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Coherence of Observed Adult Sockeye Salmon Abundance Within and Among Spawning Habitats in the Kvichak River Watershed

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Abstract: Despite coherent trends in aggregate abundance of Pacific salmon *Oncorhynchus* species at ocean-basin scales, individual populations often fluctuate out of phase with one another. However, spatial covariation in shared environmental conditions may lead to correlation among proximate populations in survival, recruitment, and subsequent adult abundance. We found strong covariation in 45 years of aerial abundance estimates of adult sockeye salmon *Oncorhynchus nerka* in 93 spawning populations in the Kvichak River system, Bristol Bay, Alaska. A significant negative relationship with geographic distance ($P<0.01$) accounted for just 2.96% of the variability in both correlation of abundance between populations, and a related similarity coefficient. There was no evidence for a threshold of rapid decay in this relationship, despite distances of up to 175 km between populations. Island beaches showed significantly higher covariation ($P<0.05$) than other types of spawning habitat, even after removing the effect of distance. We conclude that these patterns are likely a result of the commercial fishery, broad environmental patterns experienced by populations throughout the drainage, and differences in population-specific early life history survival rates among habitats. A better understanding of the degree to which spawning sites show covariation in abundance, as well as of patterns present within a single river system, could assist researchers in locating suitable control sites for experiments and may allow for more accurate interpolation of missing historical data.

INTRODUCTION

Anadromous salmonids are exposed to various agents of mortality in marine and freshwater environments over their lives, some unique to each population and some shared among populations. Pacific salmon (genus *Oncorhynchus*) populations from across North America and Asia rear in a relatively similar ocean environment in the North Pacific (Groot and Margolis 1991). Oceanic conditions experienced by these species are influenced by interannual and interdecadal climatic shifts (Mantua et al. 1997) and are related to regional aggregate changes in growth, productivity, and survival (hence abundance) across many populations (Beamish and Bouillon 1993; Hare et al. 1999; Pyper and Peterman 1999; Mueter et al. 2002). Marine environmental conditions show covariation over scales of thousands of kilometers, and recruitment variability in resident marine fish reflect this scale over distances up to 500 km (Myers et al. 1995, 1997). Regional patterns of marine survival appear strong for some salmon species (Coronado and Hilborn 1998; Pyper et al. 2002). In addition to natural sources, mortality due to fishing in the marine environment generally affects many populations simultaneously. This source of mortality is thus shared among populations, to the extent that fisheries exploit salmon populations from within a region or watershed.

The freshwater phase of Pacific salmon life history accounts for slightly more than half of the variability observed in egg to adult survival and contributes greatly to recruitment variation and subsequent abundance (Bradford 1995). Bradford (1995) further noted that freshwater habitat effects may extend to river and estuarine habitat, and so may be underestimated in his research. The extent to which populations experience common freshwater conditions depends on their specific life histories, habitats, and the coherence of environmental conditions.

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Some of the variability in freshwater production is population specific due to local response to environmental conditions, density, and stochastic processes. A greater correlation in abundance has been identified for resident and anadromous salmonid populations within tributaries than at greater spatial scales (Milner et al. 1995). However, even among proximate populations, the length of available spawning habitat (Bradford et al. 1997) and low covariation in climatic influence among lakes within a small geographic area (Magnuson et al. 1990) may lead to differential productivity. At an even smaller scale, surveys of index reaches, or representative subsets of a population, within a single stream may be as accurate as full enumeration of spawning adults under some circumstances (e.g., Shardlow et al. 1987; Irvine et al. 1992). This seems to imply that significant covariation exists at smaller spatial scales, but raises the question of how to characterize the decay from strong aggregate covariation over tens of kilometers to the weak patterns observed among individual populations spread across thousands of kilometers.

Recent research has focused on defining the spatial scale over which salmon abundance, estimated at various life stages, varies coherently among individual populations. Bradford (1999) reported a sharp decline in the correlation of coho salmon *Oncorhynchus kisutch* smolt abundance as geographic distance between populations increased, as well as a proximity threshold, at 20 to 30 km, beyond which he observed no covariation in smolt abundance between populations. This threshold was attributed to effects of comparing data from several river systems, and potential discontinuity in environmental factors between them. Myers et al. (1997) reported a threshold of about 200 km in correlation of recruitment for chum *O. keta*, pink *O. gorbuscha*, and sockeye *O. nerka* salmon, but had little data to examine below that distance and did not stratify comparisons among and within river systems.

Adult salmonid population abundance is determined by environmental and biotic factors at each stage of development. Studying spatial variability within a single watershed reduces effects of confounding factors such as differential marine survival, fishing mortality, and differences in juvenile rearing conditions. Sockeye salmon populations within a watershed that spawn in discrete locations, rear in the same lake, and migrate to sea from a common outlet provide a good opportunity to examine small scale spatial patterns in variation of abundance. Spawning and incubation periods should be important influences on abundance of adult sockeye salmon and we expected that the observed covariation would be greater than that found among populations of coho salmon, which rear in population-specific freshwater environments.

For our study, we used adult sockeye salmon abundance data from the Kvichak River system in Bristol Bay, Alaska, one of the largest sockeye salmon metapopulations in the world. To determine whether significant covariation was present among populations within this large, geographically diverse watershed, we first characterized the historical survey effort and then tested for confounding temporal changes in the composition of aggregate sockeye salmon abundance (diversity) for the entire watershed. We tested the hypothesis that geographic proximity influences the similarity of abundance among discrete spawning locations. We specifically tested for the presence of a proximity threshold for covariation of abundance that might be related to environmental differences in spawning and incubation conditions. We thought that the degree to which environmental conditions were shared within habitat types would influence the level of correlation or similarity in abundance among individual populations, and we compared similarity among habitats after controlling for effects of distance.

METHODS

Study area

The Kvichak River system has a drainage basin of 19,700 km^2 and contains two large lakes, Iliamna Lake and Lake Clark (Figure 1). Annual sockeye salmon returns to the Kvichak River system have ranged from 0.3 to 55 million fish (Cross et al. 1997; Fair 2000), making it the largest producer of sockeye salmon in Alaska (Eggers and Rogers 1987). For many years the system was characterized by a five-year cycle of high abundance, but more recently both average abundance and variation have declined (Eggers and Rogers 1987; Cross et al. 1997; Fair 2000).

