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Changing central Pacific El Niños reduce stability of North American salmon survival rates

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Pacific salmon are a dominant component of the northeast Pacific ecosystem. Their status is of concern because salmon abundance is highly variable—including protected stocks, a recently closed fishery, and actively managed fisheries that provide substantial ecosystem services. Variable ocean conditions, such as the Pacific Decadal Oscillation (PDO), have influenced these fisheries, while diminished diversity of freshwater habitats have increased variability via the portfolio effect. We address the question of how recent changes in ocean conditions will affect populations of two salmon species. Since the 1980s, El Niño Southern Oscillation (ENSO) events have been more frequently associated with central tropical Pacific warming (CPW) rather than the canonical eastern Pacific warming ENSO (EPW). CPW is linked to the North Pacific Gyre Oscillation (NPGO), whereas EPW is linked to the PDO, different indicators of northeast Pacific Ocean ecosystem productivity. Here we show that both coho and Chinook salmon survival rates along western North America indicate that the NPGO, rather than the PDO, explains salmon survival since the 1980s. The observed increase in NPGO variance in recent decades was accompanied by an increase in coherence of local survival rates of these two species, increasing salmon variability via the portfolio effect. Such increases in coherence among salmon stocks are usually attributed to controllable freshwater influences such as hatcheries and habitat degradation, but the unknown mechanism underlying the ocean climate effect identified here is not directly subject to management actions.

salmon | synchrony | persistence | North Pacific Gyre Oscillation | Pacific Decadal Oscillation

Understanding the influence of nonstationary climatic shifts on the productivity and persistence of populations is a key challenge to successful management of harvested marine and anadromous resources (1). Management of Pacific salmon fisheries in the United States and Canada exemplifies the challenges posed by climatic shifts; managers must set harvests for some stocks while protecting stocks at risk. The influence of variable survival of juvenile salmon after ocean entry complicates decision making, with increasing variability generally increasing population risk. As an example of this variability, poor ocean productivity was largely responsible for an unprecedented complete closure of the Chinook salmon fisheries in California and southern Oregon when extremely low numbers returned to spawn in 2008 and 2009 (2).

Salmon management is unique in that it focuses on stocks comprising identifiable separate populations in individual spawning streams. Recent studies show that increased covariability in abundance among separate populations of Chinook salmon has increased coherence of salmon stocks, thus increasing aggregate variability of the stocks through the portfolio effect (3–5). These effects of declining diversity among salmon subpopulations are an example of the general global concern for the loss of biodiversity in many forms (e.g., loss of genes, species, within-species variability) and its effects on ecosystem services (6–10). The portfolio effect has been a useful way of quantifying the effects on aggregate population variability in salmon stocks in terms of the loss of diversity among populations spawning in different streams (3, 4, 11). The recently detected increased

coherence of salmon populations, and associated increases in aggregate population variability, and, thus, increased risk, have generally been attributed to declining biocomplexity of freshwater habitats due to the increase in hatcheries, dams, and stream habitat homogenization (3–5, 12, 13). However, the extent to which responses to physical oceanographic conditions in the marine phase of salmon life limit the scope for reducing population variability through the portfolio effect has not been considered. We analyzed early ocean survival of hatchery coho salmon from 72 hatcheries and Chinook salmon from 104 hatcheries along western North America from central California to southeast Alaska between 1980 and 2006 using coded wire tag (CWT) data (14, 15) to show how a climatic shift has influenced the coherence in survival rates of two important salmon species in the northeast Pacific Ocean (Fig. S1).

In recent decades, El Niño events have been characterized by central Pacific warming (CPW) events more frequently than eastern Pacific warming (EPW) events typically associated with El Niño (16, 17). El Niño events drive a large fraction of both interannual and decadal variability in the northern Pacific Ocean (18), but CPW and EPW events excite different teleconnections to the northern Pacific Ocean. EPW events drive fluctuations in the North Pacific Ocean by intensifying the variance of the wintertime Aleutian Low pressure cell (19), which, in turn, drives the Pacific Decadal Oscillation (PDO). CPW events, however, influence northern Pacific Ocean climate differently by influencing

