Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the Northeastern Pacific
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Abstract

We expand on previous analyses of environmental factors related to productivity of Chinook salmon (Oncorhynchus tshawytscha) populations by analysing data on adult recruits per spawner from 24 wild (not hatchery) Chinook salmon stocks from Oregon through western Alaska. To determine the degree to which changes in productivity are shared and to help identify environmental variables that might be related to those changes, we estimated the magnitude and spatial characteristics of positive correlations in productivity trends among stocks separated by various distances. We used Dynamic Factor Analysis to characterize shared time trends in productivity and found that these trends were most closely associated with the North Pacific Gyre Oscillation (NPGO) and, to a lesser extent, with the location of the bifurcation in the North Pacific Current as it reaches North America's west coast. Chinook productivity patterns of separate populations have also become more synchronous in recent years, similar to results reported for other species of Pacific salmon. Such recent changes may reduce the resilience of the species to effects of climate change and habitat modification.

Introduction

Many Chinook salmon (Oncorhynchus tshawytscha) populations of the northeastern Pacific Ocean have recently experienced declines in abundance and productivity (Riddell et al. 2013; Schindler et al. 2013). The spatial extent and magnitude of these declines have been large enough to stimulate the formation of two separate independent scientific panels. One investigated declines of southern British Columbia (B.C.) Chinook stocks (Riddell et al. 2013), and the other examined Chinook stocks originating in the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska (Schindler et al. 2013). The mechanisms for these declines remain
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under investigation but are thought to be tied to persistent shifts in environmental conditions that affect growth and survival of juveniles in the early ocean life stage (Riddell et al. 2013; Schindler et al. 2013). Indeed, marine conditions for juveniles during that early marine period may play a substantial role in determining productivity of Chinook salmon populations (Sharma et al. 2013; Kilduff et al. 2015), as they do for populations of other salmon species (Peterman 1987; Pyper et al. 2005).

Abundance and productivity of salmon species more broadly (*Oncorhynchus* spp.) in the northeast Pacific Ocean are known to be associated with environmental factors that operate across a range of spatial and temporal scales (Mueter et al. 2002a; Stachura et al. 2014). On short-time scales (i.e., seasonal, annual), high-frequency variation in environmental conditions leads to variation in salmon survival that gives rise to typically noisy recruitment data. Longer, decadal-scale environmental factors such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) are of particular interest to resource users, managers, and scientists because these factors have been associated with longer-term variations in adult recruits per spawner (i.e., number of adult offspring [catches plus spawners] produced per spawner), abundance, and/or catches of salmon (Mantua et al. 1997; Mueter et al. 2007; Petrosky, et al. 2010; Shaller, et al. 2014; Malick et al. 2016; Ohlberger et al. 2016). Substantial changes in these potential drivers of salmon dynamics are important for managers to understand because they can lead to occasional periods of low abundance and reduced catches that cause hardship for human communities reliant on these stocks for food, economic, and cultural reasons. For example, Peterman et al. (2003) showed that optimal harvest rates of sockeye salmon in Bristol Bay, Alaska should change in response to such large shifts in productivities.
Given the critical importance noted above of the early marine life stage in determining adult recruitment in Pacific salmon, a particularly useful approach to understanding causal mechanisms underlying changes in salmon productivity has been to estimate the spatial extent of positive correlations between multiple pairs of time series of productivities in salmon stocks whose points of entry of their juveniles into the ocean are separated by various distances (Pyper et al. 2005). Generally speaking, strong positive covariation in productivity between stocks that share a common habitat for a particular life stage would indicate that environmental conditions in that shared habitat are important for determining productivity. For instance, if productivities of separate salmon populations are positively correlated across only small areas (e.g., 100 km), then that would suggest that regional or local-scale processes are likely the predominant drivers of changes in those productivities. In contrast, if positive correlations in productivities exist across separate salmon populations whose locations of early ocean life stages are separated by large distances (e.g., 1000 km), then that would suggest large-spatial-scale processes are major drivers of changes in productivity. In practice, both local-scale and large-scale drivers may be at work at the same time, and their relative importance will probably differ among populations.

Studies on several species of Pacific salmon have used this approach based on spatial patterns of covariation. For instance, time series of salmon productivity over entire life spans (i.e., recruits per spawner) for different populations of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) were found to co-vary positively at about the 500- to 700-km scale (Peterman et al. 1998; Mueter et al. 2002a,b; Pyper et al. 2005; Malick and Cox 2016). Environmental drivers may explain such spatial scales of variation in salmon productivity. For instance, productivity of pink and sockeye salmon appears to change with the early-summer sea-surface temperature in waters near where juveniles enter the ocean (Mueter et al. 2002a,b). At
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even larger, i.e., ocean-basin scales, climatic phenomena reflected by environmental indices such as the PDO and NPGO likely influence drivers of productivity that affect Chinook salmon catches and early marine survival rates (Mantua et al. 1997; Kilduff et al. 2015; Ohlberger et al. 2016). These large-scale climatic phenomena likely influence to some extent the regional and local-scale conditions experienced by juvenile Chinook salmon as they undergo the critical transition to the marine environment, although the effects of large-scale processes on local conditions and ultimately on salmon productivity may differ among regions (Pyper et al. 2005; Kilduff et al. 2014).

Only a few previous studies have conducted analyses of shared productivity trends for Chinook salmon in the northeast Pacific Ocean. Research based on data from coded wire tagged (CWT) releases from Chinook hatcheries in central California through southeast Alaska has suggested large-scale positive correlation in juvenile Chinook salmon survival rates, with gradually decreasing correlation with increasing distance between ocean entry points for juveniles from each population (Sharma et al. 2013; Kilduff et al. 2014). There also exists substantial residual variation in productivity that is not shared among Chinook stocks, suggesting that regional or local conditions are also important (Sharma et al. 2013). However, these results should be interpreted cautiously because the CWT survival data are based on hatchery, not wild Chinook salmon. They also only reflect marine life stages and thus do not capture temporal variation in freshwater productivity. Similar care should be taken when drawing conclusions from the findings of Hare et al. (1999) about negative associations between the PDO and catches of Chinook salmon at the northern (Alaska) and southern ends (California, Oregon, Washington) of its spatial distribution, because those analyses were based only on numbers of fish caught, which are influenced by harvest regulations and fishing effort, as well as salmon productivity.
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and abundance. Ohlberger et al. (2016) went beyond the limited CWT data and used estimates
of spawners and adult recruits to estimate total life-cycle productivity. They found strong
positive covariation in productivities among Alaskan Chinook salmon populations at the regional
scale. However, their analyses were restricted to Alaskan populations.