The Kvichak River watershed contains over 100 identified spawning areas (Demory et al. 1964), geographically separated by as much as 175 km from each other (Figure 1). These locations can be grouped into three general habitat types: island beaches, mainland beaches, and tributaries (rivers, streams, and ponds). Adult sockeye salmon returning to each habitat type exhibit distinct morphology and life history characteristics (Olsen 1968; Blair et al. 1993), and there appears to be little straying among habitat types (Varnavskaya et al. 1994; Quinn et al. 1999). Within each habitat, the area occupied by spawning sockeye salmon varies,

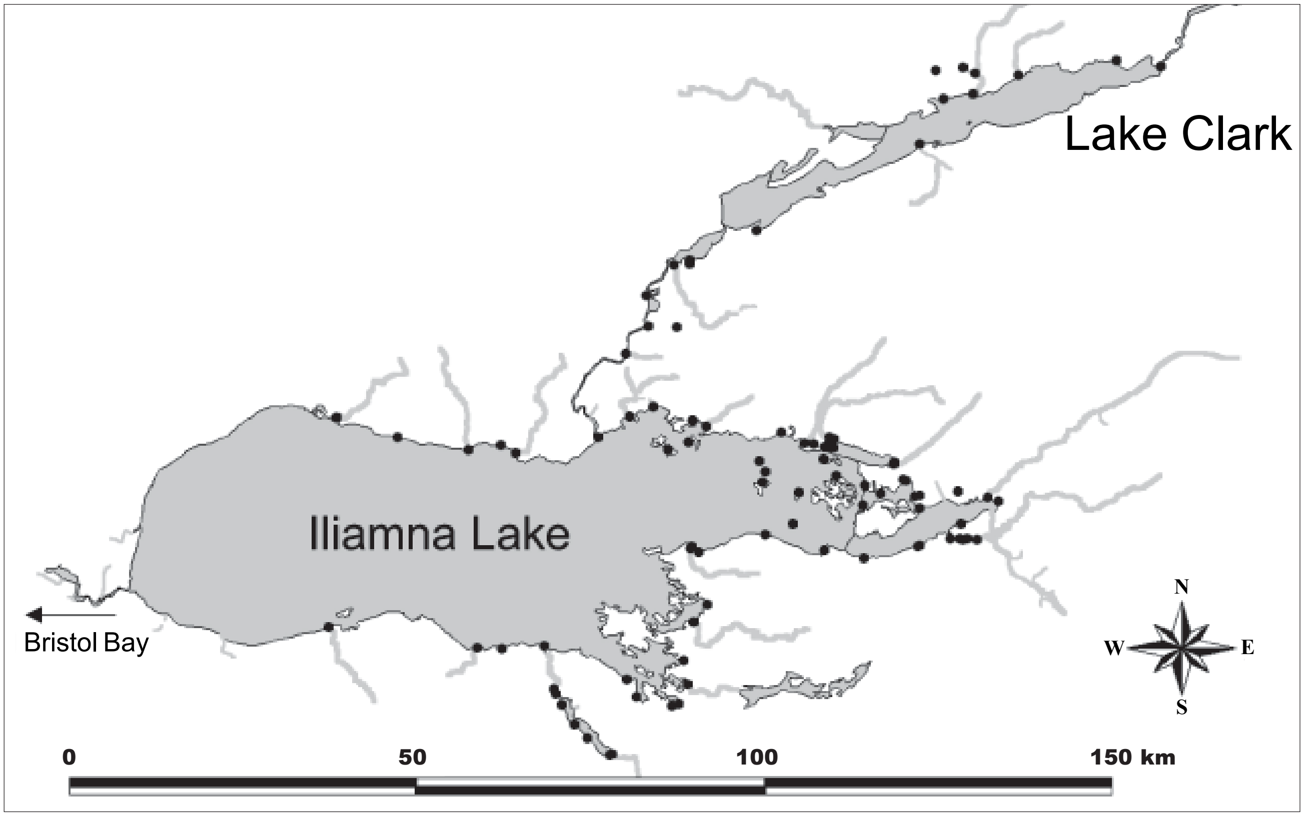

Figure 1. Map of Kvichak River watershed and study populations.

depending on density. To study the dynamics of these populations, we first grouped the populations into island beaches, mainland beaches, and tributary spawners (see below for details). We further subdivided tributary populations into major and minor populations, on the basis of aerial abundance surveys conducted by the Fisheries Research Institute (FRI; University of Washington, School of Aquatic and Fishery Sciences, Box 355020, Seattle, WA 98195) and the Alaska Department of Fish and Game (Regnart 1996). We then used survey data to determine the coherence of abundance among and within habitat types.

Most island beach spawning areas are located in the eastern end of Iliamna Lake. Sockeye salmon use beaches around more than a dozen islands, and can account for as much as 52% (mean = 9.1%) of the total observed number of spawners in the system (Olsen 1968; Kerns and Donaldson 1968; Regnart 1996; Cross et al. 1997; Fair 2000). Island beach populations spawn under similar conditions, typically on coarse substrate beaches exposed to strong wind-driven currents (Olsen 1968; Mathisen 1966; Kerns and Donaldson 1968; Leonetti 1996). Temperature regimes at these locations are usually similar to ambient lake temperature, 10°C to 13ºC, allowing embryos to hatch prior to lake freeze-up in early December (Olsen 1968; Leonetti 1996). Island beach spawners appear to balance the benefits of increased water circulation of shallower sites (Leonetti 1996) with the risks of desiccation or freezing as water levels drop and ice encroaches to nearly 1.5 m below surface level during spawning (Mathisen 1966). Duration of spawning on island beaches is short (roughly 2 weeks) and nearly synchronous among beaches in different parts of the lake (Demory et al. 1964; Kerns and Donaldson 1968; Hendry et al. 1995; Quinn et al. 1996). Interannual variability in spawner abundance is greater for island beaches than for other habitats (Figure 2; Cross et al. 1997; Fair 2000).

