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A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America

Randall M. Peterman and Brigitte Dorner

Abstract: We used data on 64 stocks of sockeye salmon (*Oncorhynchus nerka*) from British Columbia (B.C.), Washington, and Alaska to determine whether recent decreases in abundance and productivity observed for Fraser River, B.C., sockeye have occurred more widely. We found that decreasing time trends in productivity have occurred across a large geographic area ranging from Washington, B.C., southeast Alaska, and up through the Yakutat peninsula, Alaska, but not in central and western Alaska. Furthermore, a pattern of predominantly shared trends across southern stocks and opposite trends between them and stocks from western Alaska was present in the past (1950–1985), but correlations have intensified since then. The spatial extent of declining productivity of sockeye salmon has important implications for management as well as research into potential causes of the declines. Further research should focus on mechanisms that operate at large, multiregional spatial scales, and (or) in marine areas where numerous correlated sockeye stocks overlap.

Résumé : Les auteurs ont utilisé les données sur 64 réserves de saumon rouge (*Oncorhynchus nerka*) de la Colombie-Britannique (C.B.), Washington et Alaska afin de déterminer si les récentes diminutions de l'abondance et de la productivité du sockeye observées dans le fleuve Fraser, en C.B., se sont manifestées plus largement. Ils ont constaté que les tendances de diminution de la productivité avec le temps se sont manifestées sur une large étendue géographique allant de l'état de Washington, de la C.B., du sud-est de l'Alaska et jusque dans la péninsule de Yakutat, en Alaska, mais pas dans le centre et l'ouest de l'Alaska. De plus, ils ont observé un patron de tendances principalement partagées sur l'ensemble réserves du sud et des tendances opposées entre celles-ci et les réserves de l'ouest de l'Alaska, dans le passé (1950–1985), mais les corrélations se sont intensifiées depuis. L'étendue spatiale du déclin de productivité du saumon sockeye porte d'importantes implications pour l'aménagement ainsi que la recherche sur les causes potentielles des déclins. Les recherches à venir devraient se concentrer sur les mécanismes agissant en général, aux échelles spatiales multirégionales, et (ou) dans les régions marines où plusieurs réserves corrélées du sockeye se recouvrent.

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Introduction

Productivity (adults produced per spawner) and abundance of adults returning for many of the 19 major Fraser River sockeye salmon (*Oncorhynchus nerka*) populations have decreased substantially since the early 1990s, and that abundance has decreased despite major reductions in harvest rates. The 2009 adult returns were the lowest since 1947 (Peterman et al. 2010), prompting concerns serious enough to trigger a judicial inquiry. Here we quantify productivity trends in sockeye populations (stocks) throughout their geographic range in western North America to determine whether similar declines have occurred in other areas. A key component of evidence to help distinguish among multiple hypotheses about causes of reductions in fish stocks is the spatial scale of the trends (Myers. et al. 1997). Thus, our analysis provides a foundation upon which other researchers can base investigations into drivers of sockeye productivity for the Fraser River and elsewhere.

Materials and methods

We obtained data on abundance of spawners and their resulting adult returns from brood year (year of spawning) 1950 onward for a total of 64 stocks of sockeye salmon from

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R.M. Peterman. School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
B. Dorner. Driftwood Cove Designs, GD Lasqueti Island, BC V0R 2J0, Canada.

Corresponding author: Randall M. Peterman (e-mail: peterman@sfu.ca).

Fig. 1. Trends in scaled Kalman filter series of the productivity parameter, a_t, values (Scaled productivity index) by brood year for sockeye salmon stocks from Washington (WA) up the coast through the Yakutat peninsula, which is just north of southeast Alaska (SEAK) (locations in online Supplemental Fig. S2). To allow comparisons across stocks, each series of a_t values is scaled to its own mean and is shown in standard deviation units from that mean. The time series were generated by the best stock-specific model (i.e., the one with the lowest small-sample Akaike information criterion (AIC$_c$); see online Supplemental Table S2). That best model is denoted in figure legends as R for the Ricker model (black font) or L for the Larkin model (red font). Fraser River stocks are aggregated into adult run-timing groups. For the Chilko stock, brood years 1987 and 1989 through 1992 were affected by lake fertilization (highlighted in the graph by larger data points). (Time series of raw, unscaled Kalman filter series of the productivity parameter, a_t, for these same sockeye stocks are shown in the online Supplemental Fig. S5.) Horizontal lines reflect data sets in which high-frequency variation (due to natural variation and (or) observation error) was large compared with the low-frequency time trend; the Kalman filter interpreted such cases as having no time trend in the a_t productivity parameter.

