

Temporal and special changes in pattern in size-at-age were examined relative to climate variability and climate change. Good correlations were also found with climatic variables such as the Pacific Decadal Oscillation, Aleutian Low Pressure Index, or water temperature alone (Peterman, MacFarlane, Brown, Schweigert, Bonk, Tarasyuk). Competition with other pelagic species was suggested as a possible mechanism explaining changes in growth of chub mackerel (Watanabe). Ecosystem change was implicated as a factor explaining stock fluctuations in Hokkaido-Sakhalin herring whereas the co-occurring sardines stocks appear to be largely density dependent (Watanabe).

Many papers demonstrated density dependence of size-at-age. When population size was large, size-at-age was small and *vice versa*. Discussion at the workshop centered on the need to think more and work harder at identifying mechanisms that might control density dependence, with studies of the forage base being one of the prime candidates.

Discussion was also focused on the need to make better use of existing samples to study size- and weight-at age through use of scales and otoliths to generate new data sets on size- and weight-at-age.

There are many data on length and weight of fishes but not as much data on age and weight at length. Through analysis of otoliths and scales, one could determine age of fishes that have already been measured.

Finally, the workshop participants discussed the value of comparative studies and of course - this is what REX workshops are all about – providing a forum for discussion on differences in population size, growth, and life history characteristics of species that are distributed widely around the Pacific Rim. This led to the recommendation that PICES scientists need to do more comparisons of populations that are distributed in the coastal zones around the basin, but also need to compare response of fish, nekton and zooplankton populations that are found within the deeper waters of the Kuroshio, Kuroshio Extension, Transition Zone and the California Current. Interesting, this thought arose independently of the inter-sessional symposium proposed on comparative studies of North Pacific transitional areas (the symposium was held April 23-25, 2002, in La Paz, Mexico).

The following section contains extended abstracts of papers given at the workshop.

Spatial patterns of covariation in size-at-age of British Columbia and Alaska sockeye salmon stocks and effects of abundance and ocean temperature

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Introduction

Body lengths of adult Pacific sockeye salmon (*Oncorhynchus nerka*) have decreased significantly in recent years, reducing the reproductive potential of spawners and the economic value of harvests. To understand the causes of these important trends, we pursued three objectives. Firstly, we quantified the extent of

spatial covariation among age-specific body sizes of numerous stocks in the Northeast Pacific. The observed spatial scale of covariation could suggest the causes of that variation. Secondly, we compared the extent of covariation among body size and survival rate of sockeye salmon to determine whether these two variables were influenced by similar processes. Thirdly, we tested hypotheses about the relative importance of

intraspecific competition and oceanographic conditions on size of adult sockeye salmon. This paper summarizes material already published; see Pyper *et al.* (1999) and Pyper and Peterman (1999) for details.

Methods

We used 72 time series of body length at a given adult age for 31 sockeye stocks from five geographically distinct regions in British Columbia (Fraser River and Skeena River) and Alaska (Upper Cook Inlet, Copper River and Bristol Bay). Ages included were 1.1, 1.2, 1.3, 2.2 and 2.3 fish.

Patterns of covariation. To examine patterns of covariation among length-at-age data both within and between regions, we calculated Pearson product-moment correlation coefficients for pairwise comparisons among the 72 time series of lengths. Size data were aligned to have return years in common (year in which they returned to their natal streams), because Rogers and Ruggerone (1993) and McKinnell (1995) suggest that interannual variability in body size of recruits is largely determined by growth in their final year at sea. However, to estimate the importance of conditions in early ocean life, we also computed correlations after aligning the data series to have a common ocean entry year (OEY) but a different return year (*e.g.* using size data for 1.2 and 1.3 adults).

