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Assessing Extinction Risk for West Coast Salmon

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Climatic Influences on Salmon Populations in the Northeast Pacific

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1. Introduction

A number of recent studies have verified the fact that many stocks of Pacific salmon are threatened with extinction. For example, the Wilderness Society (1993) estimates that naturally reproducing Pacific salmon are mostly extinct or imperiled in 56% of their historic range in the Pacific Northwest and California. This undesirable state of affairs has developed in response to both natural variability and a legacy of human activities that are related to land use, harvest and hatchery practices (National Research Council [NRC] 1996). In this document, we examine the role that climate variability plays in driving salmon population changes. Ultimately, we develop a paradigm for the role of climate variations in the concern over future salmon extinctions.

One of the most obvious and important characteristics of the climate system is its variability. At time scales ranging from seasonal to millennial, records of climate from around the globe all highlight the fact that the normal state of the physical environment is one of dynamic change. Throughout the history of their existence, Pacific salmon and the ecological communities they are a part of have demonstrated tremendous resilience by evolving upon and adapting to a naturally variable environmental template. Thus, from a long-term historical perspective it seems clear that natural climate variability, by itself, should not be a primary concern in maintaining salmon stocks.

Anthropogenic influences on the salmon's environment play a primary role in our discussion of climate influences on salmon extinctions. Human activities have degraded, and in some cases completely eliminated much of the Pacific salmon's historic stream and estuarine habitat in the past century and a half. In many ways, human actions have forced semi-permanent changes to the salmon landscape that parallel those typically associated with climate change (Karr 1994). For example, stream temperatures, flow regimes, sediment transports, and pool-to-riffle ratios are all subject to anthropogenic and climate changes. Karr (1994) points out that one major difference between perturbations due to natural climate events versus one caused by human activities is the time scale of the resulting impacts. A warm phase of the El Niño/Southern Oscillation (ENSO) generally impacts precipitation and stream flows over the course of a single year, while the construction hydropower dam alters stream flows for decades to centuries.

In this document, we present results from two distinct types of analysis. In the first type, we adopt a Pacific Basin-scale perspective and search for linear relationships between climate and salmon-metapopulation variability along the Pacific Coast, from Alaska to California. This approach yields a robust large-scale pattern of salmon metapopulation responses to climate variability. In the second approach, we select a few case studies that illustrate complex, nonlinear relationships between climate and salmon population variability. With case studies, we examine a hierarchy of spatial scales, starting with a regional perspective of metapopulations, then step down to more local spatial scales, bringing us much closer to evolutionarily significant units (ESUs) of salmon populations. It is this latter approach that we see as most applicable to the issue of climatic influences on salmon extinctions and potential listings under the Endangered Species Act (ESA).

We will argue that the superposition of natural-climate variability upon anthropogenically stressed salmon ecosystems is an issue of grave concern for the sustainability of salmon populations. We offer some ideas about salmonid vulnerabilities to climate fluctuations, and discuss possible strategies to preserve and enhance salmon metapopulation resilience in the face of climate fluctuations.

The remainder of this document is organized as follows: In Section 2, we describe the data and methods of analysis used. In Section 3, we discuss two recurring patterns of Pacific climate variability generally believed to be important to Northeast Pacific salmon, the ENSO and the Pacific Interdecadal Oscillation (PDO). In Section 4, we discuss results of a retrospective study linking large-scale Pacific climate variability to that in Pacific salmon populations. Case studies detailing climate impacts on salmon populations over a range spatial scales are presented in Section 5. A discussion of climatic influences on salmon extinctions is presented in Section 6, and conclusions follow in Section 7.

2. Data and Methods

2.1. Climate and salmon landings data

Historical salmon-catch records and climate data were obtained from a variety of sources. In each case, we assembled annual values for each measure of interest, covered in the period of record 1925 to 1993, unless otherwise noted.

We obtained salmon-landings data from the following agencies: the Alaska Department of Fish and Game (ADFG) (1991), the Canadian Department of Fisheries and Oceans (CDFO), the Washington Department of Fisheries (WDF), the Oregon Department of Fish and Wildlife (ODFW), and the California Department of Fish and Game (CDFG). Following the various fisheries agencies listed above, we divided our salmon landings data into 10 regions: 1) western Alaska, 2) central Alaska, 3) southeast Alaska, 4) northern British Columbia, 5) the Strait of

Georgia, 6) west Vancouver Island, 7) Washington Coast, 8) Puget Sound, 9) Oregon, and 10) California (Figure 1).

