns over a very large geographic region, based on decades of salmon population data, which we believe makes them broadly applicable to the field of landscape ecology.

Methods

Study area

We analyzed three river subbasins in the Columbia River basin, USA: the John Day, Wenatchee, and Yakima (Fig. 1). The John Day subbasin is sparsely populated and cattle grazing is its predominant land use. The Yakima subbasin is dominated by

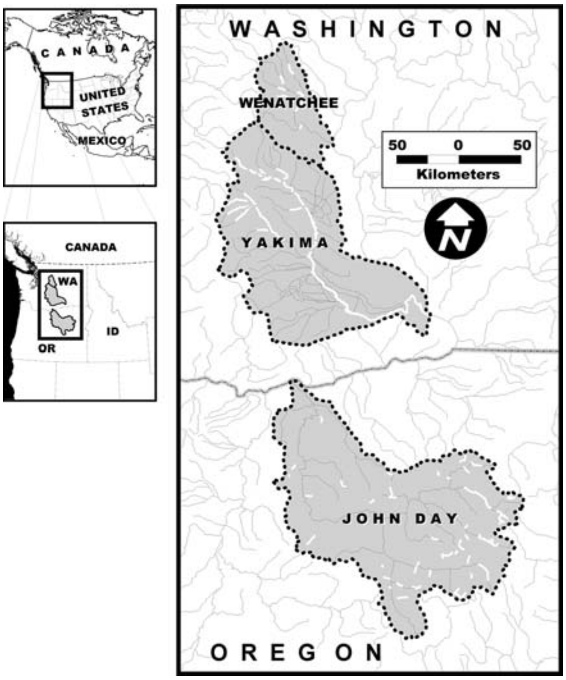

Fig. 1 Map of Columbia River basin and the three subbasins where analyses were completed. *White lines* denote locations of index reaches where salmon redd data were collected

agriculture and has a higher population density than the John Day subbasin. The Wenatchee subbasin, which is the smallest of the three, is heavily forested with relatively low levels of agricultural activity. The drainage area size, ecoregion, Evolutionarily Significant Unit (ESU) name, and ESU designation of each of the subbasins are summarized in Table 1. "An ESU is defined as a population that (1) is substantially reproductively isolated from conspecific populations and (2) represents an important component in the evolutionary legacy of the species" (Johnson et al. 1994). Further, a "population" can be defined by a geographic boundary, such as a basin.

Spawner abundance

Our analyses examined different Endangered Species Act (ESA)-listed (NMFS 2003), anadromous Pacific salmon species: spring/summer Chinook salmon (*O. tshawytscha*) and steelhead (*O. mykiss*, NMFS 1997). Redd (spawning nests constructed by females) count data were obtained from StreamNet (2002) initially, and supplemental data were obtained from other sources as necessary (including the NWFSC spawner database, unpublished data). Population data were based on annual redd count surveys (StreamNet 2002), conducted at specific river reaches ('index reaches') for many decades by various state agencies. All index reach segments were mapped to either 1:24 k or 1:100 k USGS stream networks. We examined 6, 20, and 6 Chinook index reaches in the Wenatchee (Ames et al. 1974; Schwartzberg and Roger 1986; Heindl and Beaty 1989; Hays and Peven 1990; Peven and Mosey 1995), Yakima (Horner and Bjornn 1979; Schwartzberg and Roger 1986; Fast et al. 1989, 1991; WDFW 1993), and John Day (Lindsay et al. 1986; Schwartzberg and Roger 1986; Olsen et al. 1994; Gray 1995; Unterwagner 1999; Unterwegner and Gray 1999) subbasins, respectively. We analyzed 43 years of redd data in the Wenatchee (1958–2000), 22 years in the Yakima (1980–2001), and 42 years in the John Day (1959–2000). We also examined 43 steelhead index reaches (44 years of surveys from 1959 to 2002) in the John Day subbasin only.

We used redd count data because it is the most comprehensive and complete proxy for spring/summer Chinook populations in the three subbasins we analyzed. There are surveys of juvenile abundance in

Table 1 Basin name, drainage area (km^2), ecoregion association, ESUs, and ESA status of various Pacific salmon species in the three analyzed subbasins

Basin (drainage area, km^2)	Ecoregion (s)	ESUs and ESA status
John Day (20,518)	Blue mountains; Columbia Plateau	MCR[a] Spring Chinook: not warranted; MCR steelhead: threatened
Wenatchee (3,441)	Columbia Plateau; North Cascades	UCR[b] Spring Chinook: endangered; UCR Summer/Fall Chinook: not warranted; UCR Steelhead: threatened; Lake Wenatchee Sockeye: not warranted
Yakima (16,070)	Cascades; Columbia Plateau; Eastern Cascades Slopes and Foothills; North Cascades	UCR Summer/Fall Chinook: not warranted; MCR Spring Chinook: not warranted; MCR Steelhead: threatened

[a] Middle Columbia River

[b] Upper Columbia River

these basin, but the time series are not as long and these surveys are not available for as many sites as the redd count surveys. By analyzing such a long time series of spawner data, consistently collected at the same sites over the same temporal window, we are able to reduce the influence of factors extrinsic to the basin, such as estuarine and ocean and survival. In addition, our analytical technique looks at correlation between spawner abundance across space and not across time, so interannual variability based on extrinsic factors is minimized. Finally, since we grouped our data by subbasin (and by ESU), all of the fish in a given subbasin are presumed to be affected equally by extrinsic factors (i.e., migration route, numbers of dams passed, ocean productivity, etc.)

