Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean

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ABSTRACT

We examined spatial correlations for three coastal variables [upwelling index, sea surface temperature (SST), and sea surface salinity (SSS)] that might affect juvenile salmon (*Oncorhynchus* spp.) during their early marine life. Observed correlation patterns in environmental variables were compared with those in survival rates of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon stocks to help identify appropriate variables to include in models of salmon productivity. Both the upwelling index and coastal SST were characterized by strong positive correlations at short distances, which declined slowly with distance in the winter months, but much more rapidly in the summer. The SSS had much weaker and more variable correlations at all distances throughout the year. The distance at which stations were no longer correlated (spatial decorrelation scale) was largest for the upwelling index (> 1000 km), intermediate for SST (400–800 km in summer), and shortest for SSS (< 400 km). Survival rate indices of salmon showed moderate positive correlations among adjacent stocks that decreased to zero at larger distances. Spatial decorrelation scales ranged from approximately 500 km for sockeye salmon to approximately 1000 km for chum salmon. We conclude that variability in the coastal marine environment during summer, as well as variability in salmon survival rates, are dominated by regional scale variability of several hundred to 1000 km. The correlation scale for SST in the summer most closely matched the observed correlation scales for survival rates of salmon, suggesting that regional-scale variations in coastal SST can help explain the observed regional-scale covariation in survival rates among salmon stocks.

Key words: Decorrelation scale, Pacific salmon, sea surface salinity, sea surface temperature, spatial correlation, survival rate, upwelling

INTRODUCTION

Recent studies of fish populations have shown synchrony among populations across various spatial scales for certain biological variables. For instance, survival rates of sockeye salmon (*Oncorhynchus nerka*) show positive covariation among different populations within regions, but not between regions (Adkison *et al.*, 1996; Peterman *et al.*, 1998). In contrast, adult body size of those same populations covaries not only within regions, but also over much of the north-east Pacific (Pyper *et al.*, 1999). Myers *et al.* (1997) concluded that interannual variations in recruitment of marine fish stocks in the North Atlantic and North Pacific are correlated at scales of approximately 500 km. Such spatial correlations in biological variables may be related to spatial synchrony in abiotic factors (including climatic indices) or in biotic factors related to predation or food supply (Bjornstad *et al.*, 1999; Koenig, 1999). However, few studies have thoroughly analysed spatial correlation patterns in environmental factors that are the implied causes of spatial covariation among populations (Koenig, 1999). In this paper, we investigate spatial correlations for upwelling indices, sea surface temperature (SST), and sea surface salinity (SSS) along the west

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coast of North America and compare them with spatial correlations among survival-rate indices of salmon stocks.

Many authors have investigated relationships between environmental and fish population variables by seeking correlations using time series, without regard to spatial correlation patterns in the variables of interest. This approach increases the probability of finding spurious correlations, because researchers often (1) use many environmental variables that may be correlated among themselves at various spatial scales, (2) use environmental or fish population variables averaged over a variety of temporal or spatial scales, or (3) examine various time lags. To reduce the chance of finding spurious correlations, it is important to carefully select appropriate spatial and temporal scales for such studies prior to analysis. If different populations respond similarly to environmental forcing, environmental variables can only explain changes in fish population variables if their correlation scales are similar to those in fish populations. Furthermore, similarity in correlation scales can lend strong support to observed correlations between environmental and population variables for individual fish stocks.

Previous analyses of coastal environmental variables such as wind stress, upwelling, temperature and salinity have focused primarily on the temporal domain and have revealed interannual, decadal and multidecadal oscillations in North Pacific climate (Roden, 1989; Ware, 1995; Ware and Thomson, 2000). Variations at different temporal scales have been linked to variability in the abundance, recruitment and productivity of marine fish populations (Francis *et al.*, 1998; McGowan *et al.*, 1998). While numerous studies have described spatial patterns of variability in the ocean on a basin-wide scale (for example Hanawa, 1995; Trenberth and Hurrell, 1995; Mantua *et al.*, 1997), few studies have examined spatial patterns in coastal marine climate variables along the west coast of North America. In particular, spatial scales of correlations and seasonal differences in these scales have not been described for coastal variables.

Other analyses have found that variability in salmon catches, aggregated over large spatial scales, is associated with large-scale variability in the environment (Beamish and Bouillon, 1993; Hare and Francis, 1995; Mantua *et al.*, 1997; Downton and Miller, 1998). However, recent analyses of Pacific salmon (*Oncorhynchus* spp.) stocks have found that survival rates of salmon populations exhibit positive covariation across local or regional spatial scales on the order of several hundred kilometres, but little or no covariation at larger scales (Myers *et al.*, 1997; Blackbourn, 1998; Coronado and Hilborn, 1998; Peterman *et al.*, 1998; Botsford and Paulsen, 2000; Pyper *et al.*, 2001, in press). While these latter studies did not explicitly test relationships between environmental variables and salmon survival rates, their results imply that environmental processes that affect survival rates must also show positive covariation at similar local or regional spatial scales.

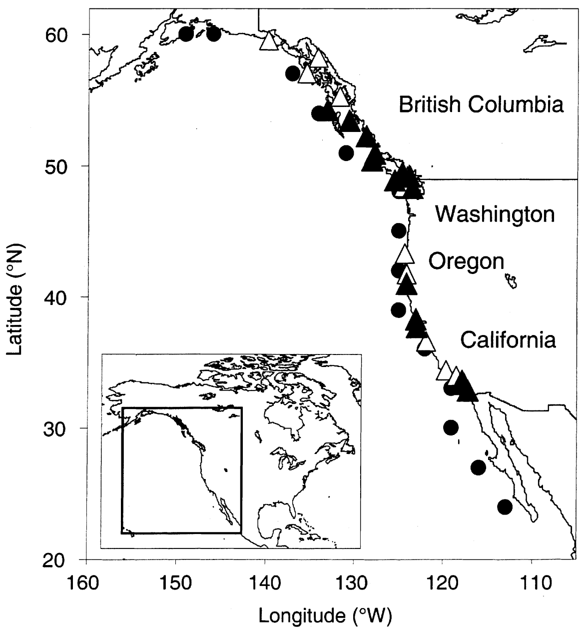
Therefore, the main goal of this study was to quantify and compare spatial scales of correlation in coastal marine environmental variables and in salmon survival rates. Our goal was to describe general patterns of correlation with distance rather than identify specific regions that show high within-region correlation. Results will help identify appropriate environmental variables to include in models of salmon productivity, and the spatial scales over which such environmental variables should be averaged. This approach should reduce the chance of finding spurious correlations and increase the power to detect true underlying relationships. We first examine spatial correlations for three environmental variables (an index of upwelling, coastal SST, and coastal SSS) that might affect juvenile salmon during their early marine life or other marine species inhabiting nearshore areas (within approximately 100 km from shore). Nearshore conditions are particularly relevant to the early marine life stages of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*), the species included in our analysis. Empirical evidence suggests that most of the variability in survival rates of these species occurs in the first few months (April–September, earlier in this period for southern stocks than for northern stocks) after fry and smolts enter the ocean (Peterman, 1987). Secondly, we compare the observed correlation patterns and scales of correlation in the environment with those in the survival rates of pink, chum and sockeye salmon stocks from the north-east Pacific.

