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The influence of scale on salmon habitat restoration priorities

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Abstract

Habitat loss and alteration is the leading cause of species' declines world-wide, therefore habitat restoration and protection is a prominent conservation strategy. Despite obvious connections between habitat and threatened or endangered species, conservationists have been hard pressed explicitly to link abundance or population health with habitat attributes. Given that habitat relationships with species are often characterized at a spatial scale that does not account for the functional relationships between habitat and populations, it is not surprising that the habitat–population conundrum persists. In order to explore the influence of spatial scale on the apparent relationship between habitat and populations, we examined the relationship between GIS-based habitat data and spring/summer chinook salmon (*Oncorhynchus tshawytscha*) redd (spawning nests built by females) densities in the Salmon River basin, Idaho, at two very different spatial scales: stream reach and watershed. Redd density was strongly correlated with climate, geology, wetlands and terrain. However, our stream-reach scale models provided poor predictive power compared with the watershed scale models. Based on these results, we conclude that our perception of which habitat attributes were important was clearly a function of our scale of observation, and that restoration efforts should focus on conditions at the watershed or landscape scale when attempting to do local or reach scale restoration projects.

INTRODUCTION

Habitat restoration is a widespread and important tool for the recovery of species at risk of extinction. The problem is that, although it is obvious that habitat has a huge influence on a species' well-being, it can be very hard to establish explicit links between the abundance or population health of a species and attributes of the habitat. A major source of error in such analyses may be that habitat variables are not being measured at the appropriate spatial scale. If an organism is influenced by habitat factors in the surrounding tens of kilometres, but habitat is measured only in the surrounding hundreds of metres, one would not be able to identify functional relationships between habitat and population. The challenge of identifying an 'appropriate scale' for analysis is general to all of ecology (Levin, 1992), yet very few studies deal with analyses at multiple spatial scales. In this paper we present the first population–habitat analysis that uses the same population data, but seeks relationships with habitat data summarized over two very different spatial scales (1–10 km^2 versus 100–1000 km^2). Specifically, we contrast the ability of statistical habitat models to describe spatial variation in the abundance of spawning salmon at the reach scale (defined here as the area within a 500 m buffer of any given sampled stream segment) versus the watershed scale (defined here as the total area draining into any given sampled stream segment).

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TWO KEY INNOVATIONS IN THE ANALYSES

Our analytical approach was unique, so it is important to emphasize two key problems with existing salmon habitat models that motivated our approach: spatial scale and temporal variability. The relationship between freshwater habitat condition and salmon productivity has traditionally been examined at very fine spatial scales (hundreds of metres) and over short periods of time (less than 5 years, Fausch, Hawkes & Parsons, 1988). However, extrapolating these site- and life-history-specific relationships to watershed (10^1–10^3 km^2) or regional (>10^4 km^2) scales is difficult because of spatial (stream reach to stream reach) and temporal (inter- and intra-annual) variation in salmon production (Holtby & Scrivener, 1989; House, 1995; Elliot *et al.*, 1998).

First we wanted to analyze the link between salmon redd (spawning nests built by females) abundance and habitat, using habitat variables representing two different spatial scales. This would enable us to explore the effect our scale of observation had on the conclusions we made about habitat influences on redd densities. A variety of influential computer models that purport to predict the consequences of regional management scenarios for salmon are built up from reach-level sub-models (Lichatowich *et al.*, 1995). However, they assume that processes operating at a local scale operate the same way at a landscape or regional scale.

A second key idea underlying our analysis is the importance of redd distribution patterns that are consistent over time, regardless of population size. Many analyses aimed at salmon consider 'mean salmon abundance' over long time-spans. In fact, habitat models for wildlife species in general usually consider 'average abundance'; however, high population years have a large effect on average abundance over many years. To understand relationships between habitat characteristics and fish response, it is important to identify habitat–fish relationships that affect species distribution in both high-and-low population years. In addition, management decisions are currently being made in a time of generally low population sizes. Analyses using metrics heavily weighted towards large population sizes may provide inappropriate management recommendations. Our statistical approach allowed us to examine annual patterns of salmon distribution and make conclusions that are robust to population size. We maximized our statistical power by using all available data rather than reducing it to summary statistics while also accounting for the lack of independence between annual redd counts at the same index reach. Identification of annually consistent relationships between salmon abundance and habitat characteristics improves our confidence in the applicability of our results to future years.

THE CONSERVATION PROBLEM AND BIOLOGICAL SYSTEMS

The Pacific Northwest of the United States (including Idaho, Oregon and Washington State) has been dramatically altered by humans: its river and stream networks have been extensively diked, channelized, dammed, logged, mined, farmed and urbanized (Sedell & Luchessa, 1982). These alterations, in combination with a long history of commercial fishing exploitation (NRC, 1996), have so depleted salmonid fishes in the region, that several species are listed as threatened or endangered under the Endangered Species Act (ESA). Snake River spring/summer chinook salmon (*Oncorhynchus tshawytscha*) were one of first salmonids listed (NMFS, 1992), and there is an enormous urgency to reverse their population decline. Hatchery supplementation (NMFS, 2003; Waples, Ford & Schmitt, 2003) and harvest pressure reductions (currently estimated at ~8%, table 4 in McClure *et al.,* 2003) apparently have not reversed population declines. In addition, Kareiva, Marvier & McClure (2000) concluded that removal of the lower four Snake River dams, in and of itself, was unlikely to recover Snake River chinook salmon, and Levin & Tolimieri (2001) found that Snake River dams were not preventing chinook stocks from recovering. Finally, there is evidence that habitat condition in the Snake River basin can influence chinook salmon stocks (Levin *et al.*, 2002). Consequently, current efforts to recover Snake River spring/summer chinook are now focusing on habitat restoration (NMFS, 2000). Given the enormous area (roughly the size of Switzerland) over which Snake River spring/summer chinook complete their freshwater life-history stages, it is necessary to predict population responses to habitat restoration at a regional scale.

If resource managers are to invest in broad-scale habitat restoration it is important to know where to pursue those efforts, and what type of habitat improvements are likely to yield the greatest increases in salmon population growth rates. In the past, science has offered guidance on these questions either by creating habitat classification schemes or by ranking habitats in terms of suitability for salmon. Lacking, however, are explicit analyses that make a link between measured habitat variables and measured salmon spawner abundance. In this paper, we relate a time series of salmon redd abundance data measured *in situ* in the Salmon River basin, Idaho, to habitat attributes derived from geospatial datalayers, characterized at two spatial scales (watershed and reach scale). We do not purport to model the habitat features important to all chinook salmon life stages; rather, we describe a methodology and create a spatially explicit model of redd density that can be used as a starting point for models of juvenile abundance, life-stage specific survival or productivity. This model, when integrated with existing protocols to evaluate watershed processes, will provide resource managers with a tool to locate, design and prioritize conservation efforts and management experiments aimed at salmon recovery.