Spatial analyses

In order to explore the influence of spatial extent on the apparent relationship between habitat and salmon redd density, we overlaid existing geospatial "habitat" datalayers with the aforementioned locale-explicit salmon redd abundance data. For the sake of simplicity, the term "habitat" will be used as a proxy for GIS based landscape datalayers for the remainder of the methods section and throughout the results section. We characterized each habitat type and ran our models at three different spatial scales: local (e.g., stream reach as defined by the area within a 500 m buffer of a given index reach, $\overline{X} = 11.9\,km^2$, SD = 21.8, across all 4 data sets), intermediate (all 6th field hydrologic units contacting a given reach, $\overline{X} = 230.2\,km^2$, SD = 302.4, across all 4 data sets) and catchment (total area upslope, i.e., the catchment, of the downstream end of a given reach, $\overline{X} = 644.5\,km^2$, SD = 1,970.1, across all 4 data sets). We chose these three scale categories for the following reasons: local scale was designed to capture the habitat conditions *generally* within the riparian zone of a given reach; intermediate scale was chosen as a hydrologically accurate representation of an area intermediate between local and catchment; and, catchment was chosen to represent the total area that could possibly affect a given index reach. It is important to note that we did not vary the grain of these geospatial datalayers, only the size of our analysis window. Our landscape geospatial data were derived from a variety of sources (Table 2). We classified each predictor into one of five categories: "land use" (agriculture, cattle grazing, clearcut, dams, mines, road density, diversions, sheep grazing or urban); "land cover" (alpine forest, arid vegetation, conifer forest, hardwood forest, pine forest, riparian, water, wetlands or wilderness, e.g., areas that have not been significantly altered by humans); "structure" (area of extent, channel slope, slides, stream junctions or terrain slope); "climate" (precipitation or mean air temperature); or "geology" (alluvium, glacial, igneous, metamorphic or sedimentary). All of the geospatial data we used in this study were "static" in that they were collected at one point in time, most often the year 2000, which was the most recent year of the spawner surveys. The fact that these data were not sampled every year did not necessarily degrade the quality of our analyses. For example, variables within the structure and geology categories, varied little if at

Table 2 Geospatial datalayers used in habitat analysis and measured at each corresponding extent (local, intermediate or catchment)

Geospatial datalayer	Map scale grain	Description
CLIMATE[a]	N/A	Mean annual temperature for 1989 (Thornton et al. 1997, acquired from Interior Columbia Basin Ecosystem Management Project (ICBEMP 1999), which was considered a "normal" year
(mean air temperature)	2 km	
CLIMATE[a]	N/A	Total annual precipitation for 1989, considered a "normal" year from Precipitation Elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 1994), acquired from the ICBEMP (1999)
(precipitation)	500 m	
GEOLOGY[b]	1:500 k	USGS classification of geologic map units according to major lithology
(Alluvium, Glacial, Igneous, Metamorphic, or Sedimentary)	N/A	Alluvium (alluvium)
		Glacial (glacial drift)
		Igneous (calc-alkaline intrusive, felsic volcanic flow, calc-alkaline volcanoclastic, mafic intrusive, mafic volcanic flow, calc-alkaline meta-volcanic, ultramafic, tuff, felsic pyroclastic, or mafic meta-volcanic)
		Metamorphic (granitic gneiss, mafic gneiss, meta-sedimentary phyllite and schist, interlayered meta-sedimentary, argillite and slate, carbonate, or shale and mudstone)
		Sedimentary (sandstone, mixed eugeosynclinal, or siltstone)
LAND COVER[b]	1:100 k	Land use and land cover from Northwest Habitat Institute (NHI 2000) GIS data layer of recent (ca. 2000) wildlife-habitat types. Wildlife-habitat types maps originally published in Johnson and O'Neil (2001)
(Alpine Forest, Arid Vegetation, Conifer Forest, Hardwood Forest, Pine Forest, Riparian, Water, or Wetlands)	25 m	Alpine Forest (alpine grasslands and shrublands, or subalpine parklands)
		Arid Vegetation (eastside [interior] grasslands, shrub-steppe, or western juniper and mountain mahogany woodlands)
		Conifer Forest (montane mixed conifer forest, eastside [interior] mixed conifer forest, or lodgepole pine forest and woodlands)
		Hardwood Forest (westside hardwood forest);
		Pine Forest (ponderosa pine and eastside white oak forest and woodlands)
		Riparian (eastside [interior] riparian wetlands);
		Water (lakes, rivers, ponds, and reservoirs)
		Wetlands (herbaceous wetlands, or montane coniferous wetlands)
LAND COVER[b]	1:24–1:500 k	Designated wilderness areas on Forest Service, Bureau of Land Management and National Park lands. Acquired from and compiled by ICBEMP (1999)
(Wilderness)	N/A	
LAND USE[b]	1:100 k	Land use and land cover from Northwest Habitat Institute (NHI 2000) GIS data layer of recent (ca. 2000) wildlife-habitat types. Wildlife-habitat types maps originally published in Johnson and O'Neil (2001)
(Agriculture, Clearcut, or Urban)	25 m	Agriculture (agriculture, pasture, or mixed environs)
		Clearcut (grass/shrub and/or regenerating forest);
		Urban (urban and mixed environs)
LAND USE[b]	1:24–1:126 k	Livestock grazing allotments. US Forest Service, and BLM delineations of areas where livestock can graze (ICBEMP 1999)
(Cattle Grazing)	N/A	
LAND USE[c]	N/A	Dams with greater than 50 acre feet storage capacity. Acquired from ICBEMP (1999) and derived from the National Inventory of Dams, US Army Corps of Engineers, and State Water Resource Department Dam Safety Divisions
(Dams)		
LAND USE[c]	1:100 k	US Forest Service database of water irrigation diversions, screens, ladders, and pumps, supplemented by BPA, and State Fish and Game data. Only used diversions for our analyses (screened, unscreened, and unknown). Acquired from and compiled by ICBEMP (1999)
(Diversions)	N/A	

Table 2 continued

Geospatial datalayer	Map scale grain	Description
LAND USE[c] (Mines)	1:24–1:100 k N/A	Mining related hazard potential sites (ICBEMP 1999). Compiled by ICBEMP (1999) from 7.5′ & 15′ USGS paper quads (site investigation field maps), published and unpublished literature, mining company records, and public land records
LAND USE[d] (Road Density)	1:100 k N/A	Polyline representation of road networks. Source material includes USGS DLG, USGS road/street maps, field compilation, survey data, and Census Bureau TIGER/Line files as provided by Wessex Corp. Acquired from and compiled by ICBEMP (1999)
LAND USE[b] (Sheep Grazing)	1:24–1:126 k N/A	Livestock grazing allotments. US Forest Service and BLM delineations of areas where livestock can graze (ICBEMP 1999)
STRUCTURE (area of extent—local)	1:24 k N/A	Total area (km^2) within 500 m of any given index reach. Generated around each index reach in ESRI ARC/INFO using BUFFER command
STRUCTURE (area of extent—intermediate)	1:24 k N/A	Total area (km^2) represented by all 6th field hydrologic units (HU's) that touch a given index reach. Generated using ICBEMP (1999) sixth field hydrologic units (HU's)
STRUCTURE (area of extent—catchment)	1:24 k N/A	Total area (km^2) upslope of the downstream end of any given index reach. Generated from a USGS 30 m DEM
STRUCTURE (channel slope)	1:24 k 30 m	Calculated from USGS 1:24 k, 30 m digital elevation models (DEM). Defined as rise (upstream elevation minus downstream elevation of index reach) over run (river km length of index reach) multiplied by 100
STRUCTURE[b] (slides)	1:500 k N/A	USGS classification of geologic map units according to major lithology: landslide category
STRUCTURE[c] (stream junctions)	1:24 k N/A	Density of stream junctions calculated from USGS 1:24 k stream network data layer. Used for steelhead only in the John Day subbasin
STRUCTURE[b] (terrain slope)	1:24 k 30 m	Hillslope gradient generated from USGS 30 m Digital Elevation Model (DEM), using ARC/INFO. Calculated the slope of every 30 m gridcell in the DEM. Hillslope for any given index reach was calculated by summing all of the 30 m DEM gridcells with a slope less than 6% (for steelhead) or 1.5% (for Chinook) contained in any index reaches' associated local, intermediate or catchment extent

