

# Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys

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**Abstract:** Spatially continuous sampling designs, when temporally replicated, provide analytical flexibility and are unmatched in their ability to provide a dynamic system view. We have compiled such a data set by georeferencing the network-scale distribution of Chinook salmon (*Oncorhynchus tshawytscha*) redds across a large wilderness basin (7330 km<sup>2</sup>) in central Idaho for 9 years (1995–2003). During this time, the population grew at a rate of 5.3 recruits per spawner, and redd numbers increased from 20 to 2271. As abundances increased, fish expanded into portions of the stream network that had recently been unoccupied. Even at the highest escapements, however, distributions remained clustered, and a limited portion of the network contained the majority of redds. The importance of the highest density spawning areas was greatest when abundances were low, suggesting these areas may serve as refugia during demographic bottlenecks. Analysis of variance indicated that redd numbers were strongly affected by local habitats and broad climatic controls, but also revealed a space–time interaction that suggested temporal instability in spatial patterns. Our results emphasize the importance of maintaining habitats with high densities of individuals, but also suggest that broader views may be needed to accommodate the dynamics of natural salmonid populations.

**Résumé :** Les plans d'échantillonnage spatial en continu, répétés dans le temps, fournissent une flexibilité d'analyse et sont sans pareil pour générer une perspective dynamique d'un système. Nous avons compilé une telle banque de données en établissant par géoréférencement la répartition à l'échelle du réseau des frayères de saumons quinnat (*Oncorhynchus tshawytscha*) dans un grand bassin versant sauvage (7330 km<sup>2</sup>) du centre de l'Idaho pendant 9 ans (1995–2003). Pendant cette période, la population a crû à un taux de 5,3 recrues par reproducteur et le nombre de frayères est passé de 20 à 2271. Au fur et à mesure de l'accroissement de l'abondance, les poissons ont envahi des sections du réseau hydrologique encore récemment inoccupées. Même dans les escarpements les plus élevés, cependant, la distribution demeure contagieuse et une partie restreinte du réseau abrite la majorité des frayères. L'importance des sites de frai à densité très élevée est maximale aux densités faibles, ce qui laisse croire que ces sites servent de refuges durant les goulots d'étranglement démographiques. Une analyse de variance indique que le nombre de frayères est très affecté par les habitats locaux et les facteurs généraux de contrôle climatique; elle montre aussi une interaction espace–temps qui laisse croire à une instabilité temporelle des patrons spatiaux. Nos résultats mettent l'emphase sur l'importante de préserver les habitats de grande densité de poissons, mais ils laissent aussi entrevoir que des perspectives plus larges seront peut-être nécessaires pour tenir compte de la dynamique des populations naturelles de saumons.

[Traduit par la Rédaction]

## Introduction

Pacific salmon populations have declined during the last century across much of North America outside of Alaska, especially at inland and southern peripheries of historical ranges (Nehlsen et al. 1991; Thurow et al. 2000). Many re-

maining populations persist at low levels, which has prompted federal protection under the US Endangered Species Act and costly restoration efforts. Initial attempts to restore populations focused on curtailment of adult harvests, supplementation of wild stocks with hatchery fish, and modification of hydrosystems to reduce mortality (Independent

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Scientific Group 1999). Results from these efforts have been mixed, and emphasis has recently turned to freshwater rearing habitats, where modeling results suggest that increases in juvenile survival could improve population growth rates (Kareiva et al. 2000; for an alternative view see Wilson 2003).

Most knowledge regarding the basic ecology of salmon comes from studies on freshwater environments. Unfortunately, most of this knowledge is derived from studies conducted at relatively small spatial and temporal extents (Fausch et al. 2002), which provides a poor fit to the broader spatiotemporal themes that underlie most species conservation efforts (e.g., metapopulation theory, source–sink dynamics, landscape ecology). Growing awareness of this gap, combined with advances in remote sensing, spatial sampling strategies, georeferencing capabilities, and broad usage of geographic information systems (Fisher and Rahel 2004) have motivated a new generation of studies designed to understand interpopulation processes (Rieman and Dunham 2000), the importance of natural disturbance regimes, terrestrial–aquatic linkages, and landscape genetics (e.g., Costello et al. 2003; Dunham et al. 2003; Miller et al. 2003).

Increasingly common among this new generation of studies are spatially continuous survey techniques (Fausch et al. 2002), which overcome many of the limitations associated with traditional sampling designs. Most sampling designs have two basic assumptions that must be met for valid inference to be drawn. First, the statistical population about which inference is desired must be correctly identified. Second, a statistically valid sample, involving the randomized selection of sample units, must be drawn from the population (Scheaffer et al. 1990). Inferential bias may still occur if broad-scale trends or unanticipated local factors impinge upon sample elements — a process that can result in spatially or temporally correlated error structures (Legendre 1993). The potential for this sort of bias has long been recognized in the temporal domain, where it motivates many books on the topic of time-series analysis. More recently, similar awareness has spread to the spatial domain, perhaps spurred by the emergence of theories that emphasize the importance of spatial context, connectivity, and habitat geometry (Hanski and Gilpin 1997). Regardless, insufficient or poorly designed sampling in either domain may yield a skewed picture of reality (Wiley et al. 1997). Spatially continuous sampling, especially if surveys are repeated through time, can minimize these error sources and provide more accurate system views that may yield novel insights to aquatic ecosystems (Fausch et al. 2002).

As one example, many biological systems are thought to be characterized by spatial variation in demographic rates, often referred to as source–sink dynamics (Pulliam and Danielson 1991). In practice, it is difficult to infer source–sink behavior in the absence of detailed demographic data (Watkinson and Sutherland 1995), which greatly restricts the spatial extents that can be studied. Changes in population size, however, often have profound and sometimes unpredictable effects on the distribution of a species because these adjustments are rarely uniform (Channell and Lomolino 2000). Populations occurring in productive habitats may show little change despite large declines in regional abundance, whereas less productive sink habitats may quickly

gain or lose populations, depending on the level of demographic support from source areas (Pulliam and Danielson 1991; Schlosser and Angermeier 1995). Simple observation of range contractions and expansions, therefore, if done using spatially continuous surveys so that the proportional contribution of different areas can be calculated, may reveal some areas to be more or less ephemeral. Although results would not provide conclusive proof for source–sink dynamics, insights might be gained regarding where more detailed studies should be conducted or which areas may be especially robust and therefore warrant conservation priority.