METHODS

Data

We examined spatial patterns of covariation in upwelling indices, SST and SSS using four data sets. Monthly upwelling indices from 1946 to 1998 were obtained for 14 locations between 24°N and 60°N along the west coast of North America (Fig. 1) from the Pacific Fisheries Environmental Group, National Marine Fisheries Service, Pacific Grove, California (Bakun, 1990) (URL: http://www.pfeg.noaa.gov/index.html). Monthly SST and SSS records spanning different periods were obtained for 22 (SST) and 15

Figure 1. Map of upwelling stations (circles), sea surface temperature stations (all triangles), and sea surface salinity stations (filled triangles).



(SSS) coastal stations between California and Alaska (Fig. 1, Table 1). The geographical range of coastal SST and SSS stations (Fig. 1) only partially overlapped with that of the salmon stocks in our analysis (Fig. 2), because of the limited number of coastal records for Alaska. In order to describe spatial correlation patterns adequately and obtain reasonable confidence intervals for spatial correlation scales, we needed at least 10–15 stations for each variable. Therefore, we included stations from California and Oregon, although these were located south of the southernmost stocks in our analysis. We assumed that patterns of correlation identified across all stations are representative of spatial correlation patterns in the region for which we have salmon data, an assumption that we examine below. To increase the overlap between environmental data and salmon data, we obtained additional monthly SST records from 1951 to 1997 for selected coastal locations (Fig. 3) from the Comprehensive Ocean–Atmosphere Data Set (COADS) (Woodruff et al., 1998). Unfortunately, no long-term SSS records are available for stations along the coast of Alaska. The COADS SST data had numerous missing values, particularly for winter months.

To examine spatial patterns of covariation among salmon populations, we used spawner and recruit data for 120 wild stocks of sockeye (37 stocks), pink (43), and chum (40) salmon. The stocks ranged geographically from Puget Sound, Washington, to Norton Sound, Alaska, a range of over 3000 km (Fig. 2). Spawner and recruit data were available for brood years between 1948 and 1996. Individual time series ranged in length from 15 to 47 years with an average of 31 years. For each stock we fit a Beverton–Holt model to log(recruits-per-spawner) as a function of spawner abundance (Quinn II and Deriso, 1999). Residuals from the Beverton–Holt fits were used as indices of survival rate (SR indices). For a detailed description of data sources, see Peterman *et al.* (1998) and Pyper *et al.* (2001, in press). We added eight sockeye salmon stocks to the 29 stocks in Peterman *et al.* (1998). These were Lake Washington (brood years 1967–93; Jeff Haymes, Washington Department of Fish and Wildlife, Montesano, Washington, personal communication), Long Lake in British Columbia (BC) (1973–94; Chris Wood, Canadian Department of Fisheries and Oceans, Nanaimo, BC, personal communication), and six stocks from the Kodiak Island and Chignik regions of Alaska (Patti Nelson, Alaska Department of Fish and Game, Kodiak, Alaska, personal communication): Upper Station early run (1969–93), Upper Station late run (1970–93), Fraser Lake (1965–93), Ayakulik (1965–93), Chignik Lake (1948–93), and Black Lake (1948–93). To test the sensitivity of our results to the form of the stock–recruitment relationship, we repeated the analysis with residuals from fits of a Ricker model (Ricker, 1975).

Statistical analysis

Coastal SST, COADS SST and SSS data had approximately normal distributions, whereas the upwelling index had an extremely heavy-tailed distribution with numerous outliers. We therefore used, where possible, robust statistical methods for the analysis of upwelling indices. Indices of survival rates were generally close to normally distributed with a few large outliers. To examine the influence of outliers, we repeated the analysis of SR indices after removing outliers.

Spatial correlations

To describe spatial correlation patterns in the environmental data and in the SR indices, we computed pairwise correlations between sites (environmental monitoring stations or ocean-entry points of stocks) and modelled the relationship between correlations and great-circle distances. The environmental data consist of monthly time series measured at many stations and were analysed for each month separately. That is, correlations were computed based on series of,

Table 1. Name and location of coastal stations and length of data record for sea surface temperature and sea surface salinity data. 'Missing periods' indicate a series of months with no data after as many individual missing values as possible were estimated based on linear interpolation or regression on data for a given month at nearby locations.

			Sea surface temperature			Sea surface salinity		
Location	Latitude	Longitude	Start	End	Missing periods	Start	End	Missing periods
Yakutat, AK*	59.55	139.8	10/1940	12/1998				
Juneau, AK*	58.25	134.1	5/1936	12/1998	9/1940–9/1941			
Sitka, AK*	57.05	135.4	5/1943	12/1996				
Ketchikan, AK*	55.33	131.7	12/1921	12/1996				
Langara Pt., BC†	54.25	133.1	10/1936	12/1998	9/1937–2/1940	3/1940	12/1998	
Bonilla I., BC†	53.50	130.6	4/1960	12/1998	1/1960–3/1960	4/1960	12/1998	
McInnes I., BC†	52.27	128.7	1/1955	12/1998		1/1955	12/1998	
Pine I., BC†	50.97	127.7	1/1937	12/1998		1/1937	12/1998	
Kains I., BC†	50.45	128.0	1/1935	12/1998		1/1935	12/1998	
Chrome I., BC†	49.47	124.7	4/1961	12/1998	1/1962–3/1962	4/1961	12/1998	1/1962–3/1962
Entrance I., BC†	49.22	123.8	5/1936	12/1998		5/1936	12/1998	
Amphitrite Pt., BC†	48.92	125.5	8/1934	12/1998	3/1939–6/1939	8/1934	12/1998	3/1939–6/1939
Neah Bay, WA‡	48.37	124.6	1/1955	12/1994				
Race Rocks, BC‡	48.30	123.5	2/1921	12/1998	7/1940–4/1941	10/1936	12/1998	7/1940–4/1941
Charleston, OR‡	43.35	124.3	5/1966	7/1997				
Crescent City, CA‡	41.75	124.2	1/1955	12/1994	4/1964–7/1964 6/1975–8/1976			
Trinidad Beach, CA‡	41.06	124.2				1/1975	12/1994	1/1976–4/1977
Bodega, CA‡	38.32	123.1	1/1957	12/1997	10/1957–2/1958	1/1975	12/1994	
Farallon I., CA‡	37.70	123.0				1/1957	12/1994	
Pacific Grove, CA‡	36.62	121.9	1/1919	5/1999	1/1940–12/1940 5/1975–6/1977			
Santa Barbara, CA‡	34.40	119.7	1/1955	10/1999	7/1959–12/1959			
Santa Monica, CA‡	34.01	118.5	1/1955	12/1997	1/1983–7/1983 1/1995–12/1996			
Balboa, CA‡	33.60	117.9	11/1924	10/1999		11/1924	12/1994	
San Clemente, CA‡	33.42	117.6				7/1965	12/1994	
La Jolla, CA‡	32.87	117.3	8/1916	9/1999		8/1916	12/1996	

*Data for four Alaska (AK) stations were obtained from US Geological Survey Open File reports (URL: http://geology.usgs.gov/open-file). The SST data for the period after 1977 (Ketchikan), 1978 (Juneau), and 1982 (Sitka, Yakutat) were reconstructed using linear regressions of SST on air temperature for the period of overlap (28–33 years, R^2 between 0.214 and 0.790). Air temperature records for the four locations were obtained from the Western Regional Climate Center, Reno, Nevada (URL: http://www.wrcc.sage.dri.edu).