All data layers were generated by other entities (such as federal, state and academic institutions), with the exception of hillslope, channel slope and stream junctions, which we generated for this study. The "*k*" after the map scales represents 1,000 (e.g., a map scale of 1:100 k = 1:100,000). "Grain" is the size of each individual pixel or gridcell for raster-based datalayers. Grain is separated from map scale by a horizontal dotted line for clarity

[a] Expressed as an area-weighted mean value, where each gridcell was multiplied by its value, summed over all gridcells and then divided by the total area of corresponding extent

[b] Expressed as a percentage, for each individual category, of the total area of each corresponding extent

[c] Expressed as a density (the number of points per km^2) for each corresponding extent

[d] Expressed as a density (linear km of given feature per km^2) for each corresponding extent

all during the temporal window of this study. Therefore, measuring them repeatedly every year would have been pointless. The climate variables were representative of average temperature and precipitation values, calculated over a 30-year window that coincided with the temporal window of the spawner data. However, the land use and land cover categories contained variables that could conceivably had been different from their 2000 classifications, which would likely have reduced the fit of our models. While we had no way of knowing which sites were significantly different from when the geospatial data were collected, we assumed that all of the land use categories had likely been in those states (for most of the sites) for the full window of the spawner survey data. All of the sites in our study were far away from urbanized areas, and urbanization would have been the variable most likely to change over the spawner data temporal window. We also assumed that the number of sites that would have experienced significant land cover change before the geospatial data were collected would be low. In addition, our analyses were designed to catch sites that may have been driving the relationship in a given regression, so this would reduce the risk.

Statistical analyses

We used mixed models that included a random intercept and an autoregressive correlation structure. This model structure was selected to manage time series of data with some missing data and was used successfully in analyses of similarly structured data (Steel et al. 2004). The mixed models included fixed effects of habitat on redd density and a random intercept to model population fluctuations over years. The autoregressive correlation structure was necessary because redd counts at a particular site are somewhat auto-correlated over years. The dependent variable in all cases was redds/km which was log-transformed (natural log) to meet normality assumptions. To identify the best extent for each potential predictor, three sets (local, intermediate and catchment) of single-predictor models were fitted for each basin-species combination. All models were fit using Proc Mixed in SAS (Littell et al. 1996).

Conclusions about significant difference between scales were made at three levels: the individual predictor, classes of predictors, and all predictors. Whether an individual predictor had a significantly stronger relationship with redd density at one scale versus the others was estimated from differences in Akaike Information Criterion (AIC) values, with differences greater than 4 generally considered significant (Burnham and Anderson 2002). Of greater interest was the question of whether the five categories of predictors had a stronger relationship with redd density at one scale versus another.

At what extent is each predictor best correlated with salmon redd density?

Single-predictor models for each landscape variable were fit to redd density in each basin/species dataset and at each extent independently. To combine results from all individual predictors or all individual predictors within a class, we used a randomization test. The null hypothesis of the randomization test was that predictors within a class had an equal chance of performing best (smallest AIC value) at each scale for which they were available. The randomization test considers each independent predictor variable to be a replicate trial within a larger class experiment. Some predictors were available at all three scales and some were available at only two scales, so we designed a customized randomization test based on a binomial distribution (where the predictor variable was only tested at two extents, thus the probability for each extent was 0.5) or a multinomial distribution (where the predictor variable was tested at all three possible extents, and the probability for each was 0.333). Note that variables included at only one scale could not be included in this analysis. We simulated 1,000 data sets from each basin/species dataset to estimate the distribution of observing any particular number of variables being best at a particular scale. We then compared the observed number of variables that were best at a particular scale to the expected number under the null hypothesis, as estimated from the Monte Carlo simulations, and estimated the probability of observing the pattern we saw. Note that the randomization test did not require all individual predictors to have a significantly stronger relationship with redd density at one scale. If, for example, all 9 land-use predictors had the strongest relationship with redd density at the catchment scale, it would indicate that for this class, catchment scale predictors had a significantly stronger relationship with redd density, even though the association for each individual predictor may or may not have been statistically significant. We drew this conclusion because under our null model, the probability of all 9 predictors having had the smallest AIC at the catchment scale was very small.

At what extent is overall model fit maximized?

To determine at which extent the overall model fit was maximized, we identified and compared the set of best multiple regression models at each extent using a model selection procedure on previous analyses of similar data sets (Feist et al. 2003, Steel et al. 2004). Models were built and selected for each extent and for each basin-species combination. The model selection procedure we used is a modified all-subsets procedure in which we considered all three-variable models, ruling out models based on AIC values, high colinearity, low stability, or low predictive power. We fit the null model (intercept only), all single-predictor models, and all two-variable models. To save computer time, we fit three variable models by adding all potential predictors only to two-variable models with an AIC less than that of the null model. We then calculated the difference in AIC values between each model of any size and the lowest AIC among all models (ΔAIC) and retained all models with a ΔAIC less than four. This relatively conservative cut-off (Burnham and Anderson 2002) was applied in order to reduce the list of candidate models.

We further refined the set of best models using three criteria to remove unstable models. The condition index (Belsley et al. 1980) was used to identify models in which the predictor variables were correlated with one another; models with a condition index >10, indicating moderate collinearity, were rejected. Cook's D was calculated to identify unstable models due to data points with high leverage; models with data points for which $D > 1.00$ were eliminated (Cook 1977). Finally, we conducted a cross-validation analysis to eliminate models with low predictive power (Steel et al. 2004). If, after applying these three criteria, fewer than 10 models remained in the candidate set, the ΔAIC criteria in step two was adjusted to increase the pool of potential models.