In this paper, we introduce a unique data set that consists of annual censuses of Chinook salmon (*Oncorhynchus tshawytscha*) nests, often referred to as redds, that have been georeferenced across a large wilderness basin located in central Idaho. Chinook salmon redds are readily observed because of their large size and high visibility for several weeks after construction. Although redd counts are often used as an index of abundance, the fact that they are the breeding structure for salmonid fishes suggests their distribution across a landscape may also serve as a useful proxy for understanding important biophysical processes (Montgomery et al. 1999). The goal of this paper is to describe the data set and examine spatial and temporal patterns in network-scale redd distributions. More specifically, we determine whether redds were randomly distributed in space, examine temporal changes in distributions relative to population size, decompose the variance associated with redd numbers to understand the relative importance of spatial and temporal factors, and discuss the conservation implications associated with these patterns. We also describe patterns associated with population expansion because salmon abundance increased dramatically during this study, probably stimulated by a combination of improved ocean productivity and juvenile migration conditions (Fish Passage Center 2003; Beamish et al. 2004).

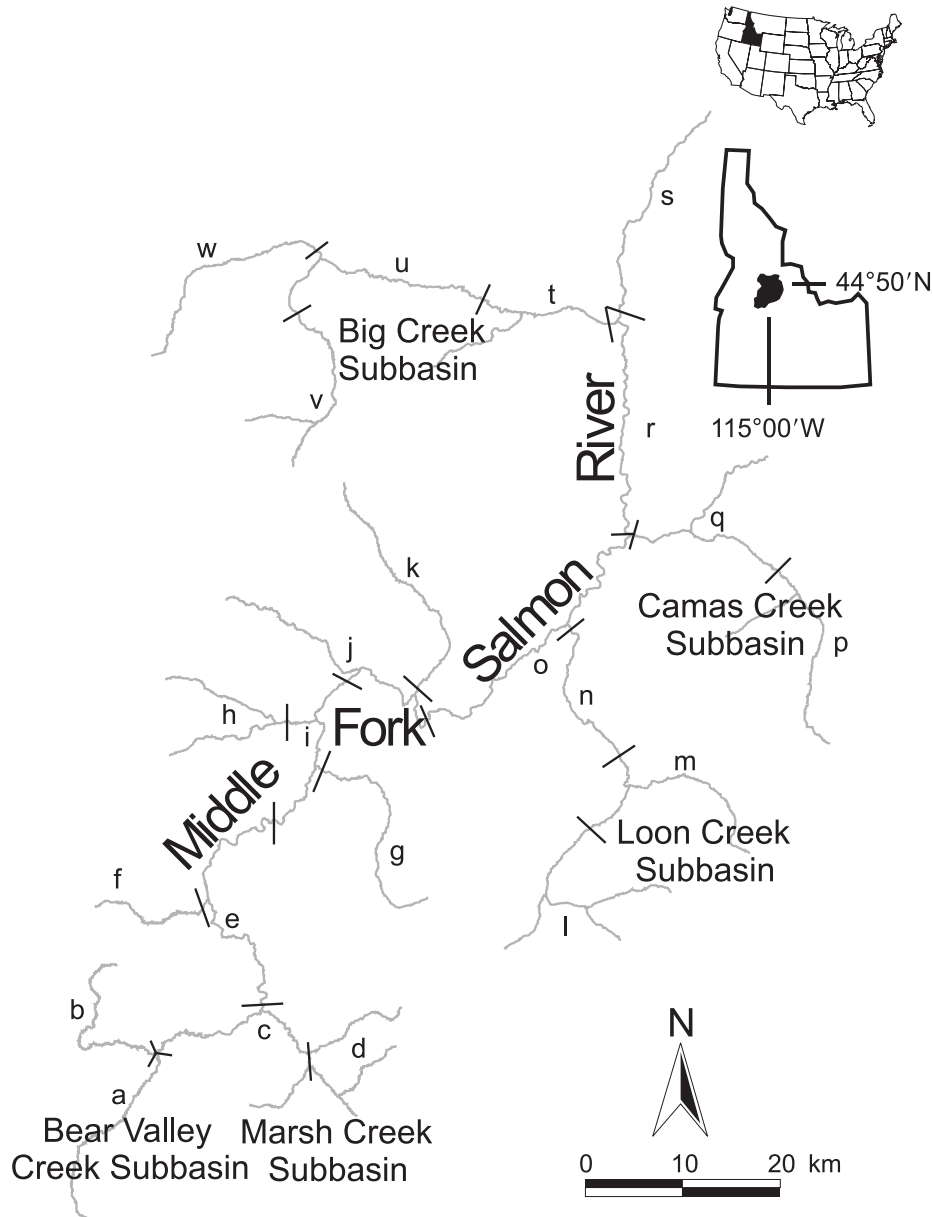
## Materials and methods

### Study area

This study was conducted in the Middle Fork of the Salmon River (MFSR) in central Idaho (Fig. 1). The MFSR drains 7330 km<sup>2</sup> of forested and steeply mountainous terrain in central Idaho that ranges in elevation from 1000 to 3150 m. Most of the area (>95%) is administered by the USDA Forest Service and was managed as a primitive area from 1930 to 1980 before receiving permanent protection as part of the Frank Church – River of No Return – Wilderness in 1980. As a result, road and trail densities are low and most areas exist in relatively pristine condition. Some areas continue to recover from the effects of grazing or mining, but cessation of many of these activities has occurred since wilderness designation and listing of Snake River salmon stocks under the Endangered Species Act. Natural disturbances from fires, hillslope movements, and floods persist, and these processes maintain a dynamic mosaic of landscape conditions.

Streams across much of the MFSR flow through narrow, V-shaped valleys, except for short reaches where valleys are unconfined. In the Bear Valley Creek and Marsh Creek subbasins, however, thick deposits of Quaternary alluvium and Pleistocene glacial drift fill the main valleys and result

**Fig. 1.** Stream network in the Middle Fork Salmon River that was accessible to Chinook salmon (*Oncorhynchus tshawytscha*) and was sampled for redds from 1995 to 2003. Letters next to stream segments denote areas used in later data summaries. Inset (upper right) shows location in Idaho, USA.

