

CHINOOK SALMON USE OF SPAWNING PATCHES: RELATIVE ROLES OF HABITAT QUALITY, SIZE, AND CONNECTIVITY

DANIEL J. ISAAK,¹ RUSSELL F. THUROW, BRUCE E. RIEMAN, AND JASON B. DUNHAM²

U.S. Forest Service, Rocky Mountain Research Station, Boise Aquatic Sciences Laboratory, 322 East Front Street,
Suite 401, Boise, Idaho 83702 USA

Abstract. Declines in many native fish populations have led to reassessments of management goals and shifted priorities from consumptive uses to species preservation. As management has shifted, relevant environmental characteristics have evolved from traditional metrics that described local habitat quality to characterizations of habitat size and connectivity. Despite the implications this shift has for how habitats may be prioritized for conservation, it has been rare to assess the relative importance of these habitat components. We used an information-theoretic approach to select the best models from sets of logistic regressions that linked habitat quality, size, and connectivity to the occurrence of chinook salmon (*Oncorhynchus tshawytscha*) nests. Spawning distributions were censused annually from 1995 to 2004, and data were complemented with field measurements that described habitat quality in 43 suitable spawning patches across a stream network that drained 1150 km² in central Idaho. Results indicated that the most plausible models were dominated by measures of habitat size and connectivity, whereas habitat quality was of minor importance. Connectivity was the strongest predictor of nest occurrence, but connectivity interacted with habitat size, which became relatively more important when populations were reduced. Comparison of observed nest distributions to null model predictions confirmed that the habitat size association was driven by a biological mechanism when populations were small, but this association may have been an area-related sampling artifact at higher abundances. The implications for habitat management are that the size and connectivity of existing habitat networks should be maintained whenever possible. In situations where habitat restoration is occurring, expansion of existing areas or creation of new habitats in key areas that increase connectivity may be beneficial. Information about habitat size and connectivity also could be used to strategically prioritize areas for improvement of local habitat quality, with areas not meeting minimum thresholds being deemed inappropriate for pursuit of restoration activities.

Key words: chinook salmon; connectivity; habitat fragmentation; habitat geometry; metapopulation; nest; *Oncorhynchus tshawytscha*; patch; redd; sampling artifact.

INTRODUCTION

Widespread population declines, extirpations, and a growing list of endangered, threatened, and sensitive fish species in riverine ecosystems (Williams et al. 1989, Nehlsen et al. 1991, Williams 2006) have caused natural-resource agencies to reassess management goals and change priorities from consumptive uses to species preservation (Hanna 1999). Underpinning this transition are advances in the fields of conservation biology and landscape ecology that have altered perceptions about how fish populations relate to the environment (Schlosser and Angermeier 1995, Rieman and Dunham 2000, Fausch et al. 2002). The traditional view focused on population isolates and local habitat quality, whereas the emerging view recognizes that population persistence

often depends on an array of spatial processes that may include complementation, supplementation, neighborhood effects, size, and connectivity (Dunning et al. 1992, Bond and Lake 2003).

Metapopulation theory, with its emphasis on groups of discrete, interacting populations, places population dynamics in a broader context and has strongly influenced conservation efforts for many species (Hanski 1991, Hanski and Ovaskainen 2003). Although archetypical metapopulation structures may be representative for a limited number of species, populations in natural environments are usually spatially structured and fall along a continuum from mainland–island systems to patchy single populations (Harrison and Taylor 1996, Rieman and Dunham 2000). Regardless of which spatial structure is most relevant, the discretization of populations emphasizes the importance of dispersal movements, which can provide either demographic support for populations with low growth rates (Dias 1996) or colonists to refound suitable habitats after local extirpations have occurred (Brown and Kodric-Brown 1977). A spatially explicit view also emphasizes habitat

Manuscript received 9 December 2005; revised 25 May 2006; accepted 8 June 2006. Corresponding Editor: T. E. Essington.

¹ E-mail: disaak@fs.fed.us

² Present address: U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 Southwest Jefferson Way, Corvallis, Oregon 97331 USA.

size, which is important because larger habitats tend to support larger populations that are usually less susceptible to extirpations from demographic or genetic stochasticity (Lande 1993). Additionally, larger habitats can absorb environmental disturbances without all individuals being adversely affected (White and Pickett 1985, Sedell et al. 1990). Although case studies of spatially structured fish populations are not yet common, a growing body of evidence supports this view (Rieman and McIntyre 1995, Dunham and Rieman 1999, Lafferty et al. 1999, Labbe and Fausch 2000, Morita and Yamamoto 2001, Koizumi and Maekawa 2004, Neville et al. 2006a).

As a logical outgrowth of a broadened population perspective, considerations regarding what constitutes relevant habitat characteristics also have evolved. Traditional measures of local habitat quality in streams (e.g., substrate conditions, undercut banks, pool depths, etc.) must now be considered with habitat size and connectivity. Because this perspective is relatively new, however, it is rare for comparative assessments of different habitat components to have been conducted. Proponents of the geometric aspects of habitat have argued that conservation efforts need only consider these factors (Hanski 1994, Moilanen and Hanski 1998), but dismissal of habitat quality information has sparked objections from others who argue that quality metrics often provide better predictions of species occurrence (Thomas et al. 1998). More recently, these disparate views have begun to merge and could yield valuable insights for prioritization of management activities (Thomas et al. 2001, Fleishman et al. 2002, Armstrong 2005). For example, models designed to evaluate the relative importance of different habitat elements could provide guidance about the effectiveness of increasing the size of existing areas, improving habitat quality, or creating new habitats that would increase connectivity among existing areas.

Inherent to most spatial population models are the assumptions that local populations will occasionally be extirpated and that colonists from nearby populations will later re-found vacant habitats (Hanski 1991, Harrison and Taylor 1996). Despite the dynamism this implies, many studies offered in support of spatial population models are derived from single, cross-sectional surveys of species distributions (Clinchy et al. 2002). The static view thus afforded is most valid only for equilibrium distributions that are not undergoing regional declines or expansions (Clinchy et al. 2002, Wagner and Fortin 2005). A better approach, although more costly, is to repeatedly survey the distribution of a target species at the same geographic locale. Not only would the replicate surveys provide more representative, time-averaged views of habitat use, but they also may reveal temporal changes in the importance of different habitat components. If such shifts occur, appropriate management responses would be at least partially

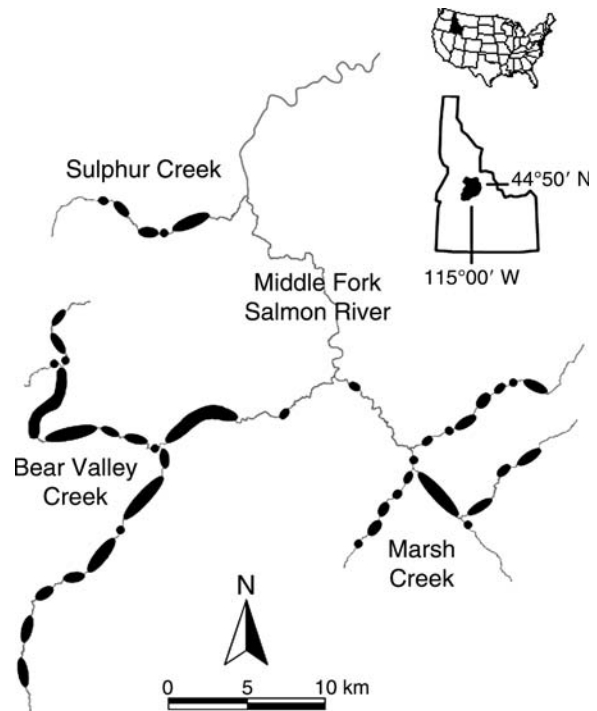


FIG. 1. Stream network in the Middle Fork Salmon River, Idaho, USA, that was accessible to chinook salmon and was annually censused for redds from 1995 to 2004. Black ovals represent patches of suitable spawning habitat.

contingent on landscape setting and population status (Moilanen and Hanski 1998).