METHODS

Study area

The Salmon River basin, Idaho, is in the Snake River basin/High Desert Ecoregion and covers an area of some 36,260 km^2 (Fig. 1). It is completely within the Snake River spring/summer chinook salmon evolutionarily significant unit (ESU) as defined by NMFS (1992). The entrance to the basin, where the Salmon River flows into the Snake River, is about 800 river km from the Pacific Ocean. Natural vegetation varies across the basin from alpine forests to arid grassland. The basin is spatially heterogeneous with respect to elevation (296 to 3717 m above mean sea level), precipitation (135 to 2498 mm, cumulative annual, Daly, Neilson & Phillips, 1994), and air temperature (–4 to +11°C, mean annual, Thornton, Running & White, 1997). Timber harvest, mining and agriculture (primarily livestock grazing, 50% of the basin is allotted for livestock grazing) are the dominant land-use practices. Most of the livestock grazing occurs in the eastern part of the basin, where the climate is arid and hot.

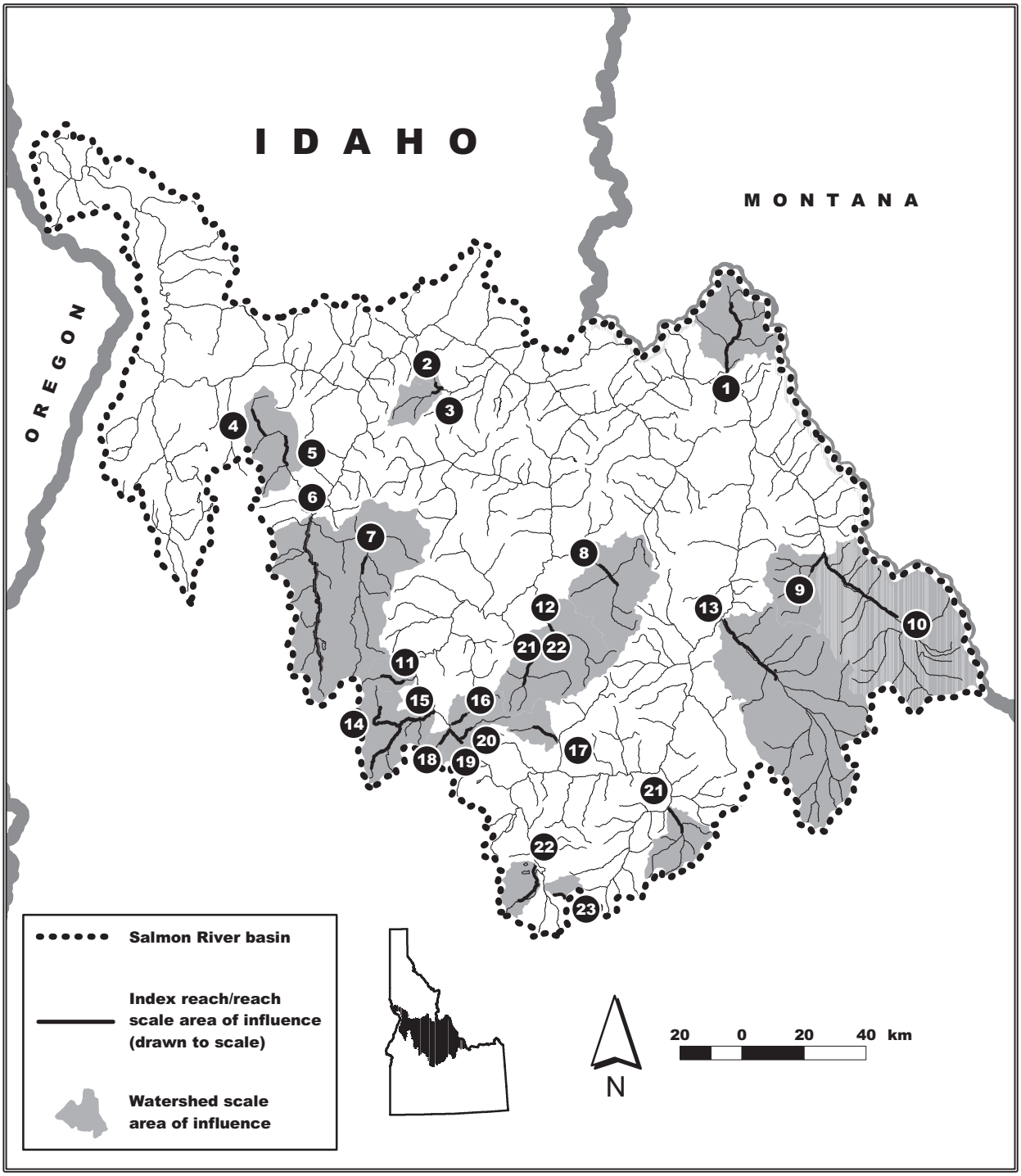

Fig. 1. Twenty three spring/summer chinook salmon index reaches used for modeling potential redd densities in the Salmon River basin, Idaho. Original redd counts collected by Idaho Department of Fish and Game (IDF&G). Reach scale area of influence (500 m buffer around index reach) drawn to scale. 1 = north fork Salmon River; 2 = west fork Chamberlain Creek; 3 = Chamberlain Creek; 4 = Lake Creek; 5 = Secesh River; 6 = South Fork Salmon River; 7 = Johnson Creek; 8 = Camas Creek; 9 = Hayden Creek; 10 = Lemhi River; 11 = Sulphur Creek; 12 = Loon Creek; 13 = Pahsimeroi River; 14 = Elk Creek; 15 = Bear Valley Creek; 16 = Beaver Creek; 17 = West Fork Yankee Fork; 18 = Cape Horn Creek; 19 = Marsh Creek; 20 = Knapp Creek; 21 = Herd Creek; 22 = Alturas Lake Creek; 23 = Pole Creek.

