

Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho

Daniel J. Isaak, Russell F. Thurow, Bruce E. Rieman, and Jason B. Dunham

Abstract: Metapopulation dynamics have emerged as a key consideration in conservation planning for salmonid fishes. Implicit to many models of spatially structured populations is a degree of synchrony, or correlation, among populations. We used a spatially and temporally extensive database of chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho to examine patterns in synchrony as these fish underwent a sixfold decrease in abundance. Our results suggested that populations became strongly synchronous as abundances decreased and that the range, or diversity of correlations, exhibited among populations also decreased. These changes indicate that the likelihood of simultaneous extirpations has increased, which could have long-term detrimental consequences for metapopulation persistence. Implications for management are that the resilience of many metapopulations to large-scale disturbance and anthropogenic suppression may not depend solely on attempts to maintain large and productive component populations, but also on efforts to desynchronize populations that have become strongly correlated. Such efforts could entail promoting the existence of a broad distribution and diversity of habitats that support a wide array of life-history forms and ensuring that some habitats are sufficiently spatially disjunct so that risks from catastrophic stochastic events are minimized.

Résumé : La dynamique des métapopulations est devenue un élément primordial de la planification de la conservation des poissons salmonidés. Plusieurs des modèles de population à structure spatiale supposent l'existence d'un degré de synchronisation ou de corrélation entre les populations. Une importante banque de données, tant spatiales que temporelles, de dénombrements de saumons quinnat (*Oncorhynchus tshawytscha*) sur les frayères dans une région sauvage du centre de l'Idaho nous a permis d'examiner la synchronisation au moment où ces poissons subissaient un déclin de leur abondance par un facteur de 6. Nos résultats montrent que les populations se synchronisent fortement à mesure que leur abondance diminue et que l'étendue ou la diversité des corrélations entre les populations décroît aussi. Ces changements indiquent un accroissement de la vraisemblance d'une extirpation simultanée, ce qui pourrait avoir des conséquences néfastes sur la survie de la métapopulation. Il y a aussi des implications pour la gestion : la résilience de plusieurs métapopulations aux bouleversements à grande échelle et à l'extermination par l'activité humaine peut ne pas dépendre uniquement d'efforts pour maintenir des populations constitutives importantes et productives, mais aussi d'efforts pour désynchroniser les populations qui sont en forte corrélation. On pourrait penser au développement d'une large répartition et diversité d'habitats où prévaudrait une gamme étendue de types de cycles biologiques et à la précaution que certains habitats soient suffisant éloignés les uns des autres pour que les risques engendrés par des événements catastrophiques stochastiques soient minimisés.

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Introduction

The Columbia River Basin once harbored abundant populations of spring and summer chinook salmon (*Oncorhynchus tshawytscha*; Lichatowich 1999), but populations of these fish have declined precipitously over the last century. Thurow et al. (2000) estimated that spring and summer chinook salmon in the interior Columbia River Basin presently

occur in only 21% of the historical range. Many remaining stocks persist at dangerously low levels (Nehlsen et al. 1991; Huntington et al. 1996), which has prompted federal protection under the U.S. Endangered Species Act (ESA). Whereas much of the recent debate regarding salmon conservation efforts has focused on the relative importance of various factors, including dams, ocean productivity, hatcheries, and habitat alterations (Ruckleshaus et al. 2002), there is little

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debate that populations have declined. Although these declines have obvious implications for the persistence of individual populations, repercussions may also occur with regards to how populations interact across larger spatial and temporal scales.

The dynamics of multiple, potentially interacting local populations, often described as “metapopulations” (Hanski 1999), has emerged as a key consideration in conservation planning for salmonid fishes. Although understanding metapopulation dynamics in salmonid fishes is limited (Rieman and Dunham 2000), all models of spatially structured populations are characterized by some degree of synchrony, or correlation, among populations (Harrison and Taylor 1996). A low level of correlation is often regarded as beneficial because habitats vacated by local extirpations can be recolonized by dispersal from nearby populations that were fluctuating out of phase (Sutcliffe et al. 1997). Conversely, a high level of correlation among populations can result in simultaneous extirpations when abundances are low and is predicted to decrease the probability of metapopulation persistence (Heino et al. 1997). Many aspects of reserve design and effective conservation thus hinge on understanding the level of synchrony that exists among local populations (e.g., Pickett and Thompson 1978; Moyle and Sato 1991; McElhany et al. 2000).