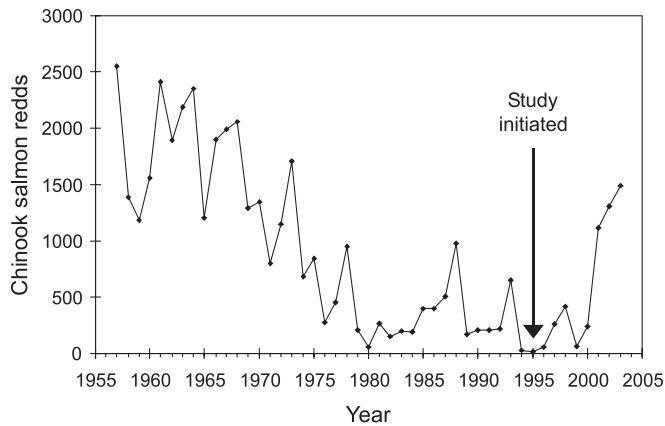


in broad, U-shaped valleys throughout these areas (Bond and Wood 1978). Channel morphologies in Bear Valley – Marsh Creek and other areas where valleys are not constrained consist of meandering pool–riffle sequences that are heavily used by spawning salmon. Channels associated with constrained valleys are usually higher-gradient planebed and step–pool configurations (sensu Montgomery and Buffington 1997). Stream hydrographs are driven by snowmelt runoff, with high flows occurring from April through June and low flows during the remainder of the year.

The Chinook salmon that occur in the MFSR are wild, indigenous fish and are referred to as spring–summer stocks based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). Redd counts conducted by the Idaho Department of Fish and Game at index sites within the MFSR since the 1950s sug-

gest that these populations have declined dramatically, although escapements increased during the span of this study (Fig. 2; Brown 2002). Chinook salmon enter the MFSR drainage in early summer, migrate to natal areas that occur primarily in larger tributaries, and stage in pools before spawning. Spawning time varies among sites, but redd construction usually begins during the last week of July at high elevations (1800–2100 m) and is completed by mid-September at low elevations (1000–1300 m; R. Thurow, unpublished data). Females deposit eggs in redds that are 2–4 m in diameter and are constructed in riffle crests or other areas that have similar hydraulic and substrate characteristics. Embryos incubate in the gravel and emerge as fry the following spring. Most juveniles rear in natal areas for one year before migrating seaward, although this time frame is variable (Bjornn 1971). Chinook salmon spend 1–3 years in

**Fig. 2.** Time series of Chinook salmon (*Oncorhynchus tshawytscha*) redd counts for index areas in the Middle Fork Salmon River. Data are from annual Idaho Department of Fish and Game surveys (Brown 2002).



the ocean, during which time growth is rapid and maturity is reached at total lengths ranging from 60 to 120 cm. Adult returns to the MFSR are dominated by age-4 and age-5 fish (Kiefer et al. 2002).

In addition to Chinook salmon, other fishes occurring within the MFSR include bull trout (*Salvelinus confluentus*), brook trout (*Salvelinus fontinalis*), westslope cutthroat trout (*Oncorhynchus clarkii lewisii*), rainbow trout (resident and anadromous forms; *Oncorhynchus mykiss*), mountain whitefish (*Prosopium williamsoni*), torrent sculpin (*Cottus rhotheus*), mottled sculpin (*Cottus bairdi*), shorthead sculpin (*Cottus confusus*), Pacific lamprey (*Lampetra tridentatus*), speckled dace (*Rhinichthys osculus*), longnose dace (*Rhinichthys cataractae*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*Catostomus columbianus*), reidside shiner (*Richardsonius balteatus*), and northern pikeminnow (*Ptychocheilus oregonensis*; Thurow 1985).

### Redd surveys

Low-level helicopter flights were used to conduct annual, spatially continuous surveys of Chinook salmon redds from 1995 to 2003 within that portion of the stream network (670 km) that was accessible to Chinook salmon (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 biologists familiar with the drainage. Aerial surveys were conducted between 0900 and 1800 h to facilitate visibility, and all surveys were conducted by the same observer (R. Thurow) at the end of the spawning period. During counts, the pilot maintained airspeeds of 20–40 km·h<sup>-1</sup> and altitudes of 15–50 m, depending on the surrounding terrain. When a redd was observed, a global positioning system (GPS; Pathfinder ProXL, Trimble, Sunnyvale, California) was used to georeference the location. In several sections of stream where tree canopy precluded aerial observation, trained observers walked the stream and recorded coordinates with a GPS at redd locations. All GPS locations were later differentially corrected and assembled into a geographic information system for use in subsequent analysis. Discerning Chinook salmon redds

from those of other fall-spawning salmonids was not problematic, given the large size of salmon redds as well as their distribution and timing of construction. Stream shading, habitat complexity, turbidity, and redd superimposition can affect the accuracy of redd counts (Dunham et al. 2001), but ongoing validation work suggests the relationship between aerial counts and “true” counts based on more reliable ground surveys is strong ( $r = 0.78$ ,  $n = 52$  reaches; R. Thurow, unpublished data).

### Population expansion

Population growth was described in three ways. Inter-generational pairs of redd distributions were mapped for years when spawner-year abundance was especially low and many stream segments were unoccupied. Intergenerational lags were determined from female age structures estimated using finray cross-sections (Kiefer et al. 2002). Population expansion was also examined by splitting the network within each of the five major subbasins where most (87%) of the spawning occurred (labeled in Fig. 1) into contiguous, 500 m reaches and calculating the proportion of reaches that contained at least one redd during each survey year. Lastly, age structure information, combined with basin-wide redd count totals, were used to calculate population growth rates based on the number of recruits per spawner:

$$(1) \quad R = \frac{(N_{i4} + N_{i5} + N_{i6})}{N_i}$$

where  $R$  is recruits per spawner,  $N_i$  is the number of redds in spawner year  $i$ , and  $N_{i4,5,6}$  are number of redds attributable to spawner year  $i$  four, five, and six years later, respectively.