Positive autocorrelation and time trends were present in many of the time series of body length, indicating that low-frequency (*i.e.*, slowly-changing) variability is important. However, such autocorrelation and time trends increase the chance that statistically significant but spurious correlations will occur in standard inference tests. Therefore, we used two approaches to examine correlations. Firstly, we computed them using the original time series and based significance tests on the method recommended by Pyper and Peterman (1998), which adjusts degrees of freedom to account for autocorrelation and maintains Type I error rates near the specified α in the presence of autocorrelation. Secondly, we first-differenced the time series (subtracting each data point from the next) to remove the low-frequency variation and

re-computed correlations. Comparing the results from these two approaches allowed us to quantify the potential importance of low-frequency causes of the positive covariation that we found.

Effects of oceanographic conditions and intraspecific competition. We also used principal components analysis (PCA) to further examine spatial and temporal covariation among lengths for 1967-1997. The PCA was done on 13 regional average length-at-age series, which better depicted the “signal” shared by given age classes and stocks in each region. This method reduced patterns of variability shared by each age class and region to a few defining time series (principal components). Copper River data were omitted due to missing data.

We then used the dominant principal component (PC1) to test hypotheses about the causes of variation in sockeye growth rate. Because our covariation results indicated that adult body size was affected primarily by conditions in the last year of ocean life, we generated indices of oceanographic conditions and intraspecific competition during the final year at sea. These indices were consistent with the area of overlap in ocean distributions of B.C. and Alaska sockeye, which roughly encompasses the Alaskan Gyre and is occupied by sockeye salmon from North America but not Asia (French *et al.* 1976). We used total ocean abundance of maturing North American sockeye salmon as an index of intraspecific competition, based on annual adult recruits (catch plus escapement) summed across the major B.C. (Fraser, Skeena, and Nass River) and Alaska stocks (Copper River, Cook Inlet, and Bristol Bay), which together account for the vast majority of sockeye abundance in the Gulf of Alaska (see Peterman *et al.* 1998 for details).

To reflect ocean conditions that might affect growth, we generated time series of annual sea-surface temperature (SST) deviations from the long-term mean. We used monthly SST data (°C) on a 5-by-5 degree latitude-longitude grid across the area stated above of general overlap in ocean distributions of B.C. and Alaska sockeye (see Pyper and Peterman 1999 for details). Deviations were computed for a given grid cell and month by subtracting its long-term mean SST for 1947

through 1997. These deviations were then averaged to create two time series, with each corresponding to a different period preceding the return (generally in July) of sockeye salmon to their rivers: 1) winter months (November through February), and 2) a combination of winter and spring months (November through June). Climatic forcing during winter months is thought to be an important determinant of ocean productivity in the subsequent spring and summer (*e.g.*, Brodeur and Ware 1992), while in spring, maturing sockeye are feeding and growing at high rates before and during migrations back to their natal streams.

We then used multiple regression to examine relationships among the dominant pattern of covariation for length (PC1), total sockeye abundance in millions of fish (A), and ocean temperature (SST) for either November-February or November-June:

$$PC1 = a + b_1A + b_2SST + \epsilon$$

Because of positive autocorrelation in the residuals, we simultaneously computed maximum likelihood estimates of the lag-1 autocorrelation coefficient and regression parameters. Due to time trends in the data, we first computed regressions using the original data and then repeated the regressions using detrended data (deviations from a linear time trend fit to each data series) to test for effects at shorter time scales.

Results and discussion

Patterns of covariation. There was widespread positive covariation among the 72 body-length time series, aligned by return year, across ages and across stocks. Of the 2,556 correlations, 91.4% were positive (and 43%, or 1,006, of the positive ones were significant at $p < 0.05$, whereas only 3 negative cases were significant). There was strong evidence of positive covariation in age-specific body size among sockeye stocks even between distant regions, as indicated by the predominance of positive correlations in these comparisons (*e.g.*, Bristol Bay vs. Fraser River; Fig. 1C). However, there was a stronger positive covariation among body length of stocks within regions (*e.g.*, among the 8 stocks in Bristol Bay and among the 20 in the Fraser River; Fig. 1A and 1B). Generally, the

percent of variation in length shared by stocks in the same region was about twice that shared by stocks from different regions (see Pyper *et al.* (1999) for detailed results).