†Data obtained from lighthouse data compiled by the Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia (BC) (URL: http://www.pac.dfo-mpo.gc.ca/).

‡Data obtained from the Physical Oceanography Research Division and Marine Life Research Group of the Scripps Institution of Oceanography, La Jolla, California (CA) (URL: http://nemo.ucsd.edu). Missing values in monthly SST series were reconstructed using either linear interpolation or regressions on SSTs at nearby coastal stations for the same month where possible.

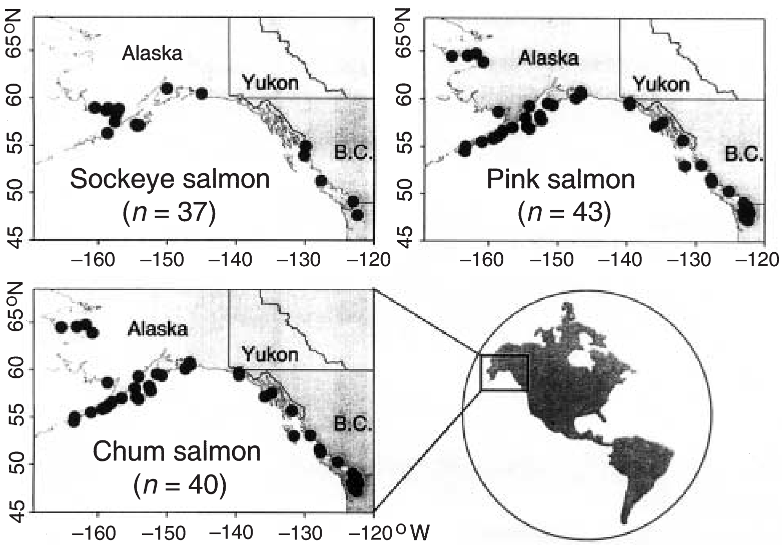
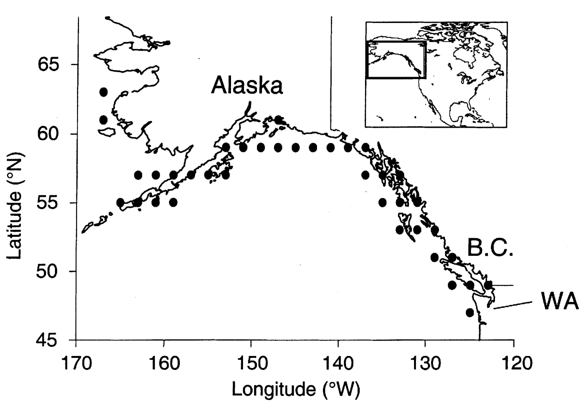


Figure 2. Approximate ocean entry points of all stocks of sockeye, pink and chum salmon included in analysis of spatial correlation patterns (n number of stocks).

for example, January SST anomalies from 1955 to 1999 at each station. In contrast, SR indices consist of annual values for each stock. Time-series correlations between each pair of stations (or stocks) i and j were computed as lag-0 cross-correlation coefficients (r_{ij}) and were plotted against the corresponding pairwise distances between sites (great-circle distances d_{ij}). Pearson's product–moment correlations were used for SST, SSS and salmon SR indices. Spearman rank correlations, which are less sensitive to extreme values, were used for upwelling indices. For the environmental data, we computed cross-correlations using either (1) years for which data were available for all stations (deletion of all years with any missing values), or (2) years for which data were available for both stations in a pairwise correlation (pairwise deletion of missing values). Results were similar in both cases and we therefore present only cross-correlation patterns by distance based on those years for which data were available for all stations. For the salmon SR indices, we only computed correlations based on pairwise deletion of missing values because there were few years with data for all stocks. However, pairwise correlations were only computed for series that had 15 or more years in common.

Figure 3. Map of COADS grid points used in the analysis of sea surface temperatures. Each point represents the centre of a 2° × 2° cell.



To estimate the relationship between correlation and geographical distance, we fit non-parametric covariance functions to plots of time-series correlation (r_{ij}) by distance (d_{ij}) following Bjornstad and Falck (2000). Point-wise bootstrap confidence intervals for the estimated functions were computed using a bootstrap procedure with 2000 bootstrap replicates (Bjornstad and Falck, 2000). Other functional forms for the decline in correlations with distance were examined (linear, exponential and spherical models), but did not adequately describe spatial correlation in one or more of the data sets. When comparing spatial correlation patterns across different variables it is important to fit the same model and use the same summary statistics for each variable. The estimation of any covariance function assumes that covariance is a function of relative distance only and does not vary in space or over time (Cressie, 1993). To check this assumption, we fit non-parametric covariance functions to subsets of the data. Spatially, we split all data sets roughly in half to examine correlation patterns in southern and northern subregions, where possible. Splits occurred at different locations because of differences in geographical coverage of the data sets and to ensure that a reasonable number of stations were included in each subregion. Upwelling indices were analysed separately for 24–42°N and 45–60°N. The SST and SSS for coastal stations were analysed separately for the regions south and north of 48°N. The COADS SST and SR indices were analysed separately for a southern region including Washington, BC and SE Alaska, and for a northern region including central and western Alaska. Differences in spatial correlation patterns over time could not be analysed because of the limited length of many series.

We quantified the spatial scale of correlation for each variable using two univariate measures of spatial correlation. First, as a convenient, although arbitrary, reference point, we estimated the distance at which average lag-0 cross-correlation declined to 50% of its maximum value at zero distance (50% correlation scale). For the environmental variables, estimates were computed separately for each month to examine seasonal differences in spatial correlation scales. We also computed a second measure of spatial correlation (decorrelation scale) that removes large-scale monthly or annual means from each data set. Correlations between time series result from a combination of both spatial and temporal correlations in the data and tend to overestimate spatial correlations when autocorrelation and time trends are present in the individual data series (Gunst, 1995). We therefore estimated decorrelation scales based on Moran's I, a commonly used measure of spatial autocorrelation that is not confounded by temporal trends in the data (Cliff and Ord, 1981). Moran's I was computed for each year of data for which data were available for all stations or stocks and was then averaged across these years. We then fit a smooth non-parametric function to scatterplots of Moran's I by distance. The decorrelation scale was estimated as the distance at which Moran's I declined to its expected value in the absence of spatial autocorrelation (Cliff and Ord, 1981).

To estimate decorrelation scales for COADS SST and SR indices of salmon, we had to exclude some data series from the analysis. Specifically, in order to retain a minimum of 10 years of complete data for computing Moran's I, we excluded 17 pink and six chum salmon stocks (out of 43 and 40 total stocks, respectively), as well as the two northernmost COADS grid cells in the Bering Sea (Fig. 3). We could only estimate Moran's I and decorrelation scales for COADS SST from May through October because of numerous missing values in other months.