There also is an extensive network of water diversions that provide irrigation for pasture land and crops. There are 85,986 mining claims, and 2789 mining hazard sites (ICBEMP, 1999). The Bureau of Land Management and the US Forest Service manage about 89% of the basin, and about 27% of the entire basin is designated as wilderness area. Spring/summer and fall chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*) and steelhead (*O. mykiss*) are all listed as threatened or endangered under the ESA (NMFS, 1991, 1992, 1997).

Study population

We focused our analysis on ESA listed (NMFS, 1992) spring/summer (stream type) chinook salmon. Historically, the entire run of Columbia River basin spring/summer chinook was dominated by Snake River stocks (Petrosky, Schaller & Budy, 2001), and run sizes in the Snake River basin as a whole have declined nearly 80% over the past 40 years. Redd count data from the 23 index reaches used in our analyses show that the total number of redds and redd densities, are a fraction of what they were even as recently as the 1960s (Fig. 2). Construction and operation of the Columbia and Snake River hydropower system has contributed to declines in spawner abundance (Schaller, Petrosky & Langness, 1999; Petrosky *et al*., 2001), in addition to influences from habitat degradation and loss, commercial harvest, and hatchery influence (Sedell & Luchessa, 1982; NRC, 1996). Spring/summer chinook juveniles rear in freshwater for 1 year before migrating seaward in the spring (Bjornn, 1971; Matthews & Waples, 1991; Achord *et al*., 1996). They return to the Columbia River in early spring when they are 4 or 5 years old, and reach the Snake River by April. They arrive at their natal streams, predominantly located in higher elevation tributaries, by May and June (Chapman *et al*., 1990).

Data sets

Salmon spawner abundance

We used redd count data for spring/summer chinook salmon, collected by the Idaho Department of Fish and Game, as our proxy for salmon spawner abundance (IDF&G, unpubl. data). The IDF&G conducts annual surveys of redd abundance (on the ground and by helicopter) at nearly three dozen specific stream segments throughout the Salmon River basin. These stream segments are called 'index reaches', since they are followed over time in order to track changes in spawner abundance within the basin. They range in length from 3.5 to 69.9 river km (Table 1). While the IDF&G redd surveys are conducted separately on each group or run (spring or summer), both runs belong to the same ESU (Matthews & Waples, 1991), so we lumped them together and refer to them as spring/summer chinook.

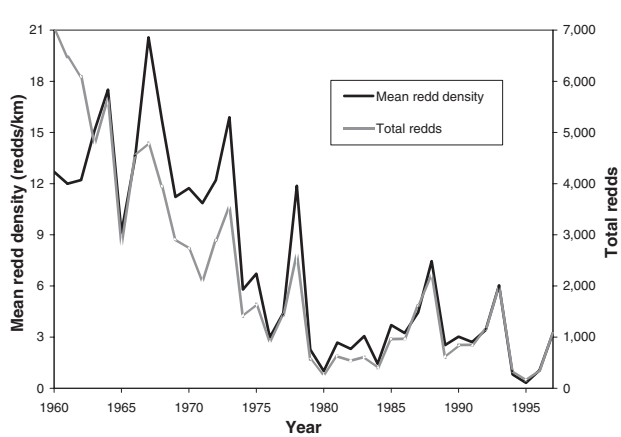

Fig. 2. Time series from 1960 to 1997 of total redd counts and mean redd densities (redds/km of stream) from the 23 index reaches used in our analyses.

Table 1. General characteristics of the index reaches used in our analyses. See Fig. 1 for corresponding 'Map no.' locations. 'Run' refers to the run timing of chinook salmon. 'Length' is the length of the index reach (in river km). 'Area' is the total area of the catchment or watershed draining into the index reach. 'Redd survey years' is the years of index reach redd survey data available for and used by our analyses.

Map no.	Index reach name	Run	Length (km)	Watershed area (km^2)	Redd survey years
22	Alturas Lake Creek	Spring	16.5	182	1960–77
15	Bear Valley Creek	Spring	42.5	497	1960–77
16	Beaver Creek	Spring	6.7	142	1960–77
8	Camas Creek	Spring	9.8	679	1960–77
18	Cape Horn Creek	Spring	6.6	72	1960–77
3	Chamberlain Creek	Spring	4.3	150	1960–65
14	Elk Creek	Spring	22.0	206	1960–77
9	Hayden Creek	Summer	7.5	369	1961–77
21	Herd Creek	Summer	11.6	301	1960–77
7	Johnson Creek	Summer	6.2	498	1960–77
20	Knapp Creek	Spring	7.9	141	1960–77
4	Lake Creek	Summer	11.0	122	1960–77
10	Lemhi River	Spring	38.4	1896	1960–77
12	Loon Creek	Summer	25.1	791	1960–77
19	Marsh Creek	Spring	9.0	141	1960–77
1	North Fork Salmon River	Spring	29.1	549	1960–77
13	Pahsimeroi River	Summer	34.2	2151	1960–67
23	Pole Creek	Spring	4.6	64	1977
5	Secesh River	Summer	11.9	441	1960–67
6	South Fork Salmon River	Summer	69.9	954	1960–67
11	Sulphur Creek	Spring	11.9	132	1960–67
2	West Fork Chamberlain Creek	Spring	3.5	56	1960–62 1965
17	West Fork Yankee Fork	Spring	11.9	148	1960–67

We used redd count data because it is the most comprehensive and complete proxy for spring/summer chinook populations in the Salmon River basin. There are surveys of juvenile abundance in the basin, but the time series are not as long and these surveys are not available for as many sites as the redd count surveys. We limited our analysis to 1960–77 and used the subset (23) of all IDF&G redd survey index reaches with minimal sampling problems within this time window (see Table 1 and Fig. 1 for general descriptions and locations of the 23 index reaches that we used, and the years of redd counts available for our analyses). We limited our analyses for a number of reasons. First, redd surveys conducted before 1960 were sporadic and methods were inconsistent since protocols were being established. Second, by the late 1970s, most salmon hatcheries were operational in the Salmon River basin (Matthews & Waples, 1991), which could bias redd count data, regardless of habitat conditions. For example, straying by hatchery adults could increase redd density, irrespective of habitat type and condition. This might make certain habitat types seem beneficial, when they are not. We expected to observe a large degree of temporal autocorrelation between redd counts at individual index reaches and we expected the

pattern might coincide with 4-year chinook salmon population cycles. However, within this time period, there were no consistent temporal autocorrelation patterns in the individual index reaches. The Lemhi River, Bear Valley Creek and the south fork Salmon River displayed significant autocorrelation with a 1-year lag; though significant, the autocorrelation for the Lemhi River and Bear Valley Creek was small, less than 0.6. The south fork Salmon River also displayed significant autocorrelation with a 2- and 3-year lag. Lake Creek had small but significant autocorrelation at a 2-year lag and Beaver Creek had marginally significant autocorrelation at a 4-year lag. We could also detect small, less than 0.04, but significant autocorrelation with a 1-year lag for all index reaches lumped together over all available years of record (1960–97).