Significance

Historically, many Pacific salmon species were thought to be influenced by the Pacific Decadal Oscillation (PDO), an indicator of ocean conditions, associated with El Niños. As the nature of El Niños has changed recently, another ocean indicator, the North Pacific Gyre Oscillation (NPGO) has become more important. By comparing time series, we find that coho and Chinook salmon survival rates along the west coast of North America are more strongly connected to the NPGO than the PDO. This was accompanied by increased similarity in survival rates of both species. Society seeks to maintain biodiversity among ecosystem components to provide a stable supply of ecosystem services through a portfolio effect. Increasingly similar salmon survivals implies reduced stability of these ecosystem services.
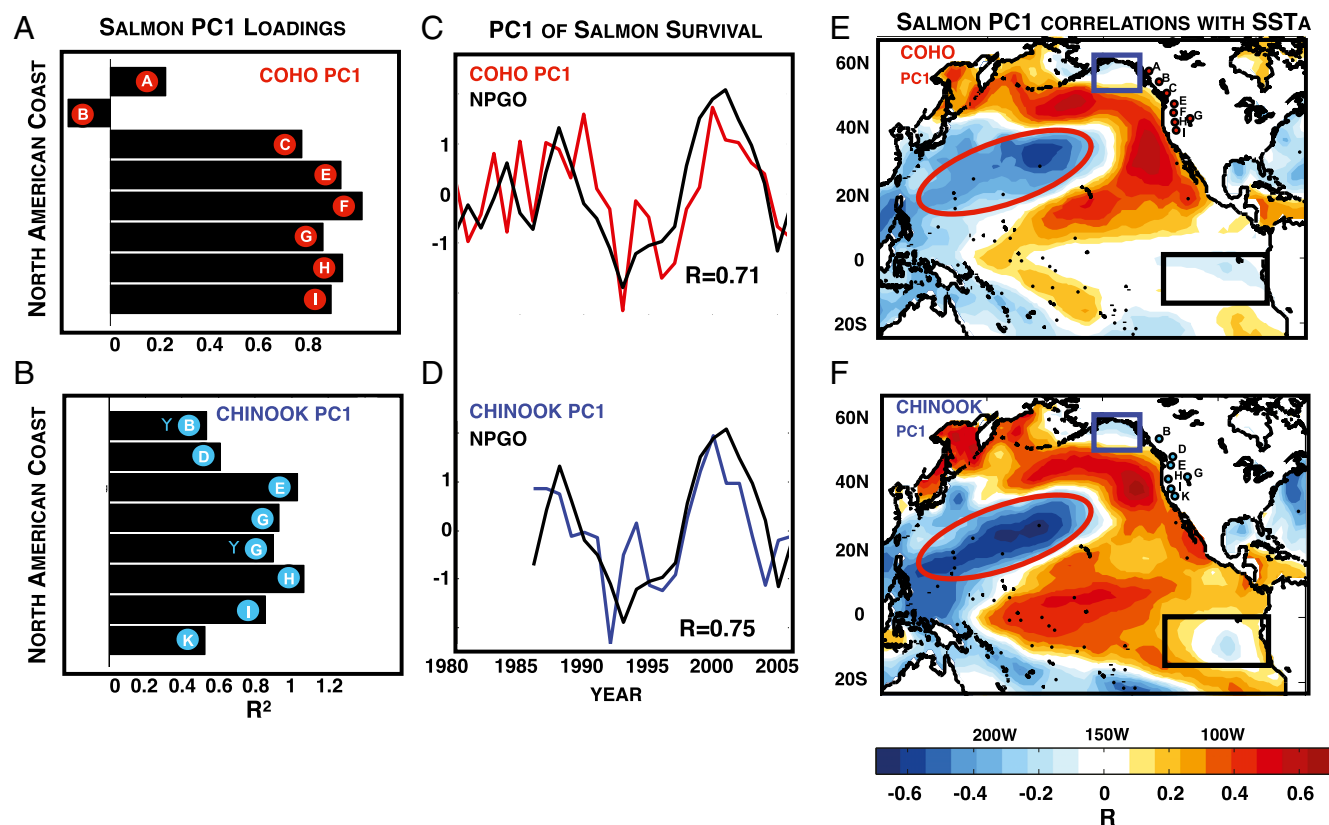
Fig. 1. Loadings on the first principal component from regional time series of (*A*) coho salmon and (*B*) Chinook salmon indicate alongshore coherence (filled colored circles contain geographic regions indicated in Fig. S1). Dominant modes of variability in (*C*) coho (red line, coho-PC1) and (*D*) Chinook (blue line, Chinook-PC1) salmon survivals are significantly correlated with the annual NPGO signal (black). This coherence is also seen in spatial correlation maps of (*E*) coho and (*F*) Chinook PC1s with mean January–March SSTas. In *E* and *F*, the blue and black rectangles and the red oval highlight spatial patterns consistent with NPGO-type variability.