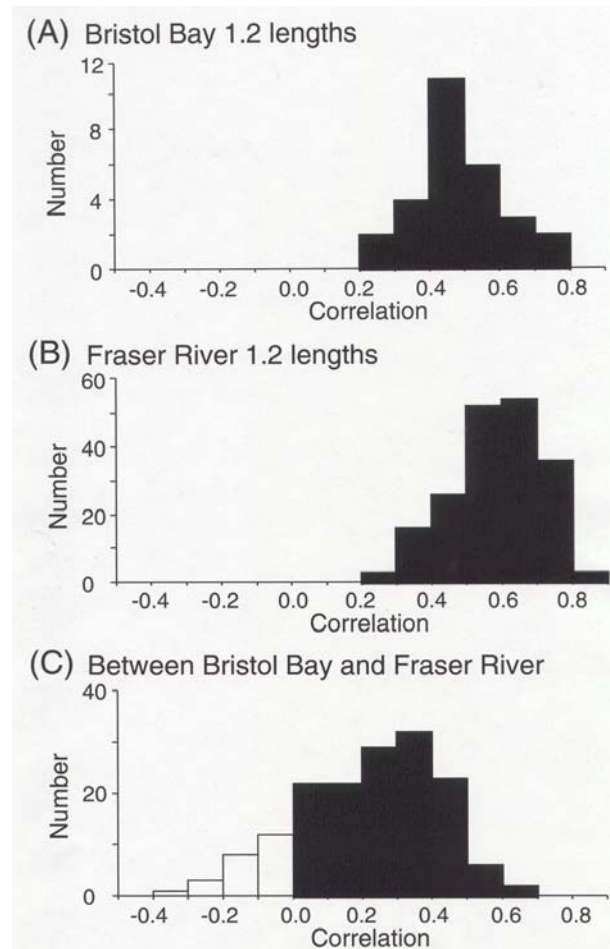


Fig. 1 Histograms of correlations between lengths of age 1.2 sockeye: A) among Bristol Bay stocks (all 28 correlations positive; 23 significant at $p < 0.05$); B) among Fraser River stocks (all 190 correlations positive; 161 significant); and C) between Bristol Bay and Fraser River stocks (136 of 160 correlations positive; 25 significant positive correlations). Open bars represent negative correlations; solid bars are positive correlations. Reprinted from Pyper *et al.* (1999).

Correlations using first-differenced data support the suggestion from the PCA reported below that slowly changing, low-frequency patterns of variability, such as the declining time trends in body size, were important sources of covariation

among average lengths of stocks. After autocorrelation and time trends in the 72 stock-specific length series were removed by first-differencing, widespread positive covariation was still evident both within and between regions. However, correlations were consistently and often substantially lower than those computed using the original data. The average of the 2,556 correlations was reduced from 0.37 to 0.23, the number of negative correlations increased to 578, and the number of significant ($p < 0.05$) positive correlations decreased to 745. Thus, there is little evidence that the general patterns of covariation in lengths could be solely a spurious result of unrelated time trends; instead, to the extent that the observed covariation in length-at-age of sockeye salmon arises from shared processes, such processes appear to be largely characterized by low-frequency patterns of variability.

In contrast to the above analyses, when the body-length time series were aligned to share the same ocean entry year (OEY) but to have a different return year (RY), the correlations among stocks decreased dramatically (*e.g.* for Bristol Bay stocks, the average correlation in the original data series decreased from 0.67 when lined up by RY to 0.29 when lined up by OEY). This decrease was even greater when possible confounding effects of autocorrelation were removed from both analyses (see Pyper *et al.* 1999). Like other analyses, (Rogers and Ruggerone 1993; McKinnell 1995), these findings imply that variable growth conditions during early marine life are not nearly as important a determinant of temporal variation in final sockeye body length as conditions during late marine life.