We georeferenced the spawner index reaches (Fig. 1) to United States Geological Survey (USGS) 1:100,000 scale hydrographic datalayers, using Environmental Systems Research Institute ARC/INFO (v. 8), a geographic information system (GIS). We then normalized redd counts to the length of stream surveyed (redds/km), as measured from the aforementioned geospatial datalayer.

Environmental variables (geospatial datalayers)

We chose our environmental variables (represented by several geospatial datalayers), based on the current understanding of the habitat factors deemed most important for spring/summer chinook salmon in the Salmon River basin (Thurow, 2000, see Table 2 for detailed descriptions of each datalayer that we used). We acquired the majority of our geospatial datalayers from various federal, state and academic institutions (Table 2). We tested the same suite of habitat variables for two scales of analysis area (reach versus watershed), using the same 23 index reaches for each scale. For the reach scale analysis, however, we added three variables appropriate only for this spatial scale: channel gradient, channel sinuosity and network distance (see datalayers marked with * in Table 2). These variables were not appropriate for the watershed scale analysis, since they were specific to any given index reach itself, and not the surrounding watershed. The conditions found in any given index reach are not necessarily representative of conditions found elsewhere in its associated watershed.

Data analysis

Characterize habitat

At the watershed scale, we defined the area of influence for each index reach as the total area draining into that index reach (70–2,000 km^2, Figs 1 & 3). For the reach scale analysis, the area of influence was a 500 m buffer around each index reach that we created using the 'BUFFER' command in ARC/INFO (Figs 1 & 3). We overlaid the watershed and reach scale representations of the 23 different index reaches with each habitat datalayer (Table 2) in ARC/INFO using the 'INTERSECT' command. By using ARC/INFO, we were able to keep track of each polygon from the separate overlays (area, index reaches name, and attribute for each habitat class/sub-class). We characterized each habitat class/sub-class in the watershed and reach scale analysis areas using area weighted mean (AWM) for continuous variables (i.e. air temperature, precipitation) or by fraction of total area for categorical variables (i.e., geology, land cover, etc.). We chose not to include fine-scale variables such as large woody debris, water temperature, instream flow, etc., because these variables were not available for all of the index reaches, nor were they available for the basin as a whole.

Spatially explicit model

We used a simplified hierarchical linear model (HLM) to characterize the relationship between habitat characteristics and salmon abundance, and to develop a predictive model, at the 6th field hydrologic unit (HU) scale (6th field HUs are a standardized catchment size, each with an average area of about 6210 ha (ICBEMP, 1999)), of redd densities in the Salmon River basin (Bryk & Raudenbush, 1992).

Hierarchical models are commonly used in the social sciences for modelling nested social units (e.g. students within classrooms, Bryk & Raudenbush, 1992). Since our response variable could be considered a nested observation (redd counts within years), HLM was appropriate. In biometric applications, these and similar types of models are often called mixed-effects or random-effects models (Laird & Ware, 1982). Our version of HLM was considered 'simplified' (i.e. not a full hierarchical linear or mixed effects model), since our small sample sizes precluded our ability to examine trends in redd distributions over time. The benefit of using a simplified model structure was increased model complexity within years (multiple habitat descriptors).

This simplified hierarchical linear model had two steps. In the first step, a weighted linear model, which used the natural log of redds/km as the response variable, was fitted independently to each year of data. The model was weighted by the inverse of the coefficient of variation in redd densities; index reaches with a greater variability in redd density were down-weighted as compared to index reaches with less variability. In the second step, the distribution of the regression coefficients associated with each predictor variable over all years was examined for consistent patterns. The statistical significance of the pattern of regression coefficients was assessed using a randomization test (Good, 1997). The observed t-statistic, which tested whether the mean regression coefficient (over all years) was significantly different from zero, was compared with 1000 t-statistics calculated from random permutations (within year) of the dependent variable. We tested for index reaches that may have had a particularly large effect on observed patterns using a leave-one-out approach. This analysis identifies those index reaches that might have confounded our analysis, if they had data collected for them only during a period when spawner densities were particularly high or low.

Table 2. Geographic information system (GIS) datalayers used in habitat analysis for the Salmon River basin, Idaho. Datalayers with an asterisk were only used for the reach scale analyses. All datalayers were generated by other entities (such as federal state and academic institutions), with the exception of datalayers 1, 3 and 4, which we generated ourselves. The 'k' after all of the map scales is an abbreviation for 'kilo or 1000. Therefore, a map scale of 1:100k is equal to 1:100,000. 'Gridcell size' is the size of each individual pixel or gridcell for raster based datalayers. Gridcell size is separated from map scale by a horizontal dotted line for clarity.