the North Pacific Oscillation (NPO), which, in turn, modulates the strength of the North Pacific Current indexed by the North Pacific Gyre Oscillation (NPGO) (17). This shift in El Niño signals influences teleconnections to the northern Pacific Ocean, with less variability ascribed to PDO, which is the dominant mode of northern Pacific Ocean low-frequency variability, and an increasing fraction to the second mode of low-frequency variability, the NPGO (17, 20, 21). Because the PDO explained important shifts in salmon productivity in the past (22), the increased variability related to the NPGO raises the question of how it affects salmon productivity.

Results

Survival time series (see Tables S1 and S2) derived from CWT show a spatially coherent dominant mode of early ocean salmon survival since 1980 in both coho and Chinook salmon (14, 15) (Fig. 1). The dominant spatial principal components of both coho and Chinook salmon survival indicate synchronous variability along the coast in each species (Fig. 1 *A* and *B*). First principal components account for 42.0% and 43.8% of the variability in coho (coho-PC1) and Chinook (Chinook-PC1) salmon survivals, respectively. Loadings on Chinook-PC1 have similar values from north coastal Oregon to north coastal Washington, with lower loadings from the southernmost and northernmost regions (Fig. 1*B*). All loadings on coho-PC1 are positive, with similar magnitudes from southern coastal Oregon to the west coast of Vancouver Island, whereas loadings from southeast Alaska are lower (Fig. 1*A*).

Correlation analyses indicate that the dominant mode of low-frequency variability in survival of both coho and Chinook salmon is better explained by the NPGO (Fig. 1 *C* and *D*, $\rho_{coho\_NPGO} = 0.71$, *P* value < 0.01; $\rho_{chinook\_NPGO} = 0.75$, *P* value < 0.05) than by the PDO (Figs. S2 and S3, $\rho_{coho\_PDO} = -0.41$, *P* value > 0.05; $\rho_{chinook\_PDO} = -0.40$, *P* value > 0.05). The physical basis for these differences in correlations between the PDO and the NPGO for both coho and Chinook salmon survival rates can be seen by comparing the patterns of spatial correlation between each salmon species' PC-1 time series and Pacific Ocean winter sea surface temperature anomalies (SSTa) to patterns of correlations between these anomalies and the NPGO and the PDO (Fig. 1 *E* and *F*). Salmon–SSTa correlations more closely resemble a plot of similar correlations between the NPGO and SSTa than those between the PDO and SSTa (see Fig. S4 *A* and *B* for PDO spatial patterns). A distinct difference between the NPGO and PDO spatial signatures is in the eastern equatorial Pacific Ocean, where the NPGO is uncorrelated with SSTa (Fig. 1 *E* and *F*), but the PDO is highly correlated (black rectangles in Fig. 1 *E* and *F* and Fig. S4 *A* and *B*). The dominant mode of salmon survival rates shares two additional features with the NPGO spatial signature. First, correlations with coastal SSTa in the Gulf of Alaska are opposite to those in the California Current system (CCS; blue rectangles in Fig. 1 *E* and *F* and Fig. S4 *A* and *B*). Second, there is a region of common negative correlation from the western equatorial Pacific Ocean to the central Pacific (red ovals in Fig. 1 *E* and *F* and Fig. S4 *A* and *B*). Hence, principal modes of recent coho and Chinook salmon survival

Fig. 2. Coherence of coho salmon and Chinook salmon survival from Oregon to Vancouver Island has increased since the early 1980s, whereas within-species covariability has changed little. (*A*) Ten-year sliding correlation between detrended time series of coho and Chinook salmon early ocean survival from common regions from 1980 to 2006. Ten-year sliding correlation of Chinook (*C*) and coho salmon (*E*) survival for neighboring regions from 1980 to 2006. (*B*, *D*, and *F*) Mean correlation of each 10-y window for within-region (*A*) and neighboring region (*C* and *E*) comparisons. Blue and red circles indicate regions for Chinook and coho salmon, respectively. See Fig. S1 for region codes.

share the same basin-scale spatial pattern of covariability with temperature as the NPGO, rather than that of the PDO.