Mainland beach spawning areas are located on the shores of Iliamna Lake, Lake Clark, and other tributary lakes (Figure 1). Sockeye salmon using this habitat type account for up to 51% (mean = 15.1%) of the total observed escapement. Mainland beaches typically have relatively fine substrate and are fed by upwelling water forced underground by topographic convergence (Olsen 1968; Blair et al. 1993; Quinn et al. 1995). Temperatures are generally 1°C to 4ºC below ambient lake temperatures (Olsen 1968). Compared to island beaches, spawning at mainland beaches occurs later in

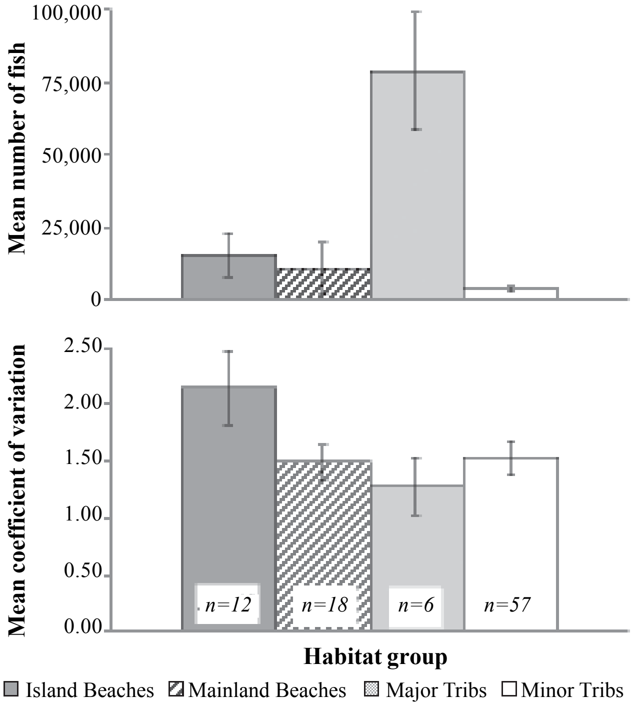

Figure 2. Mean number and mean coefficient of variation of observed spawning sockeye salmon by habitat group (1955–1999). Bars represent two standard errors.

the season, embryonic development is slower, and the risk of freezing is less because upwelling water is insulated by the ground and (at least at some sites) spawning occurs at greater depth (Demory et al. 1964; Olsen 1968; Mathisen 1966). The duration of spawning at mainland beach locations is protracted, extending for up to three months at some locations (Demory et al. 1964).

More than 60 sockeye salmon populations spawn in Kvichak River system tributaries, including large connecting rivers, glacially turbid rivers, and a variety of small spring-fed streams and ponds. Temperature regimes in small streams may be strongly influenced by air temperature, but spring-fed streams and ponds may remain at constant temperatures nearly year-round (Mathisen 1966; Quinn et al. 1999). Tributaries could be divided into functional groups based on presence of a headwater lake (Mathisen 1966), amount of available spawning habitat (Demory et al. 1964), or geographic region (Regnart 1996), but there appears to be a continuum of sites used by spawning sockeye salmon. We recognized two tributary groups (major and minor) for the purposes of this study based on observed spawning abundance. The major tributary group consisted of six populations, the Copper River, Gibralter River, Iliamna River, Lower Talarik Creek, Newhalen River, and Tazimina River. Each of these major tributaries averaged over 40,000 spawners per year, more than twice as many as any of the other 57 locations, referred to as minor tributaries (Figure 2) and most contain more spawning habitat. Sockeye salmon spawning in major tributaries account for up to 81% (mean=56%) of the total observed escapement. Minor tributaries represent the most numerous and geomorphically diverse group of spawning populations but account for a mean of only 20% of the total observed escapement.

All sockeye salmon populations in the Kvichak River system are managed collectively and commercially harvested in a single fishery district within Bristol Bay. Sockeye salmon from all populations in the system, and from the entire temporal range of spawning, pass through the fishery and by the counting tower at the outlet of Iliamna Lake, nearly simultaneously over a period of one to three weeks (Smith 1964; Mathisen 1966; Jensen and Mathisen 1987).

Data sources

Data used for this study were peak annual aerial survey counts of adult sockeye salmon for spawning sites in the Kvichak River system made from 1955 to 1999 (Regnart 1996). Aerial surveys are used to monitor more than one-third (33.9%) of the salmon populations in the United States (Knudsen 2000), and are widely used in Alaska and British Columbia (Cousens et al. 1982; Bue et al. 1998). Aerial surveys allow broad geographic coverage and provide access to remote and roadless areas. Aerial surveys are often constrained by weather, water clarity, and observer error that can limit the extent and accuracy of counts (Cousens et al. 1982). These factors result in incomplete or missing data for populations in some years. In general, aerial surveys are more accurate in shallow, clear streams and lakes than in glacial streams, sites with overhanging vegetation, or in very deep water areas (Cousens et al. 1982). Their red color and high densities make sockeye salmon relatively easy to accurately see and count from the air (Bevan 1961; Cousens et al. 1982).

Even under ideal conditions, peak spawning counts do not represent a total population census, but rather an index of abundance dependent on the residence time of individual fish, the total duration of spawning by the population and the efficiency of the observer (Bevan 1961; Cousens et al. 1982; Shardlow et al. 1987; Bue et al. 1998; Hilborn et al. 1999). Aerial surveys tend to underestimate the actual abundance (recorded by weir counts) of pink salmon (Bue et al. 1998). In addition, the variability between counts made by the same observer increases as abundance increases, and different observers may have different patterns of error (Bevan 1961; Bue et al. 1998).