Our research objective was to improve upon these past studies of Chinook salmon in four
ways. First, we focused on data from 24 naturally produced ("wild", not hatchery) Chinook
salmon stocks to permit a greater understanding of Chinook survival dynamics without the
confounding influence of hatchery practices (Figure 1; Table 1). Second, these 24 populations
were from regions ranging from Oregon in the south through to western Alaska in the north,
which is a broader geographical range than previously covered in any single study. Third, we
estimated total life-cycle productivity (adult recruits per spawner) based on abundance estimates
for spawners and the resulting recruits. Fourth, we estimated the magnitude and spatial
characteristics of shared productivity trends among stocks and then compared these not only to
PDO and NPGO time series, but also to an index describing the north-south location (latitude) of
the bifurcation in the North Pacific Current as it reaches the west coast of North America. The
latter has shown promise for explaining shared productivity trends in other salmon species
(Malick et al. 2016).

Materials and Methods

Southern data

For the "southern" part of our study area, ranging from Oregon through Southeast Alaska,
we used reconstructed historical abundances of spawners and the resulting adult recruits that
were derived from the Pacific Salmon Commission's (PSC) Chinook coast-wide model (CTC
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These data were provided by Dr. Gayle Brown (Fisheries and Oceans Canada, Nanaimo, B.C., personal communication). The PSC model is a stock assessment and forecasting model that integrates various sources of information, including spawning surveys, juvenile data, tag recoveries, and landings from commercial and sports fisheries, to track the population dynamics of a set of ‘model stocks’. The PSC model stocks correspond either to individual Chinook populations, or, more commonly, to population aggregates that are assumed to share similar characteristics. Because hatchery production of Chinook salmon is a widespread practice throughout this southern part of the study area, most of the PSC model stocks in this region have a substantial hatchery component. However, our aim was to minimize the potentially confounding effect of hatchery enhancement on our estimates of productivity by examining data on wild stocks. Therefore, we limited our analysis for the southern part of our study area to the 10 model stocks for which hatchery contributions were estimated by local biologists to be below 10%. These 10 model stocks that were selected to represent the southern part of the study area span the geographical range from Oregon to the southern tip of Alaska (Table 1). Data from these model stocks typically span 30 years, comprising brood years 1979 to 2008 and ocean-entry years 1980 to 2009. The exception is Harrison, for which data are only available starting in 1984.

Northern data

For the "northern" part of our study area, we used data on 14 wild Chinook salmon stocks that have no hatchery production. These northern stocks span the geographical range from southeast Alaska through central Alaska and to the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska. Data for Alaskan stocks were obtained from the Alaska Department of Fish and
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Game (Steve Fleischman, ADF&G, Raspberry Road, Anchorage, Alaska). Data coverage for the Alaskan data was somewhat less consistent than for the PSC model stocks, with duration ranging from 21 to 34 years, starting between brood years 1973 and 1986 and ending between 2003 and 2008, depending on the stock (Table 1). For the Alaskan Chinook stocks, all but one (Situk River) were stream-type populations consisting mostly of age 1.1, 1.2, 1.3, 1.4, and 1.5 individuals (i.e., fish that spent one winter in fresh water and between 1 and 5 winters in the ocean). Fleischman et al. (2013) estimated abundances of spawners and recruits for these Alaskan Chinook stocks by fitting Ricker stock-recruitment models for each stock using a Bayesian age-structured state-space model with an embedded abundance reconstruction process. Inputs to the Fleischman et al. (2013) analysis included each stock's unique mix of weir counts, tower counts, aerial surveys, direct mark-recapture exploitation rate estimates, and catch estimates. The catch estimates were taken from daily trip tickets summed across the entire year. Subsistence harvests were tallied from post-season surveys, and sport harvest was estimated from mail surveys.

Chinook salmon exhibit a wide variety of life history traits. Timing of their out-migration to the ocean varies – stream-type Chinook spend their first year in freshwater, whereas ocean-type Chinook migrate to the ocean in their first year. Adult run timing also varies widely; adults may return to their native streams in spring, summer, or fall. In our preliminary analyses, we investigated the potential effect of adult run timing and stream residence time of smolts on productivity trends. These analyses did not show any consistent relationships, indicating either that temporal patterns in productivity were not substantially affected by these life history traits, or that our data were not adequate to discern life history effects (unpublished data). Therefore, we did not differentiate groups of fish by life history for the analyses presented in this paper.
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Indicators of life-cycle productivity

Abundance of adult Chinook recruits \((R)\) is a function of spawner abundance in the parental generation \((S)\), as well as life-cycle productivity, which in turn is determined by fecundity of the parent generation and subsequent survival rates over the entire spawner-to-recruit life cycle. In this study, we used two measures of that life-cycle productivity that we calculated from time series of estimates for \(S\) and \(R\) for each stock.

The first indicator of productivity was \(\log_e(R/S)\), the natural logarithm of the number of adult recruits produced per spawner. However, at high spawner abundances, density-dependent effects can reduce that number of recruits produced per spawner (Ricker 1975). Because we were primarily interested in changes in productivity due to processes other than within-stock, within-brood-year density dependence, we therefore also analyzed a second measure of productivity, one that explicitly accounts for, and factors out, such density-dependent effects. This second measure was the time series of residuals, \(v_t\), from the Ricker (1975) spawner-to-recruit model,

\[
\log_e(R_t/S_t) = a + bS_t + v_t,
\]

where \(S_t\) is the number of spawners in brood year \(t\), \(R_t\) is the nominal number of adult recruits of all ages resulting from those spawners, \(a\) represents the intrinsic productivity of the stock at low spawner abundance, and \(b\) reflects within-stock density-dependent effects. The “Ricker residuals” \(v_t\) were assumed to follow a normal distribution in log space (i.e., \(v_t \sim N(0, \sigma_v^2)\)). These residuals represent changes in productivity attributable to factors other than within-stock density-dependence.
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Other papers on similar topics to ours (e.g., Peterman et al. 2003) have used a Kalman filter to screen out random short-term variability and highlight the underlying longer-term productivity trends. In this paper, the Dynamic Factor Analysis fulfills a similar role.