In this paper, we focus on a population assemblage of chinook salmon (*Oncorhynchus tshawytscha*) located in central Idaho. Within this area, salmon nests, often referred to as redds, have been georeferenced during spatially continuous, basinwide surveys conducted annually from 1995 to 2004 (Isaak and Thurow 2006). These data were used to determine the occupational status of suitable spawning areas, which was modeled as a function of habitat quality, size, and connectivity. Our specific objectives were to assess the relative importance of these general classes of habitat descriptors in determining redd occurrence, to determine whether habitat factors changed in importance for different population densities, and to discuss the conservation implications of our results.

METHODS

Study site

This research was conducted in central Idaho across a stream network that encompassed three subbasins in the Middle Fork Salmon River (MFSR) headwaters (Fig. 1). The area comprises 1150 km² of forested and mountainous terrain at elevations ranging from 1700 to 2900 m and is administered by the U.S. Forest Service. Thick deposits of Quaternary alluvium and Pleistocene glacial drift fill the main stream valleys and

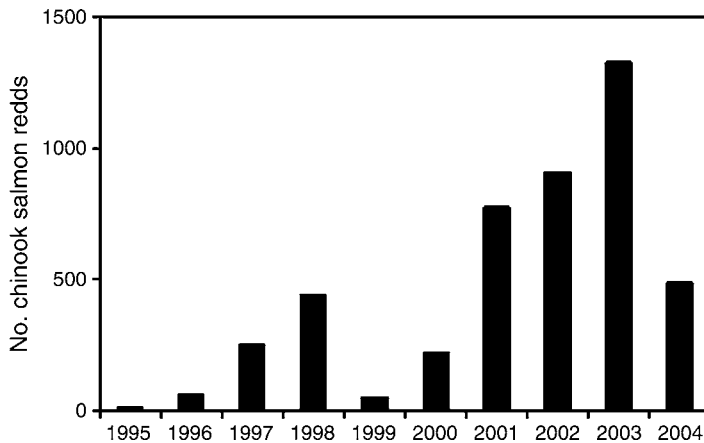


FIG. 2. Number of chinook salmon redds counted during aerial surveys of the Middle Fork Salmon River from 1995 to 2004.

result in broad floodplains (Bond and Wood 1978). Channel morphologies consist of meandering pool-riffle sequences (sensu Montgomery and Buffington 1997), except where valley walls confine streams and steeper channel morphologies are present. Stream hydrographs are characteristic of snowmelt-driven systems in the northern Rockies, with high flows occurring from April through June and low flows during the remainder of the year.

Chinook salmon populations are composed of wild, indigenous fish and are referred to as spring chinook based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). Adult salmon enter the MFSR in early summer, migrate to natal areas in larger tributaries, and stage in pools before spawning. Redd construction usually begins during the last week of July and is completed by early September (R. Thurow, unpublished data). Females typically deposit eggs in single redds (Bentzen et al. 2001) that are 2–4 m in diameter and are constructed in riffle crests or other areas that have similar hydraulic and substrate characteristics (Vronskiy 1972, Healey 1991). Embryos incubate in the gravel, emerge as fry the following spring, and rear in channel margins and side channels for one year before migrating to the ocean (Bjornn 1971, Hillman et al. 1987). Maturity is reached 1–3 years later at lengths ranging from 60 to 120 cm (Kiefer et al. 2002).

Similar to most anadromous salmonids in the Pacific Northwest (Nehlsen et al. 1991), populations of MFSR chinook declined from the 1950s into the 1990s (Brown 2002), which prompted federal listing in 1992 under the Endangered Species Act and protection of critical habitats. During the course of this study, however, populations grew and abundances increased from 10 redds in 1995 to 1326 redds in 2003 (Fig. 2), the highest number observed since the early 1970s. Increases are believed to have occurred in response to a combination of improved ocean productivity and juvenile migration conditions (Fish Passage Center 2003, Beamish et al.

2004), as significant changes in generally high-quality rearing habitats have not occurred in the last decade.

In addition to chinook salmon, other native fishes within the MFSR include: bull trout (*Salvelinus confluentus*), westslope cutthroat trout (*Oncorhynchus clarkii lewisii*), rainbow trout (resident and anadromous forms; *O. mykiss*), mountain whitefish (*Prosopium williamsoni*), torrent sculpin (*Cottus rhotheus*), mottled sculpin (*C. bairdi*), shorthead sculpin (*C. confusus*), Pacific lamprey (*Entosphenus tridentatus*), speckled dace (*Rhinichthys osculus*), longnose dace (*R. cataractae*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*C. columbianus*), reddsider shiner (*Richardsonius balteatus*), and northern pikeminnow (*Ptychocheilus oregonensis*) (Thurow 1985). Brook trout (*S. fontinalis*) have been introduced and are common within Bear Valley and Marsh creeks but appear to be absent from Sulphur Creek (Levin et al. 2002).

Redd surveys

Low-level helicopter flights were used to conduct annual, spatially continuous surveys for chinook salmon redds from 1995 to 2004 within that portion of the stream network that historically supported this species (Fig. 1). Range determination was made by reviewing records of juvenile chinook salmon occurrence (Thurow 1985), Idaho Department of Fish and Game redd survey reports (Brown 2002), and anecdotal accounts of spawning (Hauck 1953, Gebhards 1959), and by interviewing local biologists. When a redd was observed, a global positioning system was used to georeference the location. All locations were later differentially corrected and assembled into a geographic information system for use in subsequent analysis. Additional details are provided in Isaak and Thurow (2006).

Habitat patch delineation

Environmental heterogeneity, combined with species and life-stage-specific physiological requirements, result in patchy distributions of suitable habitats across stream networks (Hall et al. 1992, Dunham et al. 2002). To

delineate discrete patches of suitable spawning habitat, we used a combination of biological and physical descriptors. A preliminary set of patch boundaries was defined based on gaps in the cumulative spatial distribution of redds from 1995 to 2004 that exceeded 400 m. These boundaries were modified during subsequent foot surveys to coincide with changes in channel morphology from pool-riffle reaches that contained abundant spawning and rearing habitats to steeper channels where these habitats were uncommon (e.g., Montgomery et al. 1999, Buffington et al. 2004). Patch boundaries were also defined where spawning streams were joined by significant tributaries (i.e., third order or larger). We reasoned that salmon would perceive up- and downstream areas as distinct environments given their acute sense of smell (Quinn 2005) and the marked changes in physicochemical conditions that occur in these areas (Rice et al. 2001, Benda et al. 2004).

Using redd distributions to aid in determination of suitable patch boundaries reduced the need for subjective habitat assessments and ensured that areas deemed suitable could actually be used by the fish. However, this approach made it possible that some suitable habitats not used during this study were excluded from consideration. We believe these omissions were minor, given that channels with steep gradients constituted most of the excluded areas. Additionally, earlier research suggests that areas used for spawning have remained relatively constant across a wide range of redd densities (Isaak and Throw 2006).