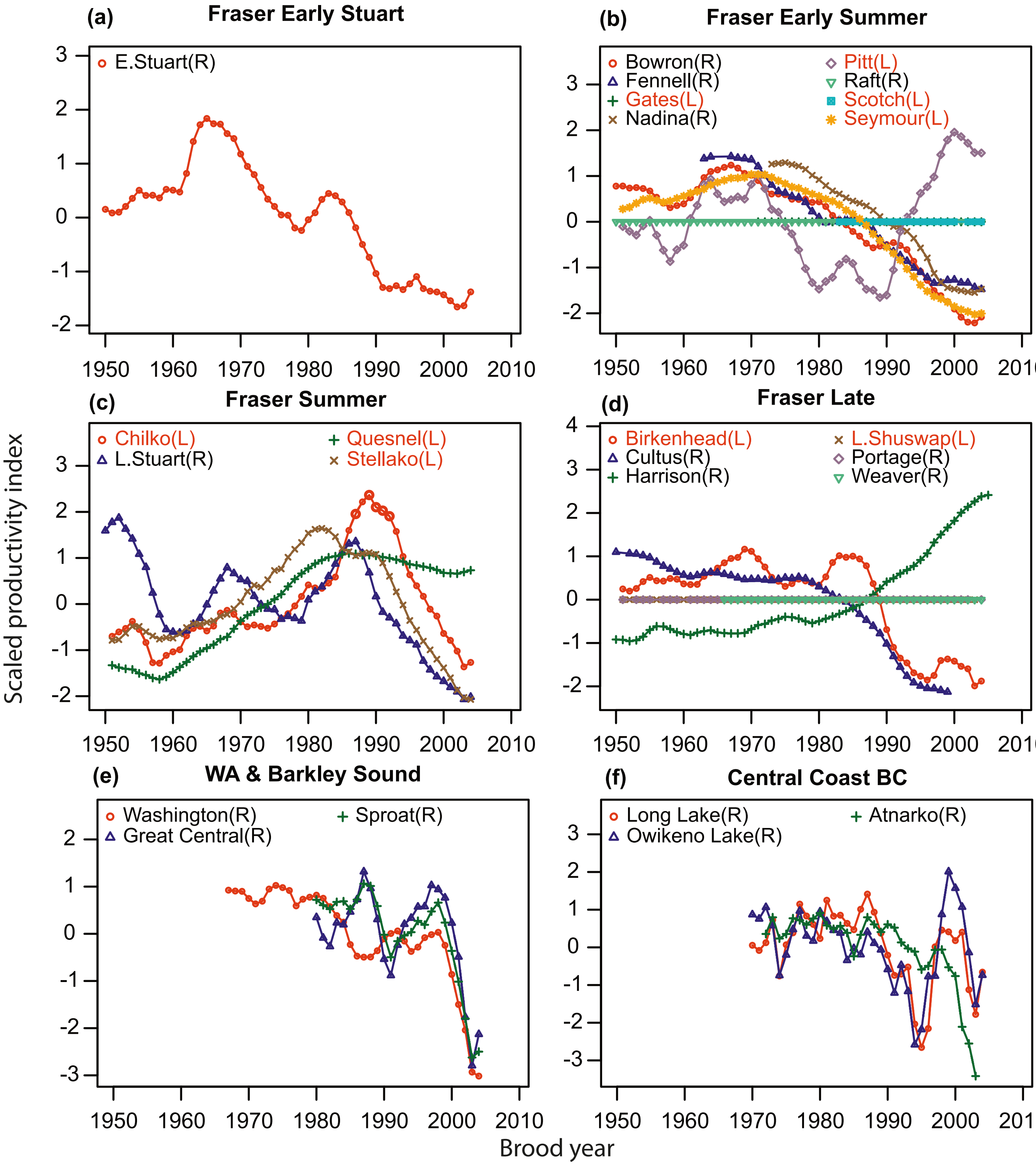