RESULTS

Spatial correlation patterns in environmental variables

Anomalies in the upwelling index from 1946 to 1999 were strongly correlated over large distances and correlations primarily remained positive up to at least 3000 km, except in summer (Fig. 4a). Spatial correlations were higher at a given distance and decayed more slowly with increasing distance in winter (for example January) than in summer (for example July; Fig. 4a). In July, upwelling at stations separated by more than about 1500 km was uncorrelated. The estimated 50% correlation scale for upwelling was significantly lower in the summer months and ranged from 746 km in June to 1749 km in February (Fig. 5a).

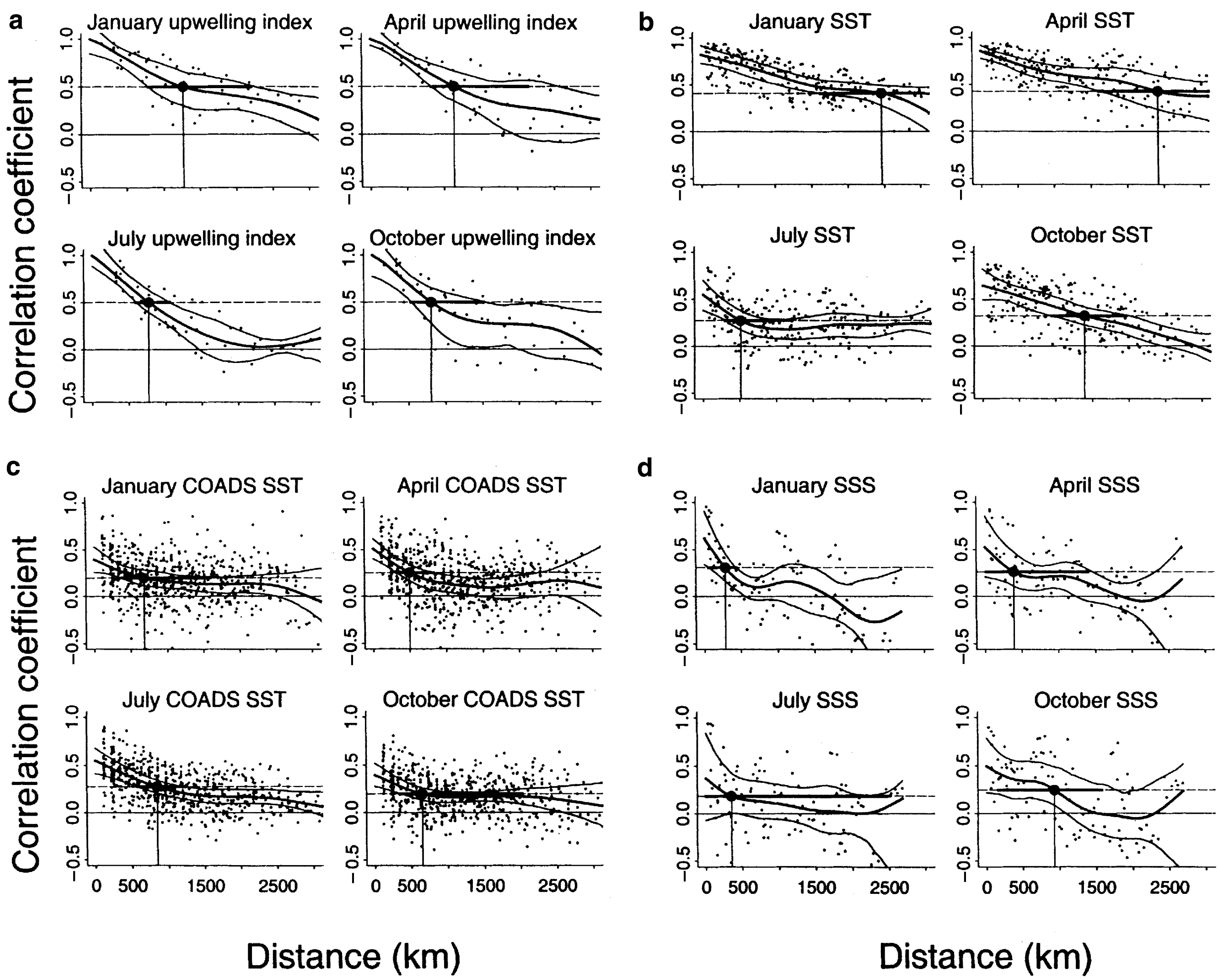
The SST anomalies (1966–94) at coastal stations were highly correlated over the entire range of stations during the winter, but not in the summer (Fig. 4b). The 50% correlation scale for time series of SST varied between 500 and 600 km from July through September, but was considerably larger during the rest of the year (Fig. 5a). In contrast, correlations among COADS SST series were generally lower and more variable than correlations among coastal SST series. Furthermore, COADS SSTs did not show a pronounced difference in the 50% correlation scale between summer and winter (Figs 4c and 5a).

Correlations among SSS series (1975–94) were generally weak and highly variable. The declining trend in correlation with increasing distance was not pronounced in the summer months (Fig. 4d) and correlations between many station pairs were negative, even at short distances. Estimates of the 50% correlation scale indicate that, as with the upwelling index and coastal SST, the correlation scale tends to be shortest in the summer (Fig. 5a). However, estimates were highly variable and confidence intervals included zero in all months. The estimated 50% correlation scale for SSS was consistently much shorter than for the upwelling index and SST (Fig. 5a).

Spatial decorrelation scales, which remove effects of common time trends, showed similar differences among variables and seasons (Fig. 5b). The upwelling index had the largest decorrelation scale, SST had intermediate values, and SSS had the smallest decorrelation scale (Fig. 5b). Confidence intervals for the decorrelation scales of SSS (not shown) included zero in all months, suggesting that SSS did not show significant spatial autocorrelation at any distance.

The covariance functions and scales of correlation for SST (coastal stations) and SSS may differ between

Figure 4. Lag-0 cross-correlations between stations for time series of (a) Bakun's upwelling index, (b) coastal sea surface temperature, SST, (c) COADS sea surface temperature and (d) sea surface salinity, SSS, for 4 months. Each point corresponds to the correlation coefficient between one pair of stations, plotted at the great-circle distance separating the stations. Smooth lines are fitted non-parametric covariance functions with approximate 95% bootstrap confidence intervals. Dashed horizontal lines indicate correlation corresponding to 50% of the correlation at zero distance. Large dots and vertical lines indicate the estimated correlation scale with a 95% confidence interval indicated by the heavy horizontal line.