Connectivity

Connectivity for each habitat patch was quantified using a metric developed by Moilanen and Nieminen (2002) that incorporates a negative exponential dispersal kernel, as well as the size and spatial arrangement of neighboring populations throughout a habitat network. The generic formula for calculating connectivity of focal patch i was

$$S_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij}) A_j^b \quad (1)$$

where p_j was the observed incidence (0 or 1) in a neighboring patch j , α was a dispersal scalar wherein $1/\alpha$ was average dispersal distance, d_{ij} was the Euclidean distance between patches i and j , and A_j^b was the area of neighboring patch j . Area is used as a surrogate for population size; the exponent, b , scales the expected emigration rate, with larger patches expected to have lower per capita emigration rates due to smaller edge-to-area ratios (Hanski et al. 2000, Moilanen and Nieminen 2002).

To adapt this metric to a stream system and the unique attributes of our data, we modified Eq. 1 by using stream distance rather than Euclidean distance, accommodating observations from different years, and using the number of redds within neighboring patches to provide direct estimates of population sizes. Substituting

redd abundance for a population surrogate based on area was especially powerful because connectivity values then reflected the dynamics of interannual shifts in spawning distribution and abundance. The formula for the revised connectivity metric was

$$S_{ik} = \sum_{j \neq i} p_{jk} \exp(-\alpha d_{ij}) N_{jk} \quad (2)$$

where p_{jk} was the observed incidence (0 or 1) of redds in neighboring patch j during year k , α was the dispersal scalar wherein $1/\alpha$ was the average dispersal distance for chinook salmon, d_{ij} was the stream distance between patches i and j measured between the nearest edges of these patches, and N_{jk} was the number of redds in neighboring patch j during year k .

Direct estimates of dispersal in chinook salmon are rare, but McClure et al. (2003) summarized unpublished tag return studies and suggested that it was uncommon for hatchery chinook to be recaptured >30 km from their natal sites. Wild fish may disperse smaller distances, however, and indirect estimates based on spatial autocorrelation analysis and fine-scale genetic patterns suggest that dispersal distances ~10 km may be more realistic (Neville et al. 2006b; D. J. Isaak, *unpublished manuscript*). To account for this uncertainty, we included a range of dispersal distances (2–30 km) in initial models to determine whether variation in this parameter affected our results.

Habitat quality

Attributes commonly linked to egg incubation success, early juvenile rearing, and adult spawning preferences were measured in all habitat patches during baseflow conditions in July 2004. Field crews measured wetted width and water depths at one-fourth, one-half, and three-fourths the width along 15 evenly spaced transects within each patch. Undercut banks (>30 cm of undercut) important for sheltering returning adults and rearing juveniles (Hillman et al. 1987, Bjornn and Reiser 1991) were measured along 10 m of both banks at each transect location. As crews moved between transects, they counted pieces of wood (>1 m in length and >10 cm in diameter) that contributed to pool formation, recorded the number of channel-spanning pools with lengths of at least one channel width, and measured the lengths of backwater and side channel habitats that serve as important rearing and refuge areas for juvenile salmonids (Hartman and Brown 1987, Scrivener et al. 1994).

Potential spawning sites within patches were defined as areas of substrate at least 2 m wide and 2 m long that were uninterrupted by large cobbles and where substrates were in the 16–64 mm range preferred by chinook salmon (Kondolf and Wolman 1993). These areas also had to have water velocities ranging from 30 to 90 cm/s and water depths that exceeded 10 cm (Bjornn and Reiser 1991). Suitable spawning sites were usually located in riffle crests and shallow glide habitats where

others have observed spawning by chinook salmon (Vronskiy 1972, Healey 1991). Detailed measurements were obtained from the first two suitable sites encountered after each transect, and subsequent sites were counted until the next transect was reached. Measurements included the areal dimensions of a site, prevalence of fine substrates, and intermediate axis lengths of five randomly selected substrate particles, which were measured with a template (US SAH-97; Wildco, Buffalo, New York, USA). In several instances, we supplemented data on substrate size with measurements from earlier surveys (R. F. Thurow, *unpublished data*). Fine substrate, which is often negatively associated with egg incubation success (Hicks et al. 1991), was quantified by placing a square metal grid (7-cm spacing) on the substrate at the downstream end of suitable areas and counting grid intersections that overlaid sand size and smaller substrates (≤ 8 mm).

These habitat measures were summarized at the patch scale by conversion to densities, ratios, proportions, and measures of central tendency and variability. Pool counts, wood counts, and lengths of rearing habitats were converted to areal densities. Fine substrate, overhead bank cover, and suitable spawning area were expressed as proportions. Calculations for spawning area were made by dividing patch size into the total potential spawning area within a patch. Patch size was obtained by multiplying average wetted width by the length of stream flowing through a patch. Stream length was measured from a 1:24 000-scale stream hydrology layer that was derived from the blue-line network on 7.5-minute U.S. Geological Survey topographic maps. Variables summarized as central tendencies included median substrate size (D_{50}) within suitable spawning sites, average stream depth, and wetted width, the latter of which could be interpreted as measures of stream size that connoted environmental stability (Taylor and Warren 2001). Width-to-depth ratios (W/D) were calculated and frequently have been used as indicators of bank stability and grazing intensity (Beschta and Platts 1986, Ebersole et al. 2003). We also calculated coefficients of variation (CV) from width, depth, and width-to-depth ratios (reasoning that greater variability would be associated with habitat diversity).

Hyporheic exchange, which involves subsurface flow through the streambed, is an important determinant of redd site selection because it moderates temperatures, increases oxygen delivery, and removes waste from incubating eggs (Curry et al. 1995, Baxter and Hauer 2000). Unfortunately, obtaining direct measures of hyporheic exchange across our study site was impractical. Therefore, we used proxy variables, reasoning that greater hyporheic exchange would occur in association with the lateral irregularities of sinuous channels or where changes in bed topography forced flow paths into the stream bed (Harvey and Bencala 1993, Poole and Berman 2001, Kasahara and Wondzell 2003). Bedform topography was measured as amplitude by subtracting

minimum depths at downstream ends of suitable spawning areas from maximum depths in the pools or glides immediately upstream. A sinuosity index was also calculated as the stream length through a patch divided by the straight-line distance between end points (Fukushima 2001).

Water temperatures were recorded with thermographs (StowAway TidbiT; Onset Computer Corporation, Pocasset, Massachusetts, USA) that were deployed at up- and downstream patch boundaries during mid-June and were retrieved in mid-September. Thermographs were set to record temperatures at 30-minute intervals and were placed in areas of flowing water after being mounted inside opaque cylinders that provided shade. Temperature data were summarized by calculating standard deviations and means, which are strongly correlated with most common temperature metrics (Isaak and Hubert 2001, Dunham et al. 2005). We also calculated patch-specific, stream heating rates from differences in mean temperatures at up- and downstream boundaries. We reasoned that low heating rates would be indicative of well-buffered patches that were associated with extensive hyporheic processes. During thermograph retrieval, stream conductivity (microsiemens) was measured with a temperature-compensating meter at each site (ExStik EC400; Extech Instrument Corporation, Waltham, Massachusetts, USA). Conductivity measures the dissolved ion content in a liquid, strongly correlates with numerous water quality metrics (e.g., salinity, alkalinity, and total dissolved solids), and is often used as a measure of stream productivity (e.g., Koetsier et al. 1996).