Average annual catch of all salmon (in millions) and fractional composition by species for each region for the period of record 1925 to 1993 are shown in Figure 2. On average, the largest salmon catches have been recorded in Alaskan waters where sockeye salmon and pink salmon are the dominant species. In contrast, southern salmon catches (and populations) are primarily composed of coho salmon and chinook salmon, and overall numbers in the southern regions are typically an order of magnitude lower than those in the far north. In British Columbia, between the extremes in the Northeast Pacific salmon's range, annual-average salmon landings have been both relatively large and evenly distributed among each of the five commercially exploited species. The average landings data for the period of record studied here are regarded as generally reliable indicators for the variability in adult salmon populations (Beamish and Boullion 1993, Francis and Hare 1994, Hare and Francis 1995).

An alternative approach is to compare salmon survival to climate variability, but such information is available for only a few select stocks and for a relatively short period of time (Coronado-Hernandez 1995). It is our hope and expectation that by averaging over relatively broad regions, variability in the catch data that is coherent with that in the climate data will emerge if the relationships are robust. The results presented in Section 4 suggest that, indeed, a climate signal does exist in the admittedly difficult-to-interpret fishery data set.

Our analysis of climate relationships with coast-wide salmon populations utilizes three indices for naturally occurring marine climate variability in the Pacific Basin. These are: 1) the Pacific Interdecadal Oscillation (PDO) index, 2) an index of sea-surface temperature (SST) variability along the coast of British Columbia and Washington State (BCSST), and 3) an index for SST variability in the eastern equatorial Pacific, hereafter the cold-tongue (CT) index. Each index was chosen to represent the time history of recurring climate patterns thought to be important to Pacific salmon and/or climate variability in the Northeast Pacific. The source regions for each of the SST indices are shown in Figure 3, and the time series are plotted in Figure 4.

The PDO index, derived from a principal component/empirical orthogonal function (PC/EOF) analysis (Preisendorfer 1988) of North Pacific SST for the period of record from 1900 to April 1996, is the dominant pattern of SST variability in the extratropical North Pacific (Zhang et al. 1996). The PDO has clear signatures in North American winter-air temperatures, precipitation, stream flows, and select salmon populations (Mantua et al. 1997). PDO-related SST and sea-level pressure (SLP) patterns are shown in Figure 5a.

The CT index is the average SST anomaly in the region from latitude (lat.) 6ºN to 6ºS, longitude (long.) 180ºW to 90ºW. It is a commonly used ocean-based measure of the ENSO (a recurring phenomenon that has been linked to large-scale climate anomalies) that are similar, in many respects, to those associated with the PDO (Zhang et al. 1996). The ENSO is known to impact a number of fisheries in the nearshore waters of the eastern Pacific (Baker and Chavez 1983, Mysak 1986, Sharp and McClain 1993). CT-related SST and SLP patterns are shown in Figure 5b.