Supplementary Figure S1 shows the productivity time series for $\log_e(R/S)$ and Ricker residuals that were reconstructed for each stock in their approximate geographical context. Because survival during the year of ocean entry tends to be the most important determinant of year class strength of Pacific salmon (Peterman 1987; Peterman et al. 1998), productivity indicators were aligned by ocean entry year for all analyses in this paper and are also shown aligned by ocean entry year in Figure S1 for this reason.

Shared productivity patterns

We used several methods to identify common productivity trends across stocks within the study area and to determine how widely these trends were shared through space and time. Unless stated otherwise, we conducted analyses for both of the two productivity indicators, $\log_e(R/S)$ and Ricker residuals.

To investigate potential changes in more recent years in the spatial extent and magnitudes of positive correlation among productivity trends of different stocks, as reported for sockeye salmon (Peterman and Dorner 2012), Chinook salmon (Kilduff et al. 2014), and pink and chum salmon (Malick and Cox 2016), we repeated our analyses for two periods, first using data for ocean-entry years 1981 through 2009 (‘full data period’) and then broken up into a pre-1995 and a post-1995 time period. For the following analysis, we limit ourselves to presenting results from the ‘full data period’ and the 1995 through 2009 period (‘recent period’), since comparison of
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pre- and post-1995 period did not produce insights that were qualitatively different from those
gained from the comparison of the full period and recent period.

To gain a more nuanced understanding of regional versus larger-scale patterns and reduce
the influence of local fine-scale variability, we also grouped stocks into geographical regions,
based on the geographical location of their ocean entry points.

Our first set of analyses aimed to quantify the spatial extent of covariation in
productivity. We calculated Pearson correlation coefficients between productivity time series for
each pair of Chinook salmon stocks. We then estimated the average within-region correlation by
averaging across the correlation coefficients for all pairs of stocks within a given region. Next,
we calculated correlations between pairs of stocks in which each stock was from a different
region. Then, for each pair of regions, we averaged those pairs of correlations to obtain the
average between-region correlation for those two regions. For example, the strength of the
correlation between Snohomish and Skagit time series serves as a measure of coherence of
productivity patterns within Puget Sound (within-region correlation), whereas the average of two
 correlation coefficients, one for the Snohomish-Washington Coast pairing and the other for the
Skagit-Washington Coast pairing, serves as a measure of similarity between Puget Sound and the
outer Washington coastal area (between-region correlation).

While correlation is useful for measuring degrees of similarity or dis-similarity, other
tools, such as dimensional reduction techniques, are needed to identify and describe the
underlying trends in productivity that are shared through time and space. We experimented with
several dimensional reduction techniques, but we focus on results obtained from a Dynamic
Factor Analysis (DFA, Zuur et al. 2003a) for the main body of this paper, because DFA results
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proved the most informative. In particular, the ability of the DFA to handle missing values
gracefully was a key asset in working with a dataset containing both missing values and
coverage periods that did not fully overlap. For interested readers, results from a Principal
Components Analysis, another dimensional reduction technique, are presented as part of the
Supplementary Material.

DFA is a variation on factor analysis specifically developed for time series data. It has
been applied in fisheries research (e.g., Zuur et al. 2003b; Strachura et al. 2014; Ohlberger et al.
2016). The objective is to express the original set of multiple time series \( y_t \) as a linear
combination of a smaller number of shared factors, or hidden ‘trends’ \( x_t \), i.e.,

\[
y_t = Zx_t + \alpha + \nu_t \quad \text{where} \quad \nu_t \sim \text{MVN}(0, P),
\]

where \( Z \) is a matrix of factor loadings, \( \alpha \) is a vector of offsets, and \( \text{MVN}(0, P) \) is a multivariate normal
distribution with mean \( 0 \) and variance-covariance matrix \( P \) (Holmes et al., 2014). Note that \( \alpha \) is
zero in our case, since our input time series were scaled to a mean of zero and standard deviation
of 1.

DFA incorporates the concept of temporal continuity by modeling the trends as smooth
random walks, i.e.,

\[
x_t = x_{t-1} + w_t \quad \text{where} \quad w_t \sim \text{MVN}(0, I) \quad \text{and} \quad x_0 \sim \text{MVN}(0, 5I),
\]

with \( I \) being the identity matrix. DFA allows for a range of different assumptions about the number of common trends,
structure of the variance-covariance matrix \( P \), and covariates, the combinations of which result in
competing DFA models. These alternative models can be compared using the Akaike
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Information Criterion with small sample correction ($\text{AIC}_c$). We tested DFA models with two different formulations of the variance-covariance matrix, namely a diagonal matrix with equal variance or a diagonal matrix with unequal variance. Because Zuur et al. (2003b) caution that using diagonal forms of $P$ may result in trends only related to a small subset of time series, we also initially considered models with non-diagonal structure for $P$. These proved hard to fit because of convergence problems and ultimately had to be dropped from the analysis. Regardless of the above caution, in our case, results for models with diagonal structure for $P$ resulted in trends that were relevant to the majority of productivity-index time series.

We used the R package MARSS (Holmes et al. 2014) in conjunction with constraints and initial values proposed by Zuur et al. (2003a, see also Holmes et al. 2014) to fit consecutive DFA models with an increasing number of trends, from 1 up to a maximum of 7, at which point $\text{AIC}_c$ values became successively and consistently larger for both productivity indices, indicating that the simpler models were a better representation of the data.

The DFA model coefficients estimated by MARSS represent just one of many equivalent solutions for the hidden trends and associated loadings. Other equivalent solutions can be obtained by factor rotation. Here, we show trends and factors resulting from the varimax rotation (see Holmes et al. 2014 for computational details). The varimax rotation creates the largest difference in factor loadings, thereby aiming for a combination of factors and trends where time series tend to be most closely associated with a small number of leading trends, which makes results easier to interpret.

Note that the varimax rotation does not result in a set of trends ranked in order of explanatory power. Instead, the importance of individual trends is inferred from the loadings.
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(i.e., the numerical values of the coefficients). Thus, for example, a trend that has positive
loadings throughout the study area represents a productivity pattern that is shared widely among
Chinook stocks, and the magnitude of the loadings can be used to infer both the explanatory
power of this trend, and the degree to which individual stocks share the trend.