Studies on a wide range of animal taxa have addressed the topic of spatial synchrony (see reviews by Bjornstad et al. (1999) and Koenig (1999)). Almost invariably, these studies document a negative relationship between correlation in a population parameter — typically abundance — and the geographic distance separating populations. At short distances, dispersal of individuals between populations is believed to be a primary synchronizing factor (Sutcliffe et al. 1997; Ranta et al. 1997), but correlated environments also synchronize population dynamics and may act over greater distances (Heino et al. 1997). Local factors, such as density dependence, heterogeneities in habitats, or small-scale stochastic events, can override or decrease the importance of synchronizing agents and result in population asynchronies (Haydon and Steen 1997; Kendall et al. 2000).

The life histories of salmonid fishes provide ample opportunity for a complexity of factors to interact and affect spatial and temporal correlation of local populations. This is particularly true for salmon that migrate long distances and use a broad diversity of habitats during their life cycle. Salmon often spawn in headwater stream habitats, where local environmental factors can have important influences (Gomi et al. 2002), possibly affecting the synchrony of dynamics among local breeding areas. Other key features of salmon life histories are migration and ocean residence, which may lead to changes in synchrony, dependant on the timing, specific location, and types of activities that occur within these habitats (Peterman et al. 1998; Pyper et al. 2001).

Spatial synchrony studies are just beginning to describe patterns and their potential causes for salmonid fishes. Rieman and McIntyre (1996) noted weak but significant correlations among bull trout (*Salvelinus confluentus*) populations across northern Idaho and northwest Montana. Salmon recovery efforts have used synchrony analysis in attempts to identify unique or independent populations with mixed results (Currens et al. 2001). Other studies have used patterns in synchrony

to make inferences about the spatial scales at which environmental controls act on individual stocks in efforts to develop improved management policies (Pyper et al. 1999; Botsford and Paulsen 2000; Pyper et al. 2001). In most cases, however, previous studies have been conducted at spatial scales of regional extent, where questions pertaining to metapopulation dynamics are largely negated. In this paper, we focus on a population assemblage of chinook salmon within a wilderness area drained by the Middle Fork of the Salmon River (MFSR) in central Idaho. Within this area, a database that encompasses 45 years of redd counts from multiple sites within close proximity allows us to ask questions not only about spatial patterns in correlations, but also about the temporal stability of these patterns, and to do so at a scale relevant to metapopulation considerations.

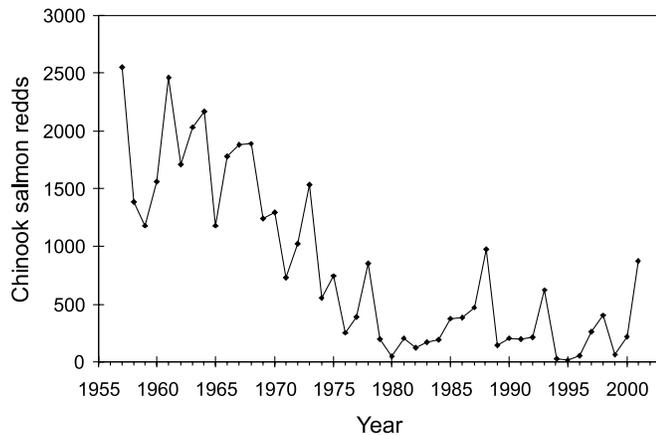
Materials and methods

Sample site

Chinook salmon populations that occur within the MFSR are composed of wild, indigenous fish. Redd counts conducted by the Idaho Department of Fish and Game (IDFG) suggest that these populations have declined to less than 20% of their abundance in the 1950s (Fig. 1; Brown 2002). These populations have been afforded federal protection since 1992, when all species of Snake River salmon were ESA listed. Populations within the MFSR are referred to as “spring/summer” chinook salmon based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). Chinook salmon enter the MFSR drainage in early summer, migrate to natal areas, and stage in pools before spawning. Eggs are deposited and fertilized in nests or redds from late July to mid-September. Embryos incubate in the gravel and emerge as fry the following spring. Although variable, juveniles typically rear in natal areas for 1 year before migrating seaward in the spring (Bjornn 1971). Migrating juveniles and returning adults must navigate eight hydroelectric dams on the lower Snake and Columbia rivers. Adults spend 1–3 years in the ocean, with the proportion of 1-, 2-, and 3-ocean fish varying across years and streams (Kiefer et al. 2002). Other salmonids that occur within the MFSR include bull trout, westslope cutthroat trout (*Oncorhynchus clarki lewisi*), mountain whitefish (*Prosopium williamsoni*), rainbow trout (resident forms and migratory steelhead; *Oncorhynchus mykiss*), and brook trout (*Salvelinus fontinalis*; Thurow 1985). Other species of salmonids are stocked in headwater lakes within the basin but are generally not found within areas used by chinook salmon (Pilliod and Peterson 2001).