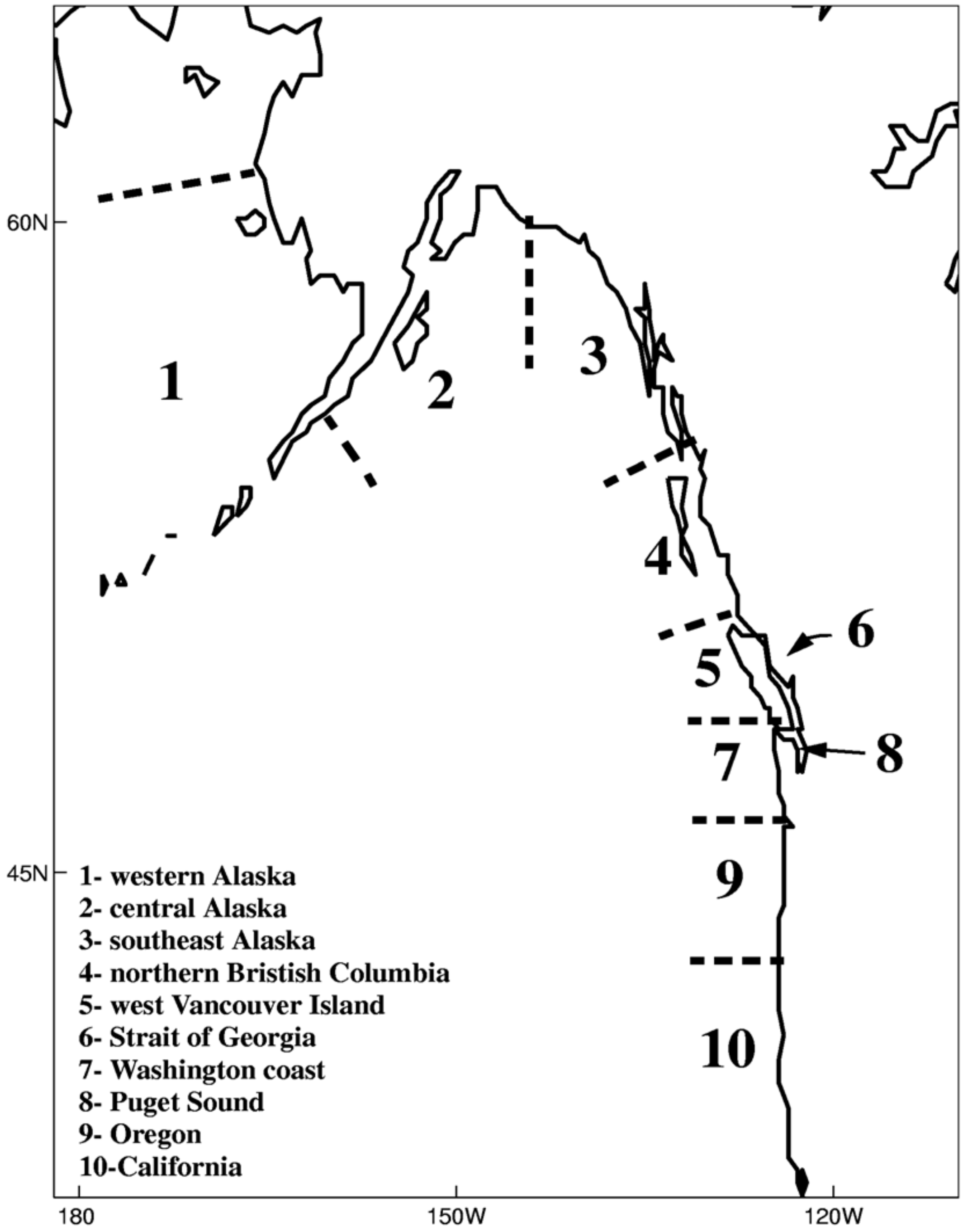


Figure 1. Salmon catch data regions.