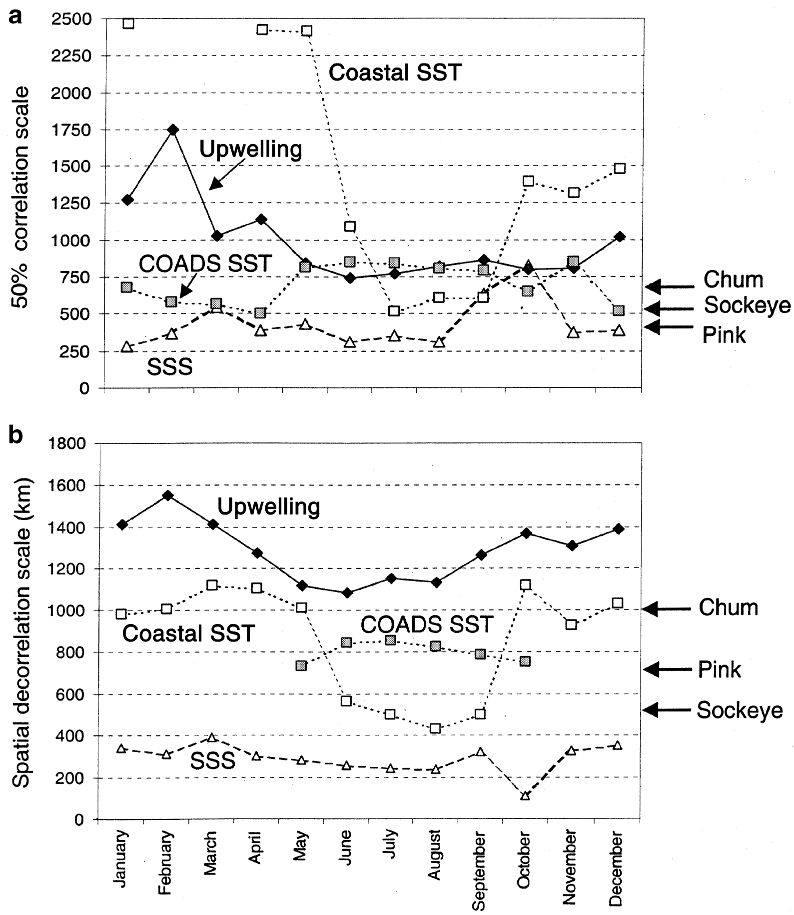


northern and southern parts of the study region (Fig. 6). Coastal SST typically had higher correlations at a given distance and a larger 50% correlation scale north of 48°N, but confidence intervals in any given month generally overlapped. In contrast, the estimated covariance function for SSS reflected considerably higher correlations south of 48°N and spatial correlations in the summer tended to increase in this subregion. The northern region for SSS included stations in BC only, which generally showed weak correlations declining to zero over very short distances. The estimated correlation scales for the upwelling index and COADS SST did not show obvious differences between regions (not shown).

Spatial correlation patterns in survival-rate indices of salmon

Average correlations in the SR indices of sockeye, pink and chum salmon were relatively high at short distances and declined rapidly with increasing distance, suggesting that positive covariation in survival rates of salmon is largely confined to relatively small, regional scales (Fig. 7). The estimated 50% correlation scales were 532 km (95% confidence interval: 199–1223 km) for sockeye salmon, 399 km (298–525 km) for pink salmon, and 662 km (344–1067 km) for chum salmon (Fig. 5a). Neither sockeye nor pink salmon showed evidence of significant correlations

Figure 5. (a) Estimated 50% spatial correlation scales (distance at which a fitted covariance function decreases to 50% of its estimated value at zero distance) for upwelling index, SST and SSS by month and (b) estimated spatial decorrelation scale (see text) by month. Arrows indicate the estimated 50% correlation scales and decorrelation scales for spawner-to-recruit survival rate indices of sockeye, pink and chum salmon.

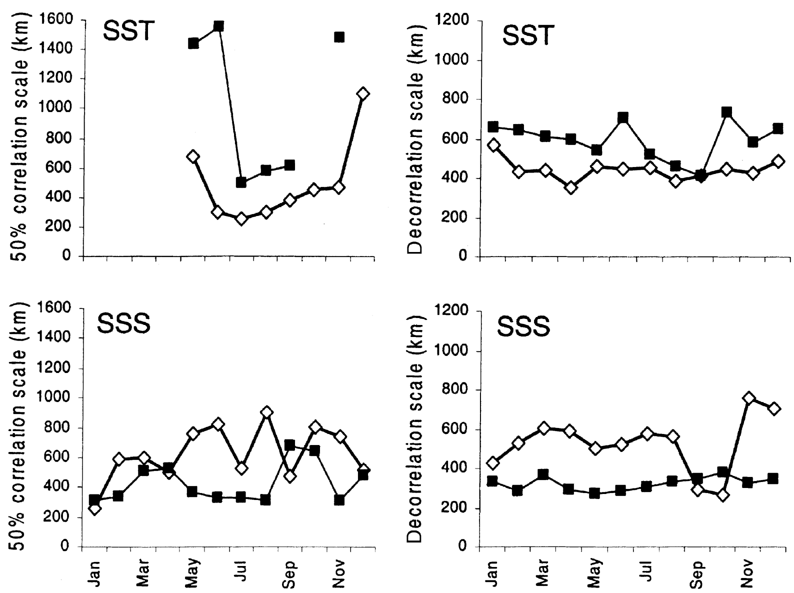


beyond approximately 800 km, as indicated by the estimated bootstrap confidence bands (Fig. 7). In contrast, chum salmon showed some evidence of significant but weak correlations up to approximately 2500 km. Estimated spatial decorrelation scales suggest that SR indices within a given year (after removing large-scale year-to-year variations) were uncorrelated at distances above 523 km for sockeye salmon, 736 km for pink salmon and 1017 km for chum salmon (Fig. 5b). For all three species, spatial correlation scales for southern stocks (from Washington to south-east Alaska) were similar to those for northern stocks.

The observed correlation patterns for salmon were insensitive to the form of the stock–recruit relationship and to outliers. When residuals from the Ricker model were used as indices of survival rate (instead of Beverton–Holt residuals), the observed decline in correlations with increasing distance was very similar. The 50% correlation scale and the decorrelation scale changed by less than 20 km for all species. Similarly, removing outliers (more than 2.5 standard deviations from the mean) did not change the estimated correlation patterns appreciably. The largest change occurred in the 50% correlation scale for chum salmon, which increased from 662 to 707 km.

The observed 50% correlation scales and spatial decorrelation scales for salmon were most similar to those for SST in the summer (Fig. 5). Both measures of spatial correlation were smaller throughout most of the year for SSS than for salmon survival rates, while correlation scales for the upwelling index, particularly in winter, were generally larger. However, chum salmon had a decorrelation scale that was only slightly smaller than that for upwelling in the summer. The 50% correlation scale (Fig. 5a) is confounded by time

Figure 6. Estimated 50% correlation scales (left) and decorrelation scales (right) for coastal sea surface temperature and sea surface salinity by month, estimated separately for southern (open diamonds) and northern (filled squares) subregions. The southern region includes stations from 33 to 48°N. Missing points could not be estimated based on the data.



trends in the data series, which strongly influence the correlations. For example, the large scale of correlation for coastal SST in the winter is a result of widespread increases in winter SST after the mid-1970s, which was not clearly evident in the COADS SST data. The spatial decorrelation scale, which removes common trends in time series from different sites, more clearly separates the environmental variables (Fig. 5b) and shows the similarity in decorrelation scales of COADS SST, coastal SST and salmon survival rates.