### Cumulative distribution curves

Similar to Walters and Cahoon (1985), we used cumulative distribution curves to summarize the spatial distribution of redds. Cumulative curves provide a visually intuitive means of describing a population, facilitate comparison to other distributions, and are simple to construct. This technique was applied by dividing the stream network into 23 segments of approximately equal length ( $\mu = 28.2$  km, standard deviation = 2.1 km; Fig. 1). Summaries were also done using smaller segments, but results were qualitatively similar and are not presented. Attempts were made to place divisions at major tributary junctions and to maintain approximately equal segment sizes, which simplified randomization of redd distributions that were later used to construct null model distributions for comparison. Once the network was partitioned, the proportions of redds within individual stream segments were calculated and ranked relative to other stream segments within the same year. Cumulative proportions were then plotted against stream segment rank order.

Null model distributions were created by generating populations of 1000 curves from the random allocation of redds to stream segments. For each population of curves, the number of redds randomly allocated equaled the number of redds observed during one of the study years. We then calculated Shannon–Wiener diversity (Zar 1996) scores for the observed and randomized redd distributions. Higher scores were indicative of greater evenness. The form of the Shannon–Wiener diversity index used was as follows:



$$(2) \quad H' = \sum_{i=1}^k p_i \log p_i$$

where  $H'$  is Shannon–Wiener diversity,  $k$  is the number of stream segments, and  $p_i$  is the proportion of redds found in stream segment  $i$ . Diversity scores within individual years were compared and assigned probability values based on the proportion of the 1000  $H'_{\text{random}}$  values that  $H'_{\text{observed}}$  exceeded. To determine whether discrepancies between observed and random distributions were related to population size, we regressed average  $H'_{\text{random}} - H'_{\text{observed}}$  values against yearly redd totals. A trend was taken as evidence that changes in observed redd distributions were nonrandom and driven by biological processes related to fish movements or spatial variation in growth rates.

### Space–time interaction

As a complement to the cumulative distributions, we considered whether the relative importance of individual stream segments remained constant through time. If no segment  $\times$  year interaction occurred, it would indicate that areas most important for spawning one year were important in other years. In the context of recovery planning, this scenario would be desirable because it allows easy identification of key areas and facilitates targeting of restoration activities on a small subset of reaches. The presence of an interaction is more problematic because it indicates that site selection through time is less consistent, and conservation or restoration activities may need to be more diffuse.

We tested for a segment  $\times$  year interaction using a repeated measures analysis of variance (ANOVA) design in which year was the repeated measure and the treatment factor was stream segment. Segments were bisected and redds were tallied by subsegments, which provided replicate samples and facilitated estimation of the interaction term (von Ende 2001). All factors were considered fixed, and the analysis was conducted in PROC MIXED in SAS (Littell et al. 1996) after redd counts were  $\log_{10} + 1$  transformed to achieve residual normality. The MIXED procedure allowed specification of different covariance matrices to account for correlated error structures, so we initially ran the analysis using several error types to determine the most appropriate structure. The relative performance of different covariance structures was assessed using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The covariance structures tested were a first-order, autoregressive structure; a banded Toeplitz matrix, which included lags out to 5 years (typically the maximum intergenerational lag); an unstructured matrix in which no a priori structure was assumed; and a standard covariance matrix, which assumed error independence (Littell et al. 1996). The Toeplitz matrix performed best and was used for the final analysis, although the choice of covariance structure had a minimal effect on the results.

### Variance partitioning

We were also interested in determining the relative roles of spatial, temporal, and error sources on variance structure, as well as the effect that study duration may have had on the ability to accurately discern these roles. Variance structure is of interest because it reveals much about different types of biological, environmental, and sampling processes that may

be relevant (Wiley et al. 1997). In the present study, for example, spatial variability represented site-to-site differences in numbers of redds among stream segments that arose from local habitat factors that affected where salmon spawned (e.g., spawning gravels, suitable temperature regimes, adequate flow depths, etc.). Temporal variability, in contrast, represented yearly changes in redd numbers that occurred consistently, or synchronously, across stream segments. Broad-scale climatic factors that affected areas similarly, such as ocean productivity or flow conditions during juvenile migrations, would have fallen into this category. Interactions between spatial and temporal factors represent variability attributable to local, site-specific forcing factors. Examples could include spatial variation in density-dependent mortality factors or a stochastic event that altered habitat conditions within a stream segment after study initiation. Finally, residual variation lumps two sources of variability: those due to intrayear variability and measurement errors (Larsen et al. 2001). In this instance, intrayear variability resulted from differences in redd counts between the two subsegments used to estimate the segment effect, and measurement error stemmed from miscounts in the field, data transcription problems, or any other process that resulted in deviations from the actual number of redds.

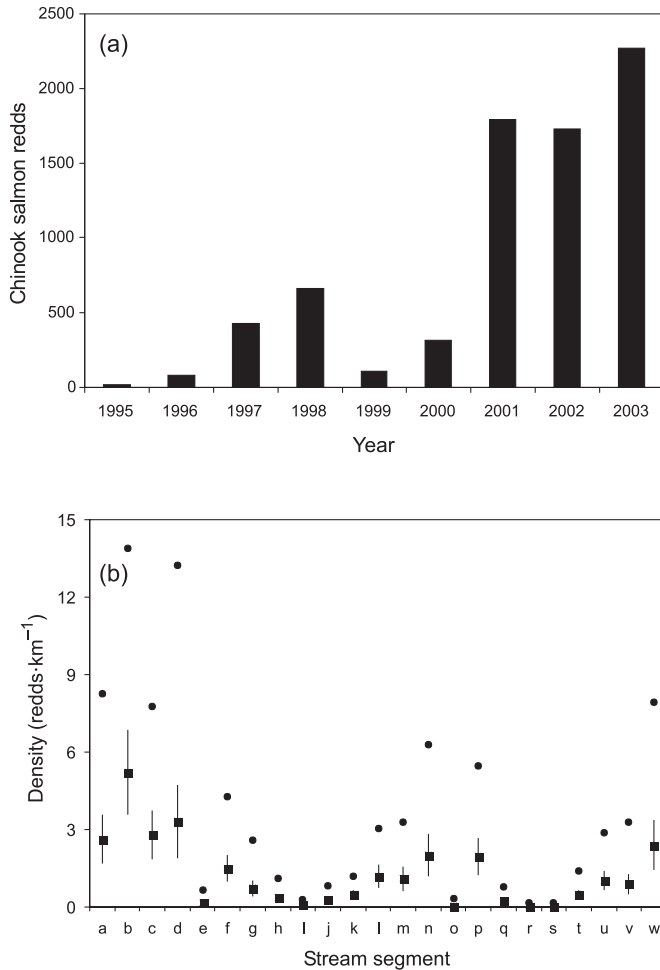
Variance partitioning was accomplished by decomposing total sums of squares (SS) into proportional contributions by segment, year, segment  $\times$  year interaction, and residual error. PROC VARCOMP was used to estimate SS because PROC MIXED does not use SS (Littell et al. 1996). Using the observed time series, SS were calculated using data from 1995, then data from 1995–1996, 1995–1997, etc. Answers derived from this approach, however, depended entirely on the observed data sequence, so we also calculated average variance contributions from analyses run on all possible yearly combinations in which years were not repeated. To determine variance contributions based on 1 year of data, nine separate analyses were run, variances were partitioned, and the proportional contribution of stream segment was calculated as an average across the nine analyses. This procedure was repeated for all possible combinations of 2 years of data, 3 years of data, etc., until the entire time series had been summarized accordingly.