Comparison of body size and survival rates. We found weak and inconsistent correlations between average length and survival rate, suggesting that different processes drive interannual variability in these components of recruitment. This conclusion is further supported by evidence that environmental processes influence these two variables at different spatial scales. Whereas both adult body size and survival rate show strong positive covariation among stocks within regions, only body size shows strong between-region covariation (*e.g.*, compare Fig. 1C here with

Fig. 1C of Peterman *et al.* 1998). These differences in spatial characteristics of covariation suggest that models for body size or forecasting annual salmon abundance (reflecting survival rates and changing age-at-maturity schedules) should be based on appropriate measures of environmental conditions that reflect this information about spatial scales. For example, we found that large, basin-scale SST was significantly associated with variation in body size (see below), whereas Mueter *et al.* (2001) found that smaller, regional-scale SST was much more important in explaining variation in survival rates of salmon.

Effects of oceanographic conditions and intraspecific competition. Principal components analysis (PCA) of the 13 age-specific regional body length series defined the temporal characteristics of variation shared among regions. The PCA yielded three principal components with eigenvalues greater than one; the best one accounted for 65% of the total variance and the other two combined accounted for only 19%. The time series (scores) of this dominant component, PC1, had an obvious declining trend from 1967-1997 ($p < 0.001$; linear regression with autocorrelated error) (Fig. 2A). All 13 length series correlated strongly with PC1 (range 0.64 to 0.89), suggesting that much of the covariation among lengths of Alaska and B.C. sockeye salmon resulted from a similar declining trend over this period.

The multiple regression for the PC1 (reflecting shared variation among body size) using the original data was highly significant (multiple $r^2 = 0.71$, $p < 0.001$), as was the estimated slope on abundance ($b_1 = -0.03 \pm 0.005$ [± 1 standard error], $p < 0.001$) (Fig. 2B). The slope on November-February SST was also significant ($b_2 = -0.72 \pm 0.29$, $p = 0.014$) (Fig. 2C). Partial r^2 values were 0.56 for abundance and 0.18 for SST.

The multiple regression using detrended data (to remove possible confounding due to time trends in the original data) showed similar results. Both abundance and November-February SST were significant ($b_1 = -0.035 \pm 0.007$, $p < 0.001$ and $b_2 = -0.87 \pm 0.31$, $p = 0.004$). Overall, the multiple $r^2 = 0.54$, $p < 0.001$, and multicollinearity was

negligible ($r = 0.04$). Partial r^2 values were 0.48 for abundance and 0.23 for SST.