To identify the final set of best models, we ranked the remaining models by ascending AIC and calculated AIC weights (Burnham and Anderson 2002). The final set of best models were those where the AIC weight of the next model was less than 0.05 or the AIC-weight of the next model was less than 0.10 and the sum of the AIC-weights for the current set of models was greater than 0.50 (Burnham and Anderson 2002).

How does a mixed extent model compare with single extent models?

Multi-extent mixed-models were generated to address the third question, "How does a mixed extent model compare with single extent models?" We identified the best extent for each potential predictor in each basin-species combination and entered the variable into the pool of potential predictors for that particular basin-species combination only at that extent. We then used the same model selection approach, as described above, to identify the set of best models using the new mixed-extent pool of potential predictors. Note that approximately the same number of potential predictor variables was available for the mixed extent analysis as in each of the single extent analyses.

Results

Predictor variables had the strongest relationships with redd density when they were summarized over the catchment scale. Meanwhile strong models could be developed using only habitat variables summarized at a local scale. Model performance did not improve when we used suites of potential predictors summarized over multiple scales.

At what extent does each predictor have the strongest relationship with salmon redd density?

Redd densities were both positively and negatively correlated with a wide variety of habitat variables at all three spatial extents (Table 3). While there were substantial differences in terms of which habitat variable produced the best relationship (lowest AIC) to the different extents, the strongest relationships overall occurred when the habitat variables were summarized over the catchment extent (Table 3). For variables describing geology or structure, significantly fewer than expected variables had the strongest relationship with redd density at the intermediate extent ($P = 0.051$ and 0.025, respectively). For land use variables, significantly fewer than expected variables had the strongest relationship with redd density at the local extent ($P = 0.021$), and there were fewer, though not significantly, than expected land cover variables in which the best relationship with redd density occurred at the local extent ($P = 0.068$). When considering all five categories of habitat variables together, there were significantly more variables than expected with the strongest relationship between habitat condition and redd density when habitat condition was summarized over the catchment extent ($P = 0.049$). When habitat conditions were summarized at the local extent, however, the number of

Table 3 Summary of model results assessing at what extent each predictor has the strongest relationship with salmon performance (Question 1, see text)

		CHINOOK									STEELHEAD		
		John Day			Wenatchee			Yakima			John Day		
Class	Subclass	Local	Intermediate	Catchment	Local	Intermediate	Catchment	Local	Intermediate	Catchment	Local	Intermediate	Catchment
Climate	Mean Air Temp	■	0	0	■	1	1	1	■	1	0	0	■
	Precipitation	0	1	■	0	0	■	6	5	**	6	*	0
Geology	Alluvium		0	■	0	1	■	*	3	4	■	0	0
	Glacial		1	■									
	Igneous	1	■	1		■	0		1	■	■	0	0
	Metamorphic	■	0	1	■	0	0	6	*	3	0	0	■
	Sedimentary		2	■		2	■	■	3	1	**	7	7
Land Cover	Alpine Forest		■	0	■	2	2		0	■		■	0
	Arid Vegetation		0	■	0	0	■	3	1	■	0	■	0
	Conifer Forest	2	1	■	0	■	0	2	■	0	■	1	2
	Hardwood Forest						■	1	0	■			
	Pine Forest	0	0	■	■	0	0	2	2	■	**	6	5
	Riparian						■	■	2	3			
	Water				2	■	1	7	6	**	4	3	*
	Wetlands		■	0	0	■	0	0	*	4		■	
	Wilderness	2	1	■		■	0		0	■		0	■
Land Use	Agriculture				0	■	1	2	■	1	1	2	■
	Cattle Grazing	■	2	1					■	0	4	*	1
	Clearcut		1	■	1	0	■	3	■	3	5	*	2
	Dams			■			■	4	*	1	■	1	1
	Mines	1	2	■	3	■	1	1	*	4	■	1	2
	Road Density	0	■	0	1	1	■	**	6	6	3	■	1
	Screens							1	1	■	■	1	1
	Sheep Grazing		■			■	0	1	1	■	10	1	*
	Urban		0	■				2	1	■		■	
Structure	Area of Extent	0	■	0	1	4	*	■	0	1	2	*	4
	Channel Slope	■			■			■			■		
	Slides		1	■							■	0	0
	Stream Junctions										1	■	0
	Terrain Slope	0	0	■	4	3	*	■	1	1	2	■	1

Gray boxes denote variables that were not present at that extent, and so could not be tested. White and black boxes denote variables that were tested at a given extent. Black boxes denote the extent with the minimum AIC for a given variable. Numbers inside the white boxes indicate the difference between AIC at that extent and the minimum AIC. Values greater than 4 can be considered significant. One asterisk in a black rectangle indicates significantly outperforming one other extent and two asterisks indicates significantly outperforming both other extents. A comparison of the best scale for each individual predictor should be considered one trial in the overall experiment to identify the best scale. Determination of a best scale and of significant differences between extents was estimated using randomization tests based on these trials

variables that contributed to a strong relationship between habitat condition and salmon redd density were fewer, but were not significantly ($P = 0.083$) less than the expected variables.

At what extent is overall model fit maximized?

A subset of the many potential predictor variables was used in the final set of 27 best models for Chinook and 11 best models for steelhead (Tables 4 and 5). All variables except sheep grazing, mean air temperature, precipitation, stream junctions, slides, terrain slope, conifer forest and hardwood forest, were included in at least one of the Chinook models. Across subbasins, the suite of best predictor variables changed considerably. Cattle grazing, for example, was in every best model for the John Day basin, but was not in the set of best models for the other basins. Agriculture was in nearly half of the best models for the Yakima, but did not appear in the other basins. Geology was important in the best models for all basins; it included alluvium, glacial, igneous, sedimentary, and/or metamorphic depending on the basin and the extent. About 77% (10 of 13) of the Chinook models involved at least one land use variable and those models that did not contain any land use variables were never observed at the catchment extent (Table 5). All of the steelhead models had at least one land use variable (Table 5). Only agriculture, area of extent, channel slope, clearcut, diversions, sedimentary geology, sheep grazing, and terrain slope made it into the 11 steelhead models (Table 5).