## Results

Stream conditions usually made it possible to count all designated areas each year, but high turbidities caused by thunderstorms limited visibility in parts of Loon and Camas creeks during 1995 and sections of Big Creek in 1997, 1998, and 2001. Basin-wide totals for redd counts ranged considerably — from 20 redds in 1995 to 2271 redds in 2003. Years of low escapements were intermixed with years of higher escapements, although the general trend was one of increase (Fig. 3a). In addition to temporal variation, spatial variability also occurred, and some segments of stream contained average redd densities as low as 0.023 redds·km<sup>-1</sup>, whereas other segments averaged up to 5.2 redds·km<sup>-1</sup>. Maximum redd densities for individual stream segments typically exceeded the mean density by a factor of three or four (Fig. 3b).

As recruits from the first redd surveys began to return, occupation of previously unused stream segments was rapid —

**Fig. 3.** (a) Basin-wide totals for annual Chinook salmon (*Oncorhynchus tshawytscha*) redds counted during aerial surveys from 1995 to 2003. (b) Mean redd densities ( $\pm 1$  standard error) within stream segments shown in Fig. 1. Points above mean values indicate the maximum number of redds that occurred within a stream segment during this study.



increasing from 6 to 16 segments between 1995 and 1999 and from 16 to 22 segments between 1996 and 2000 (Fig. 4). Distributional expansions were less dramatic in subsequent years, given that baseline redd numbers were usually larger, but in some subbasins, these expansions appeared to be ongoing across the range of observed densities (Fig. 5a). In two subbasins with the highest redd densities, however, the proportion of 500 m reaches that were used for spawning appeared to approach asymptotes at ~70% of the network (Fig. 5b). These asymptotes were reached at low densities ( $\approx 3$  redds·km<sup>-1</sup>), and the proportion of reaches occupied then remained constant across a threefold density increase, which suggested that suitable reaches were rapidly colonized, but were not being fully utilized at the densities observed. Recruits per spawner during the 9 study years ranged from 2.7 to 9.1, with an average of 5.3 (Table 1).

Visual comparison of cumulative redd curves suggested that observed spawning distributions were more clustered than random distributions (Fig. 6). This observation was confirmed by the Shannon–Wiener diversity scores, in that

all  $\bar{H}'_{\text{observed}}$  values were smaller than  $\bar{H}'_{\text{random}}$  scores, indicating  $p$  values  $< 0.001$ . As redd numbers increased, distributions became less clustered, which resulted in flatter curve profiles, and decreased the proportion of redds that occurred in the densest spawning areas. Despite this pattern, no trend occurred in  $H'_{\text{random}} - H'_{\text{observed}}$  values relative to population size ( $b_1 = -1.51 \times 10^{-5}$ ;  $df = 8$ ;  $p = 0.35$ ), suggesting that changes in observed redd distributions occurred at rates similar to those expected in a random distribution.

The repeated-measures ANOVA suggested that a significant interaction occurred between year and stream segment ( $F = 2.17$ ,  $p < 0.001$ ,  $df = 176$ ). Not unexpectedly, given the spatial and temporal variation in our data, sample year ( $F = 95.8$ ,  $p < 0.001$ ,  $df = 8$ ) and stream segment ( $F = 11.5$ ,  $p < 0.001$ ,  $df = 22$ ) also had significant effects on redd abundance. We repeated this analysis after excluding the 1995 data, reasoning that the low abundance and strongly clustered distribution observed that year may have unduly influenced our results, but all effects remained significant after this omission ( $p < 0.001$ ).