Relationships with environmental indices

We also investigated potential links between productivity trends and large-scale
atmospheric indices and ocean circulation patterns. We included the Pacific Decadal Oscillation
(PDO, Mantua et al. 1997) and the ‘spring’ North Pacific Gyre Oscillation (NPGO, Di Lorenzo
et al. 2008), which was calculated by averaging monthly values for January to June of each year
(www.o3d.org/npgo). The PDO and NPGO are the two dominant modes of North Pacific
atmospheric variability as expressed through impacts on sea surface temperature and sea-surface
height, respectively. Both indices go through decadal-scale oscillations between below-average
and above-average values, both have been associated with changes in ocean productivity and
hence food availability, and both have been linked to productivity of Chinook and other salmon
species (e.g., Mantua et al. 1997; Kilduff et al. 2015). In addition to PDO and NPGO, we
included another index that captures an important aspect of ocean circulation patterns in the
North Pacific, namely the ‘Bifurcation’ index, ‘BI’. The BI represents annual changes in the
north-south location of the bifurcation of the North Pacific Current as it approaches the west
coast of North America. The BI was estimated using the OSCURS model (Ingraham 1997) as
described in Malick et al. (2016), a paper that contains further details on the derivation of ‘BI’.
In their analysis of productivity patterns for pink, chum, and sockeye salmon, Malick et al.
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(2016) found ‘BI’ to be a potentially important explanatory variable for shifts in productivity. The effect of ‘BI’ in that study was comparable in magnitude to that of the NPGO.

We evaluated the respective ability of PDO, NPGO, and BI to explain regional or basin-scale variability in Chinook salmon productivity observed in our dataset by correlating these three environmental values with shared salmon productivity trends obtained from the DFA analysis.

Results

Correlations between productivity index time series

For the ‘full data period’ (ocean entry years 1981-2009), correlation matrices for both productivity indices indicated that Chinook populations tended to exhibit more positive than negative pairwise correlations in productivity patterns throughout the entire study area, from Oregon to western Alaska (Figure 2a for log(R/S), Figure 3a for Ricker residuals). For this period, average correlations between pairs of individual stocks were 0.23 for log(R/S) and 0.13 for Ricker residuals (Table 2). The average of between-region correlations for this period was 0.27 for log(R/S) and 0.18 for Ricker residuals (Table 2). Stocks within the same region tended to have stronger positive correlation than stocks in different regions, averaging 0.37 for log(R/S) and 0.26 for the Ricker residuals (Table 2).

The strongest regional coherence for stocks was observed at the southern limit and the northern limit of the study area, whereas stocks in the central part of the study area (from Puget Sound to Southeast Alaska (SEAK)) tended to show less coherence and also less similarity with stocks to the north or south (Figure 2a, Figure 3a). Some stocks, most notably Unalakleet (in the AYK area), and also the three southeast Alaska stocks (Situk, Alsek, and South SE), stood out.
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consistently as having distinct patterns in the results -- patterns that were predominantly negatively correlated with patterns for other stocks in the study area (Figure 2a, Figure 3a).

However, the correlation matrices did not clearly indicate larger spatially defined groups that have regionally coherent patterns and that were also distinct or diverging from time series in other regions.

For the recent period (1995 – 2009), overall spatial patterns of similarity largely matched those for the full period (Figure 2b, Figure 3b), although average correlations for all productivity indices were moderately higher in the recent period compared to the full period of 1981-2009 (Table 2), indicating overall stronger coherence in productivity trends in the most recent years.

Such higher correlations are also evident graphically through the greater prevalence of darker blue cells in the correlation matrices for the recent period (Figure 2b, Figure 3b) compared to those for the entire period (Figure 2a, Figure 3a). Unalakleet's negative correlations stood out even more strongly in the recent period as an exception to the patterns of predominantly positive correlations (Figure 2b, Figure 3b).

**DFA**

The DFA analysis resulted in a best-fit model for the full data period (1981-2009) with 6 trends for $\log_e(R/S)$ (Figure 4) and 4 trends for Ricker residuals (Figure 5; see Supplementary Table S1 for a full ranking of models by AIC$_c$ value). For both measures of productivity, the best model was based on a diagonal covariation matrix with unequal variance terms.

Loadings were predominantly positive throughout the study area for DFA-derived Trends 1, 3, and 6 for $\log_e(R/S)$ (Figure 4), as well as Trends 1 and 4 for the Ricker residuals (Figure 5). These numerous positive loadings indicate that there are aspects of those temporal productivity
patterns that are widely shared across the broad study area. This finding matches the general conclusion from the correlation analysis (Figure 2 and Figure 3), which indicated that correlations between productivity index time series are mostly positive throughout the area we considered. The Alsek and Situk stocks stand out in addition to Unalakleet; in this case, these stocks have negative loadings on Trend 1 in the best-fit DFA model for Ricker residuals, which correspond with the results from the correlation analysis for Ricker residuals (Figure 3).

The relatively large number of DFA trends identified for the 1981-2009 period indicates that there was considerable diversity among stocks in productivity patterns throughout the study area during this period. As indicated by the loadings, most trends were not strongly associated with unique geographically defined regions, although some trends were more prominent in certain parts of the study area than in others. Most notable in this latter respect are Trend 5 for log e(R/S) (Figure 4) and Trend 2 in the best-fit DFA model for the Ricker residuals (Figure 5). Both of these trends show an increase in productivity through the 1980s followed by a period of decline and then another sustained increase after 2000 (Figure 4 and Figure 5). The strongest loadings for these trends occur for stocks in the ‘central’ part of the study area (from Puget Sound to Southeast Alaska). The loadings are negative in this case, meaning the productivity pattern actually observed for those stocks is opposite to the one expressed in the DFA trends.

There were some clear associations in patterns between DFA-derived trends for Ricker residuals and DFA-derived trends for log e(R/S). Trend 1 for the Ricker residuals (Figure 5) is positively correlated with Trend 2 for log e(R/S) (r = 0.59, p < 0.001, Table 3a) and negatively correlated with Trend 4 for log e(R/S) (r = -0.79, p < 0.001, Table 3a). Trend 2 for the Ricker residuals is positively correlated with Trend 5 for log e(R/S) (r = 0.74, p < 0.001, Table 3a), while Trend 3 for the Ricker residuals is negatively correlated with Trends 1 (r = -0.56, p = 0.001), 3
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\( r = -0.67, \ p < 0.001 \), and \( 4 \ (r = -0.66, \ p < 0.001) \) for \( \log_e(R/S) \) (Table 3a). Finally, Trend 4 for the Ricker residuals, which is primarily characterized by a steep decline in productivity starting around the year 2000, is correlated with Trends 1, 4, 5, and especially Trend 6 for \( \log_e(R/S) \) (all \( r \) values \( \geq 0.7 \) and \( p \)-values < 0.001, Table 3a).