DISCUSSION

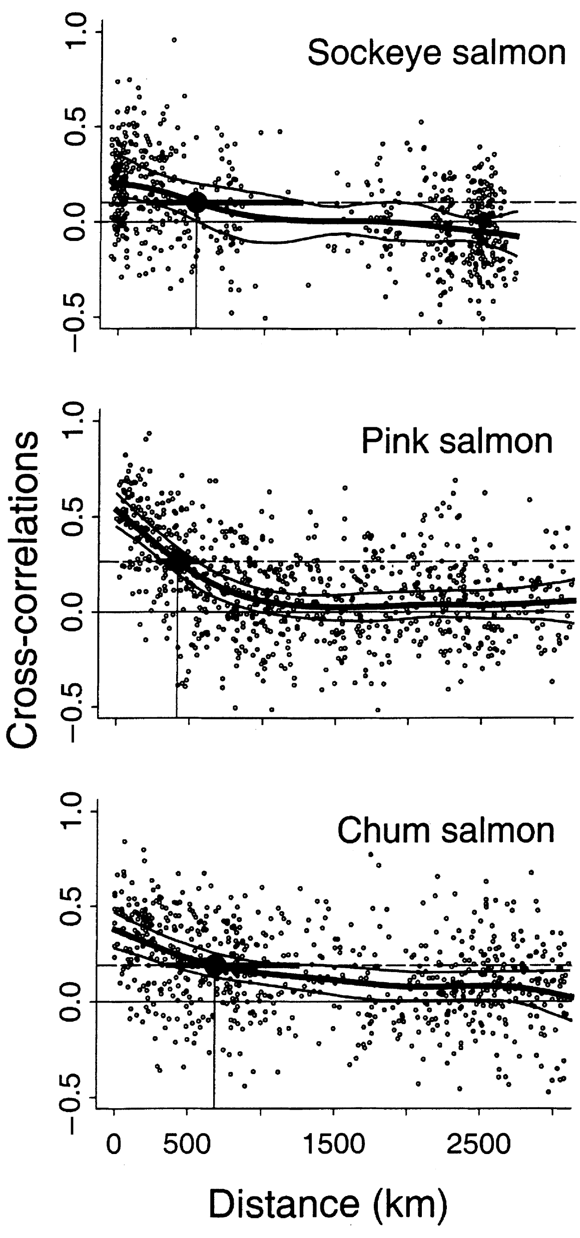
Our findings suggest important similarities between spatial correlation scales in salmon survival rates and certain coastal marine environmental variables. In general, survival rates of salmon stocks along the coasts of BC and Alaska are positively correlated over relatively short, regional scales (on the order of several hundred kilometres). In contrast, there is little or no evidence for either positive or negative correlations at distances over 1000 km (Peterman *et al.*, 1998; Pyper *et al.*, 2001, in press). Similarly, at least during the summer when salmon are present in coastal waters and their mortality rates are high, coastal environmental variables appear to be strongly correlated at distances less than 1000 km, with much weaker or no correlation at larger distances. Among the three variables examined (upwelling index, SST, SSS), correlation scales for SST in the summer most closely matched the observed correlation scales for survival rates of salmon. This suggests that regional-scale variations in SST along the coast are related to the processes causing the observed regional-scale covariation in survival rates among salmon stocks. By separately analysing spatial correlations in environmental variables and in salmon survival rates, we have provided independent evidence for including regional-scale measures of SST variability in correlative studies and in models of survival rates or recruitment of Pacific salmon.

While we observed intriguing similarities in the correlation scales of some coastal environmental variables and survival rates of salmon, there were important differences among different environmental variables and among seasons. These differences are discussed in more detail below, followed by a discussion of their implications for salmon.

Spatial correlation patterns in environmental variables

Correlation patterns for the upwelling index, SST and SSS were characterized by high positive correlations at short spatial scales and decreasing correlations with distance. We expected high correlations at short distances because each of the variables reflects spatially continuous processes. If measurement errors are

Figure 7. Lag-0 cross-correlations between survival-rate indices of sockeye, pink and chum salmon as a function of distance. Each point corresponds to the correlation coefficient between two stocks, plotted at the great-circle distance separating their ocean-entry points. Smooth lines are fitted non-parametric covariance functions with approximate 95% bootstrap confidence intervals. Dashed horizontal lines indicate correlation corresponding to 50% of the correlation at zero distance. Large dots and vertical lines show the estimated 50% correlation scale with a 95% confidence interval indicated by the heavy horizontal line.



negligible, cross-correlations should increase to 1 as the distance between locations decreases to 0. However, extrapolating the estimated covariance functions for SST and SSS resulted in estimated correlations at zero distance that are much smaller than 1, particularly in the summer (Fig. 4). This suggests a strong discontinuity in SST and SSS at small spatial scales, that is, at a scale smaller than the smallest distance between stations in our data set ('nugget effect', see Cressie, 1993). A likely explanation for this effect is the presence of frontal structures associated with eddies, river plumes and tidal currents in the nearshore environment, which lead to large changes in coastal SST or SSS over short distances. The strong nugget effect for COADS SST is unlikely to result from such frontal structures because of the large scale over which the data are averaged (2° latitude by 2° longitude). In this case, the nugget effect most likely results from measurement errors in the data. In contrast, the upwelling index shows no apparent nugget effect (Fig. 4a).

The nugget effect has implications for how point measurements of these variables can be used in predictive models. Unless a fish population of interest is confined to a small area in close proximity to where the environmental variable is measured, the latter's explanatory power for a fish response variable will always be limited by the nugget effect. This may be particularly relevant for relating juvenile salmon survival to coastal SST and SSS because the nugget effect is largest during the summer months when juvenile salmon enter coastal waters. For example, the nugget effect for salinity in July reduces cross-correlations at short distances (< 100 km) to approximately 0.37 (Fig. 4d). Thus, the correlation between SSS and a biological variable that reflects conditions over a spatial scale exceeding the scale of the nugget effect could not be expected to exceed 0.37, and may be considered spurious if it does. Therefore, the use of a point measurement in correlative studies should be avoided if there is a large nugget effect because of a high chance of finding spurious relationships.

The three variables differed in the magnitude of correlations at a given distance and in their correlation scales. Generally, the upwelling index had the highest correlations and largest spatial scales of correlation, SST had intermediate values, and SSS had the smallest correlations and correlation scales throughout the year (Figs 4 and 5). However, the upwelling indices reflect average alongshore wind stress conditions over large areas that extend a considerable distance offshore. Nearshore upwelling likely has a shorter correlation scale because of local orographic and stratification effects. Furthermore, spatial correlation scales for the upwelling index are to some extent biased by the smoothing inherent in calculating the index (Halliwell and Allen, 1987).

We observed much shorter correlation scales during the summer months for upwelling and coastal SST. Seasonal differences in correlation scale in part reflect differences in atmospheric circulation patterns between summer and winter. For example, the Aleutian Low displays strong seasonality in storm intensity and frequency, which in turn causes strong seasonality in coastal wind forcing (Wilson and Overland, 1986). During the winter, intense, large-scale weather systems result in high spatial correlations in coastal upwelling anomalies. Weaker and spatially variable winds in the summer cause smaller spatial correlations and shorter correlation scales for upwelling in the summer. Indirectly, wind conditions also contribute to the pronounced decreases in spatial correlations of SST in the summer. A shallower mixed layer and reduced stratification in the summer are conducive to the formation of local patchiness, which reduces correlations.