This coherence in survival rates in these two species and their common covariability with a recently strengthened indicator of ocean state, the NPGO, raises the question of how these characteristics developed in recent decades. Sliding correlation analyses show increasing local correlation between coho and Chinook salmon survival rates in common regions from western Vancouver Island south (Fig. 2 *A* and *B*), beginning in the early 1990s and continuing to 2006 (except the final window for northern coastal Washington). The strongest correlations bracket the turn of the century, when the PDO changed sign and the NPGO signal reached a peak (Fig. 1 *C* and *D* and Fig. S2 *A* and *B*). Short-term spatial covariability within each species, between adjacent regions, has remained positively correlated since 1980 ($\rho > 0.4$, Fig. 2 *C*–*F*).

This between-species coherence in survival rates has direct ecological and economic consequences, because it reflects a dynamic ecosystem process that has changed aggregate salmon variability in the context of the portfolio effect. The increase in within-region coherence between these two species from near zero in the 1980s to values near 0.8 in the 2000s indicates a

substantial increase in between-species coherence of ocean survivals and consequently implies increased variance in the aggregate survival of coho and Chinook salmon in the CCS. Also, the within-species spatial coherence between neighboring regions has remained relatively high since at least the mid-1980s, indicating a continuing contribution of ocean survival to the lack of diversity in population responses among regions.

Whether the increasing coherence in same-year survivals of coho and Chinook salmon would cause increasing coherence in their spawning abundance depends on the ages at which the environment influences the survival of each species (i.e., the age at ocean entry), and the ages of spawning in each species. For example, because coho salmon enter the ocean at age 2 y and spawn at age 3 y, reproduction and catch would lag variable early ocean survival by 1 y. Ocean-type Chinook salmon, on the other hand, enter the ocean at age 1 y and spawn at three later ages, with the mean age of spawning increasing with latitude (Fig. 3*B*). This leads to lags of 1–3 y, 2–4 y, and 3–5 y, with increasing latitude (23). A model constructed with these various lags shows that because of the mismatches in lags, the coherence of spawning abundance between species also depends on the amount of autocorrelation (i.e., redness) within the survival time series. If the variability in survival were white noise (i.e., no autocorrelation), as the correlation between same-year survivals of the two species increased from 0 to 0.8, the increase in correlation between each species abundance would be high enough for the portfolio effect to cause an increase in aggregate salmon variability by a factor of only about 1.1 (Fig. 3*A*). However, if the actual observed level of lag-1 autocorrelation in the survival time series were included ($\phi = 0.5$), an increase in the correlation between same-year survivals of the two species from 0 to 0.8 would create enough correlation between the spawning abundances to cause an increase in variability by a factor that ranges from near 1.3 for the more southern stocks to slightly greater than 1.1 for the more northern stocks. The greater reduction in portfolio effect diversity

Fig. 3. (*A*) Positive correlation of survival rates increases variability in aggregate spawning abundance of coho and Chinook salmon to a greater effect when spawning ages overlap. Large increases in aggregate variability, however, require lag-1 autocorrelation in the environmental signal (solid lines, $\phi = 0.5$; dashed lines, uncorrelated). Line color differentiates aggregate variability between abundances of simulated coho salmon and three Chinook salmon life histories (black, spawn at ages 2–4 y; red, spawn at ages 3–5 y; blue, spawn at ages 4–6 y). Relative variability is defined in *Materials and Methods*. (*B*) Environmental variability during ocean entry (red stars) influences survival rates of salmon and is reflected in the catch (blue circles).

for southern stocks is due to the greater overlap in spawning age distributions of the two species.