Table 4 Summary of model results to assess at what extent is the overall model fit maximized (Question 2)

Class	Subclass	Yakima Chinook Local	Yakima Chinook Intermediate	Yakima Chinook Catchment	John Day Steelhead Local	John Day Steelhead Intermediate	John Day Steelhead Catchment
Climate	Mean Air Temp						
	Precipitation						
Geology	Alluvium		1				
	Glacial						
	Igneous						
	Metamorphic		1				
	Sedimentary	1			1	1	1
Land Cover	Alpine Forest			1			
	Arid Vegetation						
	Conifer Forest						
	Hardwood Forest						
	Pine Forest						
	Riparian	3	1	1			
	Water						
	Wetlands		1				
	Wilderness		1				
Land Use	Agriculture		2	2	1		1
	Cattle Grazing						
	Clearcut	2				3	3
	Dams		3				
	Mines						
	Road Density	1		1			
	Screens			2	1	2	
	Sheep Grazing				4	4	3
	Urban			1			
Structure	Area of Extent		1		4	1	
	Channel Slope	2	5	4	1		1
	Slides						
	Stream Junctions						
	Terrain Slope		2			1	

Gray boxes denote variables that were not present at that extent, and so could not be tested. Variables with white boxes were not included in any of the final models. Variables with black boxes were included in the final models; the number of models in which a given variable was used is indicated in each of these boxes

Model fit appeared better for Chinook salmon than steelhead (Table 5; Fig. 2). However, differences in available data for the two species prevent direct cross-species comparisons. For the same reasons, inter-subbasin comparisons of model fit are not appropriate. Instead, we compared model fit across the three extents within subbasin and species. For Chinook salmon, local extent models generally had lower AIC values than intermediate and catchment extent models (Fig. 2). Intermediate extent models had the highest AIC values. For steelhead, the catchment extent models had the lowest AIC values, while the intermediate and local extent models resulted in slightly higher values.

How does a mixed extent model compare with single extent models?

For Chinook salmon, the mixed extent models produced lower AIC values than the intermediate and catchment extent models (Table 6; Fig. 2). However, the AIC values for the mixed extent models were similar to those of the local extent models. For steelhead, the AIC values of the mixed extent models were similar to that of the local and intermediate extent models, but lower than that of the catchment extent models (Fig. 2). Half (1 of 2) of the Chinook and all (4) of the steelhead models involved at least one land use variable (Table 6).

Discussion

The extent over which landscape conditions are summarized influences the degree to which landscape condition is correlated to biological response, specifically, salmon redd density. There is no single 'best' extent over which to summarize landscape condition. Instead, the choice of extent is a function of the landscape feature in question and should reflect our understanding of the underlying mechanism by which landscape condition influences aquatic habitats. The

Table 5 Independent variables, associated coefficients and AIC values for the set of best multivariate models used to assess at what extent the overall model fit is maximized (Question 2)

Subbasin species extent	Equation	AIC	r^2
Yakima	−105.77(*Channel Slope*) −0.15(*Clearcut*) −0.43(*Riparian*)	666.4	0.926
Chinook	−0.35(*Riparian*) −0.18(*Clearcut*) + 0.73(*Road Density*)	667.3	0.919
Local	−0.32(*Riparian*) −92.90(*Channel Slope*) −0.06(*Sedimentary*)	667.5	0.918
Yakima	−90.76(*Channel Slope*) −5.45(*Terrain Slope*) + 0.53(*Wetlands*)	674.4	0.835
Chinook	−76.00(*Channel Slope*) + 64.57(*Dams*) −6.18(*Terrain Slope*)	674.6	0.833
Intermediate	−0.05(*Agriculture*) + 0.03(*Alluvium*) −76.26(*Channel Slope*)	674.8	0.829
	−0.0009(*Area of Extent*) −91.95(*Channel Slope*) −0.86(*Riparian*)	675.2	0.822
	−0.036(*Agriculture*) −69.84(*Channel Slope*) + 39.31(*Dams*)	675.5	0.817
	0.080(*Metamorphic*) + 0.022(*Wilderness*) + 62.51(*Dams*)	675.9	0.810
Yakima	−0.14(*Agriculture*) −136.18(*Channel Slope*) −81.06(*Diversions*)	672.5	0.864
Chinook	−0.14(*Agriculture*) −139.16(*Channel Slope*) + 0.05(*Alpine Forest*)	673.4	0.851
Catchment	−124.36(*Channel Slope*) −4.05(*Riparian*) −0.81(*Road Density*)	673.7	0.847
	−141.71(*Channel Slope*) −118.50(*Diversions*) −1.49(*Urban*)	673.9	0.844
John Day	−0.06(*Area of Extent*) −7.32(*Channel Slope*) −0.0074(*Sheep*)	2,077.0	0.519
Steelhead	−0.04(*Area of Extent*) −0.0049(*Sedimentary*) −0.0081(*Sheep*)	2,077.5	0.509
Local	−0.05(*Area of Extent*) −0.01(*Agriculture*) −0.0081(*Sheep*)	2,077.7	0.503
	−0.05(*Area of Extent*) −0.0083(*Sheep*) −0.15(*Diversions*)	2,077.8	0.501
John Day	−0.22(*Clearcut*) −0.0079(*Sedimentary*) −0.0088(*Sheep*)	2,077.3	0.513
Steelhead	−0.3058(*Clearcut*) −1.6707(*Diversions*) −0.0074(*Sheep*)	2,077.9	0.499
Intermediate	0.0013(*Area of Extent*) −0.26(*Clearcut*) −0.0056(*Sheep*)	2,078.5	0.486
	−0.0086(*Sheep*) −1.34(*Terrain Slope*) −1.58(*Diversions*)	2,079.0	0.473
John Day	−0.22(*Clearcut*) −0.0079(*Sedimentary*) −0.0088(*Sheep*)	2,074.1	0.579
Steelhead	−0.38(*Agriculture*) −0.0083(*Sheep*) −0.23(*Clearcut*)	2,074.7	0.568
Catchment	−0.27(*Clearcut*) −7.70(*Channel Slope*) −0.0081(*Sheep*)	2,075.0	0.562

The response variable in all cases is the natural log of redds/km

strength of relationships at the catchment extent suggests that mechanisms controlling aquatic conditions are operating over these large spatial extents and data collection efforts that ignore the larger context of local conditions are likely to be incomplete. However, local conditions should not be ignored, rather, they should be viewed within the context of the landscape they are contained within.

At what extent is each predictor best correlated with salmon redd density?