Spawning ground counts of sockeye salmon in the Kvichak River system were standardized in the early 1960s so that annual comparisons could be made (Kerns and Donaldson 1968). From 1964 to 1987, the same FRI observer conducted nearly all of these aerial surveys (P. H. Poe, Bonneville Power Administration, Portland, Oregon, personal communication). In 1988, reduced funding decreased the number of replicate observations at each site (Regnart 1996; Cross et al. 1997; Fair 2000), making the individual survey timing more variable and survey coverage less complete. Although aerial surveys account for only a mean of 16.3% of the total number of spawners estimated by tower counts each year (Figure 3; Regnart 1996), these data provide long-term information on spawner abundance among different habitat types and for different spawning populations within the Kvichak River system.

Analyses methods

We selected 93 spawning sites for this analysis, each with a minimum of eight years of observation (mean = 27.4 years, standard deviation (SD) = 10.1). These sites included 12 island beach locations, 18 mainland beach locations, 6 major tributaries, and 57 minor tributaries. We did not filter individual observations for quality (e.g., adverse weather conditions, poor timing relative to spawning activity, or decreased visibility due to turbidity) because this type of qualitative classification was not available for all observations. We were also not able to estimate observer efficiency, due to a lack of site-specific weir counts for validation. These corrections, combined with accurate stream-life estimates would be expected to significantly improve the quality of these data (Bue et al. 1998). Therefore, substantial variability does exist in the accuracy of counts among sites and years. Ideally, inclusion in analysis and weighting of data points might be made based on a "quality" index assigned by the observer, but this was not possible for the current data set. We address some possible systematic effects of this source of variability in the discussion.

Prior to assessing covariation of observed abundance, we examined the diversity of observed spawning escapement in the Kvichak River system over time. A decline in the diversity of production across different populations would be expected as a consequence of mixed-population fisheries exploiting populations of differing productivities (Ricker 1958, 1973; Paulik et al. 1967; Hilborn 1985). We followed the methods of Walters and Cahoon (1985) to see if there were changes in the number of populations contributing to relative levels of observed escapement. We calculated 5-year mean escapements at each site over nine historical periods (1955–1959, 1960–1964, …, 1995–1999). This period length was selected to balance the ability to discern potential temporal trends with substantial interannual variability in abundance and survey coverage. The 5-year periods also allowed the large cyclic abundances over part of the time series to be distributed relatively evenly among the periods. Some researchers have opted to consider "peak" years separately in analyses of this type (e.g., Cross et al. 1997; Fair 2000) and the choice of period length may be important in interpreting our results. We ranked each site in each 5-year period based on mean escapement for that period. Within each period, we did not

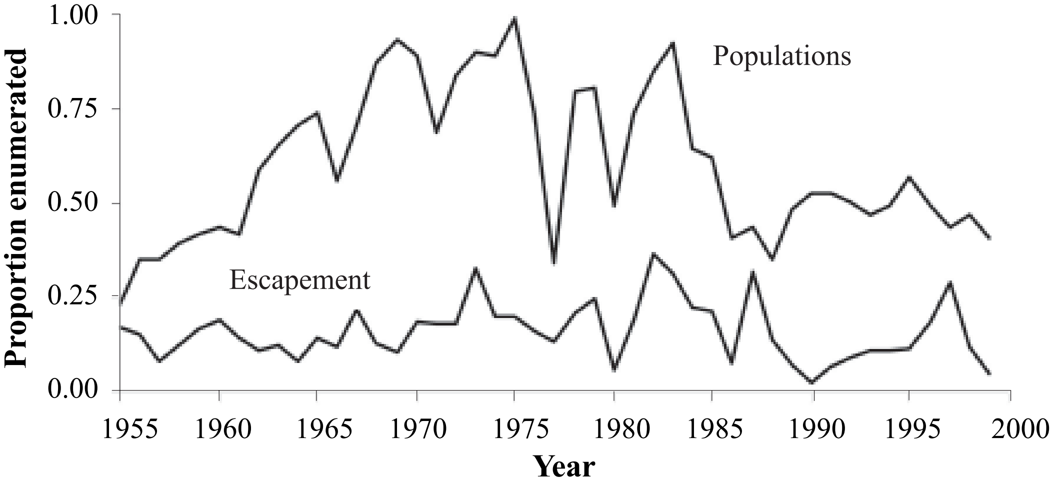

Figure 3. Proportion of spawning populations (*n*=93) and estimated total escapement enumerated in annual aerial surveys.

rank sites without at least one abundance observation to avoid confounding changes in abundance with changes in survey coverage. This was also a subjective choice, but was considered an improvement over the assumption that lack of survey data represented zero abundance for that period (Walters and Cahoon 1985). The absolute number of rankings therefore varied depending on the total number of sites enumerated in that period. We then calculated the cumulative observed escapement beginning with the first ranked site in each period. This method allows comparison of how many sites were required to achieve 70%, 80% or 90% of the total observed escapement, despite different rankings of individual sites among periods. If a decline in diversity were present, we expected the number of sites required to reach each specified level of cumulative escapement to decrease.

For spatial analysis, we used lake and river data maps included with ArcView GIS software, version 3.1 (ESRI 1998) and located spawning sites visually based on areas identified in Demory et al. (1964) and conversations with Mr. Poe (P. H. Poe, Bonneville Power Administration, Portland, Oregon, personal communication). Using ArcView GIS 3.2 (ESRI 1999), we calculated the shortest geographic distance over water between all 4,278 possible pairs of sites. These distances were generally much greater than straight-line calculations, especially between the Lake Iliamna and Lake Clark subbasins, and likely reflect the ecological separation between sites more accurately.

For all pairs of sites, a simple correlation coefficient (r) was calculated based on observed abundance in all years with data (no longer using the period means from above). Because they have been applied in other studies, we used a nonlinear weighted least squares method to fit two decay models to the observed distribution of correlation coefficients (Gunst 1995; Myers et al. 1997; Bradford 1999). In the exponential model,

$$p(d) = p_1 e^{-d/v},$$

and in the Gaussian model,

$$p(d) = p_2 e^{-(1/2)(d/\sigma)^2},$$

where $p(d)$ = the predicted correlation; p_1, p_2 = the expected correlations at a distance of zero; v = the distance at which the correlation has decayed to e^{-1} (0.37) of the initial value; and σ = one-half the distance at which the correlation has decayed to e^{-1}. To incorporate variable sample sizes, analysis of pairwise data was weighted by the number of years of data in common for each pair. Those pairs with less than five years in common ($n = 58$) were excluded from the analysis.