The MFSR drains 7330 km² of forested and steeply mountainous terrain in central Idaho that ranges in elevation from 1550 to 3150 m (Fig. 2). Major tributaries along the 171 km length of the MFSR provide spawning habitat for chinook salmon. Spawning also occurs within portions of the mainstem river but has been uncommon in recent years (Thurow 2000). Most lands within the MFSR (>95%) are administered by the U.S. Forest Service, and the area 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 streams exist in rela-

Fig. 1. Aggregated time series of chinook salmon (*Oncorhynchus tshawytscha*) redd counts for the Middle Fork Salmon River basin. Data are from annual Idaho Department of Fish and Game surveys of chinook salmon spawning index areas (Brown 2002).



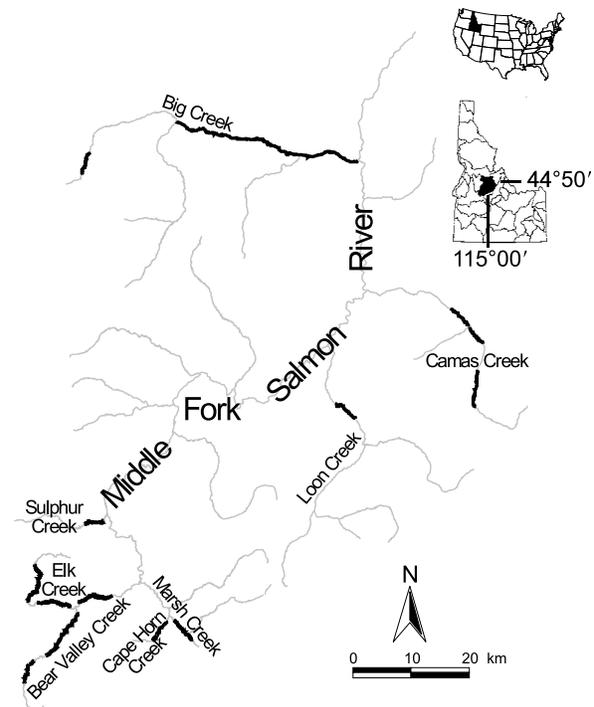
tively pristine condition. Some areas continue to recover from the effects of past grazing or mining, but cessation of many of these activities has occurred since wilderness designation and ESA listing. Natural disturbances from fires, hill-slope movements, and floods persist, and these processes help maintain the dynamic mosaic of stream habitats that exist within the MFSR (e.g., Miller et al. 2003; Nakamura et al. 2000). Most precipitation occurs as snowfall, and stream hydrographs are dominated by snowmelt with peak runoff in June, followed by low flows from late July through March.

Streams flow through wide, U-shaped valleys in the upper portion of the MFSR drainage, but elsewhere valleys are typically narrow and V-shaped. Land surfaces consist primarily of colluvium overlain by thin soils, but bedrock outcrops are not uncommon. Geology is varied, and Cretaceous-aged calc-alkaline intrusive materials of the Idaho Batholith occur across the southern half of the drainage, except where overlain by Quaternary alluvium and Pleistocene glacial drift (primarily in the Bear Valley Creek and Marsh Creek subbasins; Bond and Wood 1978). Streams in east-central and west-central portions of the drainage flow over felsic pyroclasts of the Challis Volcanics. The northern part of the drainage is a heterogeneous mix of several geologic formations (Bond and Wood 1978). Vegetation varies with elevation and aspect. Sagebrush (*Artemisia* spp.), grasses, and forbs are common at lower elevations and on southern slopes, whereas conifers predominate at higher elevations and on northern slopes.