Wang et al. (2003) concluded that the importance of "reach-scale" variables was most evident in "undegraded areas" and that "watershed-scale" variables would increase in importance in landscapes that have been altered by humans. Our results are in agreement with the latter scenario. We found that there were significantly fewer than expected "best" extent land use variables at the local extent that made substantive contributions to the predictive models. We found similar patterns for our land cover variables, which is probably due to the fact that so many land cover variables are strongly affected by land use practices (e.g., forested cover types and commercial timber harvest). It is widely believed that the geology and climate patterns of a given drainage basin drive the conditions found in streams (Knighton 1984; De Boer 1992; Richards et al. 1996). Although our results appear to support this paradigm qualitatively, the relationship was not always statistically significant. One reason for a lack of significant relationships may be the low number of index sites and insufficient statistical power. Another explanation may be that the

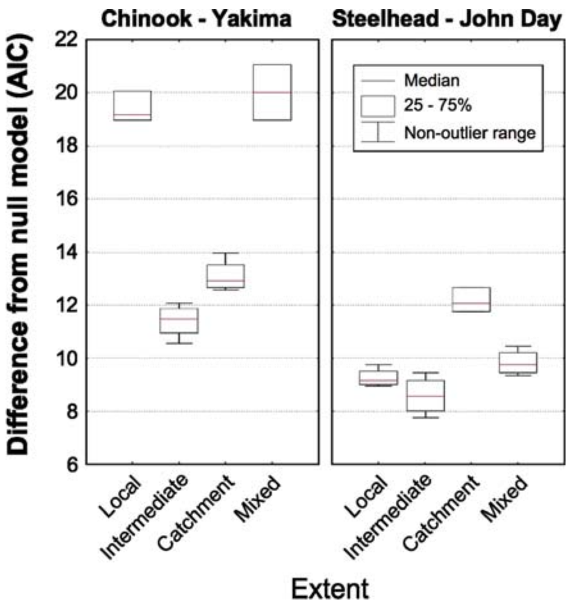

Fig. 2 *Box* and whisker plots comparing AIC for various fixed- and mixed-extent models as a function of extent, by subbasin and species (steelhead and Chinook)

extent over which a given predictor influences stream characteristics, and hence abundance of spawning fish, is highly variable, and our three extent areas did not adequately capture the scaling dynamics (Frissell et al. 1986). The relatively poorer model fit for Chinook at the intermediate extents for geology and structure variables suggests that the mechanisms through which these variables influence Pacific salmon redd density operate primarily at the local and catchment extents. There are a number of fine-grained habitat attributes, such as physical structure (large woody debris, boulders, etc.) and riparian composition that are important for anadromous salmonids (Quinn 2005), but were not resolved by our coarse-grained geospatial data. This deficiency may also explain the apparent decrease in model performance at smaller spatial extents.

Scale dependent relationships with factors other than habitat (e.g., invertebrates) may have also limited our ability to detect strong scale dependent relationships. Based on their work on macroinvertebrates, Richards et al. (1996) concluded that anthropogenic factors operate at a local “scale”, which should, in turn, influence habitat conditions in a given stream reach. Therefore, one might argue that land use practices should have the strongest relationship with Pacific salmon redd density when summarized over a small area. However, Paavola et al. (2006) and Infante et al. (2009) concluded that macroinvertebrates might respond to processes operating at smaller scales, compared with fishes that may respond more to large-scale factors. They also demonstrated that concordance between macroinvertebrates and fish species increased as a function of the spatial extent of the analysis. Given that we did not measure macroinvertebrate diversity in this study, we could not account for it in our models and it may have decreased the strength of the relationship between the various geospatial landscape data and spawner abundance, measured at various extents.

Overall, our analyses suggest that quantifying habitat in geospatial datalayers at a catchment extent provides potential predictor variables that are more closely correlated with and may therefore have a greater influence on Pacific salmon redd density. This conclusion is consistent with other research (Frissell et al. 1986; Imhof et al. 1996; Richards et al. 1996; and Davies et al. 2000). However, it is important to note that all of the relationships we observed should not be presumed causal. All we can conclude is that the characteristics of the predictor variables either

Table 6 Independent variables, associated coefficients and AIC values for mixed-extent models to determine how a mixed extent model compares to single extent models (Question 3)

Subbasin species	Equation	AIC	r^2
Yakima Chinook	−0.078(*Pine Forest*) + 0.95(*Road Density*) −1.38(*Urban*)	665.4	0.933
	−92.90(*Channel Slope*) −0.32(*Riparian*) −0.056(*Sedimentary*)	667.5	0.918
John Day Steelhead	−0.34(*Agriculture*) −0.0083(*Sheep*) −0.0079(*Sedimentary*)	2,076.3	0.534
	0.0012(*Area of Extent*) −0.0073(*Sheep*) −0.0078(*Sedimentary*)	2,076.8	0.524
	−0.064(*Mean Air Temp*) −0.011(*Sheep*) −0.0095(*Sedimentary*)	2,077.2	0.516
	−0.38(*Agriculture*) −0.25(*Clearcut*) −0.0065(*Sheep*)	2,077.4	0.511

The response variable in both cases is the natural log of redds/km. AIC values should only be compared between models predicting the same response dataset directly, or through indirect and/or associations, cause them to be coincident with redd density. Finally, it is important to note that our results may have told a different story had we analyzed juvenile salmon data as a response variable.

At what extent is overall model fit maximized?

Some of the classes of variables (e.g., geology, terrain, land cover, etc.) identified in the best models were similar to those identified by others who have studied the relationship between Pacific salmon population dynamics and landscape condition in other Pacific Northwest systems (Pess et al. 2002; Feist et al. 2003; Steel et al. 2004). Looking across all six basins and the three species studied in these previous studies, we did not find that a consistent set of landscape predictors always correlated with salmon abundance. This should not be surprising, given the variety of ecosystems analyzed and the diversity of intra- and interspecific life history patterns. Rather, our observations indicate that a unique combination of land use, land form, climate and geology variables drive salmon distribution in each basin. While climate factors are generally presumed to have profound effects on local stream conditions (Knighton 1984; De Boer 1992; and Richards et al. 1996), we found that neither precipitation nor mean air temperature were included in any of the final models. While the ranges of temperature and precipitation for both subbasins were fairly wide (up to 11C and 1,700 mm, respectively), it's possible that the coarse grain of these data (2,000 and 500 m, respectively) may have hindered our ability to detect an effect.