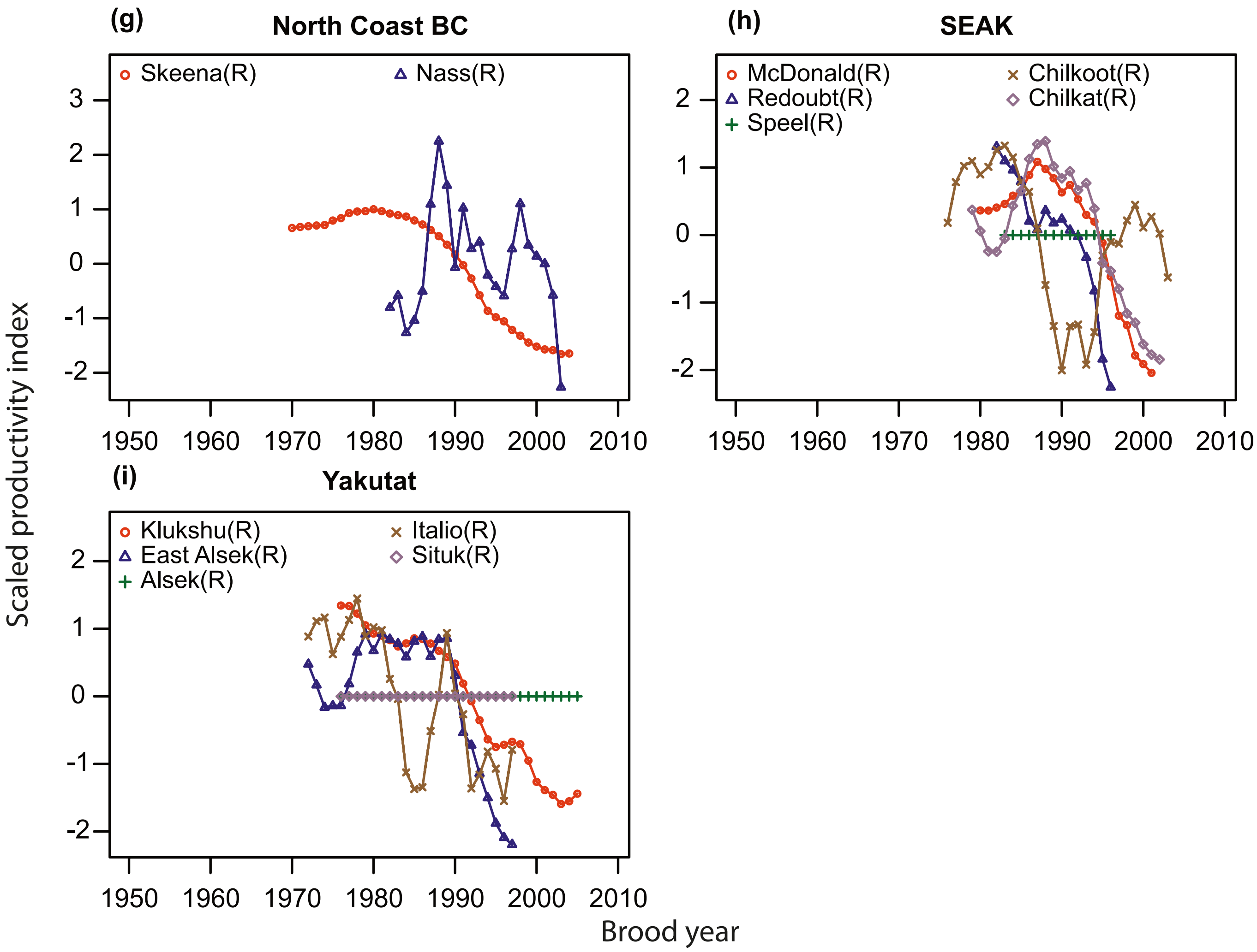