Because our primary interest was to discern the general effect of habitat quality rather than the effects of individual habitat quality variables (Armstrong 2005), we used principal components analysis (PCA) to reduce the dimensionality of these attributes (Vaughan and Ormerod 2005). Pairwise deletion was used for missing values and the PCA was performed on the correlation matrix. Principal coordinate scores from the first four axes that had eigenvalues > 1 were used to summarize habitat quality in subsequent statistical models (Table 1).

Data analysis

We used the LOGISTIC procedure in SAS (Allison 1999) to develop logistic regression models that predicted the probability of redd occurrence from patch attributes. Data were not analyzed as interannual repeated measures because parameter estimates from logistic models that incorporated correlated error structures were virtually identical to estimates derived from models that assumed temporal independence. We checked for problems associated with influential outliers using standardized residuals and DFBETA statistics and used variance inflation factors to assess the potential for multicollinearity. Model residuals were also tested for

TABLE 1. Axis loadings from principal components analysis used to summarize habitat quality attributes in models predicting occurrence of chinook salmon redds in the Middle Fork Salmon River.

Covariate	PC1	PC2	PC3	PC4
Stream width	-0.674	-0.547	0.305	0.045
CV width	0.512	-0.095	0.455	0.043
Stream depth	-0.642	0.301	0.493	0.093
CV depth	0.582	0.089	0.340	0.055
W/D	-0.048	-0.822	0.244	-0.259
CV W/D	0.366	0.099	0.546	-0.171
Bed amplitude	-0.400	0.387	0.684	0.177
Sinuosity	0.000	0.664	0.337	-0.068
Bank cover	0.491	0.283	0.115	-0.492
Large wood	0.573	-0.444	-0.024	0.405
Rearing habitat	0.619	0.477	0.076	0.201
Pool density	0.809	0.363	-0.206	0.142
Suitable spawning	0.230	0.551	-0.147	0.141
Median substrate (D_{50})	0.401	-0.560	0.008	-0.083
Fine substrate	-0.603	0.002	-0.160	0.266
Mean temperature	-0.776	0.335	0.139	-0.202
SD temperature	-0.149	0.150	-0.633	-0.552
Heating rate	-0.155	-0.130	-0.254	0.673
Conductivity	0.400	-0.530	0.404	-0.117
Variance explained (%)	25.0	17.7	12.4	8.01
Eigenvalue	4.75	3.37	2.36	1.52

spatial independence using Mantel tests (Fortin and Gurevitch 2001).

Logistic regressions were developed for a group of candidate models, which included a global model and several reduced forms with predictor subsets (Table 2). We included an interaction between patch size and connectivity to accommodate the potential for spatial or temporal shifts in the relative importance of these variables (Flather and Bevers 2002). A categorical stream variable was included in each model to account for differences among streams that were not captured by our habitat measurements (Dunham and Vinyard 1997). We selected among candidate models by ranking them based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c ; Hurvich and Tsai 1989). The difference between the AIC_c of a candidate model and the one with the lowest AIC_c provided the ranking metric (ΔAIC_c). Generally speaking, ΔAIC_c between 0 and 2 indicates substantial support for a model being the best approximating model, ΔAIC_c between 4 and 7 represents less support, and $\Delta AIC_c > 7$ indicates very little support (Burnham and Anderson 2002). Akaike weights (w_i) were calculated, which represent the strength of evidence in favor of model i being the best model. The ratio of Akaike weights (w_i/w_j) indicates the plausibility of the best-fitting model compared to other models (Burnham and Anderson 2002). Standardized parameter estimates and 95% CI were calculated to evaluate the relative importance of individual variables in the best-performing models (Allison 1999).

Similar to the issue in species richness-habitat area relationships, it was possible that an association between patch size and redd occurrence could arise as a sampling artifact (Coleman et al. 1982, Rosenzweig 1995). That is,

even if redds were distributed randomly, occurrence should be greater in larger patches simply because they encompass larger areas. For biological significance, therefore, a patch size association should exceed the expectation based on a random distribution. To test for this effect, we compared the observed proportional distribution of redds among patches to a predicted distribution based on the relative proportions of individual patch areas (Coleman et al. 1982). Separate comparisons were made for each set of three years with the highest and lowest abundances to determine whether the patch size association changed with population density. We used patch areas to determine predicted values because the random allocation of a large number of redds would result in proportions that equaled patch area proportions. This remained true for the low abundance years, when only 111 redds were built, because repeated randomization trials were required to obtain the mean expectation.

If redd occurrences were random, a match between predicted and observed values should occur and the slope of a linear regression describing this relationship would approximate one. If redds occurred nonrandomly, the regression slope should differ from one, with the departure tending towards observed values if patch size positively affected redd occurrence. Y-intercepts for these regressions were constrained to zero.

RESULTS

Forty-three patches of spawning habitat were delineated within the study area (Fig. 1). These patches composed 60% of the 165 km of stream surveyed from the air and ranged in size from 0.3 to 20 ha, although most were <3 ha (Fig. 3). The average occupancy rate for a patch was 67% (range 30–100%) among years, and 7–100% of patches were occupied within individual years. Additional patch descriptors are summarized in Table 3.

Variance inflation factors were below levels indicative of problems with multicollinearity (i.e., <3) and parameter estimates were minimally affected by influential observations. Mantel tests also suggested that residuals were spatially independent. Before starting

TABLE 2. Candidate models composed of factors hypothesized to affect occupancy of chinook salmon spawning patches in the Middle Fork Salmon River.

Model no.	Candidate model†
1	Connectivity, patch size, connect × size, habitat quality‡
2	Connectivity, patch size, connect × size
3	Connectivity, patch size
4	Connectivity, habitat quality
5	Patch size, habitat quality
6	Habitat quality
7	Connectivity
8	Patch size

† All models contain a categorical stream variable.

‡ Global model.

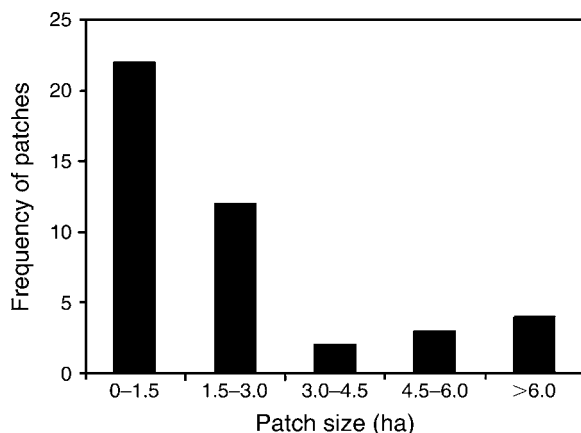


FIG. 3. Size-frequency histogram for patches of chinook salmon spawning habitat in the Middle Fork Salmon River.

model selection procedures, we included connectivity values derived using a range of dispersal distances (2–30 km) in the global model. No qualitative differences in model outcomes were observed, and model selection proceeded with connectivity values based on a 10-km dispersal distance.