To capture information from all years with survey data for each population, not just those that overlapped in time with other populations, we compared all observations over the entire record for each site, and converted these to relative abundances scaled from zero to one. We then calculated a measure of similarity between each pair of sites based on Gower's coefficient (Legendre and Legendre 1998),

$$S_{ij} = \frac{1}{n}\sum_{y=1}^{n} 1 - \left[\frac{\left|x_{iy} - x_{jy}\right|}{R_y}\right],$$

where S_{ij} = similarity coefficient between sites i, j; x_{iy} = relative abundance at site x_i in year y; n = number of years in which abundance was observed at both sites x_i and x_j; and R_y = maximum difference in relative abundance observed between any two sites in year y. In this manner, the relative abundances used to assess similarity between pairs of sites reflected observations in all years from each site through relative scaling. By using a relative metric, results are more easily interpreted and less influenced by major fluctuations in absolute abundance over time. We felt that this approach would produce results with a clearer interpretation than correlation coefficients that could be influenced by the contrast in abundance between sites over the specific years in which observations between pairs overlapped (e.g., low contrast would result in low r-values). For pairwise similarity values, we again fit both the exponential and Gaussian models, as well as a simple linear model. Although this is a common approach, fitting of parameters in this manner may be biased by non-independence of pairwise data.

To compare the distribution of similarity values we observed with an expected distribution in the absence of any covariation among sites we first had to generate a set of "no relationship" similarity coefficients. We drew a uniform random number between zero and one to represent the x_{iy} at each of two simulated sites for each of 10 years (a conservative choice, as the mean number of years in common in our data set was 18.2). We selected an R_y randomly, with replacement, from the observed values in the actual data set for each of the 10 years to be simulated. We calculated the similarity coefficient based on the x_{iy} values and the maximum of the selected R_y or the R_y of the simulated x_{iy} values. We repeated this process 10,000 times. We then calculated the interval containing 95% of these simulated values and used this to evaluate the distribution of observed values.

We performed a Mantel test (Mantel 1967), modified to a simple linear regression approach (Smouse et al. 1986), to determine if the similarity index declined with increasing geographic distance between population pairs. We randomly permuted the similarity coefficients with respect to observed distances 10,000 times and for each permutation we calculated the coefficient of determination (r^2), thus creating a sample of the distribution of possible values given our specific data; *P*-values were calculated as the frequency of statistics more extreme than our observed value. This randomization approach, sampling from a finite population without replacement by reordering the observations with respect to one or more categories or covariates (Legendre and Legendre 1998), is often used for data collected in a pair-wise manner, especially genetic distances (e.g., Excoffier et al. 1992; Wright et al. 2000), and makes no assumption of normality of error or independence between observed data points (Smouse et al. 1986; Legendre and Legendre 1998). This method thus represents an inferential approach with appropriate significance levels.

To test for significant differences in similarity between pairs of populations in the Iliamna Lake and Lake Clark subbasins, and among the habitats within them, we first computed residuals from the regression of similarity on distance. Ten types of pairwise comparisons were examined with respect to habitat: island beach pairs (only in Iliamna Lake), major tributary pairs, mainland beach pairs, minor tributary pairs, island beach × major tributary pairs, island beach × mainland beach pairs, island beach × minor tributary pairs, major tributary pairs × mainland beach, major tributary × minor tributary pairs, and mainland beach × minor tributary pairs. Mean residuals were then calculated for each comparison. Working with residuals from partial relationships has been identified as the most accurate approximation for significance estimation of basic permutation strategies (Anderson 2001). The distributions of all possible mean residual values for each comparison were sampled through 10,000 permutations of observed residuals with respect to habitat type. Observed values were then compared to these distributions. Estimated *P*-values were corrected for simultaneous tests through a sequential Bonferroni correction (Rice 1989); a global alpha of 0.05 was used within each comparison.

A cluster analysis was used as an exploratory measure of the strength of similarities within and between habitat groups and to determine if any patterns were present in the populations that did not cluster with the appropriate habitat group. The cluster analysis was performed using the software *Neighbor* (Felsenstein 1993). The data were the observed similarity values, and clusters were formed using the unweighted pair group method with arithmetic mean (UPGMA) as the clustering algorithm.

RESULTS

We observed a gradual increase in the number of populations surveyed through the 1960s and early 1970s until nearly complete survey coverage (92 of 93 populations included in this analysis) was obtained in 1974 (Figure 3). Subsequently the number of spawning sites

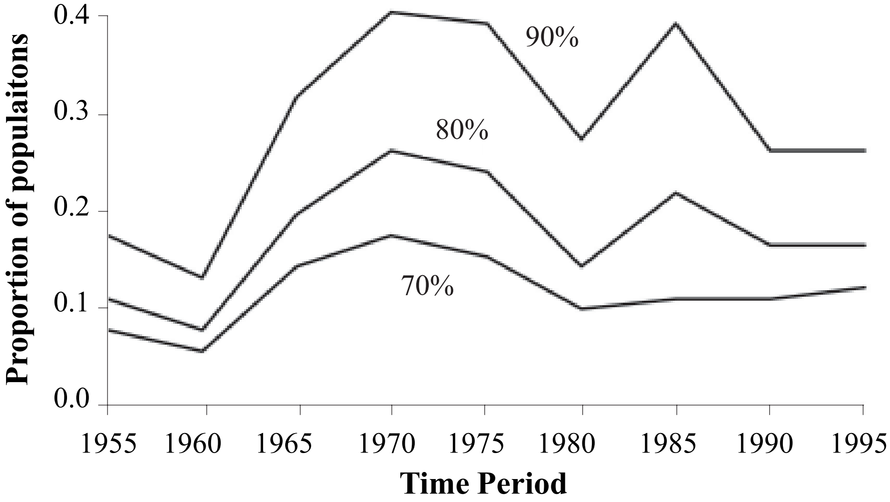

Figure 4. Proportion of the 93 spawning populations accounting for 70%, 80% and 90% of the observed escapement in nine 5-year periods, beginning 1955, 1960, …, 1995.

surveyed in each year declined, (Figure 3) with approximately 50% coverage over the most recent 15 years. Fewer than 40% of the 93 spawning sites accounted for 90% of the observed escapement in all periods (Figure 4). The proportion of sites accounting for 70%, 80% and 90% of the observed escapement was variable, but did not show a strong temporal trend.