Fig. 1 (*concluded*).



British Columbia (B.C.), Washington, and Alaska (refer to online Supplemental Fig. S2 map and Supplemental Table S1[1]). Almost all data are from wild populations; where applicable, local agency biologists removed hatchery contributions, except for the Pitt River, which is a small sockeye stock on the Fraser system. We did not include data from the 2010 returns because at the time of writing, biologists were still determining stock identifications in samples for numerous stocks (e.g., Fraser River).

We analyzed two measures of productivity that reflect survival processes between spawners and their resulting adult returns (recruits). Recruits are their offspring that return to the coast prior to fishing (online Supplemental Appendix S1[1] further explains estimation of adult recruits). It is well known that within-stock, within-brood-year density-dependent effects can reduce the number of adult recruits per spawner at high spawner abundances (Ricker 1975). Therefore, we calculated the first indicator of productivity as $\log_e$(recruits per spawner) residuals from the best-fit "stationary" spawner-to-recruit model, as explained below. These residuals represent the change in $\log_e$(recruits per spawner) that is attributable to factors other than within-stock density dependence as spawner abundance changes. For each stock we estimated a time series of these residuals, v_t, first by fitting the Ricker (1975) model:

$$(1) \qquad \log_e(R_t/S_t) = a + bS_t + v_t$$

where S_t is abundance of spawners in brood year t, R_t is abundance of adult recruits of all ages resulting from those spawners, a is the productivity parameter (in units of $\log_e(R_t/S_t)$) at very low spawner abundance, b reflects within-stock density-dependent effects, and $v_t \sim N(0, \sigma_v^2)$. We refer to this Ricker model as "stationary" because it assumes that a is constant across the entire time series of spawner and recruit data. We also fit a "stationary" Larkin (1971) model to the data. This model allows for delayed density-dependent interactions across successive brood years within a given stock, which are hypothesized to result from severe depletion of salmon food or buildup of pathogens or predators in response to occasional large abundances of spawners:

$$(2) \qquad \log_e(R_t/S_t) = a + bS_t + b_1S_{t-1} + b_2S_{t-2} + b_3S_{t-3} + v_t$$

where S_{t-1}, S_{t-2}, and S_{t-3} are the spawner abundances from brood years $t-1$, $t-2$, and $t-3$, respectively, and the b_1, b_2, and b_3 parameters reflect the corresponding delayed

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-063.

density-dependent effects between cohorts from different brood years. We included the Larkin model in our analysis because of concerns that delayed density dependence might play a role in population dynamics. This is of particular concern for some Fraser River sockeye stocks, where high spawner abundances resulting from efforts to rebuild those stocks may have caused reduced productivity and consequent decreases in total adult returns (Peterman et al. 2010).

Our second measure of productivity came from fitting "nonstationary" versions of the Ricker and Larkin models, which replaced the single a parameter in eqs. 1 and 2 with a time-varying parameter, a_t. To estimate a_t, we used a Kalman filter, assuming that a_t follows a random walk, i.e.,

$$(3) \qquad a_t = a_{t-1} + w_t$$

where $w_t \sim N(0, \sigma_w^2)$ (Chatfield 1989). Previous simulations (Peterman et al. 2000) and empirical analyses (Peterman et al. 2003) show that this Kalman filter method gave the most reliable parameter estimates, compared with the standard regression method, when applied to salmon populations in which there was an underlying time trend in productivity. A fixed-interval smoother applied to the time series of a_t estimates produced the maximum likelihood values of a_t (Harvey 1989) and also drastically reduced the random high-frequency year-to-year variation that tends to obscure underlying long-term trends. These smoothed time series of a_t values constituted our second measure of productivity. The b and variance parameters were determined by maximum likelihood estimation. Details of our Kalman filter estimation method are described in the appendix of Peterman et al. (2003).

We then used correlations to compare time trends in residuals of $\log_e$(recruits/spawner) across time and space. In addition, we used a principal components analysis (PCA) on the Kalman-filtered smoothed a_t time series from the best-fit nonstationary model to identify groupings of stocks that have shared similar productivity patterns and to obtain a description of the key components of shared productivity patterns within the study area. The best-fit model (Ricker or Larkin) within each category (i.e., stationary or nonstationary) was determined by the small-sample Akaike information criterion (AIC_c) (Burnham and Anderson 1998). To facilitate graphical presentations for stocks with substantially different magnitudes of productivity, we expressed some indicators in standard deviation units (i.e., scaled to their respective long-term means and standard deviations).