Data collection

Data were derived from annual spawning ground surveys conducted by IDFG personnel on MFSR spawning tributaries. In recent years, some of these counts have been conducted by Rocky Mountain Research Station personnel. Salmon redds were counted by individual observers during a single pass along a stream transect and were timed to occur at or soon after the peak of spawning activity. The same biologist often conducted counts for the same set of transects during many consecutive years, although the length of the data record has required that multiple individuals contribute to each time series. Redd counts have been conducted on foot and by using aircraft — either small airplanes or heli-

Fig. 2. Stream network in the Middle Fork Salmon River. Dark bars indicate Idaho Department of Fish and Game sampling transects used in this study.



copters. Foot surveys are generally used in accessible portions of the drainage, whereas aircraft are often used to sample remote areas. Redds have been counted with varying degrees of consistency at numerous areas on MFSR streams since 1952, but geographic boundaries were not standardized until 1957 (Hassemer 1993). For inclusion in this study, we selected data from 13 sample transects that were distributed across the MFSR and which had been sampled frequently within consistent geographic boundaries since 1957 (Table 1; Fig. 2). The prevalence of errors in this data set is unknown, but given the long time series and dramatic changes in populations that have occurred, we judged the data to be valuable for analyzing patterns and developing initial hypotheses.

Data analysis

The temporal extent of the redd counts made it possible to examine the consistency of spatial patterns across time and population sizes. We stratified the 13 series of redd counts into two periods — a high-abundance period from 1957 to 1973 (mean = 1624) and a low-abundance period from 1979 to 2000 (mean = 252). Analyses were completed on raw and detrended-redd numbers. Detrending was done using two methods — interannual differencing and linear regression. Annual differences were calculated as $\log_e(N_i/N_{i-1})$, where N_i was the redd count in year i . Differencing provided a measure of the instantaneous rate of population change and was independent of population size. In the regression-based method, individual series of redd counts were regressed against sample year within each stratum and subsequent analyses

Table 1. Summary of chinook salmon redd counts for three periods at 13 sampling transects in the Middle Fork Salmon River.

Sampling transect	Entire record (1957–2001)			High-abundance period (1957–1973)			Low-abundance period (1979–2000)		
	Years sampled	Mean redd count	CV	Years sampled	Mean redd count	CV	Years sampled	Mean redd count	CV
Upper Big Creek	44	68	1.06	17	120	0.72	22	28	0.94
Lower Big Creek	30	85	1.43	14	167	0.83	14	9	0.77
Lower Camas Creek	41	59	0.96	14	113	0.43	21	15	0.96
Upper Camas Creek	31	40	1.15	11	86	0.56	14	6	1.58
Loon Creek	33	37	1.06	11	75	0.52	16	9	0.85
Sulphur Creek	36	38	1.18	8	107	0.33	22	13	1.19
Marsh Creek	45	109	0.89	17	206	0.39	22	38	0.94
Cape Horn Creek	45	39	0.97	17	66	0.58	22	15	1.11
Lower Bear Valley Creek	45	92	0.89	17	176	0.38	22	31	0.98
Middle Bear Valley Creek	45	105	1.05	17	216	0.48	22	29	0.89
Upper Bear Valley Creek	45	15	1.12	17	30	0.63	22	6	1.22
Lower Elk Creek	45	87	0.94	17	176	0.35	22	25	0.99
Upper Elk Creek	45	109	0.94	17	207	0.40	22	42	1.37
Average	41	68	1.05	15	134	0.51	20	21	1.06

Note: Coefficient of variation (CV) = standard deviation/mean.

were conducted on the residuals. Detrending minimized the possibility of spurious correlations among redd counts as a result of long-term, linear trends in redd numbers and focused the analysis on local population dynamics (Koenig 1999).

We quantified synchrony by calculating Pearson correlations among all pairwise combinations of redd counts and detrended redd counts within each stratum. Because temporal autocorrelation within a time series can result in liberal estimates of significance (Type I statistical error) for inter-series correlations (Botsford and Paulsen 2000), statistical significance was determined by comparing the observed correlations with reference distributions that were obtained by recalculating correlations after each of 1000 randomizations of a time series (Howell 2002). Within each stratum, we tested whether the mean correlation equaled zero and whether a difference in mean correlations occurred across strata. Statistical significance was determined using bootstrap methods because only $(C - 1 + C - 2)$ pairwise correlations of all possible pairwise correlations $(C(C - 1))/2$ can be calculated independently (C is the number of time series considered; Ranta et al. 1997). For each test, 95 and 99% confidence intervals were constructed using the SE derived from 1000 bootstrap samples.

The relationship between population synchrony and distance was described for each stratum by regressing correlations against the stream distance that separated the midpoints of sample transects. Stream distances were measured from a 1:100 000 scale hydrology layer in a geographic information system (GIS). Significance levels for slope parameters were calculated using a randomization approach to avoid the problems with nonindependence discussed above (Legendre and Legendre 1998). Difference in the slopes of the relationships was tested by calculating the ratio of the slope difference to the SE of the slope difference and comparing this value with a t distribution (Zar 1996).