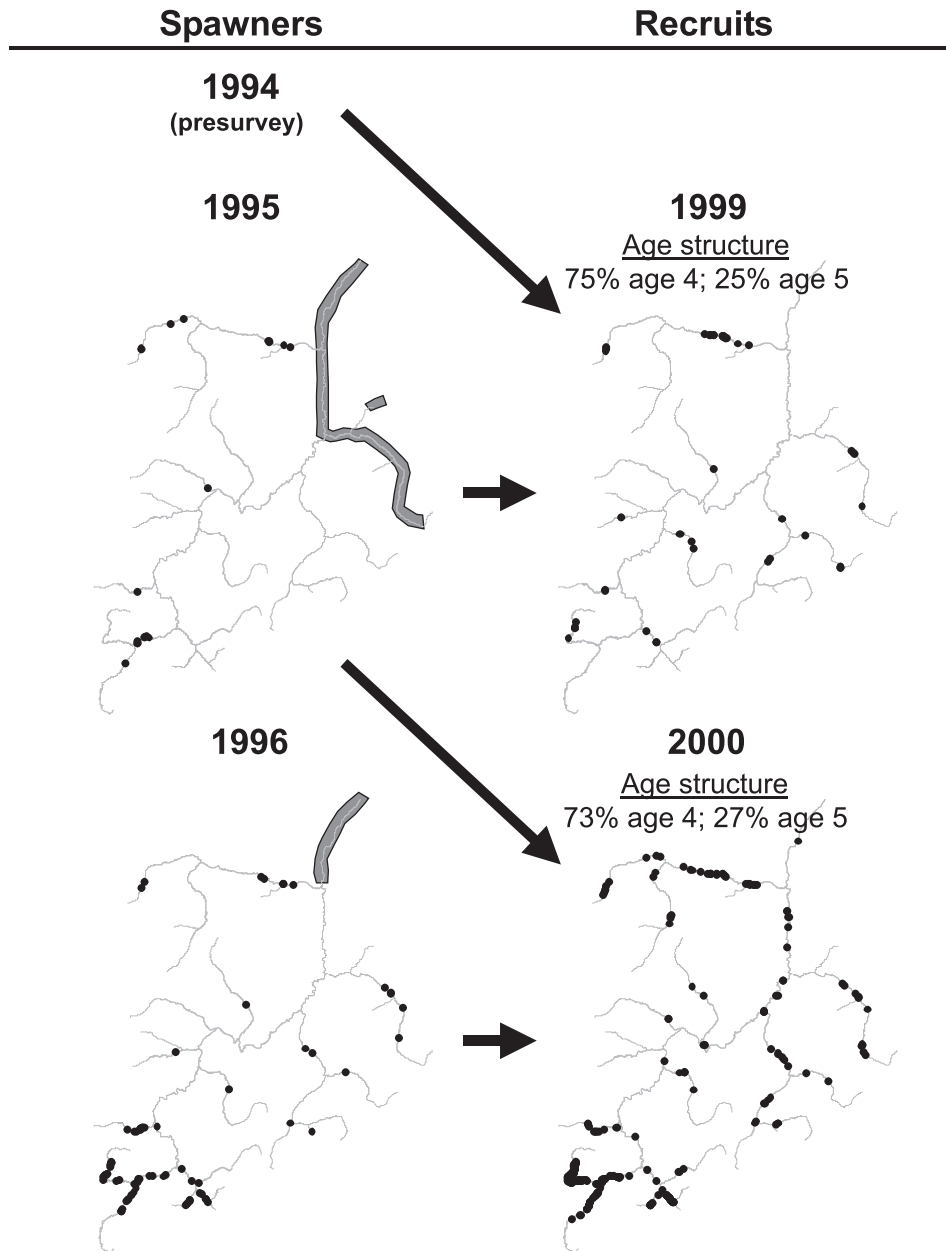
Variance partitioning suggested that inference from fewer than 3–5 years of data would have resulted in a biased view regarding the relative importance of variance components. This pattern was similar in both the observed and permuted data sequences (Fig. 7). With 1 year of data, it was impossible to estimate a year effect ( $df = 0$ ), so all variance was attributed to segment and residual error, which inflated the apparent importance of stream segments (65%–80% of total variation). Once multiple years of data were available, the strength of the segment effect decreased and stabilized at approximately 35% of total variation between years 3 and 5. Remaining variance components also stabilized by this time, with year, segment  $\times$  year, and residual error accounting for 40%, 13%, and 12% of total variation, respectively.

## Discussion

### Spatial and temporal heterogeneity

Our data set linked a spatially continuous population census with almost a decade of observation. During this time, redd densities changed by two orders of magnitude, which provided a range of variability over which population performance could be examined. Similar to previous studies for a variety of salmonids, our results confirm that Chinook salmon spawning is a spatially and temporally heterogeneous process (Walters and Cahoon 1985; Magee et al. 1996; Pess et al. 2002). Preferred areas typically consisted of low-gradient, pool–riffle channels that flowed through wide, alluviated valleys, a finding which others have documented for this species (Vronskiy 1972; Montgomery et al. 1999; Burnett 2001). Specific mechanisms accounting for this linkage are poorly understood, but a suite of interacting factors probably plays a role. The simplest explanation is that pool–riffle channels have the greatest availability of microhabitats (substrate, flow, and depth combinations) that are suitable for spawning. However, these channels also occur in association with extensive alluvial deposits, which may act as aquifers to moderate temperature and flow regimes (Brunke and Gonser 1997), and their undulating bedforms may increase hyporheic exchange, thereby facilitating oxygen and waste

**Fig. 4.** Intergenerational differences in distributions of Chinook salmon (*Oncorhynchus tshawytscha*) redds coming off low abundance years in 1995 and 1996. Shading covers those portions of the stream network that were not surveyed in 1995.

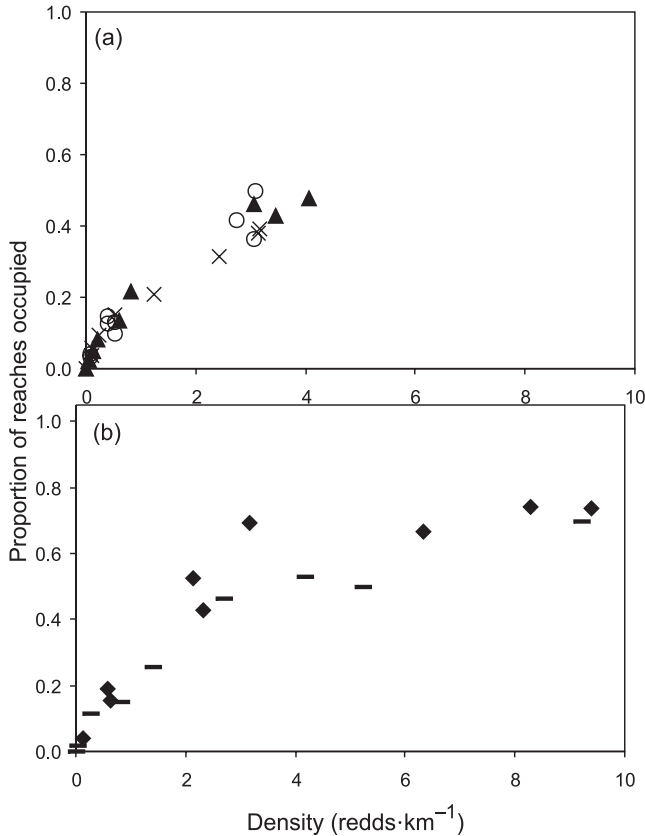


transferral through eggs pockets (Harvey and Bencala 1993; Baxter and Hauer 2000). The spatial arrangement of complementary habitats (sensu Kocik and Ferrari 1998) may also be especially conducive to successful spawning and rearing in pool-riffle reaches, where side channel habitats are commonly used by juvenile fish (Hartman and Brown 1987), either because they provide refugia from floods and predators or local productivities are enhanced by strong terrestrial-aquatic linkages.