Results and discussion

We found that the declining productivity of Fraser River sockeye is not unique among sockeye stocks from western North America. Instead, there have been relatively rapid and consistent decreases in productivity since the late 1990s, and in many cases since the late 1980s or early 1990s, in most "southern" sockeye stocks (i.e., those from the Puget Sound, Washington; Fraser River and Barkley Sound, B.C.; central coast of B.C.; north coast of B.C.; southeast Alaska; and the Yakutat peninsula; Fig. 1; stock locations in online Supplemental Fig. S2[1]). For stocks showing declines in productivity, time trends are qualitatively similar, even though starting dates may differ and a period of recovery through the late 1990s is more pronounced in some stocks than others.

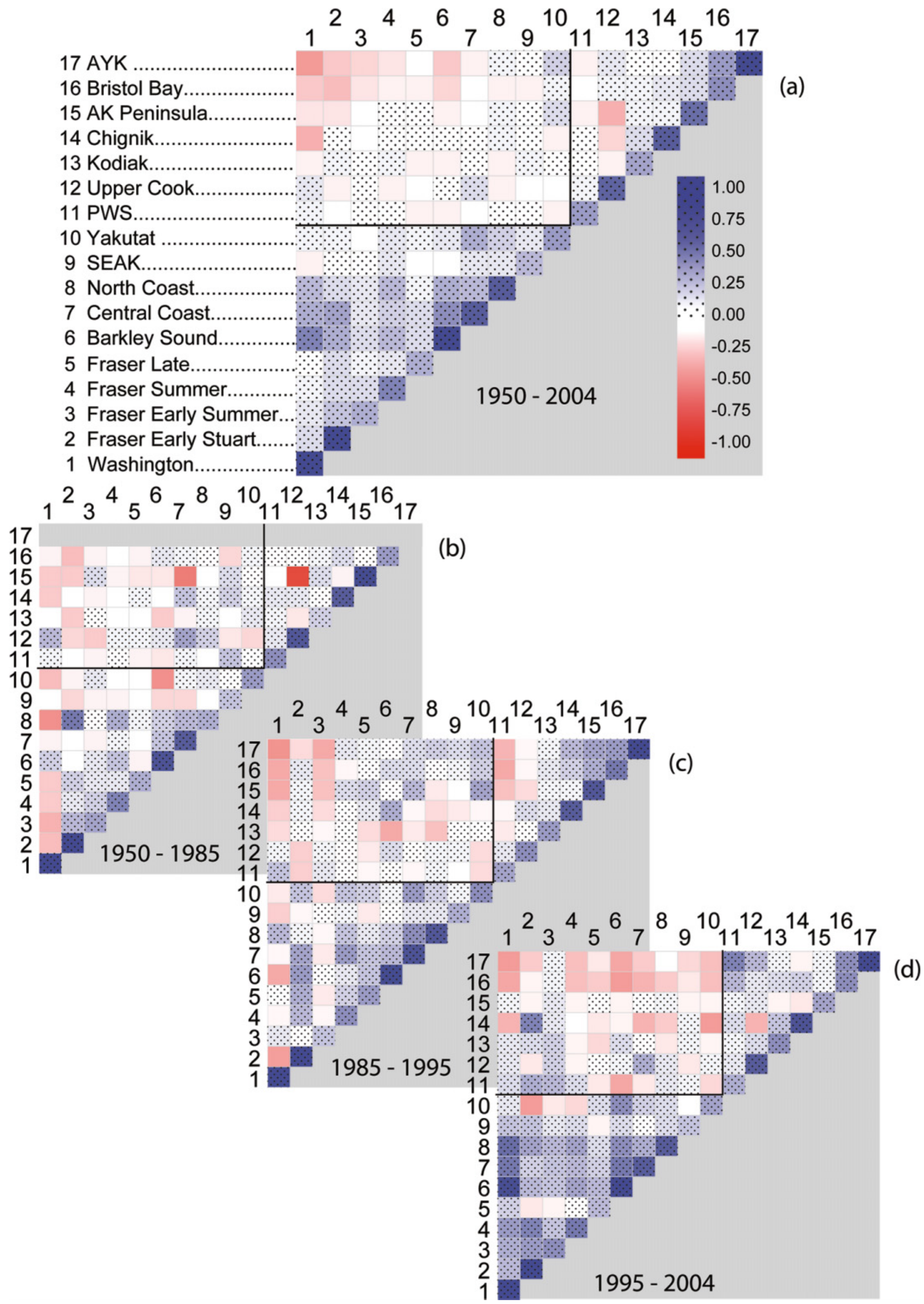
The widespread downward time trend in sockeye productivity is reflected in the among-stock correlation analysis (Fig. 2), shown here for stationary best-model residuals because correlation coefficients cannot be calculated for the stocks where the nonstationary model estimated constant Kalman filter a_t values (several occurrences in Fig. 1). Regional averages of pairwise correlations across B.C. and between B.C. and Washington stocks are positive (range 0.01 to 0.56; Fig. 2*a*). Correlations between both Washington and B.C. stocks and those in southeast Alaska and Yakutat are also mostly positive (ranging from –0.04 to 0.37; Fig. 2*a*). In contrast, over the same period, productivity of most central and western Alaskan sockeye populations (regions 11–17) generally either increased or remained stable, rather than decreased (Supplemental Fig. S5[1]), resulting in mostly negative correlations with productivity of southern stocks (Fig. 2*a*).