Correlations between pairs of sites were highly positive, exceeding the expected random distribution of correlation values within smaller data sets (Bradford 1999; Myers et al. 1997). When we fit decay functions to raw correlations, neither the exponential (p_1=0.492, v = 209, sum of squares = 5608.03) nor Gaussian (p_2= 0.438, σ = 123, sum of squares = 5608.03) models showed evidence of rapid decay or a clear threshold of decay (Figure 5). Estimated distances to decay of 0.37 of expected values at zero distance (exponential [v] = 209 km, Gaussian [2 • σ] = 246 km) did not occur within the range of observed data.

Calculated similarity coefficients between all pairs with at least five years in common averaged 0.76, reflecting strong covariation in relative abundance of all stocks over time. Only 466 (11%) of the observed similarities fell within the interval (0.31–0.66) that con-

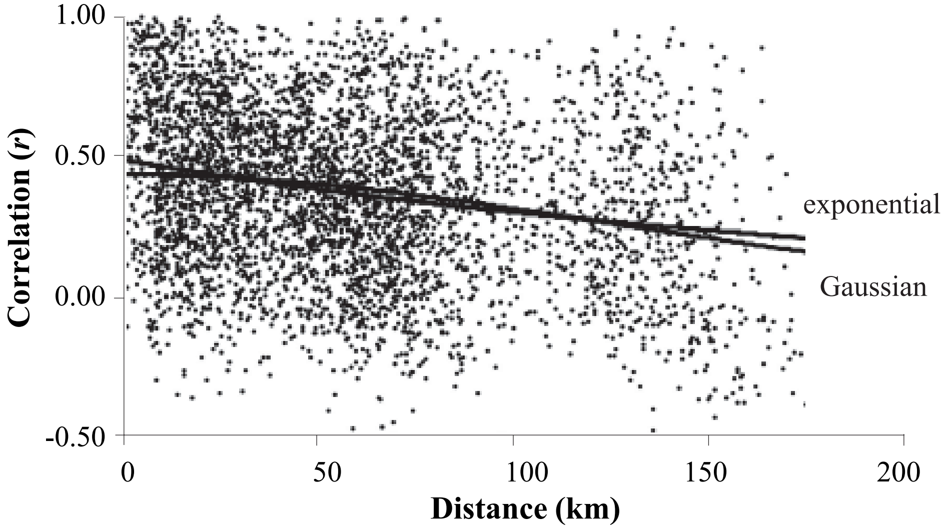

Figure 5. Fit of exponential and Gaussian decay models to observed pairwise correlation coefficients between spawning sites (n = 4,220).

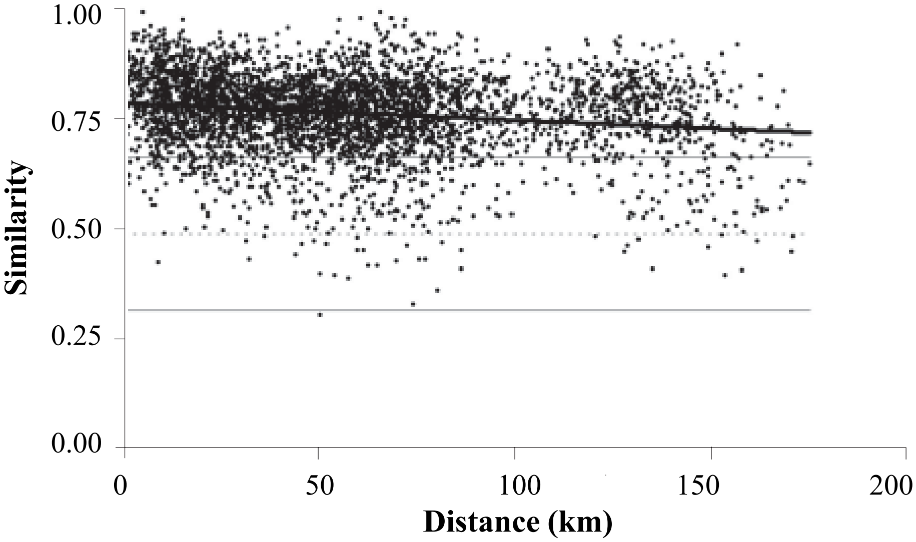

Figure 6. Linear Mantel regression of pairwise similarity and distance (r^2= 0.0296, P < 0.01, based on 10,000 random permutations of the observed distances between pairs). Horizontal lines indicate upper and lower 95% intervals for expected similarities based on a simulation of sites with random abundances, dashed line represents the mean.

Table 1. Fit of the exponential, Gaussian, and linear models to pairwise similarity coefficients.

Model	Intercept (p_1, p_2, b_0)	Decay at x km ($x = v$, 2ó)	Slope (b_1)	Sum of Squares
Exponential	0.787	2,479		460.54
Gaussian	0.778	920		463.17
Linear	0.787		-0.0003	460.59

tained 95% of simulated values for random abundance (Figure 6). Fitting exponential and Gaussian models to the similarity coefficients observed between sites showed even smaller levels of decay with distance (Figure 6) and both fits were similar to that of a simple linear model (Table 1). A significant (P<0.01) linear decline in similarity with increasing distance was found, but explained only 2.96% of observed variability of similarity coefficients.