Discussion

These analyses indicate that the population dynamics of salmon populations along the west coast of the United States have changed substantially as the nature of ocean variability at the equator has changed since the 1980s. Recent changes in ENSOs in the tropical Pacific Ocean have, through teleconnections, led to a stronger NPGO and a weaker PDO currently. Ocean survival rates of two North American salmon species reflect the increasing importance of the NPGO compared with the PDO during the study period. In addition, variability in the survivals of these two species has become more coherent since the 1980s, effectively reducing the marine component of salmon biodiversity. Because this shift was demonstrated with tagging data from hatchery fish, we note that hatchery and wild salmon occupy similar ocean habitats and have similar survival patterns (24–26), but the response of wild fish may differ. The covariability between the NPGO and the principal modes of spatial variability in coho and Chinook salmon survival rates is a previously unidentified link between low-frequency Pacific climate variability and salmon. This finding is consistent with the relative increase in NPGO-type variability of the Pacific Ocean since the late 1980s and with coherent fluctuations of fish and invertebrates along the North American west coast that covary with the NPGO signal (27, 28). Recent studies link the increasing variance of the NPO—the atmospheric driver of the NPGO—to greenhouse forcing (29). Consistent with this view, in the winter of 2013–2014, the NPO activity reached a record high, causing the warmest SSTa anomalies ever recorded in the northeast Pacific (30). These SSTa anomalies exhibit the same spatial pattern as the NPGO (31), suggesting that extremes in physical conditions linked to salmon survival rates may become more frequent in future decades.

Although the mechanisms underlying this potential shift in salmon productivity are not yet well understood, this link highlights the recent nonstationary nature of the relationship between climate and fish, and their potential ecological consequences. Coho and Chinook salmon differ in many aspects of their life history, and these differences were previously invoked to explain the distinct patterns of spatial and temporal variability in populations of these species (32). These differences include duration of freshwater residence (33, 34), offshore distributions in the early ocean phase (35–37), and ocean migration paths (24, 25, 38, 39). The difference in the distribution of spawning ages is the most obvious difference between these species: Coho salmon tend to spawn at a single age, whereas spawning in specific populations of Chinook salmon is distributed over several ages (23, 40) (Fig. 3B and Figs. S5 and S6).

The increased covariability between survival rates of these two species reduces the contribution to combined population stability by a reduced diversity in responses to ocean conditions, similar to the effects of increasing coherence within salmon species observed in other instances (3–5). This is a specific type of biodiversity, in the sense that it reflects covariability among species rather than within populations of the same species (3–5, 11). It is, specifically, variability in population rates rather than abundance itself, and thus is an example of response diversity (41). How the portfolio effect ultimately contributes to the aggregate stability of these two species depends on ongoing changes in their freshwater habitat. Importantly, however, the synchronizing influence of ocean conditions on salmon survival rates differs from freshwater factors like habitat availability or hatchery production. Managers have some capacity to modify freshwater habitat or hatchery programs to decrease their homogenizing influence. For example, there are recommendations that hatchery release times be varied more broadly to increase variability in

annual ocean survival (42). However, ultimately, these salmon are vulnerable to interannual changes in ocean conditions, and this overall variability in salmon abundance needs to be accounted for in salmon conservation and management.

Materials and Methods

CWT release and recovery data were obtained from the Pacific States Marine Fisheries Commission's Regional Mark Processing Center (www.rmpc.org). We developed regional time series of early ocean survival (log-transformed and normalized) using CWT data from Chinook and coho salmon hatcheries in California to southeast Alaska from 1980 to 2006 (see Tables S1 and S2, for additional details on CWT-based survival estimates methods; see refs. 14 and 15). Hatchery reared subyearling (yearling) Chinook salmon are released at age 1 y (age 2 y) and spend multiple years at sea. Coho salmon survival was calculated as the number of CWT returns at age 3 y divided by the number released (14). We used cohort reconstruction to estimate the number of age 2 y (age 3 y) returns for subyearling (yearling) Chinook salmon (15, 43), assuming constant ocean survival rates for later ocean periods (0.5 for survival from age 2–3 y (3–4 y) for subyearling (yearling) releases and 0.8 for older ages). Regional patterns in survival estimates were not sensitive to the values selected for older ages.