To provide a temporally detailed view of changes in population synchrony, we calculated correlations for an 8-year

sampling frame that was advanced at 1-year increments through each pair of redd count time series. Because data were collected sporadically at some transects, these calculations were made only for pairs of transects that had been sampled concurrently for more than 20 years.

Results

Chinook salmon redds were counted at the 13 sample transects included in this study from 31 to 45 years (Table 1). The number of sample years in high- and low-abundance periods ranged from 8 to 17 (mean = 15) and 14 to 22 (mean = 20), respectively. Mean redd counts during the early period of high abundance ranged from 30 to 216 redds and averaged 134, whereas mean redd counts during the subsequent low abundance period ranged from 6 to 42 and averaged 21. Coefficients of variation during the low-abundance period were larger than during the high-abundance period at 12 of 13 transects.

Patterns in synchrony for raw redd counts and both forms of detrended redd counts were virtually identical, so only results based on detrended regression residuals are presented. Significant correlations between redd counts were common during both periods (Table 2). The mean correlation for each period differed significantly from zero (high abundance $r = 0.34$, $p < 0.01$; low abundance $r = 0.50$, $p < 0.01$), as did the difference between the two periods ($d = 0.16$, $p < 0.01$), suggesting that the overall level of synchrony increased as population sizes decreased. Corroboration of this trend was provided by the number of significant correlations within each period. During high abundance, 23 of 78 correlations were significant at $\alpha = 0.05$, but this number increased to 42 of 78 correlations during the low-abundance period. Significant correlations during the high-abundance period were most common within the geographically proximate transects located in the upstream portion of the MFSR, and significant correlations became virtually ubiquitous in this area at lower escapements (27 of 28 possible correlations). Outside the

Table 2. Correlations among detrended redd count residuals at 13 transects in the Middle Fork Salmon River for two abundance periods.

Transect	Upper					Lower							
	Big Creek	Big Creek	Camas Creek	Camas Creek	Loon Creek	Sulphur Creek	Marsh Creek	Cape Horn Creek	Lower Valley Creek	Elk Creek	Upper Valley Creek	Middle Valley Creek	Upper Valley Creek
Upper Big Creek	—	0.15	0.18	-0.08	0.29	0.63	0.80	0.73	0.81	0.67	0.75	0.81	0.75
Lower Big Creek	0.01	—	0.10	0.15	-0.07	-0.02	0.06	-0.02	0.41	-0.01	0.10	0.31	0.17
Lower Camas Creek	0.24	-0.05	—	0.28	0.50	-0.02	0.34	0.35	0.28	0.35	0.41	0.32	0.48
Upper Camas Creek	0.32	0.07	0.79	—	0.49	0.14	0.03	0.64	0.32	0.51	0.52	0.25	0.43
Loon Creek	0.02	0.17	0.59	0.52	—	0.18	0.57	0.70	0.33	0.51	0.65	0.48	0.47
Sulphur Creek	0.39	-0.27	0.32	0.24	0.17	—	0.51	0.61	0.56	0.54	0.50	0.49	0.47
Marsh Creek	0.24	0.04	0.56	0.73	0.24	0.22	—	0.62	0.84	0.75	0.74	0.75	0.68
Cape Horn Creek	0.26	-0.31	0.36	0.21	0.25	-0.06	0.64	—	0.73	0.88	0.87	0.80	0.79
Lower Bear Valley Creek	0.64	-0.37	0.07	0.24	-0.42	0.41	0.44	0.23	—	0.76	0.86	0.83	0.83
Lower Elk Creek	0.44	-0.29	0.72	0.65	0.27	0.64	0.59	0.53	0.47	—	0.92	0.82	0.77
Upper Elk Creek	0.50	-0.02	0.42	0.47	-0.05	0.33	0.48	0.37	0.46	0.76	—	0.88	0.85
Middle Bear Valley Creek	0.32	0.20	0.78	0.66	0.34	0.68	0.53	0.50	0.20	0.74	0.54	—	0.91
Upper Bear Valley Creek	0.14	-0.27	0.63	0.41	0.31	0.50	0.70	0.66	0.36	0.68	0.38	0.59	—

Note: Correlations below the diagonal are for the high abundance period from 1957 to 1973; correlations above the diagonal are for the low abundance period from 1979 to 2000. Correlations with significance levels ≤ 0.05 are shaded; correlations with significance levels ≤ 0.01 are solid black. Box encompasses sites within the upstream portion of the Middle Fork Salmon River.

upper MFSR, redd counts in Loon Creek and upper Big Creek became more synchronous with other areas, whereas lower Camas Creek became less synchronous.