Temporal variation in the distribution of spawning was also noteworthy, and cumulative distribution curves suggested that redds became more evenly distributed as population size increased. The rate at which observed distributions changed, however, did not differ from the rate expected in random dis-

tributions, which suggests that changes were a statistical artifact associated with population size rather than the result of biological processes. Failure to reject the null hypothesis may have been the result of limited inferential power, possibly stemming from limitations associated with the number of years for which data were available, measurement errors, or simply using data that were too crude for the task at hand. Most studies that describe source-sink dynamics rely on detailed mark-recapture information, location-specific growth rates, or assignment tests based on genetic information (e.g., Gunderson et al. 2001; Berry et al. 2004). If a pattern due to biological processes were to exist, either fish must be dispersing from areas of high abundance to low abundance or spatial inequities in population growth rates

**Fig. 5.** Occurrence of Chinook salmon (*Oncorhynchus tshawytscha*) redds within five subbasins in the Middle Fork Salmon River. (a) Patterns in subbasins where population expansion was ongoing (▲, Loon Creek; ×, Camas Creek; ○, Big Creek); (b) patterns in subbasins where population expansion appears to have reached an upper limit (◆, Bear Valley Creek; ■, Marsh Creek).



**Table 1.** Summary of recruits per spawner in an expanding population of Chinook salmon (*Oncorhynchus tshawytscha*) in the Middle Fork Salmon River.

Spawner year	<i>R</i>
1995	9.1
1996	5.9
1997	6.6
1998	3.9
1999	2.7 <sup>a</sup>
Average <sup>b</sup>	5.3

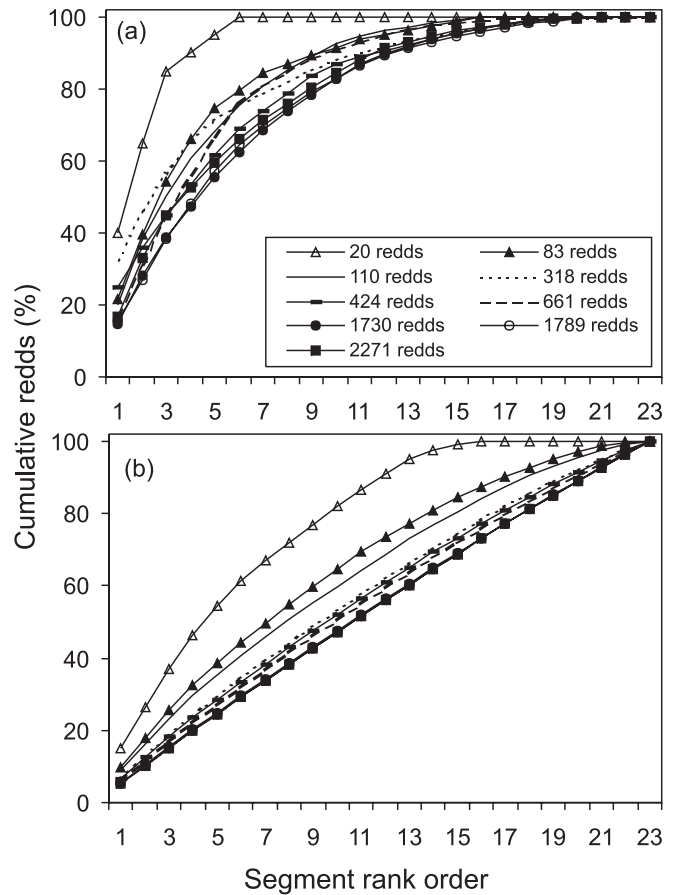
**Note:** Values were calculated using female age structures in return years and basin-wide redd count totals.

<sup>a</sup>Estimate is biased low by lack of data on age-6 fish that returned in 2005.

<sup>b</sup>Average is weighted by relative population sizes determined by summing spawners and recruits.

exist, with populations in low density areas growing more rapidly than high density areas. That dispersal would play a role seems likely, given our observations of unoccupied stream segments that were later used by progeny from the earliest year classes, but determining the relative effects of both mechanisms will be challenging.

**Fig. 6.** Rank-ordered cumulative distributions for (a) observed redd distributions and (b) random redd distributions.

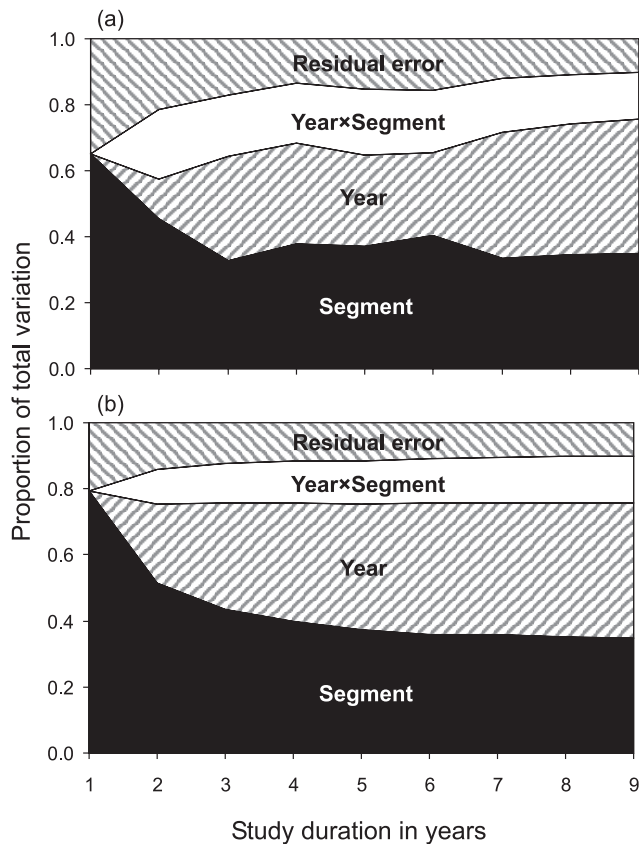


Chinook salmon populations grew rapidly during the course of this study, and the rate of this growth was higher than other values published for this species (McClure et al. 2003). Because the stream habitats in the MFSR have been protected by wilderness and primitive area designations for many decades, it is unlikely that this increase was caused by changes in spawning and rearing conditions. Instead, improved marine productivities and favorable juvenile migration conditions must have increased out-of-basin survival rates (Fish Passage Center 2003; Beamish et al. 2004). Although this population rebound probably occurred in response to the alignment of important environmental factors that were largely beyond management control, it was remarkable to note the resilience displayed by these populations. Such resilience suggests that attainment of robust population sizes may be achievable over several generations under the right conditions.