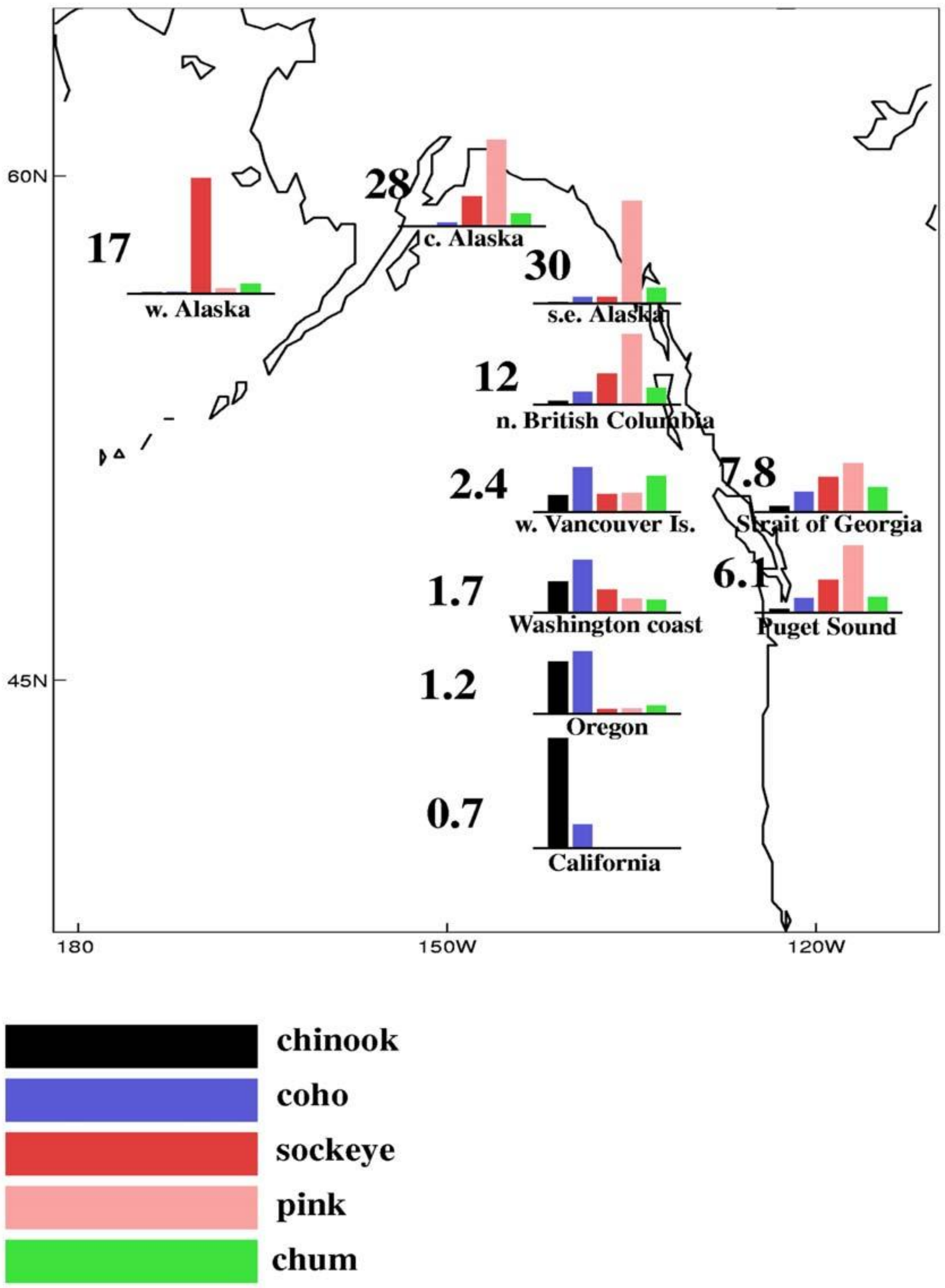


Figure 2. Annual mean total salmon catch by species for each of ten regions along the Pacific Coast of North America. Bold-faced numbers represent the annual mean catch of all salmon in millions of fish for the period of record 1925-1993. The length of each bar corresponds to the average relative contribution of each species to the catch of all salmon in the region.