The DFA for the recent period (1995-2009) indicated stronger coherence in productivity trends among stocks, as well as less variety among them, compared to the full data period. The best-fit DFA models of the recent period for both productivity indices had covariation matrices with equal variance terms (Supplementary Tables S1c and S1d). The best DFA model for \( \log_e(R/S) \) for the recent period had only a single trend (Trend 1R), and that trend showed a decline starting around ocean-entry year 2000 followed by a period of recovery after 2005 (bottom left panel of Figure 4). That Trend 1R had a similar shape to the post-1995 part of Trends 1 and 2. Loadings for this Trend 1R for the recent period (bottom right panel of Figure 4) were much more consistently and strongly positive across almost all stocks than loadings for the DFA Trends 1-6 that were derived from data over the entire period (top six right-hand panels of Figure 4). Exceptions to these positive loadings for Trend 1R were negative loadings for Alsek and, most notably, Unalakleet.

The best DFA model for Ricker residuals for the recent period had two trends (bottom left panels in Figure 5). Trend 1R shows an initial increase in productivity through the second half of the 1990s, followed by a brief period of high productivity until 2002, and then a steep decline. Similar to the loadings shown in Figure 4 for Trend 1R of \( \log_e(R/S) \), the loadings on Trend 1R for the Ricker residuals were consistently positive across 21 of the 24 stocks, with Situk, Alsek, and especially Unalakleet standing out as the only stocks with negative loadings.

Trend 2R identified in the best-fit model for Ricker residuals in the recent period differed from
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The residuals' Trend 1R in two key respects: the clear increase through the second half of the 1990s in Trend 1R is missing, and there is a strong recovery after 2005 in Trend 2R. This aspect of pattern captured in Trend 2R is expressed most strongly through central Alaska (Alsek and Situk through to Karluk and Ayakulik), whereas negative loadings predominate for stocks in British Columbia and parts of Southeast Alaska.

Relationship with environmental indices

We calculated Pearson correlation coefficients to estimate the strength of correlation between DFA trends from the best-fit DFA models and the three environmental indices. The strongest and most consistent relationship was for the North Pacific Gyre Oscillation (NPGO). For the full data period (1981-2009), NPGO was most strongly correlated with DFA Trend 2 for log$_e$(R/S) and Trend 1 for the Ricker residuals (correlation coefficients 0.57 and 0.59, respectively, \( p < 0.001 \) and \( p = 0.001 \), Table 4a). We also found somewhat weaker (inverse) correlations between the Pacific Decadal Oscillation (PDO) and Trends 1 and 2 for Ricker residuals \( r = -0.41 \) and \(-0.45 \), respectively, \( p = 0.025 \) and \( p = 0.015 \), Table 4a), as well as Trend 4 for log$_e$(R/S) \( r = -0.48 \), \( p = 0.009 \), Table 4a). The bifurcation index of the North Pacific Current (BI) was most strongly correlated with Trends 1 and 4 of the Ricker residuals \( r = 0.41 \) and \(-0.40 \), respectively, \( p = 0.028 \) and 0.032).

For the recent data period (1995 – 2009), NPGO was correlated with Trend 1R for the Ricker residuals as well as the sole Trend 1R for log$_e$(R/S), with coefficients in strength similar to those observed for the entire data period \( 0.60 \) and \( 0.56 \), respectively, \( p = 0.018 \) and \( p = 0.031 \) Table 4b), whereas BI was most strongly correlated with Trend 2 of the Ricker residuals \( -0.47 \), \( p = 0.075 \), Table 4b). Trends for the recent period were only weakly correlated with the PDO,
suggesting that PDO had little influence on Chinook productivity in that period (Table 4b).

Figure 6 illustrates in graphical form the relationship between NPGO and the DFA time series most strongly associated with the NPGO. Recall that for the recent period, the loadings for the two Chinook productivity trends labeled 1R shown in Figure 6b are predominantly positive throughout the study area (Figure 4 and Figure 5), indicating that these two trends represent patterns that are widely shared among Chinook salmon populations.

Discussion

One of the biggest challenges facing fisheries scientists and managers is the non-stationarity of stock productivity (i.e., where the mean and/or variance changes substantially over time) (Walters 1987). Regardless of whether such changes occur because of altered ocean or freshwater conditions, the success of efforts to sustainably manage Pacific salmon harvests and rebuild low-abundance populations depends on understanding the causes of changes in salmon productivity. Important clues about these causal mechanisms in Pacific salmon can result from analyses that compare time series of productivity indices for numerous stocks from different regions (e.g., Botsford and Paulsen 2000; Mueter et al. 2002a; Pyper et al. 2005; Sharma et al. 2013; Stachura et al. 2014). Similar time trends in productivity across numerous salmon stocks from different regions would suggest that processes that operate at that across-region scale may play an important role in driving productivity patterns. Such large-scale phenomena could be atmospheric conditions that influence the ocean regions shared by the stocks, and/or conditions in widely-separated marine and/or freshwater habitats that are driven by shared atmospheric events. To reflect such broad perspectives, our analysis encompassed wild Chinook populations from more northern areas of Alaska and southern areas of Oregon than in any previous single
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analysis. We also used whole-life-cycle productivity, which also captures freshwater survival, and we focused on wild stocks, not hatchery ones, to avoid confounding our interpretations with hatchery activities.

Our analysis of productivity patterns highlights a substantial degree of temporal variation among Chinook salmon stocks, coupled with a moderate amount of synchrony throughout the study area, ranging from Oregon to western Alaska. There was also relatively little division into distinct regional groups with unique productivity trends. The predominance of positive correlations among even widely separated Chinook salmon stocks of the northeastern Pacific is similar to that found previously for Chinook based on CWT hatchery data (Sharma et al. 2013; Kilduff et al. 2014). There are two interpretations of the observed similarities in productivity patterns across such large distances. Either the similarities are being caused by shared factors that are affecting Chinook stocks throughout the study area in similar ways, or by separate factors that have similar effects on Chinook productivity and that are occurring coincidentally in distant regions of the study area (or both). An example of the latter might be increased predation in one region and decreased salmon food supply in another, both of which would cause reduced productivity. However, the relatively strong correlation between some of the DFA trends and environmental indices suggests that large-scale ocean and atmospheric circulation patterns are likely candidates for drivers of the shared productivity patterns.