Regressions of correlational strength on distance had negative slopes that were different from zero for both periods (high abundance $b_1 = -0.0012, p < 0.01$; low abundance $b_1 = -0.0014, p < 0.01$; Fig. 3), suggesting that redd count synchronies were stronger among proximal transects than among distant transects. Slopes of the two regression lines were not different ($t = 0.35, p = 0.73$), but as would be expected given the difference in mean correlations, the Y intercept was significantly larger for the low-abundance period ($t = 2.34, p = 0.02$).

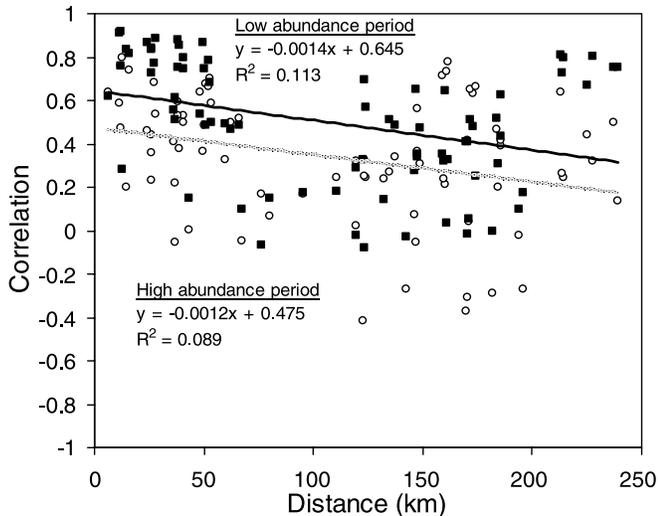
The moving window analysis suggested that the mean correlation among redd count time series steadily increased from an initial value of 0.23 to the most recent value of 0.88 as population abundance decreased (Fig. 4). Coincident with this increase, the range of associated interseries correlations has narrowed. Whereas correlations early in the time series were negative, near zero, or positive, correlations later in the series were usually strongly positive. Also noteworthy is that interseries correlations varied considerably during the time series — often exhibiting large changes in magnitude over the span of a few years. Part of this variability could be attributable to sampling variation given the relatively short 8-year length of the sampling frame, but similar patterns were observed when sampling frame lengths were extended to 13 years.

Discussion

Our results provide insight into how a group of wild, indigenous chinook salmon populations in a relatively pristine setting have functioned during the last half century. The picture that emerges is one of a system that has been highly dynamic in both space and time. Coincident with sometimes dramatic short-term fluctuations among populations, overall abundance has undergone a sixfold decrease, correlations among populations have increased, and the range of interseries correlations has narrowed. Combined, these patterns are indicative of a system that has transitioned from a high level of stability and resilience to a state in which these qualities appear greatly reduced. The diversity and low level of synchrony once manifest within this system appear to have provided the capacity necessary to maintain some level of functionality while undergoing severe population declines. At the present time, however, further capacity for change seems limited and scenarios involving multiple simultaneous extirpations could become reality and have long-term detrimental consequences for metapopulation persistence.

The diverse life history of chinook salmon includes occupation of several distinct environments and opens the possibilities to a range of hypotheses that may explain the dramatic changes in correlations among these populations. One possibility may be the decreased availability of nutrients in freshwater rearing environments that has undoubtedly resulted from massive declines in adult carcasses. Previous studies suggest that salmon carcasses, either through direct consumption (Chaloner and Wipfli 2002) or through the release of inorganic nitrogen and phosphorus (Schuldt and Hershey 1995), may increase productivity of lower trophic levels and