There were no significant ($P > 0.05$) differences between pooled similarity residuals either within or between Iliamna Lake and Lake Clark (Table 2). However, when compared across the entire watershed, two habitat-specific types of population pairs showed residual values (from the regression of similarity on distance) significantly different ($P < 0.05$) to those of random permutations (Table 2). Island beaches had an average similarity residual of 0.1156, reflecting a significantly higher ($P < 0.05$) similarity than expected. Thus, abundance among island beach populations was more similar than among other types of habitat pairs. Minor tributaries had an average residual of –0.0058, reflecting a small but significant ($P < 0.05$) negative pattern of similarity relative to other types of pairs. Average similarity residuals for the other eight types of pairs did not differ significantly from expected values. When separated by lake subbasin, average similarity residual for island beach pairs was unchanged (not present in Lake Clark), but the significant value for the minor tributaries was found to be present in the between subbasin pairings (Table 2). Additionally, a significant negative average residual was observed for pairs between mainland beaches and minor tributaries within the Iliamna Lake subbasin.

Cluster analysis supported the results from residual analysis. The algorithm produced no clear patterns for major or minor tributaries, or mainland beaches, but all island beaches were clustered very tightly. The smallest cluster that contained all 12 island beach populations included only 4 other populations, one mainland beach and 3 minor tributaries (Figure 7); there were thirty-eight clusters at that resolution. Two of these 4 other populations, Chekok beaches and Pedro Creek and ponds, were located in the eastern end

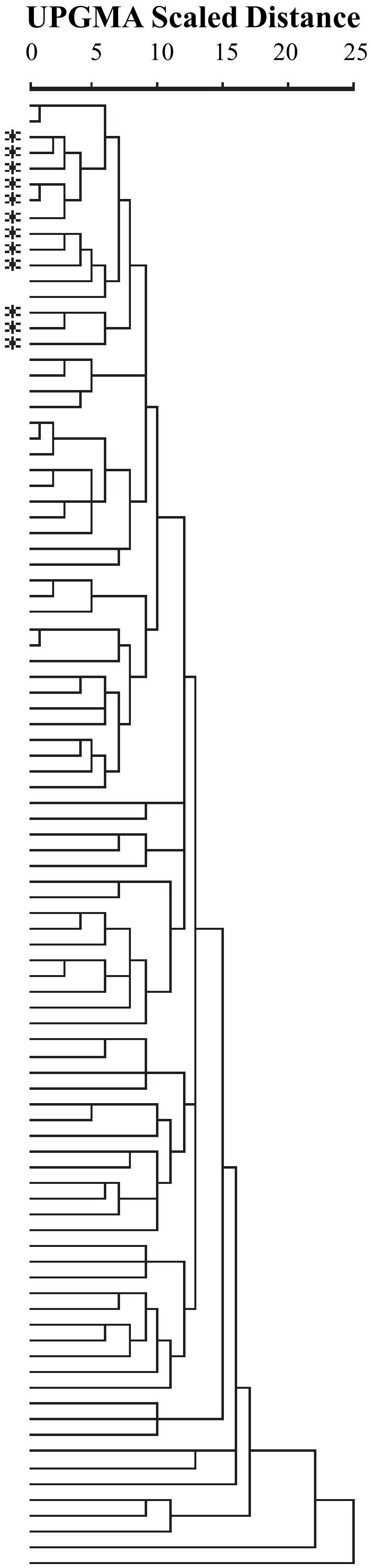

Figure 7: Clustering of the 93 study sites by similarity in abundance, 1955–1999. Stars indicate island beach spawning sites.

of Iliamna Lake near the major island beach spawning populations.

DISCUSSION

Aerial survey effort within the Kvichak River system has decreased markedly since a peak in the early 1970s, but the number of sites accounting for most of the observed sockeye salmon spawners has shown no clear temporal trend. This result differs from observations of declining diversity among other salmon species in British Columbia (Walters and Cahoon 1985). It is possible that diversity within the Kvichak River system has been lost among less productive populations that were not regularly enumerated, as expected

Table 2: Observed, lower, and upper critical (95%) mean residual values from the Mantel regression of similarity and geographic distance. Asterisks (*) indicate significant ($P < 0.05$) values based on 10,000 random permutations of residuals with a sequential Bonferroni correction for multiple tests within each set of comparisons.

Comparison	Observed Similarity	Lower Bound	Upper Bound
Within Iliamna Lake and Lake Clark	-0.0014	-0.0018	0.0018
Between Iliamna Lake and Lake Clark	0.0029	-0.0033	0.0033
All pairwise comparisons:			
Island beaches	0.1156*	-0.0279	0.0261
Major tributaries	0.0173	-0.0383	0.0358
Mainland beaches	0.0058	-0.0117	0.0115
Minor tributaries	-0.0058*	-0.0044	0.0044
Island beaches-Major tributaries	-0.0092	-0.0168	0.0168
Island beaches-Mainland beaches	0.0134	-0.0140	0.0142
Island beaches-Minor tributaries	0.0037	-0.0050	0.0051
Major tributaries-Mainland beaches	0.0036	-0.0137	0.0134
Major tributaries-Minor tributaries	0.0040	-0.0076	0.0074
Mainland beaches-Minor tributaries	-0.0059	-0.0060	0.0059
Iliamna Lake only:			
Island beaches	0.1156*	-0.0282	0.0248
Major tributaries	0.0254	-0.0880	0.0703
Mainland beaches	-0.0003	-0.0196	0.0179
Minor tributaries	-0.0026	-0.0054	0.0047
Island beaches-Major tributaries	-0.0222	-0.0309	0.0283
Island beaches-Mainland beaches	0.0144	-0.0174	0.0161
Island beaches-Minor tributaries	-0.0002	-0.0057	0.0051
Major tributaries-Mainland beaches	0.0019	-0.0264	0.0231
Major tributaries-Minor tributaries	-0.0058	-0.0144	0.0133
Mainland beaches-Minor tributaries	-0.0102*	-0.0083	0.0076
Lake Clark only:			
Major tributaries	0.0993	-0.2309	0.1283
Mainland beaches	-0.0078	-0.0652	0.0218
Minor tributaries	-0.0415	-0.0422	0.0014
Major tributaries-Mainland beaches	0.0358	-0.0868	0.0404
Major tributaries-Minor tributaries	0.0150	-0.0603	0.0172
Mainland beaches-Minor tributaries	-0.0280	-0.0389	-0.0021
Between Iliamna Lake and Lake Clark:			
Major tributaries	0.0009	-0.0521	0.0531
Mainland beaches	0.0149	-0.0237	0.0285
Minor tributaries	-0.0084*	-0.0051	0.0109
Island beaches-Major tributaries	0.0159	-0.0425	0.0433
Island beaches-Mainland beaches	0.0109	-0.0238	0.0282
Island beaches-Minor tributaries	0.0202	-0.0171	0.0215
Major tributaries-Mainland beaches	-0.0014	-0.0255	0.0294
Major tributaries-Minor tributaries	0.0156	-0.0158	0.0205
Mainland beaches-Minor tributaries	0.0040	-0.0050	0.0106