ID	Datalayer	Categories	Map scale - - - - - - - - - Gridcell size	Description
1	* Network distance	Continuous, values ranged from 272 to 663 km	1:100k - - - - - - - - - N/A	Number of river km that the bottom or downstream end of any given index reach is from the entrance or mouth of the basin. Calculated using ARC/INFO with USGS 1:100k hydrolayers as underlying network.
2	* Channel sinuoisity	Continuous, values ranged from 0 to 1%	1:100k - - - - - - - - - N/A	Extracted from existing USGS 1:100k hydrolayers. Calculated by USGS, relative measure of stream within any given index reach.
3	* Channel gradient	Continuous, values ranged from 0 to 1%	1:24k - - - - - - - - - N/A	Calculated manually using USGS 1:24k quad maps. Defined as rise (upstream elevation minus downstream elevation of index reach) over (river km length of index reach) multiplied by 100.
4	Hillslope less than 1.5%	Hillslope gradient	1:100k - - - - - - - - - - 90 m	Hillslope gradient generated from USGS 90 m Digital Elevation Model (DEM), using ARC/INFO. Calculated the slope of every 90 m gridcell in the DEM. Hillslope for any given index reach is then calculated by summing all of the 90 m DEM gridcells contained in any index reaches' associated watershed or reach scale area of influence that has a slope less than 1.5%.
5	Major lithology	Carbonate and shale metamorphosed carbonate and shale, mixed carbonate and shale) Conglomerate Granitic (granite, granitic gneiss, mafic gneiss, calc-alkaline intrusive, quartzite, argillite and slate) Sedimentary (siltstone, sandstone, shale and mudstone, interlayered meta-sedimentary, meta-siltstone) Surficial deposits (alluvium, glacial drift) Syncline (mixed eugeosynclinal, mixed miogeosynclinal) Volcanics (felsic pyroclastic, calc-alkaline volcanoclastic, mafic volcanic flow, calc-alkaline metavolcanic)	1:500k - - - - - - - - - N/A	USGS classification of geologic map units according to major lithology. Generalized to seven classes from original 25.
6	USGS Land Use and Land Cover	Forest Land (deciduous, evergreen, mixed) Wetlands (forested and non-forested) Agricultural (cropland, pasture, orchards, groves vineyards, nurseries, confined feeding operations, other) Rangeland (herbaceous, shrub and brush, mixed)	1:250k - - - - - - - - - N/A	United States Geological Survey (USGS) classification of land use and land cover (LULC) from aerial photographs. Generated by USGS using Anderson *et al*. (1976) protocols.
7	GAP Land Use and Land Cover	Non-forested riparian wetlands (graminoid or dominated ('grass-like' wetland plants) shrub dominated, mixed non-forest Forested riparian wetlands (needleleaf dominated, broadleaf dominated, needle/ broadleaf dominated, mixed (forest and non-forest)	1:100k - - - - - - - - - 30 m	United States National GAP Analysis program classification of LANDSAT TM imagery into various vegetation and land-cover categories. Original LANDSAT image *c*. 1990 (Redmond, 1997; Homer, 1998)
8	Mean daily mean, maximum and minimum air temperature	Continuous, values ranged from +1 to +19°C (max), –13 to +5°C (min)	Unknown - - - - - - - - - 2 km	Mean, max, and min annual temperature for 1982, 1988 and 1989 (Thornton *et al*., 1997, acquired from ICBEMP, 1999) 1989 was considered a 'normal' year. Expressed as an area weighted mean, where each gridcell is multiplied by its temperature value, summed over all gridcells, and then divided by the appropriate area of influence (reach or watershed).
9	Cumulative annual precipitation	Continuous, values ranged from 135 to 2498 mm	Unknown - - - - - - - - - 500 m	Total annual precipitation for 1989, considered a 'normal' year from Precipitation Elevation Regressions on Independent Slopes Model (PRISM, Daly *et al*., 1994, acquired from ICBEMP, 1999). Expressed as an area weighted mean, where each gridcell is multiplied by its precipitation value, summed over all gridcells, and then divided by the appropriate area of influence (reach or watershed).
10	Livestock grazing allotments	Sheep Cattle	1:24–1:126k - - - - - - - - - N/A	US Forest Service, and BLM delineations of areas where livestock can graze. Used only on sheep and cattle categories.
11	Mining claims	Points expressed as density (number/km^2)	1:500k - - - - - - - - - N/A	Mining claims are sites where an individual possesses a mining claim. This does not necessarily imply that there is a mine in existence at the site (ICBEMP, 1999).
12	Water diversions	Points expressed as density (number/km^2)	1:100k - - - - - - - - - N/A	US Forest Service database of water irrigation diversions, screens, ladders and pumps, supplemented by BPA, and Idaho Fish and Game data. Only used diversions for our analyses (screened, unscreened and unknown).

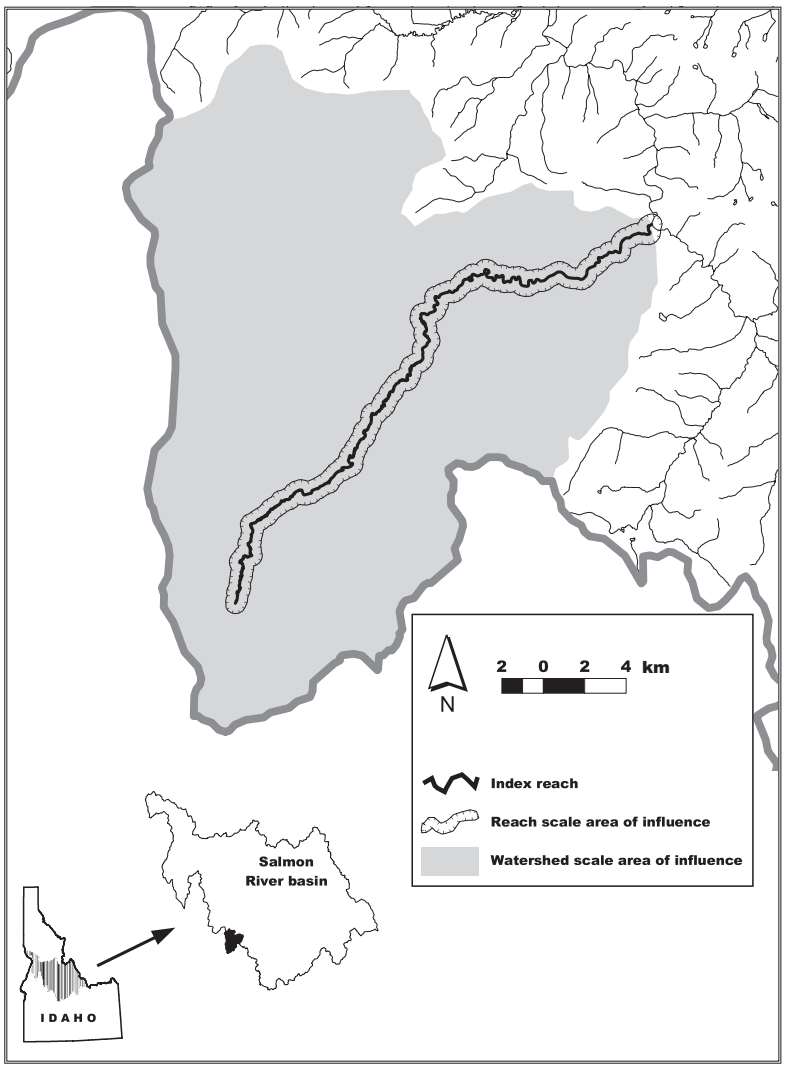

Fig. 3. Representative map of an index reach, its 500 m buffer reach scale area of influence, and its watershed scale area of influence. Example is for Bear Valley Creek watershed, one of the 23 index reaches used in our analysis.