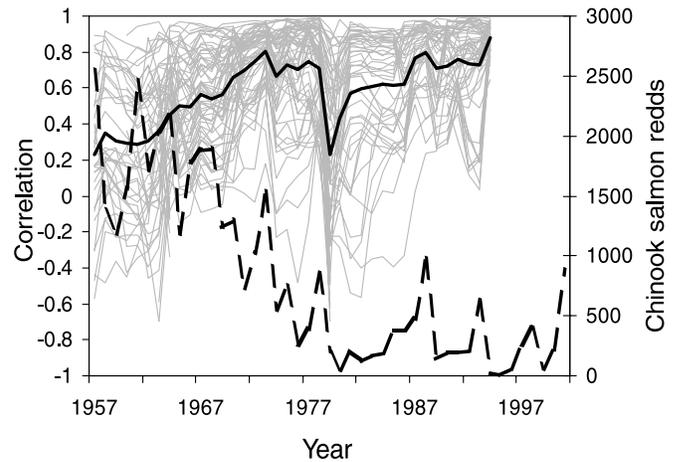
Fig. 3. Trends in correlations among detrended redd counts relative to stream distance for all pairwise combinations of Idaho Department of Fish and Game transects during two abundance periods. Open circles are correlations exhibited during the high-abundance period (shaded trend line); solid squares are correlations exhibited during the low-abundance period (solid trend line).



the growth rates and size of fish (Mundie et al. 1991). Although little evidence exists for decreases in survival or productivity of MFSR stocks during freshwater rearing (Petrosky et al. 2001), other more subtle changes are possible. For example, the timing of migration and even the expression of some life histories appear to be partially dependent on juvenile growth (Healy and Heard 1984). Changes in growth, therefore, could have altered the developmental trajectories and environments experienced by a fish, and as carcasses decreased within the MFSR, juvenile growth and the range of available life-history options may have simply become restricted (e.g., Gende et al. 2002).

Another possibility is that changes in synchrony are related to decreases in the importance of density-dependent regulatory mechanisms. Stock–recruitment theory suggests that density dependence decreases to zero as stock size decreases, whereas the relative importance of density-independent mortality factors increases (Hilborn and Walters 1992). As a result, the buffering effect that density dependence provides individual populations against stochastic events and that also helps maintain asynchrony among populations (Kendall et al. 2000) is minimized, and populations could become correlated in response to stronger density-independent control. Although a density-dependent mechanism could exert influence during several life stages, researchers working with both freshwater (Rieman and McIntyre 1996) and anadromous fishes (Peterman et al. 1998) have argued that patterns in synchrony are largely determined before establishment of residence in lentic or oceanic habitats, which may only serve to enhance preexisting patterns, given the relative homogeneity of these habitats. Rieman and McIntyre (1996) predicate their argument upon the establishment of relative year-class strength early in life, whereas Peterman et al. (1998) suggest that only minor changes in synchrony occur after juveniles emigrate from rearing habitats. If this scenario is applicable to the MFSR, current conditions probably differ

Fig. 4. Temporal trends in correlations among all pairwise combinations of redd counts at Idaho Department of Fish and Game transects. Correlations were calculated based on an 8-year sampling frame that was advanced at 1-year increments through paired time series. Shaded lines represent interseries correlations; heavy solid line represents the mean correlation; heavy broken line represents the aggregated time series of chinook salmon redd counts from Idaho Department of Fish and Game trend sites in the Middle Fork Salmon River.



from historical conditions when population responses were metered by the degree of density dependence. Under historical conditions, similar environmental stimuli, acting upon a range of population abundances, would have resulted in differential responses and may have generated asynchronous dynamics.

Land management activities and the suppression of natural disturbance regimes have resulted in the homogenization of stream habitats in many landscapes (Bisson et al. 1992; McIntosh et al. 2000). As the diversity of available rearing habitats is diminished, populations increasingly occur in similar habitats and experience similar environments. This trend could be an important synchronizing agent in many managed areas but seems unlikely in the wilderness setting in which our study was conducted. Minimal anthropogenic effects and a geographic size that facilitates the existence of natural disturbance processes ensure the continual generation and maintenance of a diversity of stream habitats. Although the array of stream habitats available to fish under such conditions may constantly be changing (Bisson et al. 1997), it is doubtful that a sustained unidirectional shift in the physical characteristics of stream habitats could occur over a time span sufficient to evoke a systemic response in population synchrony. Additionally, the time scale of such changes is likely to greatly exceed the length of the time series considered here (Wolman and Gerson 1978).

Factors outside the MFSR may have contributed to the pattern that we observed. The hydrosystem on the lower Snake and Columbia rivers was constructed coincident with changes that occurred in synchrony. Recent data suggest that the timing of smolt migration through the hydrosystem strongly affects juvenile survival and adult returns (J. Williams, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, unpublished data). If temporal patterns in smolt mi-

grations and hydrosystem survival are consistent among years, the hydrosystem could effectively act as a filter that selects for particular life histories, ultimately decreasing the range of viable life-history options.