Model selection results suggested two models were most likely (Table 4). The sum of Akaike weights for these models was 1.00, which indicated that all the weight of evidence for patch occupancy was in these models. The best overall model contained patch size, connectivity, and a connectivity \times size interaction, had an Akaike weight of 0.92, and was 11.5 times more plausible than the next best model. The next model was the global model, which had an Akaike weight of 0.08. Prediction accuracy for both models was good, with redd occurrence predicted correctly 84–86% of the time

at a 0.50 probability cutoff. Performance of candidate models that lacked either patch size or connectivity decreased rapidly, with models based exclusively on habitat quality metrics being the least plausible.

Parameter estimates from the two best models suggested that redd occurrence was strongly and positively associated with connectivity, which had a standardized parameter estimate ~ 3 times larger than patch size, the second strongest predictor (Table 5). A significant interaction between these predictors, however, suggested that their relative strengths varied across the range of predictor values. Associations between habitat quality and redd occurrence were small and not statistically different from zero. The stream variable suggested that patch occupancy rates were lower in Marsh and Bear Valley creeks compared to Sulphur Creek, although only the Marsh Creek and Sulphur Creek comparison was statistically significant.

A shift in the relationship between observed redd distributions and distributions predicted from patch size may have accounted for the interaction between size and connectivity. In high-density years, the slope of a regression between predicted and observed was not statistically different from 1 ($b_1 = 0.89$; $t = 1.40$; one-tailed $P = 0.084$, two-tailed $P = 0.169$; $N = 43$), suggesting that patch use could not be distinguished from a random process (Fig. 4). At low abundance, however, larger patches became more important and were used more frequently than predicted ($b_1 = 1.21$; $t = 1.86$; one-tailed $P_d = 0.035$, two-tailed $P = 0.070$; $N = 43$).

The best overall model, which contained patch size, connectivity, and a size \times connectivity interaction, was used to create response curves for Bear Valley Creek by plotting the probability of redd occurrence across the

TABLE 3. Descriptive statistics for chinook salmon spawning patches in the Middle Fork Salmon River.

Variable	<i>N</i>	Mean	Median	SD	Minimum	Maximum
Stream width (m)	43	11.0	10.0	4.64	4.16	24.9
CV width (%)	43	27.3	25.7	7.18	16.3	49.5
Stream depth (cm)	43	28.9	27.8	7.51	16.6	49.3
CV depth (%)	43	66.5	68.3	11.7	37.4	89.0
W/D	43	45.4	44.0	14.8	22.5	72.7
CV W/D (%)	43	60.2	58.6	17.1	30.6	97.2
Bed amplitude (cm)	41	67.4	59.9	21.6	36.0	125
Sinuosity	43	1.36	1.33	0.218	1.00	1.85
Bank cover (%)	43	10.2	10.5	5.02	0.00	30.4
Large wood (no./ha)	43	12.4	3.19	15.8	0.00	58.9
Rearing habitat (m/100 m ²)	43	8.05	6.89	5.67	0.00	23.1
Pool density (no./100 m)	43	2.66	2.84	1.17	0.373	5.38
Suitable spawning (%)	43	3.30	2.26	2.30	0.250	9.22
Median substrate (D_{50}) (mm)	43	37.0	37.5	9.99	17.6	64.0
Fine substrate (%)	43	5.31	4.89	2.52	1.56	16.7
Mean temperature (C°)	43	12.2	12.0	1.65	8.55	14.8
SD temperature	43	3.04	3.02	0.507	2.10	4.16
Heating rate (C°/1000 m)	37	0.159	0.084	0.316	-0.763	1.18
Conductivity (μ S)	43	53.5	52.9	12.2	32.5	72.6
Patch size (ha)	43	2.53	1.50	3.33	0.316	19.7
Connectivity (S_i)	43	76.3	47.5	84.3	0.292	381
Patch occupancy (%)†	43	0.67	0.70	0.18	0.30	1.00

† Occupancy is calculated by patch among years.

TABLE 4. Model selection results for logistic regression analysis of factors that affected chinook salmon occupancy of spawning habitats.

Model no.	Candidate model†	Log likelihood	<i>p</i>	$\Delta AIC_c \ddagger$	Akaike weight (w_i)	w_i/w_1
2	Connectivity, patch size, connect \times size	-152	6	0.00	0.92	1.00
1	Connectivity, patch size, connect \times size, habitat quality§	-150	10	4.89	0.08	11.5
3	Connectivity, patch size	-159	5	11.5	0.00	317
4	Connectivity, habitat quality	-168	8	35.6	0.00	5.25×10^7
7	Connectivity	-174	4	40.2	0.00	5.24×10^8
8	Patch size	-255	4	203	0.00	1.08×10^{44}
5	Patch size, habitat quality	-253	8	206	0.00	6.16×10^{44}
6	Habitat quality	-258	7	213	0.00	1.94×10^{46}

Notes: Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible; *p* is the number of parameters. The ratio of Akaike weights (w_i/w_1) indicates the plausibility of the best fitting model (w_1) compared to other models (w_i).

† All models contain a categorical stream variable.

‡ Minimum $AIC_c = 316$.

§ Global model.

observed ranges of patch size and connectivity (Fig. 5). These curves suggested that 9.5 ha of habitat were needed to have a 50% occurrence probability at a connectivity of 1, which typified values during the year with the fewest redds (1995, 10 redds). As average connectivity approached 50, however, even the smallest patches were predicted to have occurrence rates exceeding 50%. Calculations for Sulphur and Marsh creeks suggested 50% occurrence at a connectivity of 1 translated to patch sizes of 8.0 ha and 11.7 ha, respectively.

DISCUSSION

Our results suggest that habitat size and connectivity are important determinants of the distribution of chinook salmon spawning within the MFSR. Previous research has documented the importance of habitat geometry for stream resident salmonids (Dunham and Rieman 1999, Morita and Yamamoto 2001, Koizumi and Maekawa 2004), but this study is one of the first to document these patterns in an anadromous species and

further generalizes growing evidence for the importance of spatial considerations in stream fish ecology (Schlosser and Angermeir 1995, Rieman and Dunham 2000). Attributes associated with habitat quality were weakly associated with habitat occupancy, which was unexpected given numerous studies that document linkages between local habitat conditions and productivity of chinook salmon or fish populations in general (Fausch et al. 1988, Roper et al. 1994, Thurow et al. 1997, Thompson and Lee 2002, Feist et al. 2003). Additionally, the dispersal capabilities of chinook relative to the scale at which patch delineations were made suggests study populations were not strongly fragmented, which usually decreases the importance of habitat geometry because the need for organisms to move between areas, or for large habitats to retain local populations, is less crucial (Moilanen and Hanski 1998, Thomas et al. 2001).

Failure to detect a significant quality association may have resulted from several factors including the presence of nonnative brook trout, which may prey on juveniles

TABLE 5. Parameter estimates and significance levels for the best models predicting probability of chinook salmon redd occurrence within suitable spawning habitats.

Model	Parameter†	<i>P</i>	Parameter estimate (SE)	Standardized parameter estimate
2	Intercept	<0.001	-1.4663 (0.2748)	
	Stream 1 _(Bear Valley)	0.228	-0.2554 (0.2117)	
	Stream 2 _(Marsh)	0.001	-0.6658 (0.2020)	
	Patch size	0.090	0.1611 (0.0951)	0.29
	Connectivity	0.002	0.0226 (0.0071)	1.05
	Connect \times size	<0.001	0.0206 (0.0060)	
1	Intercept	<0.001	-1.4886 (0.3036)	
	Stream 1 _(Bear Valley)	0.133	-0.5156 (0.3428)	
	Stream 2 _(Marsh)	0.015	-0.6482 (0.2662)	
	Patch size	0.084	0.1883 (0.1089)	0.34
	Connectivity	<0.001	0.0246 (0.0073)	1.14
	Connect \times size	0.001	0.0196 (0.0060)	
	Habitat quality _(PC1)	0.366	-0.0921 (0.1020)	-0.11
	Habitat quality _(PC2)	0.806	-0.0266 (0.1080)	-0.03
	Habitat quality _(PC3)	0.358	-0.1116 (0.1214)	-0.09
	Habitat quality _(PC4)	0.266	0.1269 (0.1142)	0.09

† For categorical stream variables, parameter estimates were derived from comparison to Sulphur Creek.

