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Implications for Research From the Widespread Decrease in Productivity of Sockeye Salmon Populations in Western North America

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Researchers of Pacific salmon (*Oncorhynchus* spp.) have begun to understand how environmental factors such as freshwater and ocean conditions cause changes in abundance and productivity (the latter reflects adults produced per spawner). However, there are still many gaps in that knowledge. One key source of evidence of potential causal mechanisms comes from studies across numerous salmon populations that identify the spatial extent of occurrence of similar temporal variation in productivity (e.g., Botsford and Paulsen 2000). That is, where several salmon populations have positively correlated time trends in productivity, it is likely that they share one or more drivers of those changes (e.g., Myers et al. 1997; Mueter et al. 2002a). Furthermore, environmental variables that vary temporally on similar or larger spatial scales compared to those of salmon productivity are likely to be the most important drivers of changes in that productivity (e.g., Mueter et al. 2002b).

Thus, to extend previous research that applied this multi-population approach, we examined data series as far back as 1950 for 64 mostly-wild populations of sockeye salmon (*O. nerka*) from British Columbia (BC), Washington, and Alaska. We also sought to determine whether the decreases in abundance and productivity observed, especially since the early 1990s for Fraser River, BC, sockeye salmon, have occurred more widely or are restricted to those populations. We examined two measures of productivity that reflect survival processes between spawners and their resulting adult returns (i.e., recruits, which are the offspring that return to the coast prior to fishing). Our first indicator of productivity was $\log_e$(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) spawner-recruit model. That model was $\log_e(R_t/S_t) = a + bS_t + v_t$, 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, parameter 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. Our second measure of productivity came from fitting a "non-stationary" version of the Ricker model in which the a parameter in equation 1 is replaced 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., $a_t = a_{t-1} + w_t$, and $w_t \sim N(0, \sigma_w^2$; 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 to 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 Kalman-filter-estimated a_t values constituted our second measure of productivity. We used this Kalman filter approach to account for observation error in the data as well as natural variability.

Three main findings emerged. First, the declining productivity of Fraser River sockeye has occurred in numerous other sockeye salmon stocks from western North America. Specifically, relatively rapid and consistent decreases in productivity occurred since the late 1990s, and in many cases since the late 1980s or early 1990s, in 24 of the 37 "southern" sockeye salmon stocks. Those "southern" stocks include Puget Sound (Washington), Fraser River, Barkley Sound, BC, Central Coast of BC, North Coast of BC, Southeast Alaska, and Alaska's Yakutat peninsula (inside the ellipse in Fig. 1). In contrast, such decreases have generally not occurred in central or western Alaska (stocks 38-64), where productivity tended to either increase over time or vary around a stable mean. For the stocks that show such decreases in productivity, time trends are qualitatively similar, even though starting dates may differ. Furthermore, a period of temporary increase in productivity through the late 1990s is pronounced in a few stocks.

The widespread downward time trend in sockeye salmon productivity is also reflected in the among-stock correlation analysis and Principal Components Analysis (see Peterman and Dorner 2012 for more details). Because the productivity of most central and western Alaskan sockeye salmon populations generally either increased or remained stable instead of decreasing, their correlations with productivity of southern stocks were mostly negative or near zero.

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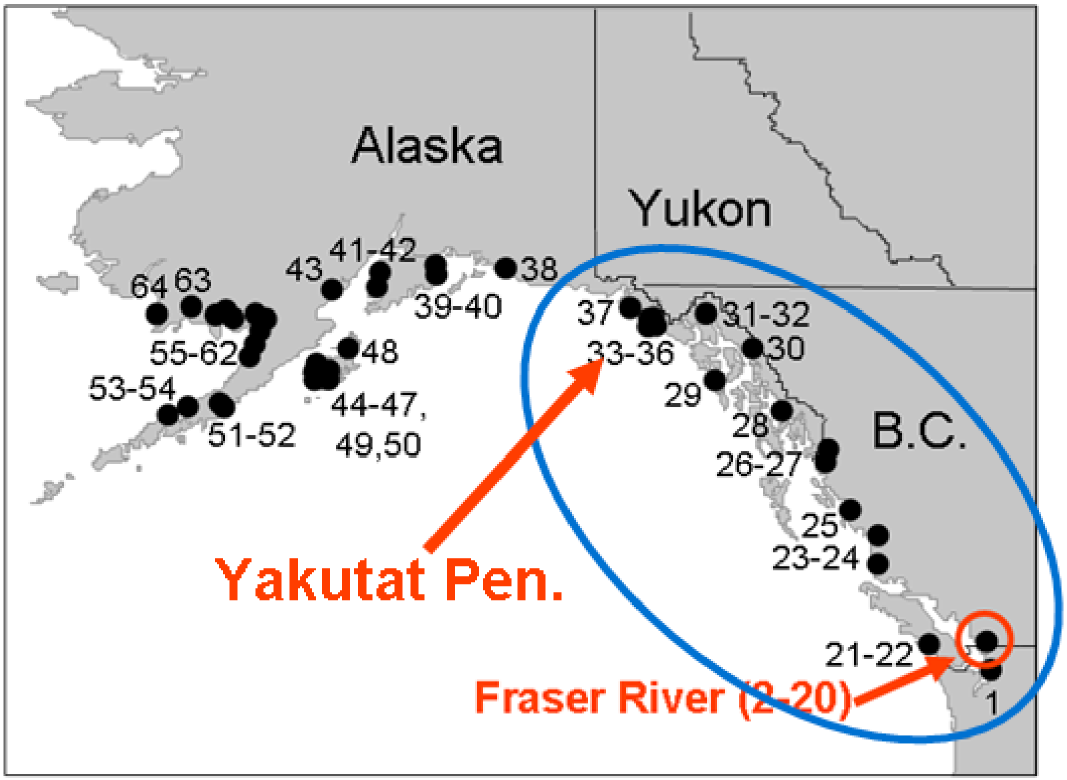