Chinook salmon appear to be distinct from other salmon species in exhibiting positive correlations in productivities across most of the species’ distribution. Evidence from pink, chum, and sockeye salmon shows little or no positive covariation at the scale of the whole northeastern Pacific; instead, those three species tend to show positive covariation in productivities at smaller, regional scales (Pyper et al. 2001, 2002, 2005; Peterman et al. 1998; Peterman and Dorner 2012).
In addition, as would be expected based on the greater similarity of physical and biological processes among stocks that spawn, rear, and/or migrate in shared habitats, pairwise correlations for Chinook salmon productivity were higher within regions than between regions for both productivity indicators and both time periods that we analyzed, consistent with the findings of Sharma and Liermann (2010), Sharma et al. (2013), and Ohlberger et al. (2016). However, while the average within-region correlation was very strong for some regions, such as Kodiak Island, other regions such as southeast Alaska and the Fraser River (B.C.) had weak or even negative within-region correlations. Moreover, on average the difference between within- and between-region correlations was only moderate. With the possible exception of the regions at the southernmost (Columbia River) and northernmost (AYK, Kodiak, and Cook) limits of the range, there were also no clearly apparent larger spatially-contiguous regions that stood out as having distinctive and cohesive patterns (Figure 2, Figure 3). This result also contrasts with the findings for pink, chum, and sockeye salmon (Pyper et al. 2001, 2002, 2005; Peterman et al. 1998; Peterman and Dorner 2012), for which there were strong within-region correlations, as well as spatially contiguous areas of covariation at larger scales, although the latter areas did not extend to the scale of the study area as a whole. These differences between Chinook and other salmon species in the degree to which the similarity in productivities is driven by spatial separation distance may result from the much wider range of life-history types (and hence timing and magnitude of exposure to various mortality agents) in Chinook salmon than in other species (Healey 1991).

Our analysis further suggests that temporal patterns in Chinook productivity have become more synchronous in recent years. For both productivity measures, average correlations in productivity across stocks were higher in the recent period (ocean-entry year 1995-2009) than in
the entire data set (1981-2009) (Table 2, Figure 2, Figure 3), and the DFA analyses showed fewer distinct shared trends and more consistent loadings across stocks in that recent period compared to the overall data set (Figure 4, Figure 5). This finding is consistent with results from other studies on Chinook, as well as other salmon species. Specifically, Kilduff et al. (2014) found evidence of stronger covariation among stocks in the area from California to the west coast of Vancouver Island since the mid-1990s compared to the previous period, and Kilduff et al. (2015) documented an increasing synchronicity in productivity patterns for coho as well as Chinook salmon. For sockeye salmon, Peterman and Dorner (2012) showed that time series of productivity for 64 stocks in the northeastern Pacific have also become more coherent since the mid-1990s. Pink and chum salmon in British Columbia and Washington also show evidence of increasingly positive correlations among stocks’ productivities since the early 1990s (Malick and Cox 2016). This tendency for productivities of Pacific salmon stocks to be more synchronous in the most recent decade or more suggests that the relative importance of the different drivers of salmon productivity may have changed in recent years. In particular, factors affecting stocks throughout the study area in a similar way may be exerting a stronger and perhaps more uniform influence now, possibly leaving less scope to see the resilience benefits of the "portfolio effect" (Griffiths et al. 2014) of diverse life histories among populations within given salmon species.

The degree to which productivity patterns in Chinook salmon have become more synchronous has important implications for fisheries. Increased synchronicity can be expected to result in more year-to-year variability in harvest levels and more frequent fishery closures because fewer stock abundances will be high when others are low, especially since the predominant trend in recent years has been towards lower productivity. A steep decline in productivity identified by the DFA in the recent period and starting in the early 2000s was the
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Between 21 and 22 of the 24 stocks tended to have that downward trend, as shown by their positive loadings on Trend 1R for Ricker residuals and Trend 1R for \log_e(R/S) (Figure 4, Figure 5).

Our findings support the conclusion of Kilduff et al. (2015) that broad-scale ocean or climate-driven conditions reflected by NPGO have a substantial effect on Chinook salmon productivity. The NPGO, which is an integrated measure of variability in sea-surface height in the North Pacific, is highly correlated with sea-surface salinity, nitrate, and chlorophyll-a (Di Lorenzo et al. 2008). The NPGO thus may reflect conditions associated with bottom-up processes such as food supply for salmon. This interpretation is consistent with our results for 1981-2009 showing that when the NPGO index is positive, productivity tends to be relatively high for Chinook stocks in the northeastern Pacific (Figure 6a). Although we found a weak correlation between DFA trends and PDO for the full data period, the lack of such a correlation for the recent period further suggests that the importance of the PDO as a driver of Chinook productivity may be decreasing. In contrast, our results suggest that processes associated with the north-south location of the bifurcation (BI) in the North Pacific Current may continue to play a role in driving Chinook productivity, albeit to a lesser degree than processes associated with the NPGO. Interestingly, loadings on Trend 2R, the recent-period trend associated with BI, suggest an opposite pattern for BC and Alaskan stocks, with the change in sign of loadings occurring in southeast Alaska while moving northward across latitude lines. This opposite north-south pattern is reminiscent of the opposite effect of the timing of spring bloom on pink salmon across those northern and southern regions as described in Malick et al. (2015) and also the opposite effects of early-summer sea-surface temperature on BC pink and sockeye salmon.
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populations compared to Alaskan populations (Mueter et al. 2002a). Those intriguingly similar results suggest that there are oceanographic processes important for salmon survival that are different in those two regions, or that large scale processes common to both regions have different effects on factors such as food supply or predator abundance.