Marine conditions are also a strong determinant of survival in anadromous salmonids (Mantua et al. 1997; Hare et al. 1999), and patterns in correlations have been documented among anadromous fish stocks in many coastal regions (Peterman et al. 1998; Pyper et al. 1999). To date, however, these patterns have emerged only at large spatial scales (e.g., coastal regions of the northeast Pacific ocean; Pyper et al. 2001; Mueter et al. 2002a), and for the marine environment to have become a stronger synchronizing factor implies either that the ocean has become more homogenous relative to the scales at which fish from the MFSR use it or that distributional patterns have changed and fish are now using more similar environments than previously. These explanations seem unsatisfactory, however, given that patchiness in many of the marine variables that affect ocean survival emerges only at geographic scales exceeding hundreds of thousands of square kilometres (Mueter et al. 2002b). Instead, rather than changes in synchrony occurring within out-of-basin environments, these environments may have indirectly precipitated the synchronization of MFSR populations by decreasing out-of-basin survival rates (Mantua et al. 1997; Deriso et al. 2001; Petrosky et al. 2001), which decreased numbers of returning adults and thereby facilitated mechanisms that operate during freshwater rearing.

Another possibility is that redd count errors have decreased through time, thus giving the appearance that an increase in correlation has occurred. This scenario implies either that improved sampling protocols and observer competences have resulted in markedly improved redd counts or that population declines and lower associated redd densities have led to fewer counting errors. The former explanation seems less likely given that Hassemer (1993) reviewed the IDFG redd count database and revised its content for consistency in the early 1990s. The data used in this study were a subset of this database that met even stricter requirements regarding sampling consistency. Additionally, although the temporal extent of the redd count time series used in this study has required contributions by numerous individuals, most of the counts have been conducted by highly experienced biologists who have surveyed the same transects for many consecutive years, even decades. Potentially more problematic is the possibility that error rates were greater when population levels, redd densities, and the amount of superimposition were higher. Unpublished data from research designed to assess the accuracy of chinook salmon redd counts suggests that miscounts do occur more frequently at redd clusters than at individual redds (R. Thurow, personal observation). However, even in reaches in which clustering and superimposition are common, reach-scale error rates appear to be relatively small, especially in comparison with other salmonid species like bull trout (Dunham et al. 2001). As a result, even if changes in redd count accuracy have occurred, this mechanism appears incapable of accounting for the entirety of the increase in synchrony that we observed.

Temporal instability in biological systems has implications for fisheries research and population assessments. Several studies of metapopulation dynamics in salmonids have

relied on cross-sectional data sets collected after populations had declined substantially (Rieman and McIntyre 1995; Dunham et al. 1997; Dunham and Rieman 1999). As our results suggest, present patterns may not be indicative of past performance. Additional evidence or longer time series may be needed before definitive conclusions can be drawn about many systems (Clinchy et al. 2002). Also potentially problematic is the use of redd counts conducted within a subset of available habitat. Depending on the amount of correlation between sampled and unsampled areas, as well as the temporal stability of these correlations, redd counts may or may not provide accurate assessment of population trends. Remedies for this problem might include surveying the entirety of an area, assessing patterns of synchrony in existing redd count data, or improving sampling designs (e.g., Larson et al. 2001).

Negative relationships were observed between population synchrony and distance during both high- and low-abundance periods, suggesting that proximal populations performed more similarly than distant populations. Rieman and McIntyre (1996) documented a similar pattern for bull trout and concluded that where correlations were weak, the existence of strong proximal populations should be promoted as a means to facilitate the exchange of individuals. This advice remains sound, but caution must be exercised in systems characterized by high levels of synchrony. In these situations, benefits of maintaining populations in close proximity must be balanced with risks of simultaneous extirpations that could threaten the regional persistence of a species, especially in regions characterized by landscape conditions that are conducive to intense and extensive disturbances like the large forest fires that have become common in the western U.S. (Hessburg and Agee 2003). Efforts to desynchronize populations that have become strongly synchronous should complement basic efforts to maintain large and productive population assemblages. These efforts could entail promoting the existence of a broad distribution and diversity of habitats that support a wide array of life-history forms and ensuring that some habitats are sufficiently spatially disjunct so that risks from catastrophic stochastic events are minimized. Of course, these considerations may be moot for many depressed up-river anadromous stocks unless accompanied by continued efforts to address out-of-basin mortality factors.

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