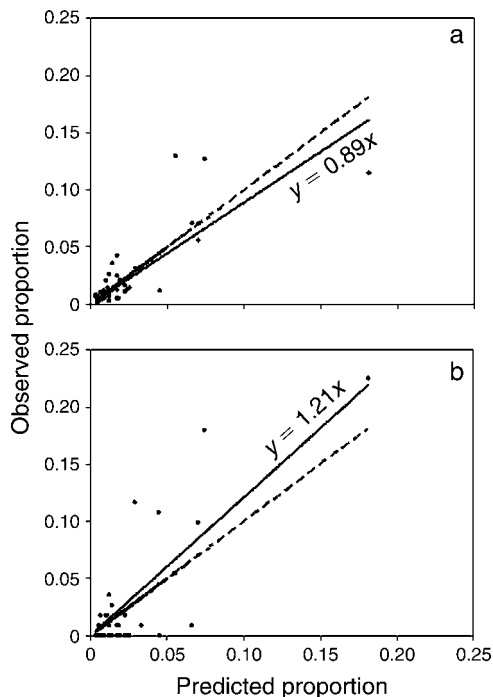


FIG. 4. Observed use of spawning patches vs. predicted use based on patch size for three years of (a) highest and (b) lowest abundance. The dashed line represents a slope of 1.

or compete for space and thereby decouple chinook populations from local habitat conditions (Levin et al. 2002). Alternatively, the stream habitats we sampled may have provided a limited range of conditions and predictive power because our study site encompassed a restricted geographic extent and generally good habitat conditions. It is also possible that the wrong habitat attributes were measured or that the correct attributes were measured inaccurately. We attempted to address the former concern by including a wide array of habitat quality variables that previous researchers have found to be relevant for salmonids, but the accuracy of these measurements was difficult to ensure. Even with experienced crews, rigorous training, and standardized protocols, stream habitats are often difficult to characterize (Roper and Scarnecchia 1995, Roper et al. 2003). Greater error in these measurements, especially relative to habitat size and connectivity, would decrease their perceived importance.

Another challenge is matching the spatial scales of habitat measurements to the scales at which organisms perceive and respond to the environment (Keitt and Urban 2005). It has been suggested that metapopulation models, with their requirements for discrete patch boundaries, may be overly simplistic and difficult to apply to organisms that acquire resources from habitats segregated in space or time (Mazerolle et al. 2005). Salmonids are in this category, given ontogenetic habitat shifts (Everest and Chapman 1972) and the frequency of migratory life histories (Quinn 2005). In the case of

chinook salmon and other anadromous salmonids, the seaward journeys are well known, but common environmental effects might be assumed during these movements, at least when populations originate from a limited geographic area, because fish encounter the same general series of riverine, estuarine, and oceanic habitats. More problematic, given that survival and year-class strength in most fishes appear to be strongly regulated during early life stages (Sinclair 1989, Nislow et al. 2004), is that newly emerged chinook juveniles often move downstream before establishing residence (Bradford and Taylor 1997). If these movements are of sufficient magnitude, juveniles may leave natal habitats and rear elsewhere, thereby confounding patch delineations and making it difficult to accurately associate habitat attributes. Without detailed understanding of these movements at our study site, it was impossible to gauge their importance, and we had to assume movements were relatively rare or that survival was most strongly controlled during spawning and incubation periods (e.g., Greene et al. 2005).

Connectivity was a strong predictor of habitat occupancy in our study, although an interaction with habitat size precluded clear separation of this association. The apparent strength of this association may have been due to the greater realism of Moilanen and Nieminen's (2002) connectivity metric, which is an improvement over previous metrics based on simple nearest neighbor or buffer-based approaches. The interaction between connectivity and habitat size revealed a shift towards greater importance of larger habitats when populations were small. We inferred a similar pattern from an earlier analysis of redd distributions at a broader spatial scale (Isaak and Thurow 2006), and combined, these observations support the general prediction that habitat size should be the dominant consideration when populations are

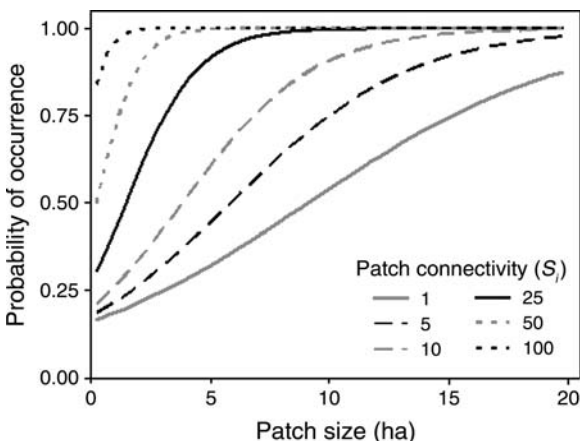


FIG. 5. Response curves for spawning-patch occupancy derived from a logistic regression model based on patch size and connectivity (model 2). Predicted values were generated for Bear Valley Creek across the observed ranges of patch size and connectivity.

reduced (Fahrig 2002, Flather and Bevers 2002). At small population sizes, persistence is thought to depend most heavily on local populations being large enough to avoid extirpation from demographic or genetic stochasticity. However, per capita emigration rates also decline at lower densities, which may decrease the importance of connectivity (Clobert et al. 2001).

As might be expected, therefore, the observed habitat size association was not an area-related sampling artifact at low abundance, and salmon built redds in larger habitats at greater frequencies than was expected if spawning were randomly distributed. However, we could not reject this hypothesis at higher abundances, which suggested that the statistical association between habitat size and patch occupancy was not attributable to biological mechanisms for all levels of abundance. Although the distinction is subtle, researchers should exercise caution when interpreting this relationship in patch occupancy models and routinely test for area-related sampling artifacts, as is often done in studies of species richness-habitat area relationships (Coleman et al. 1982, Rosenzweig 1995).

Conservation implications

Regardless of the mechanisms associated with habitat use, by definition, species need habitat to survive, and our results highlight the importance of maintaining the size and connectivity of existing chinook salmon habitats. As one of the perennial issues in conservation biology, however, it is a challenge to know how much habitat to preserve (Tear et al. 2005, Trent et al. 2005). Although answers will vary by life history stage and the complexity of factors that interact in different landscapes, our results provide general guidance at the local population level and indicate that 8–12 ha of spawning habitat are needed to ensure 50% occurrence probabilities when populations and connectivity levels are low. Habitats of this size may form resistant components of larger habitat networks and act as refugia during extreme demographic bottlenecks to ensure persistence at broader scales. Also noteworthy was that smaller habitats were needed to reach this occurrence threshold in Sulphur Creek where brook trout were absent. If brook trout do adversely affect chinook salmon populations, their removal or suppression may represent another conservation option, especially in areas where the potential for habitat improvements is limited (Levin et al. 2002, McHugh et al. 2004).