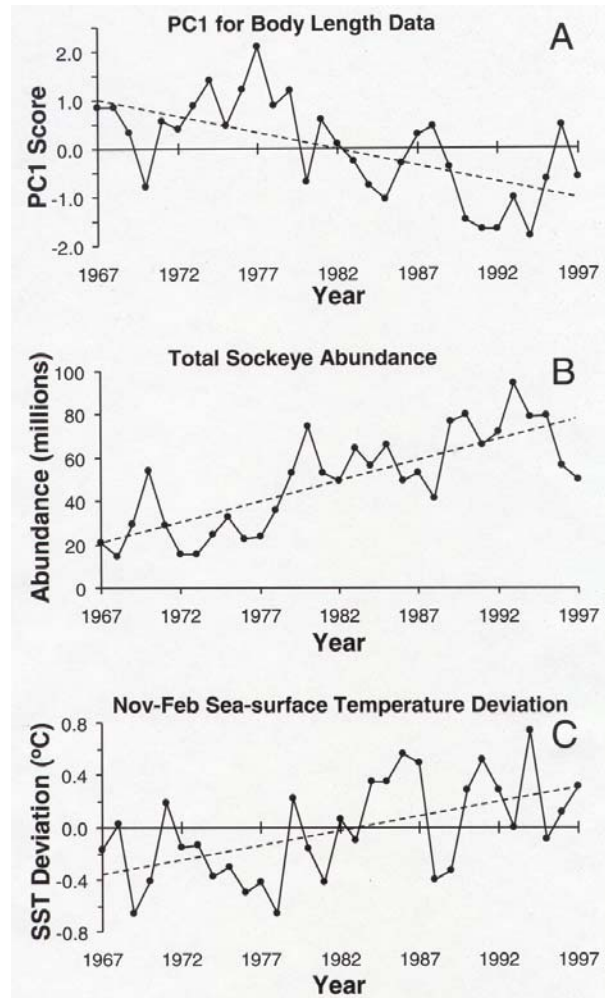


Fig. 2 (A) Scores for the dominant principal component (PC1) of length-at-age data for B.C. and Alaska sockeye salmon -- lower values of PC1, for example, reflect the tendency toward reduced body length that is shared among these stocks; (B) Total annual abundance of adult recruits (catch plus escapement) of the major B.C. and Alaska sockeye stocks; and (C) Average yearly winter (November through February) sea-surface temperature (SST) deviations in °C from the long-term (1947-1997) mean for those months (6.8°C) for the Northeast Pacific Ocean over the region where distributions of B.C. and Alaska sockeye salmon overlap. Dotted lines are the fitted linear time trends used to detrend the data. Reprinted from Pyper and Peterman (1999).

Because November-February and November-June SST data were highly correlated ($r = 0.86$), all results for the latter were similar to those for November-February, with the exception that November-June SST was not significant in either the multiple regression with original data ($p = 0.11$) or with detrended data ($p = 0.08$).

These results indicate that reduced adult body length of both B.C. and Alaska sockeye salmon are associated with increases in total sockeye abundance in the Northeast Pacific and November-February sea-surface.

Abundance and SST together account for 71% of the variability in the first principal component (PC1) of body length among the major sockeye stocks of the northeastern Pacific Ocean during 1967-1997. Furthermore, abundance appears to have a much greater effect on body size than temperature. Its partial r^2 was considerably larger (0.56 vs. 0.18), and when data in each series were transformed into standard deviation units so that slopes were in the same units, the standardized slope for abundance (-0.68) was greater than the slope for SST (-0.27). This indicates that for each standard deviation increase, abundance had about 2.5 times the contribution to reducing adult body size as did November-February SST.

In addition, both abundance and SST were significantly related to the dominant pattern of variability in body length at both long and short time scales (*i.e.*, in the original, as well as detrended data). Thus, although it is possible that relationships among the original data might be coincidental due to their co-occurring time trends (*i.e.*, that some other omitted variable actually explains the trend in PC1), the evidence in support of the effects of abundance and SST was strengthened by their very similar slopes in both the original data analysis and the analysis once time trends were removed.

Although several authors have documented increased secondary productivity in the northeastern Pacific Ocean in recent decades (*e.g.*, zooplankton and squid - Brodeur and Ware 1992, 1995), which should improve growth rates for sockeye salmon, abundance of sockeye recruits also increased (Fig. 2B). We therefore

hypothesize that increased food supply was more than offset by increased sockeye abundance, which resulted in greater competition and smaller body size in recent years.

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Influences of the 1997-1998 El Niño and 1999 La Niña on juvenile chinook salmon in the Gulf of the Farallones

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El Niño, the warm phase of El Niño/Southern Oscillation (ENSO) events, has been shown to produce dramatic effects on marine communities. Alterations in physical oceanographic properties of the marine environment can be observed as far

north as Alaska. Less is known of the influences of La Niña, the cool phase of ENSO events that follows an El Niño. During the 1982-83 El Niño, anomalous plankton distributions, altered fish community structure, and reduced fish catch