The first component identified in the PCA of best-model smoothed time series of Kalman filter a_t (Supplemental Fig. S3[1]) shows a steady decline in productivity starting shortly before 1985, establishing this downward trend as the main factor distinguishing productivity patterns in the study area. The PCA tended to separate Washington and B.C. stocks from central and western Alaska along this axis (Supplemental Fig. S4[1]), confirming the opposite productivity trends that produced positive correlations in the south and negative correlations between southern and western Alaska stocks.

It is possible that the shared downward time trends in productivity across the southern sockeye stocks result from a coincidental combination of simultaneous processes related to freshwater habitat degradation, contaminants, pathogens, predators, and (or) food supply that have each independently affected individual stocks or small groups of stocks. However, the large spatial scale of similar time trends in productivity for over 25 stocks in both relatively pristine and heavily disturbed habitats suggests that a more likely explanation is that there are shared causal mechanisms across Washington, B.C., southeast Alaska, and the Yakutat region of Alaska.

Two additional observations provide insights to help narrow down potential mechanisms. First, there was some evidence for delayed density dependence in several stocks (mostly Fraser River) (i.e., where the nonstationary Larkin model had a lower AIC_c than the Ricker; Supplemental Table S2[1]). However, there was only one stock (Quesnel on the Fraser) where delayed density dependence was a sufficient explanation for observed declines in productivity (i.e., where the Larkin model did not show declining a_t values but the Ricker model did). Thus, while delayed density dependence may have contributed somewhat to declining productivity in a few stocks, our data do not support the hypothesis that large spawner abundances are responsible for the widespread declines in productivity. Second, a previous analysis (Peterman et al. 2010) examined evidence related to the life stage most responsible for the decline in productivity. That analysis used data to estimate time series of productivities from spawners to juveniles (smolts or fry) and juveniles to adults, but such data sets were only available with sufficient duration for seven Fraser sockeye stocks. Those data show that de-