In order to choose the best set of habitat predictors over all 18 years, we used both forward and backward model selection procedures. We fitted a given set of potential predictors to each year of data independently and evaluated the results over all 18 years. For each model of a given size, for example two-variable models, we retained three models with the highest mean adjusted r^2 over all years (best over all fit), three models with the highest maximum adjusted r^2 (best fit for any 1 year), and three models with the highest minimum adjusted r^2 (best performance in years where model fit was poor). Since r^2 values increase as parameters are added to a model, we adjusted r^2 values in order to compare models of different sizes (Neter, Kutner & Wasserman, 1996). We restricted the set of best candidate models to those in which all parameters were significant (α-level = 0.002), in which no two predictors were highly correlated, and for which there were no strong linear trends in regression parameters over time. Final models were chosen from the set of best-candidate models using a weighted combination of mean and minimum Bayesian Information Criterion (BIC). Reported model coefficients are the average of the coefficients observed in all 18 years.

We applied the model to the entire Salmon River basin (including areas where redd data were not available) using a three-step process. First, we overlaid the 584 6th field hydrologic units (HUs) datalayer with each of the significant predictor variables from the watershed scale model, using ARC/INFO. This allowed us to characterize model-relevant habitat within each 6th field HU in the Salmon River basin. Second, the habitat variables for each 6th field HU were entered into the predictive models to generate a predicted redd density for each 6th field HU. Finally, we calculated the redd density for each 6th field HU as the mean from all five predictive models for that 6th field HU. Mean redd density was expressed in the map as standard deviation above or below the mean redd density for any given 6th field HUs. We excluded HUs whose habitat characteristics fell outside the range of the habitat characteristics used to build the model. We also excluded HUs with a main-channel gradient greater than 5%, as

reaches this steep are rarely used for spawning by chinook salmon. Prediction confidence intervals were calculated using 1000 bootstrap iterations (Efron & Tibshirani, 1986). The bootstrap technique used the uncertainty around the original model fit to simulate the uncertainty in predictions from the model. This did not incorporate uncertainty associated with redd count errors, which are not available for these data. Each iteration of the bootstrap randomly reassigned the original model residuals to the original fitted values. The hierarchical approach was then used on the new data to fit a new model (using the same set of predictor variables) and to predict a value for each 6th field HU. One random residual was added to the predicted value to estimate the variance around the prediction. From the distribution of 1000 predictions for each HU, the coefficient of variation was calculated.

RESULTS

The mean regression coefficient was significantly different from zero for many of the potential predictor variables, when entered independently, for both the watershed and reach scale analyses. However, many of the potential predictor variables were highly correlated, so it was difficult to determine the influence of any one variable. Based on the leave-one-out analysis, there was no single index reach responsible for the consistent patterns in regression coefficients over time.

Predictive multiple regression model

For the watershed and the reach area analyses, there were numerous 'best' models; we retained a set of best models for predictive purposes. Since there was high correlation among many potential predictor variables, the suite of habitat variables in the final models did not necessarily contain all of the most important causal drivers of overall salmon abundance. The advantage of using a set of best models is that we reduce the uncertainty associated with selecting any one particular model.

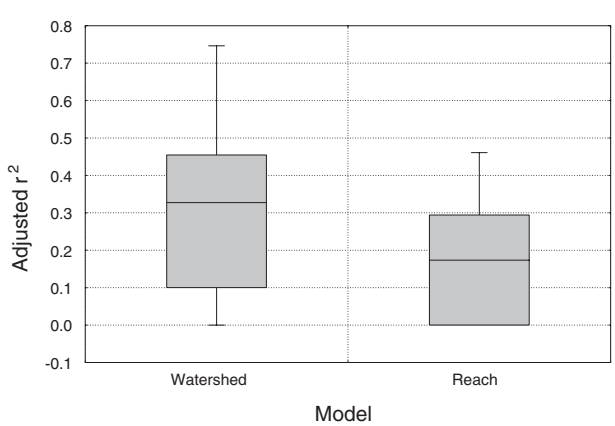

Fig. 4. Median adjusted r^2 values for watershed and reach scale models. Boxes are 25th to 75th percentile, and whiskers are minimum and maximum.

Watershed scale

The best models for predicting salmon redd density at the watershed scale, included percent non-forested riparian wetlands, air temperature, percent sedimentary geology, and percent hillslope less than 1.5%. On average, these models had an adjusted r^2 around 0.28 (Fig. 4). Maximum adjusted r^2 values, for any year, were higher than 0.70, so in many years the models explained a large amount of the variance in redd density. Model fit was worst in 1960 and 1977, and was poor in 1961, 1969 and 1971. Model coefficients, intercept and transformations for all five watershed models are presented in Table 3.

The five different models performed similarly because the four variables that differed among models were highly correlated (anywhere from –0.75 to –0.37, and +0.47 to +0.81). The high degree of correlation among land-use variables and among land-use and landscape characteristic variables prevented us from determining which habitat variables were the dominant drivers of spring/summer chinook abundance. However, our analysis indicated that from 1960 to 1977, redd densities were greatest in cool, wet areas, with small areas of sedimentary geology, large areas of low gradient topography and non-forested riparian wetlands. These areas tend to have a lower total area of rangeland, and grazing allotments, and lower densities of water diversions.

Predicted redd density for each of the 6th field HUs throughout the basin was variable across space (Fig. 5). In general, the coefficient of variation was inversely related to predicted redd density. In other words, the estimated precision of the estimates was highest in those 6th field HUs (e.g. mainstem Salmon River), where predicted redd density was highest.

Reach scale

We followed the same methodology for the reach scale data as for the watershed scale data; yet model fits were much weaker. There was no clear best model or best set of models because all models explained relatively little of the variation in redd abundance between index reaches. The top seven models are presented in Table 4; adjusted r^2 values were all below 0.160. Air temperature was the only variable that was consistently selected in the best models (Table 4). The maximum adjusted r^2 observed for any one year was only 0.460. Since these values were significantly lower than the watershed scale models, we did not attempt to predict redd densities using models developed from habitat variables characterized at the reach scale.

DISCUSSION

Which spatial scale for restoration?

Our perception of ecological processes is a function of the spatial, temporal or organizational scale of these processes, and of our observations of these processes (Levin, 1992). This was most certainly the case with our

Table 3. Predictor variables, coefficients, intercepts, mean adjusted r^2 (over all 18 modelled years) and mean BIC (Bayesian Information Criterion) for each of the five watershed scale models used in the final predictions. All models were applied to each of the 584 6th field hydrologic units in the Salmon River basin for the spatially explicit model. Response variable for all models is the natural log of redd density (redds/km) + 0.5.