We used the National Oceanic and Atmospheric Administration Extended Reconstruction Sea Surface Temperature data from 1980 to 2006 (44), computing monthly SSTa by removing climatological monthly means. Monthly PDO and NPGO indices were downloaded from research.jisao.washington.edu/pdo and www.o3d.org/npgo, respectively, and an annual (seasonal) mean for each index was calculated.

Principal components analysis was used to extract the first two dominant modes of variability in eight coho salmon and eight Chinook salmon regional survival time series (Fig. 1 A, B, E, and F). Spatial correlation maps for each signal (coho-PC1, Chinook-PC1, the PDO, and the NPGO) versus SSTa were constructed to compare the salmon spatial patterns to the two ocean indices. Correlation significance of salmon PC1s with PDO and NPGO was computed using Monte Carlo simulation (5,000 realizations) to derive empirical probability distributions of correlation coefficients for two red-noise time series with the same autoregression coefficients estimated for each data series. To investigate short-term changes in survival coherence, 10-y sliding correlations were conducted on detrended coho and Chinook salmon survival time series from the same regions and for subyearling Chinook and coho salmon from neighboring regions—ignoring missing data.

We used an age-structured, density-dependent salmon population model (45) to investigate how the observed increased correlation of coho and Chinook salmon survival rates could increase aggregate variability of simulated coho and Chinook salmon spawning abundance. Specifically, we investigated how aggregate variability of the spawning abundance of returning coho and Chinook salmon changes as survival becomes increasingly homogenous. Simulations were run with increasingly correlated survival and with and without the influence of autocorrelation in the survival rates on aggregate variability. Changes in aggregate variability depend, in part, on the time lags experienced by coho salmon and ocean-type Chinook salmon (see SI Materials and Methods for additional details).

The age-structured model with density-dependent recruitment for coho salmon and Chinook salmon with a maximum age of n has the form

$$\bar{x}(t) = F(\bar{x}(t-1), t) = \begin{pmatrix} R(P(t)) \\ sx_1(t-1) \\ (1-\delta_e)sx_2(t-1) \\ \delta_l sx_3(t-1) \end{pmatrix}$$

where $\bar{x}(t) = (x_1(t), \ldots, x_4(t))^T$, the vector of abundance at age, s is the annual survival rate, δ_e is the fraction that spawn early, before the mean age of spawning (age $n-1$), and δ_l is the fraction that spawn late, after the mean age of spawning. For both coho salmon and Chinook salmon, δ_e was 0.1056, whereas δ_l was 8.84×10^{-5} for coho salmon and 0.1056 for Chinook salmon. The annual survival rate was set to 0.8 for all ages, and the annual harvest rate was 0.4, with harvest assumed to occur only during spawning migrations. $P(t) = \delta_e x_{n-2}(t-1) + (1-\delta_l)x_{n-1}(t-1) + x_n(t-1)$ denotes the number of spawning fish in year t, and R is the Beverton–Holt stock recruitment relationship (see SI Materials and Methods for additional information on the population model).

We simulated environmental variability in survival beginning with an $N \sim (0,1)$ vector, which was used as the base case forcing vector for coho salmon. We then generated vectors correlated to the coho salmon forcing vector ($\rho = 0.0$–0.80 in increments of 0.05) that were used to force Chinook salmon. Each of these signals was then multiplied by 0.3 to yield $\varepsilon \sim$

$N(0, 0.3)$ and then "reddened" to have a lag-1 autocorrelation coefficient (ϕ) of 0.5 corresponding, approximately, to the lag-1 autocorrelation coefficient of Chinook-PC1 ($\phi = 0.51$). All simulated survival vectors were checked to ensure that they had the same mean and variance. We conducted 2,000 simulations for each level of ρ and ϕ. After a burn-in period of 500 y, simulations were run for an additional 100 y that were used in the analysis.

We used the coefficient of variability (CV) for aggregate coho and Chinook salmon spawning abundance when survival rates of both species were uncorrelated and had no autocorrelation as the basis for comparison (CV$_{base}$) to scenarios with increasing correlation and with autocorrelation (CV$_{scenario}$). The mean of the ratio of CV$_{scenario}$ to CV$_{base}$ was used to show the relative increase in aggregate variability as correlation in survival rates increased, with and without autocorrelation (Fig. 3A).

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