We compared our estimates of correlation scales for three environmental variables with previously published spatial correlation scales in the atmosphere and in the ocean. Halliwell and Allen (1987) found that cross-correlation coefficients for 6-hourly winds along the west coast declined to less than 0.35 at 600–800 km in the summers of 1981 and 1982, and at 600–1200 km in the winter of 1981. These estimates suggest smaller correlation scales than we found for the upwelling index, which may result from different time scales used in the analysis (6-hourly vs. monthly averages), or from differences between 1981–82 and the longer period (1946–99) examined in our study. Roden (1989) found that coastal air temperatures are 'highly' to 'moderately' coherent over distances of 1200 km and 'marginally' coherent beyond 1500 km. Cross-correlations of annual air temperature anomalies from 1920 to 1980 over North America have a 50% correlation scale of approximately 1000 km (Gunst, 1995), which is similar to our estimate of the 50% correlation scale for SST when averaged over all months (not shown). This suggests that on an annual scale, temperatures in the atmosphere and coastal ocean have similar scales of correlation.

The magnitude and scale of correlations are determined by the processes driving each of the variables. Upwelling is driven by large-scale atmospheric weather systems with diameters of 1200–1500 km (Roden, 1989). This agrees with the observed scales over which upwelling indices (reflecting alongshore wind stress) are positively autocorrelated (decorrelation scale in Fig. 5b). The SST along the west coast of North America is driven by heat fluxes between the atmosphere and ocean, direct solar irradiation, coastal Kelvin waves associated with El Nino/Southern Oscillation events, upwelling and wind-driven currents. All of these factors contribute to the relatively large spatial coherence in coastal SST patterns along the coast during most of the year. In contrast to SST, SSS varies on a more local scale and is strongly affected by precipitation, freshwater run-off and upwelling. Local variations in these three factors may be sufficient to explain the shorter spatial correlation scale for salinity. Precipitation patterns in the atmosphere vary at spatial scales on the order of 1000 km (Cayan *et al.*, 1998). However, most freshwater is supplied as point sources to the coastal ocean by rivers, creating small-scale variability in run-off patterns along the coast, particularly along topographically complex coastlines like the coasts of BC and southeast Alaska.

Estimated correlation scales for SST in the winter differed considerably between the COADS data and coastal SST data. Several characteristics of the two data sets contribute to this difference. First, the COADS data cover the region from Washington to western Alaska, whereas we only had coastal SSTs for stations from California through SE Alaska. Strong common trends in the winter SST at these coastal stations contribute to the large 50% correlation scale for coastal SSTs in winter. In contrast, the COADS series for most of Alaska show less evidence of common trends and therefore had a much shorter 50% correlation scale. Secondly, the paucity of COADS data in the winter months resulted in relatively low and extremely variable correlations at short distances (a large nugget effect) and unreliable estimates of correlation scales. Thirdly, differences in spatial correlations between the two measures of SST is expected because COADS data averages opportunistic measurements over large grid cells (which in some cases encompass waters as far as 250 km offshore), while the coastal stations reflect nearshore conditions and local, small-scale influences. Therefore the two different measures of SST reflect different influences but are both relevant to juvenile salmon, which most likely occupy locations very close to shore initially, but quickly disperse across and along the shelf. Importantly, the 50% correlation scales and decorrelation scales for both measures of SST are intermediate between those of upwelling and SSS and are most similar to the corresponding scales for salmon SR indices.

Differences in correlation scales of SSS between the southern and northern subregions may primarily result from the inclusion of several inshore stations between Vancouver Island and the mainland of BC in our analysis. When these inside stations were excluded, the estimated 50% correlation scales and decorrelation scales were similar to those estimated for California stations alone. This suggests that SSS has a 50% correlation scale along the outer coast on the order of 600–800 km, which is similar to that of SST in the summer. In contrast, the inside stations were essentially uncorrelated, suggesting a correlation scale shorter than the shortest pairwise distance. However, as a result of the small number of inside stations, reliable estimates of the correlation scale for SSS in BC could not be obtained. Because of a lack of long SSS records for Alaska, where most of the salmon stocks in our analysis are located, correlation scales for coastal SSS in Alaska cannot be evaluated at present.

Spatial correlation patterns in survival-rate indices of salmon

Spatial correlation patterns for survival rates of salmon were characterized by moderate correlations at short distances that decline rapidly with increasing distance (Fig. 7), similar to that of environmental variables in the summer. The large observed nugget effect (Fig. 7) results from errors in the estimated numbers of spawners and recruits (and hence survival rates), as well as true differences in survival rates of adjacent stocks (for example, caused by differences in freshwater survival). However, it is unclear which of these factors is more important. The observed decline in correlations with distance suggests that survival rates are primarily determined by processes acting over relatively short spatial scales, that is, less than approximately 500–1000 km, rather than by basin-wide processes as is often implied by studies relating recruitment or catch of salmon to large-scale climate variables.

Thus, we suggest that relevant environmental factors should be averaged over regional scales similar to the observed correlation scales in survival rates when examining relationships between salmon productivity and the environment. This recommendation contrasts with much of the recent literature on relationships between salmon and the environment, which has focused on large, basin-wide scales by using aggregate catch data and large-scale indicators of environmental variability (Beamish and Bouillon, 1993; Hare and Francis, 1995; Mantua *et al.*, 1997; Francis *et al.*, 1998; Noakes *et al.*, 1998; Beamish *et al.*, 1999). While the above studies have revealed coherence in the temporal trends of environmental indicators and large-scale salmon abundances, they do not address spatial variability in these trends and can mask important regional differences, such as the differences in catch trends between northern and southern regions shown in Hare *et al.* (1999).

Regional-scale variability in the coastal marine environment can help explain observed regional-scale covariation among survival rates of Pacific salmon. Although spatial correlations in the environment are a likely cause of spatial correlations in biological variables (Koenig, 1999), such causal links are difficult to establish. Nevertheless, in seeking to forecast or explain fish population variables (for example, salmon survival rates), researchers should focus on environmental variables that have correlation scales corresponding to those of the biological variables. An environmental variable can only explain covariation in salmon survival rates to the extent that its correlation scale is similar to that of salmon survival rates. Our results suggest that time series of coastal environmental variables, in particular SST, exhibit patterns of spatial correlation that are similar to those observed in salmon survival rates. Summer SST, and possibly summer upwelling, during the period when juveniles are present in coastal waters could therefore potentially be associated with the observed covariation in salmon survival rates, whereas the spatial correlation scale of SSS in BC in the summer may be too small. The small correlation scale of SSS implies that effects of salinity on populations will be at a more local scale and will only contribute to variability in salmon stocks that is not shared across stocks.

Differences in the observed patterns of spatial correlation among species (Fig. 7) may be the result of their different life histories. Short correlation scales in the survival rates of pink and sockeye salmon imply that survival rates are primarily determined during the freshwater or early ocean stages when fry, smolts and juveniles from geographically separated stocks have distinct distributions, as opposed to the later life stages where these species have overlapping distributions (Groot and Margolis, 1991). For chum salmon, larger correlation scales and positive covariation at most spatial scales suggest that environmental conditions in the open ocean contribute to variability in their survival rates. Unlike pink salmon, which spend only about 1.5 years in the ocean, chum salmon spend 2–6 years in the ocean, where survival rates of all stocks are similarly affected by large-scale environmental conditions, hence leading to positive covariation over larger spatial scales. Sockeye salmon also spend several years in the marine environment but did not show evidence of synchrony at large spatial scales (Fig. 7). Unlike the other species, sockeye salmon spend 2 or 3 years in freshwater before migrating to the ocean. Their longer residence time in freshwater reduces the relative contribution of ocean residence to overall survival rates, hence limiting covariation to smaller spatial scales.