If resources are available for significant habitat restoration, it may be possible to expand existing habitats or create new ones in key areas that increase the potential for interactions among existing populations. In landscapes that have been fragmented by anthropogenic modifications, connectivity could be increased by removing barriers associated with road crossings and diversion structures (Steele et al. 2004) or possibly by alleviating high stream temperatures that can act as thermal barriers (Torgersen et al. 1999). Even

if most management activities remain focused on traditional efforts at improving habitat quality (Roni et al. 2002, Bond and Lake 2003), our research could enable better strategic assessments. For example, prioritization of habitats for treatment could be made after consideration of habitat geometry, with areas not meeting minimum size or connectivity thresholds being deemed inappropriate for pursuit of costly restoration activities.

CONCLUSIONS

Several recent assessments of chinook salmon, conducted at broad regional scales, have identified the importance of habitat quality to population status (Thurow et al. 1997, Thompson and Lee 2002, Feist et al. 2003). Additional efforts have served to focus recovery strategies for many threatened salmon populations on improving the quality of habitats associated with freshwater spawning and rearing environments (Karieva et al. 2000). Our results suggest that altering habitat quality will not be a panacea and that spatial considerations will occasionally supercede the importance of local habitat conditions. Whether this apparent discrepancy results from differences among studies in geographic scale, the ranges of habitat conditions examined, or both, future assessments should be conducted across a range of environments and spatial scales. Broad, multiscale assessments would allow identification of the most important habitat features at different scales, provide context for smaller scale features, and enable more effective conservation efforts by yielding a more synthetic view of how salmon relate to their environments.

ACKNOWLEDGMENTS

Numerous individuals have contributed to the assembly of this data set over the last decade. We thank J. Pope, Sr., J. Pope, Jr., and R. Gipe for helicopter flights. D. Lee and S. Waters of the Boise Interagency Fire Center assisted with flight management, and numerous personnel from the Boise, Payette, and Salmon-Challis national forests provided logistical support for flights. J. Guzevich organized the GIS database. J. Markham, B. Ubelacher, B. Riley, A. Preston, and B. Goodman assisted with habitat measurements. Two anonymous reviewers provided comments on an earlier manuscript draft. The U.S. Forest Service Rocky Mountain Research Station provided funding for redd surveys from 1995 to 1998, and the Bonneville Power Administration (BPA) provided funding from 1999 to 2004. We thank M. Ralston, A. Meuleman, and J. Brady for BPA contract administration. D. Isaak was supported by Rocky Mountain Research Station agreement (01-JV-11222014-101-RJVA) with additional support from the Ecohydraulics Research Group at the University of Idaho.

LITERATURE CITED

- Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.
- Armstrong, D. P. 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. *Conservation Biology* 19:1402–1410.

- Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:1470–1481.
- Beamish, R. J., R. M. Sweeting, and C. M. Neville. 2004. Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. *Transactions of the American Fisheries Society* 133:1163–1175.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. *BioScience* 54:413–427.
- Bentzen, P., J. B. Olsen, J. E. McLean, T. R. Seamons, and T. P. Quinn. 2001. Kinship analysis of Pacific salmon: insights into mating, homing, and timing of reproduction. *Journal of Heredity* 92:127–136.
- Beschta, R. L., and W. S. Platts. 1986. Morphological features of small streams: significance and function. *Water Resources Bulletin* 22:369–380.
- Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. *Transactions of the American Fisheries Society* 100:423–438.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication 19. Bethesda, Maryland, USA.
- Bond, J. G., and C. H. Wood. 1978. Geologic map of Idaho, 1:500,000 scale. Idaho Department of Lands, Bureau of Mines and Geology, Moscow, Idaho, USA.
- Bond, N. R., and P. S. Lake. 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. *Ecological Management and Restoration* 4: 193–198.
- Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behaviour of newly emerged Chinook salmon (*Onchorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1585–1592.
- Brown, E. M. 2002. 2000 salmon spawning ground surveys. Pacific Salmon Treaty Program, Award Number NA77FP0445. Idaho Fish and Game Report 02-33, Boise, Idaho, USA.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Buffington, J. M., D. R. Montgomery, and H. M. Greenburg. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2085–2096.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- Clinchy, M., D. T. Haydon, and A. T. Smith. 2002. Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? *American Naturalist* 159:351–362.
- Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. *Dispersal*. Oxford University Press, Oxford, UK.
- Coleman, B. D., M. A. Mares, M. R. Willig, and Y. H. Hsieh. 1982. Randomness, area, and species richness. *Ecology* 63: 1121–1133.
- Curry, R. A., D. L. G. Noakes, and G. E. Morgan. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1741–1749.
- Dias, P. C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11:326–330.
- Dunham, J. B., G. Chandler, B. E. Rieman, and D. Martin. 2005. *Measuring stream temperature with digital data loggers: a user's guide*. General Technical Report RMRS-GTR-150/WWW. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642–655.
- Dunham, J. B., B. E. Rieman, and J. T. Peterson. 2002. Patch-based models of species occurrence: lessons from salmonid fishes in streams. Pages 327–334 in J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall, editors. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Covelo, California, USA.
- Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. *Transactions of the American Fisheries Society* 126:323–329.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1266–1280.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29:91–100.
- Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12:346–353.
- Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–1985. General Technical Report PNW-GTR-213. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52: 483–498.
- Feist, B. E., E. A. Steel, G. R. Pess, and R. E. Bilby. 2003. The influence of scale on salmon habitat restoration priorities. *Animal Conservation* 6:271–282.
- Fish Passage Center. 2003. Annual report. BPA Contract Number 94-033. Portland, Oregon, USA.
- Flather, C. H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist* 159: 40–56.
- Fleishman, E., C. Ray, P. Sjogren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* 16:706–716.
- Fortin, M. J., and J. Gurevitch. 2001. Mantel tests: spatial structure in field experiments. Pages 308–326 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Second Edition. Oxford University Press, Oxford, UK.
- Fukushima, M. 2001. Salmonid habitat-geomorphology relationships in low-gradient streams. *Ecology* 82:1238–1246.
- Gebhards, S. V. 1959. *Columbia River Fisheries Development Program*. Salmon River Planning Report. Idaho Department of Fish and Game, Boise, Idaho, USA.
- Greene, C. M., D. W. Jensen, G. R. Pess, and E. Ashley Steel. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates

- in the Skagit River, Washington. *Transactions of the American Fisheries Society* 134:1562–1581.
- Hall, C. A. S., J. A. Stanford, and F. R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos* 65:377–390.
- Hanna, S. S. 1999. From single-species to biodiversity—making the transition in fisheries management. *Biodiversity and Conservation* 8:45–54.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42:17–38.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63:151–162.
- Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239–251.
- Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* 64:119–127.
- Harrison, S., and A. D. Taylor. 1996. Empirical evidence for metapopulation dynamics. Pages 27–39 in I. A. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, New York, New York, USA.
- Hartman, G. F., and T. G. Brown. 1987. Use of small, temporary, floodplain tributaries by juvenile salmonids in a west coast rain-forest drainage basin, Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44:262–270.
- Harvey, J. W., and K. E. Bencala. 1993. The effect of streambed topography on surface-subsurface water exchange in mountain catchments. *Water Resources Research* 29:89–98.
- Hauck, F. R. 1953. A survey of the spring Chinook salmon spawning and utilization of Idaho streams. Job Completion Report, Project F-1R2. Idaho Department of Fish and Game, Boise, Idaho, USA.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 312–391 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, British Columbia, Canada.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483–518 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication 19. Bethesda, Maryland, USA.
- Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile Chinook salmon in a highly sedimented Idaho stream. *Transactions of the American Fisheries Society* 116:185–195.
- Hurvich, C. M., and C. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Isaak, D. J., and W. A. Hubert. 2001. A hypothesis about factors that affect maximum summer stream temperatures across montane landscapes. *Journal of the American Water Resources Association* 37:351–366.
- Isaak, D. J., and R. F. Thurow. 2006. Network-scale patterns of spatial and temporal variation in Chinook salmon redd distributions: patterns inferred from spatially continuous replicate surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 63:285–296.
- Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. *Science* 290:977–979.
- Kasahara, T., and S. M. Wondzell. 2003. Geomorphic controls on hyporheic exchange flow in mountain streams. *Water Resources Research* 39:1005. [doi: 10.1029/2002wr001386]
- Keitt, T. H., and D. L. Urban. 2005. Scale-specific inference using wavelets. *Ecology* 86:2497–2504.
- Kiefer, R. B., P. R. Bunn, and J. Johnson. 2002. Natural production monitoring and evaluation: aging structures. Idaho Fish and Game Report 02-24. Boise, Idaho, USA.
- Koetsier, P., G. W. Minshall, and C. T. Robinson. 1996. Benthos and macroinvertebrate drift in six streams differing in alkalinity. *Hydrobiologia* 317:41–49.
- Koizumi, I., and K. Maekawa. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology* 49:973–981.
- Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 29: 2275–2285.
- Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* 10:1774–1791.
- Lafferty, K. D., C. C. Swift, and R. F. Ambrose. 1999. Extirpation and recolonization in a metapopulation of an endangered fish, the Tidewater Goby. *Conservation Biology* 13:1447–1453.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Levin, P. S., S. Achord, B. E. Feist, and R. W. Zabel. 2002. Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat? *Proceedings of the Royal Society of London, Series B* 269:1663–1670.
- Matthews, G. M., and R. S. Waples. 1991. Status review for Snake River spring and summer Chinook salmon. NOAA Technical Memorandum NMFS F/NWC-200. National Marine Fisheries Service, Seattle, Washington, USA.
- Mazerolle, M. J., A. Desrochers, and L. Rochefort. 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. *Ecological Applications* 15: 824–834.
- McClure, M., et al. 2003. Independent populations of Chinook, steelhead, and sockeye for listed evolutionary significant units within the interior Columbia River basin. Interior Columbia Basin Technical Recovery Team. National Marine Fisheries Service, Seattle, Washington, USA.
- McHugh, P., P. Budy, and H. Schaller. 2004. A model-based assessment of the potential response of Snake River spring/summer Chinook salmon to habitat improvements. *Transactions of the American Fisheries Society* 133:622–638.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503–2515.
- Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145.
- Montgomery, D. R., E. M. Beamer, G. R. Pess, and T. P. Quinn. 1999. Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 56:377–387.
- Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109:596–611.
- Morita, K., and S. Yamamoto. 2001. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* 16:1318–1323.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4–21.
- Neville, H. M., J. B. Dunham, and M. M. Peacock. 2006a. Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* 21:901–916.
- Neville, H. M., D. J. Isaak, R. F. Thurow, J. B. Dunham, and B. E. Rieman. 2006b. Microsatellite variation reveals weak

- genetic structure and retention of genetic variability in threatened Chinook salmon (*Oncorhynchus tshawytscha*) within a Snake River watershed. *Conservation Genetics*. [doi: 10.1007/s10592-006-9155-4]
- Nislow, K. H., S. Einum, and C. L. Folt. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* 65:188–200.
- Poole, G. C., and C. H. Berman. 2001. An ecological perspective on instream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management* 27:787–802.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press, Seattle, Washington, USA.
- Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Tributaries sediment sources, and the longitudinal organization of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 824–840.
- Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* 9:51–64.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285–296.
- Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific northwest watersheds. *North American Journal of Fisheries Management* 22:1–20.
- Roper, B. B., J. L. Kershner, E. Archer, R. Henderson, and N. Bouwes. 2003. An evaluation of physical stream habitat attributes used to monitor streams. *Journal of the American Water Resources Association* 6:1637–1646.
- Roper, B. B., and D. L. Scarnecchia. 1995. Observer variability in classifying habitat types in stream surveys. *North American Journal of Fisheries Management* 15:49–53.
- Roper, B. B., D. L. Scarnecchia, and T. J. LaMarr. 1994. Summer distribution of and habitat use by Chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. *Transactions of the American Fisheries Society* 123:298–308.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium* 17:392–401.
- Scrivener, J. C., T. G. Brown, and B. C. Andersen. 1994. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) utilization of Hawks Creek, a small and nonnatal tributary of the Upper Fraser River. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1139–1146.
- Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14:711–724.
- Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197–241 in J. M. Cherrett, editor. *Ecological Concepts*. British Ecological Society Symposium. Blackwell Scientific Publications, Oxford, UK.
- Steel, E. A., B. E. Feist, D. W. Jensen, G. R. Pess, M. B. Sheer, J. B. Brauner, and R. E. Bilby. 2004. Landscape models to understand steelhead distribution and help prioritize barrier removals in the Willamette basin, Oregon, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 61:999–1011.
- Taylor, C. M., and M. L. Warren. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* 82:2320–2330.
- Tear, T. H., P. Kareiva, P. L. Angermeier, P. Comer, B. Czech, R. Kautz, L. Landon, D. Mehlman, K. Murphy, M. Ruckelshaus, J. M. Scott, and G. Wilhere. 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience* 55:835–849.
- Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London, Series B* 268: 1791–1796.
- Thomas, J. A., R. T. Clarke, G. W. Elmes, and M. E. Hochberg. 1998. Population dynamics in the genus *Maculinea*. Pages 261–290 in J. P. Dempster and I. F. G. McLean, editors. *Insect population dynamics: in theory and practice*. Chapman and Hall, London, UK.
- Thompson, W. L., and D. C. Lee. 2002. A two stage information-theoretic approach to modeling landscape-level attributes and maximum recruitment of Chinook salmon in the Columbia River basin. *Natural Resource Modeling* 15: 227–257.
- Thurrow, R. F. 1985. Middle Fork Salmon River fisheries investigations. Federal Aid in Fish Restoration Project F-73-R-6. Idaho Department of Fish and Game, Job Completion Report. Boise, Idaho, USA.
- Thurrow, R. F., D. C. Lee, and B. E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia River Basin and portions of the Klamath River and Great Basins. *North American Journal of Fisheries Management* 17:1094–1110.
- Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* 9:301–319.
- Vaughan, I. P., and S. J. Ormerod. 2005. Increasing the value of principal components analysis for simplifying ecological data: a case study with rivers and river birds. *Journal of Applied Ecology* 42:487–497.
- Vronskiy, B. B. 1972. Reproductive biology of the Kamchatka River Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Ichthyology* 12:259–273.
- Wagner, H. H., and M. J. Fortin. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology* 86:1975–1987.
- White, P. S., and S. T. Pickett. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, USA.
- Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47:501–515.
- Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14(6):2–19.
- Williams, R. 2006. *Return to the river: restoring salmon to the Columbia River*. Elsevier Academic Press. Boston, Massachusetts, USA.