Circulation patterns in the Northern Pacific have been changing in recent years, with an observed intensification of the NPGO linked to global warming (Di Lorenzo et al. 2008). As a result of this intensification, we may expect both increased synchronicity in Chinook productivity patterns, as well as more extreme highs and lows of productivity as global warming trends continue. The prognosis of more extreme values, combined with more overall synchronicity in productivity patterns, has important management implications, specifically that a period of reduced productivity for some Chinook salmon populations may not be compensated for by increases in productivity in other stocks, and that periods of coast-wide low Chinook abundance may become a more common occurrence. The predominant management paradigm is not well prepared for this situation, since most salmon management models assume that average productivity (recruits per spawner at a given spawner abundance) is constant, and analysts are generally cautious about revising estimates until several years of data clearly indicate a trend in productivity, as opposed to short-term "noise". We therefore urge salmon scientists to incorporate time-varying productivity and environmental covariates into their analyses. In addition, DFA and other statistical models able to incorporate information from multiple stocks to get a clearer picture of developing shared productivity trends would be useful tools to add to the stock assessment arsenal. We also recommend that managers prepare for the possibility that extended periods of either unusually low or high productivity and abundance of Chinook salmon
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will occur as these populations respond to decadal-scale trends in the oceanic environment that are amplified by climate change.

A key objective for future research should be to gain a better understanding of the links between large-scale circulation patterns and salmon productivities in general and Chinook productivities in particular. For instance, why do Chinook seem to respond relatively more uniformly than other species, what are the causal mechanisms behind the observed relationships, and to what degree are these relationships likely to hold up as circulation patterns change in response to global warming? One avenue towards this goal could be to expand DFA analysis to include the environmental covariates into models and examine patterns of covariation attributable to these covariates, versus as-yet unexplained covariation due to other sources (see Pollock et al. 2014 for a study that utilizes a latent-variable model to look at variability explained by environmental factors versus residual covariation). Another avenue to gain further insights might be to get a better understanding of what distinguishes stocks such as Unalakleet, Situk, and Alsek, which have experienced productivity patterns that differed substantially from the more widely shared trends. Do the productivity time series of these three stocks diverge from those of the majority of stocks because of differences in juvenile run timing, unique geographical and/or biological features of their freshwater or marine habitats, or some other characteristics? Finally, how do these differences affect productivity responses in a way that diverges from the effect of shared drivers?

Acknowledgments

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Current. We also thank Robert A. Clark for comments on the manuscript and David Mackas for pointing out the similarity between the NPGO and our preliminary DFA results. Funding was partly provided by Fisheries and Oceans Canada, the Fraser River Aboriginal Fisheries Secretariat, and the Canada Research Chairs Program, Ottawa.

References


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Table 1. Chinook salmon stocks used in the study. Locations of ocean entry of juveniles of each stock are shown on the map in Figure 1. In the third column, N is the number of brood years of data available.

<table>
<thead>
<tr>
<th>Stock</th>
<th>Region</th>
<th>Brood years (N)</th>
<th>Spawners (1000s)</th>
<th>Recruits/Spawner</th>
</tr>
</thead>
</table>
| Oregon Coast (ORC)
| Oregon Coast (ORCST)       | 1979 - 2008 (30) | 102              | 2.31             | 0.27 - 7.76     |
| Lewis River (LRW)
| Lower Columbia R. (LCOLR)  | 1979 - 2008 (30) | 11               | 2.26             | 0.37 - 15.14    |
| Lyons Ferry (LYF)
| Mid- and Upper Columbia R. (M&U.COLR) | 1979 - 2008 (30) | 1                | 5.01             | 2.37 - 13.53    |
| Washington Coastal        | Washington Coast (WACST)                    | 1979 - 2008 (30) | 24               | 3.05             | 1.09 - 8.55     |
| Snohomish (SNO)
| Puget Sound (PGSD)         | 1979 - 2008 (30) | 4                | 2.68             | 0.73 - 4.21     |
| Skagit (SKG)
| Puget Sound (PGSD)         | 1979 - 2008 (30) | 13               | 1.48             | 0.40 - 6.63     |
| Harrison (HAR)
| Fraser River (FRASER)      | 1984 - 2008 (25) | 98               | 1.43             | 0.11 - 10.50    |
| Fraser Early (FRE)
| Fraser River (FRASER)      | 1979 - 2008 (30) | 102              | 1.71             | 0.77 - 5.85     |
| North/Central BC (NTH)
| North and Central BC (N&CBC)| 1979 - 2008 (30) | 154              | 2.13             | 1.43 - 3.61     |
| Stikine (STK)
| BC-Alaska Trans-boundary Region (TBR) | 1981 - 2005 (25) | 32               | 1.07             | 0.39 - 5.18     |
| Taku (TKU)
| BC-Alaska Trans-boundary Region (TBR) | 1973 - 2006 (34) | 44               | 1.17             | 0.30 - 3.58     |
| AK South SE (AKS)
| Southeast Alaska (SEAK)    | 1979 - 2008 (30) | 14               | 1.51             | 0.23 - 4.47     |
| Situk (SIT)
| Southeast Alaska (SEAK)    | 1982 - 2007 (26) | 1                | 2.15             | 0.48 - 12.60    |
| Alsek (ALS)
| Southeast Alaska (SEAK)    | 1976 - 2003 (28) | 9                | 0.97             | 0.40 - 2.79     |
| Deshka (DES)
| Cook Inlet (COOK)          | 1979 - 2006 (28) | 26               | 1.08             | 0.12 - 5.26     |
| Anchor (ANC)
| Cook Inlet (COOK)          | 1977 - 2008 (32) | 9                | 1.18             | 0.33 - 1.99     |
| Karluk (KAR)
| Kodiak (KODIAK)            | 1976 - 2007 (32) | 9                | 0.97             | 0.15 - 2.75     |
| Ayakulik (AYA)
| Kodiak (KODIAK)            | 1976 - 2007 (32) | 9                | 1.34             | 0.13 - 6.60     |
| Yukon (YUK)
| Arctic-Yukon-Kuskokwim (AYK)| 1982 - 2006 (25) | 50               | 2.52             | 0.83 - 5.89     |
| Kuskokwim (KSK)
| Arctic-Yukon-Kuskokwim (AYK)| 1976 - 2007 (32) | 160              | 1.62             | 0.50 - 5.67     |
| Goodnews (GDN)
| Arctic-Yukon-Kuskokwim (AYK)| 1981 - 2007 (27) | 6                | 1.45             | 0.36 - 3.27     |
| Chena/Salcha (CHS)        | Arctic-Yukon-Kuskokwim (AYK)               | 1986 - 2006 (21) | 16               | 1.83             | 0.44 - 10.17    |
| Unalakleet (UNA)
<p>| Arctic-Yukon-Kuskokwim (AYK)| 1985 - 2006 (22) | 3                | 2.35             | 0.62 - 7.53     |</p>
<table>
<thead>
<tr>
<th></th>
<th>Arctic-Yukon-Kuskokwim (AYK)</th>
<th>1976 - 2007 (32)</th>
<th>4</th>
<th>1.75</th>
<th>0.43 - 6.59</th>
</tr>
</thead>
</table>

Majority of juveniles exhibit an ocean-type life history

Majority of juveniles exhibit a stream-type life history

Source: Pacific Salmon Commission (Dr. Gayle Brown, Fisheries and Oceans Canada, Nanaimo, B.C.)