Predictor variable	Model 1 coefficient	Model 2 coefficient	Model 3 coefficient	Model 4 coefficient	Model 5 coefficient
Non-forested riparian wetlands				+10.02	–3.81
Air temperature		–0.47[a]	+0.18[b]		
Sedimentary geology	–0.84		–1.12	–0.72	–0.91
Hillslope less than 1.5%	+4.35	+6.38			+5.69
Y-intercept	2.77	5.96	4.51	2.75	2.86
Mean adjusted r^2	0.272	0.258	0.242	0.243	0.297
Mean BIC	–4.189	–3.643	–3.405	–3.367	–3.178

[a]1989 Maximum Air Temperature
[b]1989 Minimum Air Temperature

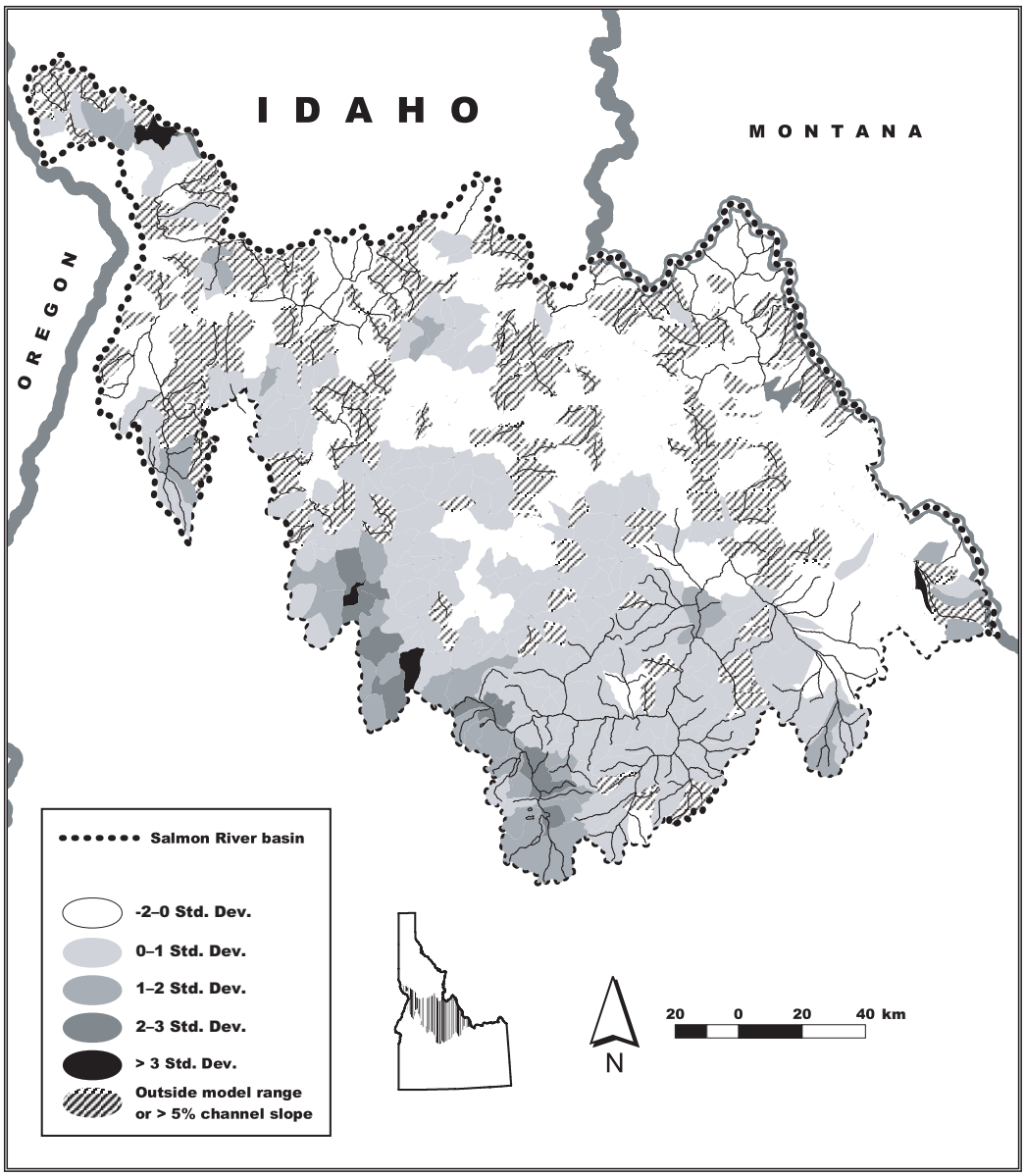

Fig. 5. Final predictive spatial model of potential spring/summer chinook redd densities in the Salmon River basin, Idaho. Potential redd densities were predicted for each of the 584–6th field hydrologic unit catchments, and are expressed as standard deviations above or below the mean.

research in that our conclusions about which habitat attributes had the greatest influence on salmon redd density were a function of our scale of observation. For example, if we had only done our analyses at the reach scale, we would have concluded that ambient air temperature was the primary driver of redd density. By also running our analyses at the watershed scale, we learn that over large spatial scales, the amount of riparian wetlands influence salmon redd density, and geology and terrain may also be important. This is an important cautionary tale in general for conservation, and an important practical result for salmon recovery planning in particular. If resource managers had made a decision based on our reach scale analyses, they would have concluded that little could be done to improve redd density, and might have decided that habitat restoration would not help salmon populations in the Salmon River basin. Correlations between the habitat variables prevented us from attributing cause and effect relationships between specific habitat characteristics and redd abundance. One of the challenges of working at large scales is that designed experiments are nearly impossible. These types of analyses can, however, be used to generate hypotheses that can be tested as restoration actions are implemented.

The watershed scale analysis worked well for our predictive model, but management actions are often aimed at the reach scale. This underscores our need to plan small-scale restoration in the context of whole watersheds. Restoring one small reach in a watershed that has had its habitat-forming processes altered is of little utility, and is unlikely to be successful (Beechie & Bolton, 1999). In addition, reach scale restoration efforts, such as large woody debris placement, may not improve stream conditions if the quality and quantity of riparian wetlands is low. Given the enormous area over which anadromous salmonids complete their freshwater life-history stages, it is not surprising that landscape scale processes have a profound influence on populations.