The relationship of predictor variables with redd density was previously found to be greater for habitat summarized over the entire drainage basin associated with a given spawner index stream, than with an area restricted to within 500 m of a given spawner index stream (Feist et al. 2003). In contrast, here we found that multivariate models that were based on habitat summarized within 500 m of a spawner index stream (local extent) had lower AIC values than models summarized at intermediate and catchment extents. This may appear to be counterintuitive, given that the "best extent" for individual predictor variables (addressed in question 1) was more often catchment extent than local or intermediate extents. The pattern can be explained with the conclusion that single variables, summarized at the local extent, were not strongly correlated, but combinations of these "local" variables have a much greater explanatory power. This implies that multiple factors influence salmon spawner abundance, and these factors likely interact. We can consider this finding conservative given that there were fewer variables available at the local extent and, all other things being equal, a greater number of candidate predictors leads to better models, particularly with small sample sizes (Harrell 2001).

How does a mixed extent model compare with single extent models?

Few published papers have compared the performance of mixed extent models with models whose variables were summarized over a single extent. Such models require that the authors calculate the variables at multiple extents and then determine the best extent for each variable. However, there have been numerous correlational studies that have characterized land use variables at a variety of extents, and then determined which extent was best correlated with instream response variables (see papers cited in Allan 2004 and Van Sickle 2003). It seems intuitive that models with mixed spatial extents should perform better than the simpler single extent models. Given that there is not one extent that yields the best fit for all of the variables, it follows that a model, which is created with variables measured at the optimum scale for that variable, would have better model fit compared with a model using variables summarized at one scale. Further, given the hierarchical arrangement of riverscapes, one would expect that measuring variables at extents that potentially match the scale of their influence might yield models with better fit. Olden et al. (2006), found that models of macroinvertebrate communities that incorporated habitat at multiple spatial scales performed better than those at a single scale. That our mixed extent models generally had model fits that were similar to those of all of the models generated to address question two was surprising, as we had hypothesized that mixed extent models would improve model fit. Our result may be due to strong positive within-extent interactions; those interactions were lost when we used mixed extent models. Another possibility is that the best extent for a particular variable, when entered alone in a model, may be different than the best extent for that same variable when entered in a model already generated with one or more parameters. Finally, the best extent for a given variable might shift as a function of other variables in the model. Mixed extent models did not perform any better than single extent models, suggesting that a simpler approach to analyzing the geospatial data may be more efficient.

Conclusion

From these data, we conclude that our perception of which habitat attributes are significant is a function of observational extent, and that restoration and conservation efforts should consider conditions at multiple extents. The spatial window size over which we summarize or examine habitat variables can be important. If it were not, we would have found similar relationships at all three extents. Our analyses indicate that coarse-grained land use and land cover predictor variables do not correlate as well with Pacific salmon redd density when summarized within 500 m of the stream channel. Much stream and river research has been conducted at the reach scale and often restoration or land-use decisions focus only on the riparian buffer surrounding a stream. That the pattern of land-use across the entire catchment might be as strongly or even more strongly associated with stream condition or salmon distribution is useful. Our results open the way for tools from the field of landscape ecology to be applied to river and salmon conservation.

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References

Allan JD (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst 35:257–284

Allen TFH, Starr TB (1982) Hierarchy: perspectives in ecological complexity. University of Chicago Press, Chicago

Ames J, Orrell R, Deschamps G, Fiscus H, Allen D, Bergh A (1974) Report on the Salmon escapement in the State of Washington, 1971. Washington Department of Fisheries, Olympia

Belsley DA, Kuh E, Welsch RE (1980) Regression diagnostics: identifying influential data and sources of collinearity. Wiley, New York

Boys CA, Thoms MC (2006) A large-scale, hierarchical approach for assessing habitat associations of fish assemblages in large dryland rivers. Hydrobiologia 572:11–31

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer, New York

Cook RD (1977) Detection of influential observation in linear regression. Technometrics 19:15–18

Daly C, Neilson RP, Phillips DL (1994) A statistical topographic model for mapping climatological precipitation over mountainous terrain. J Appl Meteorol 33:140–158

Davies NM, Norris RH, Thomas MC (2000) Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshw Biol 45:343–369

De Boer DH (1992) Hierarchies and spatial scale in process geomorphology: A review. Geomorphology 4:303–318

Everest FH, Chapman DW (1972) Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J Fish Res Board Can 29:91–100

Fast DE, Hubble JD, Scribner TB, Johnston MV, Sharp WR (1989) Yakima/Klickitat natural production and enhancement program, annual report FY. Bonneville Power Administration, Portland

Fast D, Hubble J, Kohn M, Watson B (1991) Yakima River spring Chinook enhancement study. Bonneville Power Administration, Portland

Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. Bioscience 52:483–498

Feist BE, Steel EA, Pess GR, Bilby RE (2003) The influence of scale on salmon habitat restoration priorities. Anim Conserv 6:271–282

Frissell CA, Liss WJ, Warren CE, Hurley MD (1986) A hierarchical framework for stream habitat classification—viewing streams in a watershed context. Environ Manage 10:199–214

Gilbert CH (1912) Age at maturity of Pacific coast salmon of the genus Oncorhynchus. Bull US Fish Comm 32:57–70

Gray M (1995) Oregon Department of Fish and Wildlife (ODFW) unpublished John Day District files

Harrell FE Jr (2001) Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis. Springer, New York

Hays SG, Peven CM (1990) Spring and summer Chinook spawning ground surveys on the Wenatchee River basin. Chelan County Public Utility District, Chelan

Heindl AL, Beaty RE (1989) Escapement monitoring of some naturally spawning Columbia River Basin Chinook salmon stocks, 1987. Columbia River Inter-Tribal Fish Commission, Portland

Horner N, Bjornn TC (1979) Status of upper Columbia River fall Chinook salmon (excluding Snake River populations). Idaho Cooperative Fisheries Research Unit, University of Idaho, Moscow

Howell P, Jones K, Scarnecchia D, LaVoy L, Kendra W, Ortmann D (1985) Steelhead stock summaries stock transfer guidelines–information needs. In: Stock assessment of Columbia River anadromous salmonids, vol. II. Bonneville Power Administration, Portland, OR, p 1032

ICBEMP (1999) Interior Columbia Basin ecosystem management project spatial data. Pacific Northwest Research Station, USDA Forest Service, Portland, OR. Available from http://www.icbemp.gov/. Accessed August 2000

Imhof JG, Fitzgibbon J, Annable WK (1996) A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Can J Fish Aquat Sci 53:312–326