Variance partitioning provided several insights regarding the relative importance of factors that affected MFSR Chinook salmon. Compared with similar analyses performed with coho salmon (*Oncorhynchus kisutch*; Larsen et al. 2001), our data had a stronger temporal component and little residual variation. This suggested that variation from the combination of subsegments and measurement errors was low compared with the strength of signal from spatial and temporal factors. The strong year effect was due to large



**Fig. 7.** Relative importance of variance components as a function of study duration. (a) The pattern derived from the observed data sequence; (b) the average pattern derived from different yearly combinations of data.



interannual changes in redd numbers and the population growth that occurred during our study. The strength of this effect, combined with a relatively weak segment  $\times$  year interaction, also suggested concordant changes in redd numbers across sites, which corroborated earlier findings for these populations (Isaak et al. 2003). Increased synchrony is a recent phenomenon, the cause of which is unclear, but it may be related to loss of life history diversity or decreased importance of density-dependent factors at reduced population sizes (Isaak et al. 2003).

Variance partitioning results also suggested that inferences drawn from fewer than 3–5 years of study would have led to biased views regarding the relative importance of spatial and temporal components. Conversely, surveys conducted in excess of this temporal expanse were unnecessary — assuming, of course, that the only objective had been to accurately characterize these variance components. Because system behavior during the period of observation dictates when variance components stabilize — with some systems requiring decades and others a few years (Kratz 1995; Wiley et al. 1997) — generalizable recommendations regarding study duration are not possible. It is safe to conclude, however, that more than 1 year of data are desirable so that variance components inclusive of temporal factors can be estimated and that studies relying on space-for-time substitution may tend

to overestimate the importance of spatial attributes (Clinchy et al. 2002).

### Conservation implications

Our results have several implications for population monitoring and prioritization of conservation efforts. Many early monitoring protocols were initiated using a series of index sites, which were often selected from accessible, high-density spawning areas (Larsen et al. 2001). Lack of randomization in site selection and shifts in fish distributions may bias inference from index samples and help mask population trends — a topic that we explore more fully with our data in a subsequent paper (J. Courbois, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, unpublished data). Given the magnitude of declines that have occurred in many salmon stocks, however, optimal sampling strategies were not necessary for trend detection until recently. The new challenge will be to discern relatively small population changes that will allow for accurate assessments of expensive conservation and restoration efforts (Paulsen and Fisher 2005). Failure to do so may have negative consequences for depressed populations; therefore it is important that contemporary monitoring protocols be designed with appropriate statistical rigor (*sensu* Larsen et al. 2001).

With regard to habitat conservation, one of the commonalities emerging from many prioritization strategies is that the best remaining areas within a species' range should be protected (Epifanio et al. 2003; Groves 2003). In this context, "best" often connotes high density, and part of the rationale is that once limiting factors have been alleviated, protected areas can act as sources of colonists to fuel expansion into unoccupied habitats (Schlosser and Angermeier 1995). Our work supports this idea, in that the contribution of high-density areas appeared to be larger at low escapements, which suggests these areas may be particularly resistant to declines.

A strategy focused on protection of core populations may be useful in the short term, but longer perspectives will also be needed to accommodate the dynamics of natural systems (Hilborn et al. 2003). Even over the relatively short period encompassed by this study, we observed a segment  $\times$  year interaction, and population growth rapidly expanded spawning into areas where it had recently been absent. Over longer periods, we have documented dramatic changes in inter-population synchronies (Isaak et al. 2003), and anecdotal information suggests that spawning in mainstem areas may have once been much more prevalent (Hauck 1953; Meyer and Leidecker 1999). These factors highlight temporal variation in spatial distributions, the importance of suitable but unoccupied habitats, and the fact that populations will need room to expand during recovery (Cooper and Mangel 1998; Rieman and Dunham 2000). Conservation efforts that fail to accommodate future growth, and which seek to protect species only in high density or currently occupied areas, may artificially constrain populations and actually curtail future recovery possibilities.

### Future applications

The challenges of conserving stream ecosystems extend beyond the knowledge that can be gained from traditional,

small-scale, site-specific studies and must be addressed in innovative ways. Fausch et al. (2002) provide a powerful argument for the necessity of studies conducted at landscape scales using continuous sampling techniques. Not only does the georeferencing that accompanies these surveys provide tremendous analytical flexibility, but a broader spatial extent facilitates a system view that is more commensurate with the scales at which important biophysical processes related to population persistence operate (Rieman and Dunham 2000). Although measurement errors will always remain a concern, researchers are less constrained by limitations associated with traditional sampling designs and instead may be limited chiefly by the array of interesting ideas that can be generated and tested.

By censusing the distribution of a commonly measured demographic parameter through time, we have generated a data set that has tremendous potential for revealing much about the dynamic nature of Chinook salmon in the MFSR. Currently, these data are being used in a host of studies to address key conservation issues for Chinook salmon, including examination of linkages between fine-scale genetic structure, demographic parameters, and environmental characteristics (H. Neville, University of Nevada-Reno, Department of Biology, Reno, NV 89577, USA, unpublished data), determination of dispersal ranges and environmental constraints using spatial autocorrelation analysis (D. Isaak, unpublished data), validation of hydrologic models for predicting basin-wide distributions of spawning substrates (Buffington et al. 2004), assessment of environmental covariates that affect habitat occupancy (D. Isaak, unpublished data), and validation of redd count methodologies (R. Thurrow, unpublished data). We welcome opportunities for additional collaborations that would further explore the utility of these data.

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