Restoration priorities

Our modelling efforts suggest that areas in the Salmon River basin with low-gradient streams, low amounts of sedimentary geology, cooler air temperatures and expansive riparian wetlands are most likely to support high densities of spring/summer chinook spawners. Restoration opportunities should be abundant in areas with these conditions, or in areas that historically had these conditions. While anthropogenic influences such as logging, livestock grazing and water diversions did not qualify to be in our predictive models, they appear to have a negative influence on redd density, when considered individually. This suggests that resource managers should pay close attention to the influence of livestock grazing and water diversions when choosing and prioritizing potential restoration sites. It is clear that livestock grazing (Petrosky & Holubetz, 1988; Platts, 1991; Belsky, Matzke & Uselman, 1999) and water diversions (Chapman, 1966; Junk, Bayley & Sparks, 1989) can lower the survival of anadromous salmonids. While correlation problems in our habitat data precluded separating the influence of these potentially detrimental land-use practices, it is not prudent to assume that their absence in our predictive models implies that they are innocuous in the Salmon River basin. It is possible that none of the index reaches that we analyzed was truly 'pristine', so there may not have been enough contrast to measure the effects of the aforementioned anthropogenic influences. However, it is conceivable that the apparent negative influence of a given land-use practice could be due to the fact that it is highly correlated with another detrimental habitat attribute.

Given the coarse scale of our model, all of these suggested restoration strategies require management experiments that will verify efficacy. For example, survival at various life-history stages, as well as the annual population growth rate, should be measured at restoration sites. Since existing index reaches have strong correlation with respect to habitat attributes (i.e. reaches with cattle grazing associated with them are usually in drier, hotter locales, with numerous water diversions, and generally lack granitic geology), management experiment sites should be selected in locales that represent all possible combinations of modelled habitat variables.

Data and analysis limitations

Since our model relies on simple correlation, the mechanisms linking habitat to salmon abundance are not explicitly tested. For example, riparian wetlands are

Table 4. Predictor variables, coefficients, intercepts, mean adjusted r^2 (over all 18 modelled years) and mean BIC (Bayesian Information Criterion) for each of the seven reach scale multiple regression models. Response variable for all models is the natural log of redd density (redds/km) + 0.5. The indicator for wetlands was equal to 1 if percent wetland was greater than 0.01, –1 else.

Predictor variable	Model 1 coefficient	Model 2 coefficient	Model 3 coefficient	Model 4 coefficient	Model 5 coefficient	Model 6 coefficient	Model 7 coefficient
Air temperature	–0.026[a]	–0.278[b]	–0.138[c]	–0.297[a]	–0.126[c]	–0.140[c]	–0.129[c]
Wetlands (indicator)							–0.234
Glacial deposits				–0.693		–0.388	
Granitic geology					–0.452		
Y-intercept	4.683	5.241	1.113	5.520	1.019	1.142	1.482
Mean adjusted r^2	0.140	0.143	0.134	0.158	0.144	0.127	0.128
Mean BIC	–2.602	–2.583	–2.424	–1.436	–0.8590	–0.616	–0.519

[a]1982 Maximum air temperature
[b]1989 Maximum air temperature
[c]1982 Minimum air temperature

beneficial to spring/summer chinook salmon juveniles in a variety of ways, ranging from food availability to refugia from predation. Our analyses do not determine what it is in particular about any given habitat attribute that is beneficial to salmon. As well, there are clearly other unmeasured habitat variables which may have a large effect on redd distribution. In our analysis, we did not consider non-linear or multiplicative effects of measured habitat variables. Finally, since we used adult spawner abundance as a proxy for population condition, it would seem prudent to pursue studies directed at linking habitat conditions with juvenile abundance or survivorship data. It is conceivable that our habitat restoration priorities benefit adults spawners more than juveniles.

Currently, available redd data severely underrepresent sites with lower-quality habitat. As a result, we have little information on habitat type and condition where spring/summer chinook are rare or absent. As our data for these sites are poor, the model should not be used to make conclusions about which areas in the basin are not particularly good for salmon. The higher levels of uncertainty in redd abundance predictions from our models for areas with lower than average redd density further emphasize this point. This again suggests that the model is best suited for identifying areas with high salmon redd densities. Limitations of current data make a clear argument for a sampling design incorporating sites supporting low redd densities, or sites that are not used by salmon. From examples with plant population dynamics research, there are two consequences of only sampling where an organism currently resides (Crawley, 1990). First, populations will tend to disappear or go extinct in any given area. This does not imply that they can never return, so sampling should continue. Second, recruitment of new populations is most likely to occur in areas where individuals are absent or at extremely low densities. If one only samples where one knows there are salmon, one misses recruitment events and tends to underestimate population growth rates.

SUMMARY AND CONCLUSIONS

The relative importance of habitat to salmon survival is a contentious issue. This is especially so in the Snake River basin, where various groups have become polarized over the issue of dams versus habitat, as it relates to the extinction risk of spring/summer chinook salmon (NMFS, 2000). Kareiva *et al*. (2000) concluded that increasing survival in either the freshwater rearing or estuarine/early ocean life-history stages was most likely to reverse population declines for Snake River basin spring/summer chinook. However, Marmorek, Peters & Parnell (1998) concluded that removing the four lower Snake River dams would have a stronger influence on population trajectories. While our analysis is incapable of evaluating the tradeoffs of these two policy options, one of the original objectives of our research was to predict population responses to various anthropogenic impacts in the Salmon River basin. In doing so, we had hoped to quantify the impact of habitat degradation and loss on salmon populations in any given sub-basin. However, correlation among many of the predictor variables prevented us from determining whether or not any given single habitat variable, in and of itself, was influencing redd abundance. Given the disparity of conclusions about what needs to be done to recover salmon stocks, it seems prudent to improve existing population sampling protocols in order to be freed from the constraints of correlation in the data and make definitive conclusions about the relative influence of habitat on the population dynamics of spring/summer chinook salmon in the Salmon River basin. Our analysis does not enable us to predict whether or not removing the negative influence of any given anthropogenic influence will sufficiently reverse population declines of spring/summer chinook in the Salmon River basin. However, given that increasing survival during freshwater residency may have the greatest likelihood of reversing population declines (Kareiva *et al*., 2000), addressing these impacts at locations possessing the physical attributes associated with high salmon abundance is a logical first step. Subsequent evaluation of the response of the salmon to these restoration efforts will enable an estimate of the effect on survival and productivity and permit the development of more precise restoration strategies.

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