Infante DM, Allan JD, Linke S, Norris RH (2009) Relationship of fish and macroinvertebrate assemblages to environmental factors: implications for community concordance. Hydrobiologia 623:87–103

Jenerette GD, Wu J (2000) On the definitions of scale. Bull Ecol Soc Am 81:104–105

Johnson DH, O'Neil TA (2001) Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, OR

Johnson OW, Waples RS, Wainwright TC, Neely KG, Waknitz FW, Parker LT (1994) Status review for Oregon's Umpqua River Sea-Run Cutthroat Trout. US Department of Commerce. NOAA Technical Memorandum NMFS-VWFSC-15

Johnson RK, Furse MT, Hering D, Sandin L (2007) Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. Freshw Biol 52:939–958

Knighton D (1984) Fluvial forms and processes. Edward Arnold, London

Lam NS-N, Quattrochi DA (1992) On the issues of scale, resolution, and fractal analysis in the mapping sciences. Prof Geogr 44:88–98

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Lindsay RB, Knox WJ, Flesher MW, Smith BJ, Olsen EA, Lutz LS (1986) Study of wild spring Chinook salmon in the John Day River system, final report 1985. Bonneville Power Administration, Portland

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS® system for mixed models. SAS Institute Inc, Cary 633 pp

Martin DJ, Benda LE (2001) Patterns of instream wood recruitment and transport at the watershed scale. Trans Am Fish Soc 130:940–958

Moerke AH, Lamberti GA (2006) Scale-dependent influences on water quality, habitat, and fish communities in streams of the Kalamazoo River Basin, Michigan (USA). Aquat Sci 68:193–205

Montgomery DR (1999) Process domains and the river continuum. J AmWater Resour Assoc 35:397–410

Morley SA, Karr JR (2002) Assessing and restoring the health of urban streams in the Puget Sound basin. Conserv Biol 16:1498–1509

Myers JM et al (1998) Status review of Chinook Salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum, NMFS-NWFSC-35, 443 pp

NHI (2000) Northwest Habitat Institute spatial data. Northwest Habitat Institute. Eugene, OR: Available from http://www.nwhi.org/. Accessed August 2000

NMFS (National Marine Fisheries Service) (1997) Endangered and threatened species: listing of several evolutionarily significant units (ESUs) of west coast steelhead. Fed Regis 62(159):43937–43954 [Docket No. 960730210–7193–02, 18 August 1997]

NMFS (National Marine Fisheries Service) (2003) Draft report of updated status of listed ESUs of Salmon and steelhead. US Department of Commerce, NOAA Technical Memorandum. Available from http://www.nwfsc.noaa.gov/cbd/trt/brt/brtrpt.html/. Accessed December 2003

Olden JD, Poff NL, Blesdoe BP (2006) Incorporating ecological knowledge into ecoinformatics: an example of modeling hierarchical structured aquatic communities with neural networks. Ecol Inform 1:33–42

Olsen EA, Beamesderfer PMP, McLean ML, Tinus ES (1994) Salmon and steelhead stock summaries for the John Day River basin: an interim report. Oregon Department of Fish and Wildlife, Portland

Paavola R, Muotka T, Virtanen R, Heino J, Jackson D, Maki-Petays A (2006) Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. Ecol Appl 16:368–379

Pess GR, Montgomery DR, Steel EA, Bilby RE, Feist BE, Greenberg HM (2002) Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Washington, USA. Can J Fish Aquat Sci 59:613–623

Peven CM, Mosey TR (1995) Spring and summer Chinook spawning ground surveys on the Wenatchee River basin. Chelan County Public Utility District, 1996

Poff NL (1997) Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. J North Am Benthol Soc 16:391–409

Quinn TP (2005) The behavior and ecology of pacific Salmon and Trout, 1st edn. American Fisheries Society, Bethesda

Rastetter EB, Aber JD, Peters DP, Ojima DS, Burke IC (2003) Using mechanistic models to scale ecological processes across space and time. Bioscience 53:68–76

Resetarits WJ (2005) Habitat selection behaviour links local and regional scales in aquatic systems. Ecol Lett 8:480–486

Richards C, Johnson LB, Host GE (1996) Landscape-scale influences on stream habitats and biota. Can J Fish Aquat Sci 53:295–311

Schneider DC (2001) The rise of the concept of scale in ecology. Bioscience 51:545–553

Schwartzberg M, Roger PB (1986) An annotated compendium of spawning ground surveys in the Columbia River basin above Bonneville Dam, 1960–1984. Columbia River Inter-Tribal Fish Commission, Portland

Snyder CD, Young JA, Villella R, Lemarie DP (2003) Influences of upland and riparian land use patterns on stream biotic integrity. Landscape Ecol 18:647–664

Steel EA et al (2004) Landscape models to understand steelhead (*Oncorhynchus mykiss*) distribution and help prioritize barrier removals in the Willamette basin, Oregon, USA. Can J Fish Aquat Sci 61:999–1011

StreamNet (2002) Current anadromous Chinook salmon and steelhead distribution at a 1:100,000 scale. Pacific States Marine Fisheries Commission, Newport, OR. Available from http://www.streamnet.org/. Accessed August 2000

Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. J Hydrol 190:214–251

Torgersen CE, Close DA (2004) Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentate*) at two spatial scales. Freshw Biol 49:614–630

Unterwagner T (1999) Electronic data submission. summary of Spring Chinook spawning density, John day District, 1959–1999. Electronically submitted. Unpublished. Oregon Department of Fish and Wildlife

Unterwegner T, Gray M (1999) Annual report: John Day Fish District, Northeast region, 1997. Oregon Department of Fish and Wildlife, John Day, Oregon

Urban DL (2005) Modeling ecological processes across scales. Ecology 86:1996–2006

Van Sickle J (2003) Analyzing correlations between stream and watershed attributes. J AmWater Resour Assoc 39:717–726

Wang LZ et al (2003) Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, USA. Can J Fish Aquat Sci 60:491–505

Ward JV (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. Elsevier Sci Ltd, Oxford, pp 269–278

WDFW (1993) 1992 Washington state salmon and steelhead stock inventory, Appendix three, Columbia River stocks. Washington Department of Fish and Wildlife, Olympia

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. Freshw Biol 47:501–515

Wiens JA, Van Horne B, Noon BR (2002) Integrating landscape structure and scale into natural resource management. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge, pp 23–67

Wiley MJ, Kohler SL, Seelbach PW (1997) Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshw Biol 37:133–148