Source: Alaska Department of Fish & Game (Steve Fleischman, Raspberry Road, Anchorage, Alaska)

* The Chena and Salcha River stocks were treated as one stock for the purposes of this analysis because harvests that were taken in the middle Yukon River could not be assigned with confidence to either of these two stocks in a given year.
Table 2. Average correlations among productivity index time series.

<table>
<thead>
<tr>
<th>Productivity index</th>
<th>Between pairs of stocks</th>
<th>Between regions</th>
<th>Within-regions</th>
</tr>
</thead>
<tbody>
<tr>
<td>log(R/S)</td>
<td>0.23</td>
<td>0.24</td>
<td>0.27</td>
</tr>
<tr>
<td>Ricker residuals</td>
<td>0.13</td>
<td>0.18</td>
<td>0.18</td>
</tr>
</tbody>
</table>
Table 3. Correlations between trends derived from the best-fit DFA model for $\log_e(R/S)$ and for the Ricker residuals for (a) the entire data period and (b) the recent data period.

(a) Entire data period, 1981-2009 brood years.

<table>
<thead>
<tr>
<th>Ricker Residuals</th>
<th>Log$_e$(R/S)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trend1</td>
<td>Trend1</td>
</tr>
<tr>
<td>Trend1</td>
<td>-0.40</td>
</tr>
<tr>
<td>Trend2</td>
<td>-0.30</td>
</tr>
<tr>
<td>Trend3</td>
<td>-0.56</td>
</tr>
<tr>
<td>Trend4</td>
<td>0.70</td>
</tr>
</tbody>
</table>

(b) Recent data period, 1995-2009 brood years.

<table>
<thead>
<tr>
<th>Ricker Residuals</th>
<th>Log$_e$(R/S)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trend1R</td>
<td>Trend1R</td>
</tr>
<tr>
<td>Trend2R</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Correlations between trends derived from the best-fit DFA model and the environmental indices NPGO (North Pacific Gyre Oscillation), PDO (Pacific Decadal Oscillation), and BI (bifurcation index), shown for (a) the entire data period, and (b) the recent data period.

(a) Entire data period, 1981-2009 brood years.

<table>
<thead>
<tr>
<th></th>
<th>Log$_e$(R/S)</th>
<th>Ricker Residuals</th>
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<tbody>
<tr>
<td></td>
<td>Trend1</td>
<td>Trend2</td>
</tr>
<tr>
<td>NPGO</td>
<td>0.19</td>
<td>0.57</td>
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<tr>
<td>PDO</td>
<td>0.01</td>
<td>-0.03</td>
</tr>
<tr>
<td>BI</td>
<td>-0.14</td>
<td>0.21</td>
</tr>
</tbody>
</table>

(b) Recent data period, 1995-2009 brood years.

<table>
<thead>
<tr>
<th></th>
<th>Log$_e$(R/S)</th>
<th>Ricker Residuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trend1R</td>
<td>Trend2R</td>
</tr>
<tr>
<td>NPGO</td>
<td>0.56</td>
<td>0.60</td>
</tr>
<tr>
<td>PDO</td>
<td>-0.17</td>
<td>0.10</td>
</tr>
<tr>
<td>BI</td>
<td>-0.19</td>
<td>-0.10</td>
</tr>
</tbody>
</table>
Figure captions for the main text

**Figure 1.** Ocean entry locations for the 24 Chinook salmon stocks included in the study. For further information on individual stocks, see Table 1.

**Figure 2.** Graphical summary of correlations between pairs of productivity time series (productivity estimated by \( \log_e(R/S) \)) for Chinook stocks. Positive correlations are shown in shades of blue, negative correlations in shades of red, with darker, more saturated shades indicating stronger correlations. The top part of the figure (panel a) shows correlation coefficients calculated for the full data period (ocean entry years 1981-2009); panel b below shows coefficients calculated for the recent period (ocean entry years 1995-2009). Thick black lines separate pairings of stocks from within the same region (to the right and below the line) from pairings of stocks originating from different regions. The large matrix on the left of each panel shows correlation coefficients for individual pairs of stocks, whereas the smaller matrix on the right shows correlations between pairs of regions.

**Figure 3.** Graphical summary of correlations between pairs of productivity time series (productivity estimated by Ricker residuals) for Chinook stocks. See Figure 2 for further details.

**Figure 4.** Time trends (left column) and associated stock-specific loadings (right column) derived from the best-fit DFA model for the time series of \( \log_e(R/S) \). The top model for the full data period (1981-2009) had 6 trends, shown in the first 6 panels on the left of the figure, whereas the top model for the recent period (1995-2009)
had 1 trend (Trend 1R shown below the trends for the full data period). The x-axis of the time series shows ocean entry year.

**Figure 5.** Time trends (left column) and associated stock-specific loadings (right column) derived from the best-fit DFA model for the time series of Ricker residuals. The top model for the full data period (1981-2009) had 4 trends, shown in the first 4 panels on the left of the figure, whereas the top model for the recent period (1995-2009) had 2 trends (1R and 2R shown at the bottom left below the trends for the full data period). The x-axis of the time series shows ocean entry year.

**Figure 6.** Comparisons of the North Pacific Gyre Oscillation (NPGO) with productivity patterns of Chinook salmon for (a) the full period of data, brood years 1981-2009 and (b) for just the most recent period, 1995-2009. Salmon productivity trends in this figure were those estimated by Dynamic Factor Analysis (DFA) from data on $\log_e(R/S)$ and residuals from the best-fit Ricker stock-recruitment model (Figs. 4 and 5, respectively).
(a) 1981 - 2009

(b) 1995 - 2009