Fig. 2. Summaries of correlations in productivity between pairs of sockeye salmon populations, based on annual residuals from the best stock-specific stationary model (either the Ricker or Larkin spawner–recruit model, whichever had the lowest AIC_c). To illustrate and emphasize geographical patterns, stocks were grouped by geographical location of their ocean entry points, or, in the case of the Fraser River stocks, by adult run-timing group. Average pairwise Pearson correlations between time series from the different regions (named, numbered, and ordered from north to south) are positive (stippled blue), negative (red), or near zero (white). Horizontal and vertical black lines within each correlation matrix separate the "southern" regions (1–10) from the others. To calculate the average correlation between any two regions, (*i*) each stock in the first region was paired with each stock in the second region, (*ii*) correlation coefficients were then calculated for the time series of best-model residuals for each pairing, and (*iii*) all of these correlation coefficients were then averaged to produce the mean correlation between the two regions. To calculate the average correlation coefficient for a given region, each stock within that region was paired with each other stock within the same region. Thus, the diagonal values in the matrices are typically less than one and reflect similarity of time trends within each region. Correlations are shown for various periods of brood years: (*a*) 1950–2004, (*b*) 1950–1985, (*c*) 1985–1995, and (*d*) 1995–2004. The number of pairings included for each region and number of data years included to calculate correlations for each pairing depended on data availability and thus differed somewhat between pairings and regions (number of stocks per between-region pairing ranged from 2 to 72; number of overlapping data years per pair of stocks ranged from 2 to 36, with medians of 10, 11, and 9, respectively, for the three successive time periods). A similar matrix with correlations for the period 1950–1995 was used for the analyses presented in Supplemental Appendix S2. Regional abbreviations are SEAK (southeast Alaska), PWS (Prince William Sound), AK (Alaska) Peninsula, and AYK (Arctic–Yukon–Kuskokwim).



creases in a sockeye stock's total-life-cycle productivity from spawners to adult recruits have usually been associated with declines in its juvenile-to-adult productivity, but not spawner-to-juvenile productivity (Peterman et al. 2010). These results indicate that either (*i*) the primary mortality agents causing the decline in productivity occurred in the period after estimation of juvenile abundance in fresh water or (*ii*) certain stressors (such as pathogens) that were nonlethal in fresh water caused mortality later in the marine life stage.

Given the widespread similarity in trends across many sockeye salmon stocks, we then asked whether such similarities existed historically or whether their appearance suggests recently emerging large-scale stressors that synchronize stock productivities. We therefore split the time series of productivity residuals into two periods, before and after 1985, and then broke the latter period into two intervals of approximately equal length to get a better understanding of recent dynamics. We repeated the correlation analyses for each period separately. Results suggest that the predominantly shared trends across southern stocks and opposite trends between southern stocks and stocks from western Alaska were present in the past (1950–1985), but have intensified, especially in the most recent period, in the sense that correlations within the southern area in 1995–2004 were more strongly positive, and correlations between those southern regions and western Alaska were also more strongly negative (Supplemental Appendix S2 and Supplemental Fig. S6[1]; compare with Figs. 2*b*–2*d*). In addition, the extent of the positively correlated southern area appears to have spread further north over time (Supplemental Appendix S2 and Supplemental Fig. S6[1]; also see Figs. 2*b*–2*d*). Our results are consistent with large-scale, multiregional shifts in climate-driven oceanographic patterns that were previously implicated as drivers of sockeye productivity (Mantua et al. 1997; Mueter et al. 2002), although potential time lags in the way the Kalman filter tracks changes preclude a detailed comparison between change points in ocean regime and change points in the a_t series.

Further research into the decreasing productivity of west coast sockeye salmon should therefore focus on mechanisms that have one or more characteristics. (*i*) The mechanisms operate at large, multiregional spatial scales or in marine areas where a large number of the correlated sockeye stocks overlap. (*ii*) The mechanisms are likely to affect stocks in the geographic range from Puget Sound to southeast Alaska in a similar way, but while having an inverse effect on stocks from central and especially western Alaska. (*iii*) The mechanisms have been present historically, but have intensified, or they have exacerbated the effects of drivers already present in the past. Mechanisms consistent with these three criteria include climate-driven increases in freshwater or marine mortality induced by pathogens, as well as increases in predation or reduced food availability due to oceanographic changes. The greatest progress in understanding mechanisms will come from coordinated research programs that simultaneously examine numerous stocks with contrasting levels of exposure to these multiple mechanisms. Furthermore, scientists are less likely to find spurious relationships with explanatory variables if they explore mechanisms that transcend regional and national boundaries and that match the spatial scale of the phenomenon they are trying to explain (Mueter et al. 2002), in this case, the downward trends in sockeye productivity shared among numerous southern stocks. Results of such research into mechanisms should provide critical information for managers to choose appropriate responses.

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