Fig. 1. Locations of ocean entry for seaward-migrating juveniles of the 64 sockeye salmon stocks analyzed here that had lengthy time series data on annual abundances of spawners and their resulting adult recruits. Stock names for each number are given in the Supplementary Information of Table S1 in Peterman and Dorner (2012). Regional groups of stocks include Puget Sound, Washington (1), Fraser River, BC (2-20), Barkley Sound, BC (21-22), Central Coast of BC (23-25), North Coast of BC (26-27), and the following Alaskan stocks: Southeast Alaska (28-32), Yakutat peninsula (33-37), Prince William Sound (38-40), Upper Cook Inlet (41-43), Kodiak (44-50), Chignik (51-52), Alaska Peninsula (53,54), Bristol Bay (55-63), and Arctic-Yukon-Kuskokwim (AYK, 64).

It is conceivable that the decreasing time trends in productivity that appeared across the southern sockeye salmon stocks resulted from a coincidental combination of simultaneous processes related to freshwater habitat degradation, contaminants, pathogens, predators, and/or food supply that have each independently affected particular stocks. However, the large spatial scale of similar time trends in productivity for 24 of the "southern" stocks occurred across a wide range of habitats, ranging from relatively pristine to heavily disturbed areas. This observation suggests that a more likely explanation of the widespread decrease in productivity is that there are shared causal mechanisms across Washington, British Columbia, Southeast Alaska, and the Yakutat region of Alaska.

Our second main finding was that although the positively correlated temporal patterns across numerous "southern" stocks were present in the past (1950-1985 brood years), correlation coefficients have increased since then, especially in the 1995-2004 period. These results indicate that productivity trends have become more synchronized across populations.

Third, and perhaps most importantly, we found that the extent of the positively correlated "southern" area appears to have spread further north over time. This observation suggests that ongoing climate-driven changes may be an important driver of the widespread decreases in productivity.

Our finding of a large spatial extent of changes in productivity of sockeye salmon populations has important implications for research into potential causes of the declines in productivity. Based on our findings, further research into the decreasing productivity of west coast sockeye salmon should look for mechanisms that have three characteristics. (1) The mechanisms should operate at large, multi-regional spatial scales, and/or in marine areas where a large number of the correlated sockeye salmon stocks overlap. (2) The mechanisms should be likely to affect stocks in the geographic range from Puget Sound to Southeast Alaska in a similar way, but may have an inverse effect on stocks from central and western Alaska. (3) The mechanisms should have been present historically, but have intensified in recent years.

Mechanisms consistent with these three criteria include climate-driven increases in freshwater and/or marine mortality induced by pathogens, as well as increases in predation and/or reduced food availability due to oceanographic changes. However, we did not analyze data reflecting those processes. Instead, we leave that to other researchers. We emphasize, though, that 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. At least some of those mechanisms should be ones that operate at large, multi-regional spatial scales.

The large-scale pattern of decreasing productivity also has implications for management agencies. Managers should be cautious about taking management actions based on studies that only examine small-scale local factors that potentially affect salmon productivity. That caution is justified because similar, broader-scale trends in other nearby salmon populations may indicate that such locally-driven efforts may be relatively ineffective, and that resources could be better spent addressing larger-scale processes.

More complete descriptions of methods, results, and implications of this analysis are reported in Peterman and Dorner (2012).

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