by exploitation theory (Ricker 1958, 1973; Paulik et al. 1967; Hilborn 1985), or that declines due to exploitation occurred prior to 1955, the first year within this data set. Decreases in aerial survey coverage have been achieved by eliminating observations of many of the smaller populations and maintaining observations of the larger ones. While this may initially appear to be a better use of limited funds, index populations often use better than average spawning habitat (Bocking et al. 1988), and declines in smaller populations could occur undetected when only the more productive populations are monitored. However, we found no evidence for erosion of stock structure during the period of years we examined.

Strong covariation in abundance occurred between all populations within the system; both observed correlation and similarity coefficients were well above those expected to occur by chance. We conclude that this covariation is likely related to effects of both the fishery and broad environmental patterns experienced by populations throughout the drainage system. Because sockeye salmon from different populations within a watershed generally share a longer period of common environmental conditions during their freshwater rearing phase than other Pacific salmon species, it is not surprising that we found higher correlations than those reported from studies on coho salmon (Bradford 1999).

We did find a decrease among pairwise correlations and similarity coefficients with increasing geographic distance between spawning populations within the Kvichak River system. While this relationship described only a small fraction of the observed variability, it does suggest a weak environmental gradient affecting spawning, incubation, or early juvenile survival in all habitats. We did not see evidence for a threshold in this relationship within the Kvichak River system despite relatively large geographic distances between populations. We think that reported thresholds of 20–50 km in other studies (Myers et al. 1997; Bradford 1999) are likely to be artifacts from comparisons across watersheds for all but the closest populations.

Habitat-specific patterns of similarity in abundance were much more pronounced than distance effects. The high degree of covariation in abundance among island beach spawning populations was most likely due to shared environmental influences on recruitment and mortality, geographical proximity, as well as common factors affecting the surveys. Since most island beach sockeye salmon spawn in relatively shallow water (Quinn et al. 1996) well mixed by wind-driven currents, all these populations would experience similar effects from lake level changes, and ice conditions. Island beaches are also most likely to have high similarity in survey-related variability. As spawning occurs over a short period, poor visibility and minor changes in survey date, possibly causing observers to miss the peak of spawning, are likely to affect abundance estimates for all populations. Determining whether peak spawning was missed is difficult for island beach sites where carcasses sink quickly into deep water where they cannot be observed from the air (Cross et al. 1997; Fair 2000).

In contrast to island beaches, both environmental and survey factors are likely to reduce observed similarity of sockeye salmon abundance among minor tributaries. Spawning sites grouped within this category are much less homogeneous than island beaches, and differences are likely more pronounced between the Iliamna Lake and Lake Clark minor tributaries. Different local environmental forces, such as rainstorms, melt from snow-pack and density-dependent bear predation on small populations (Quinn and Kinnison 1999; T. P. Quinn, unpublished data) tend to increase variability of spawning and incubating conditions among these sites within a given year, and degrade correlations and similarities in abundance. Minor tributaries may also be more difficult to survey in a uniform manner due to habitat heterogeneity. The combination of low abundance and variable spawning timing could make it difficult to get a representative count for some populations, and vegetation can block a large proportion of the view on some small streams. Poor visibility is also likely to be unequally distributed across minor tributary sites (Rogers 1984). This pattern of heterogeneous effects across populations is also likely to introduce variability between habitat groups. However, we did not find these differences to be significant. We do not have an explanation for the lower than expected similarity in abundance found in comparisons between the minor tributaries and mainland beaches within Iliamna Lake.

We did not find lower than expected similarity in abundance for major tributary spawning sites. These sites are similar to minor tributaries since their spawning habitat is heterogeneous and subject to greater diversity of environmental influences than island and mainland beaches. However, major tributary spawning sites show much higher levels of average salmon abundance than other groups. This may reflect a higher degree of stability in factors influencing recruitment, or could be the result of limited diversity in a less numerous group. Aerial surveys of major tributaries may be more consistent from year to year than those for minor tributaries because timing of the annual counts is more carefully targeted at these abundant populations so that they more frequently correspond to peak spawning. There may also be a lesser problem with overhanging vegetation obscuring visibility on larger streams and rivers, but deep water and corresponding poor visibility may introduce another source of survey variability.

Although they did not show a higher than expected similarity in abundance, mainland beaches should share some of the same lake effects as island beach sites. However, unlike island beaches, the spawning gravel of mainland beaches is oxygenated with upwelling water captured by local topography which allows sockeye salmon to spawn at greater depths (Demory et al. 1964) and avoid potential egg mortality from winter ice scouring. Also, unlike wind-driven currents at island beach sites, upwelling water is derived from heterogeneous landforms and could be affected differently by environmental variability at each location. Spawning at greater depths may cause more variability in the accuracy of the aerial surveys between locations.

We found patterns of sockeye salmon abundance that appear to reflect shared environmental influences on recruitment and mortality during the early life history phase. Identifying such patterns should both help us understand the factors influencing observed abundance and interpret historical patterns of productivity. Most Pacific salmon are harvested in mixed-population fisheries, with populations having different productivity and optimal harvest rates (Ricker 1958, 1973; Paulik et al. 1967; Hilborn 1985). Understanding population-specific productivity requires accurate escapement estimation specific to each population (Starr and Hilborn 1988), and estimates of abundance over multiple years. A better understanding of the degree to which spawning sites show covariation in abundance, as well as of patterns present within a single river system, could assist researchers in locating suitable control sites for experiments and may allow for more accurate interpolation of missing historical data.

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