In conclusion, the relatively confined spatial scales of correlation for both SST in the coastal environment and survival rates of salmon suggest that future studies of salmon recruitment or survival should focus on regional environmental variability rather than large-scale climate indicators. In particular, regional averages of summer SST may be useful predictors in models of survival rates or recruitment of Pacific salmon. We are currently using these results to guide development of models that link environmental variables to salmon survival rates.

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REFERENCES

Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M. and Korman, J. (1996) Alternative models of climatic effects of Sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. *Fish. Oceanogr.* **5:**137–152.

Bakun, A. (1990) Global climate change and intensification of coastal ocean upwelling. *Science* **247:**198–201.

Beamish, R. and Bouillon, D. (1993) Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* **50:**1002–1016.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V. and Kurashov, V. (1999) The regime shift concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **56:**516–526.

Bjornstad, O.N. and Falck, W. (2000) Nonparametric spatial covariance functions: estimation and testing. *EES* **8**:53–70.

Bjornstad, O.N., Ims, R.A. and Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.* **14:**427–432.

Blackbourn, D.J. (1998) The coherence scale of marine survival rates in North American pink, chum and coho salmon. *Proceedings of the 18th Northeast Pacific Pink and Chum Salmon Workshop*. Nanaimo, BC: Canadian Department of Fisheries and Oceans, pp. 143–168.

Botsford, L.W. and Paulsen, C.M. (2000) Assessing covariability among populations in the presence of intraseries correlation: Columbia River spring–summer chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **57:**616–627.

Cayan, D.R., Dettinger, M.D., Diaz, H.F. and Graham, N.E. (1998) Decadal variability of precipitation over western North America. *J. Clim.* **11:**3148–3166.

Cliff, A.D. and Ord, J.K. (1981) *Spatial Processes: Models and Applications*. London: Pion, 266 pp.

Coronado, C. and Hilborn, R. (1998) Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* **55:**2067–2077.

Cressie, N.A.C. (1993) *Statistics for Spatial Data*. New York: John Wiley & Sons, 900 pp.

Downton, M.W. and Miller, K.A. (1998) Relationships between Alaska salmon catch and North Pacific climate on interannual and interdecadal time scales. *Can. J. Fish. Aquat. Sci.* **55:**2255–2265.

Francis, R.C., Hare, S.R., Hollowed, A.B. and Wooster, W.S. (1998) Effect of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* **7:**1–21.

Groot, C. and Margolis, L. (eds) (1991) *Pacific Salmon Life Histories*. Vancouver, BC: University of British Columbia Press, 564 pp.

Gunst, R.F. (1995) Estimating spatial correlations from spatial–temporal meteorological data. *J. Clim.* **8:**2454–2470.

Halliwell, G.R. and Allen, J.S. (1987) The large-scale coastal wind field along the west coast of North America, 1981–1982. *J. Geophys. Res.* **92:**1861–1884.

Hanawa, K. (1995) Long-term variations in SST fields of the North Pacific Ocean. In: *Climate Change and Northern Fish Populations*. R.J. Beamish (ed.). Canadian Special Publications of Fisheries and Aquatic Sciences 121. Ottawa: National Research Council of Canada, pp. 25–36.

Hare, S.R. and Francis, R.C. (1995) Climate change and salmon production in the Northeast Pacific Ocean. In: *Climate Change and Northern Fish Populations*. R.J. Beamish (ed.). Canadian Special Publications of Fisheries and Aquatic Sciences 121. Ottawa: National Research Council of Canada, pp. 357–372.

Hare, S., Mantua, N. and Francis, R. (1999) Inverse production regimes: Alaska and West coast Pacific salmon. *Fisheries* **24:**6–14.

Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends Ecol. Evol.* **14:**22–26.

Mantua, N., Hare, S., Zhang, Y., Wallace, J. and Francis, R. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteor. Soc.* **78:**1069–1080.

McGowan, J.A., Cayan, D.R. and Dorman, L.M. (1998) Climate–ocean variability and ecosystem response in the Northeast Pacific. *Science* **281:**210–217.

Myers, R.A., Mertz, G. and Bridson, J. (1997) Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Can. J. Fish. Aquat. Sci.* **54:**1400–1407.

Noakes, D.J., Beamish, R.J., Klyashtorin, L. and McFarlane, G.A. (1998) On the coherence of salmon abundance trends and environmental factors. *N. Pac. Anadr. Fish Comm. Bull.* **1:**454–463.

Peterman, R.M. (1987) Review of the components of recruitment of Pacific salmon. *Am. Fish Soc. Symp* **1:**417–429.

Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D. and Walters, C.J. (1998) Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **55:**2503–2517.

Pyper, B.J., Peterman, R.M., Lapointe, M.F. and Walters, C.J. (1999) Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*On-*

corhynchus nerka) stocks. *Can. J. Fish. Aquat. Sci.* **56:**1046–1057.

Pyper, B.J., Mueter, F.J., Peterman, R.M., Blackbourn, D.J. and Wood, C. (2001) Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **58:**1501–1515.

Pyper, B.J., Mueter, F.J., Peterman, R.M., Blackbourn, D.J. and Wood, C. (in press) Spatial covariation in survival rates of Northeast Pacific chum salmon. *Trans. Am. Fish. Soc.* (in press).

Quinn, T.J. II and Deriso, R.B. (1999) *Quantitative Fish Dynamics*. New York: Oxford University Press.

Ricker, W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* **191:**382.

Roden, G.I. (1989) Analysis and interpretation of long-term climatic variability along the west coast of North America. In: *Aspects of Climate Variability in the Pacific and the Western Americas*. D.H. Peterson (ed.). Geophysical Monograph. Washington, DC: American Geophysical Union, pp. 93–111.

Trenberth, K.E. and Hurrell, J.W. (1995) Decadal coupled atmosphere–ocean variations in the North Pacific Ocean. In: *Climate Change and Northern Fish Populations*. R.J. Beamish (ed.). Canadian Special Publications of Fisheries and Aquatic Sciences 121. Ottawa: National Research Council of Canada, pp. 15–24.

Ware, D.M. (1995) A century and a half of change in the climate of the NE Pacific. *Fish. Oceanogr.* **4:**267–277.

Ware, D.M. and Thomson, R.E. (2000) Interannual to multidecadal timescale climate variations in the Northeast Pacific. *J. Clim.* **13:**3209–3220.

Wilson, J.G. and Overland, J.E. (1986) Meteorology. In: *The Gulf of Alaska: Physical Environment and Biological Resources*. D.W. Hood and S.T. Zimmerman (eds). Springfield, VA: Minerals Management Service, pp. 31–54.

Woodruff, S.D., Diaz, H.F., Elms, J.D. and Worley, S.J. (1998) COADS Release 2 data and metadata enhancements for improvements of marine surface flux fields. *Phys. Chem. Earth* **23:**517–527.