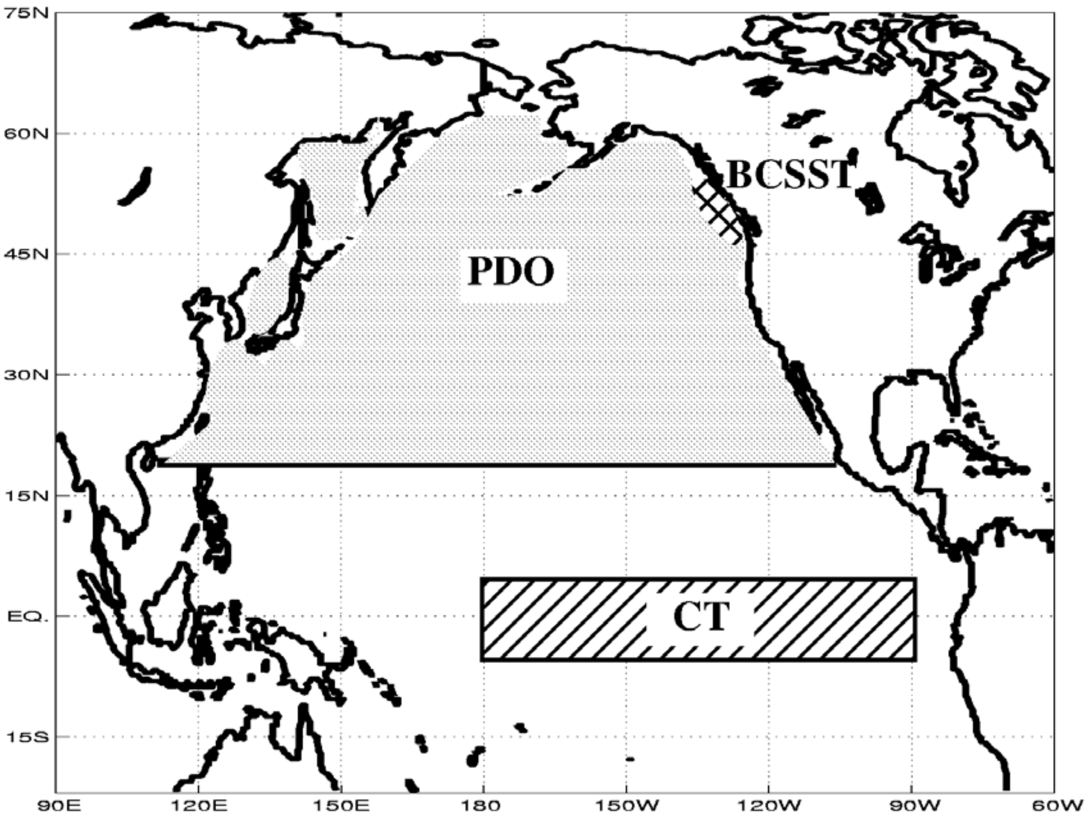


Figure 3. Source regions for the SST indices described in Section 2.1 and discussed in Section 3: Pacific Interdecadal Oscillation (PDO), coastal British Columbia SST (BCSST), and the Cold-Tongue (CT).

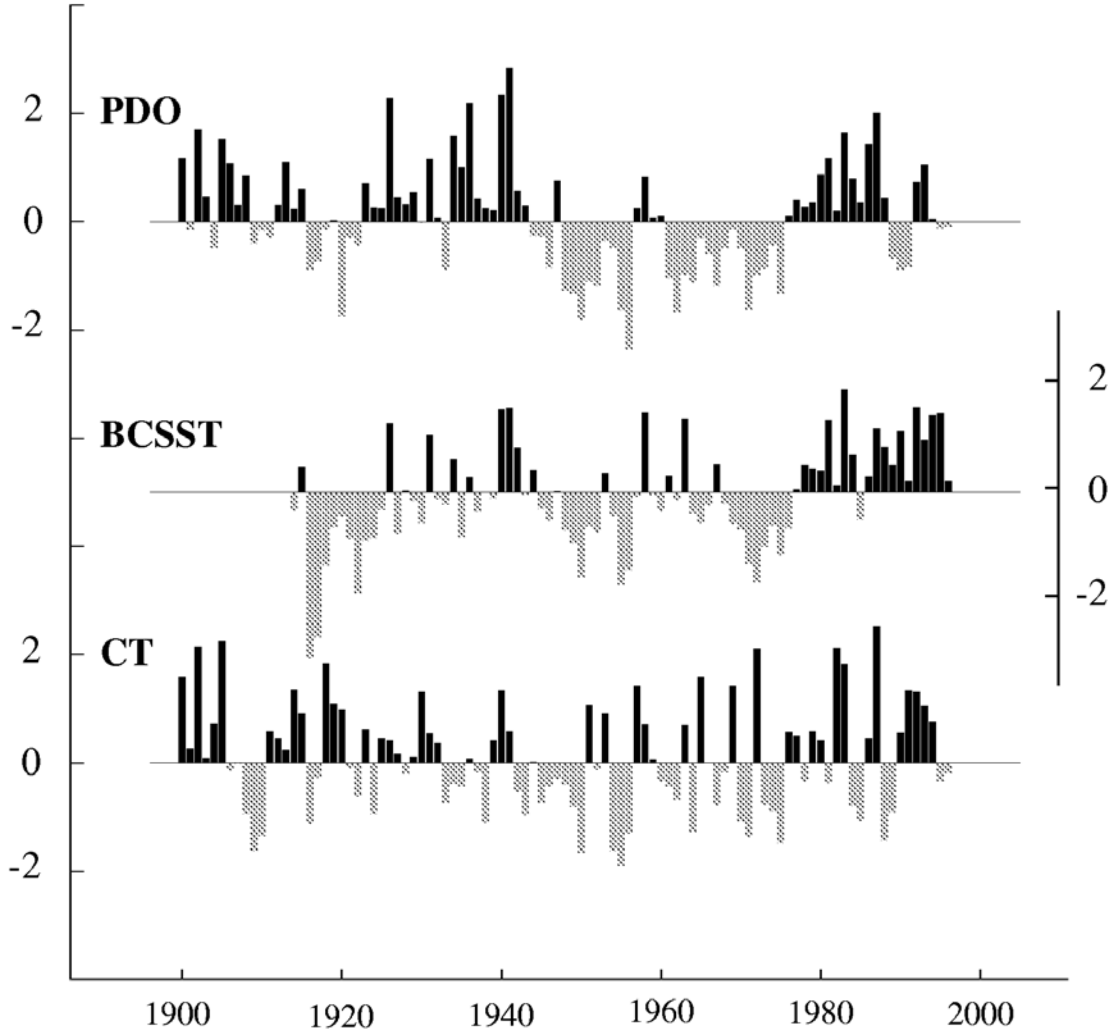
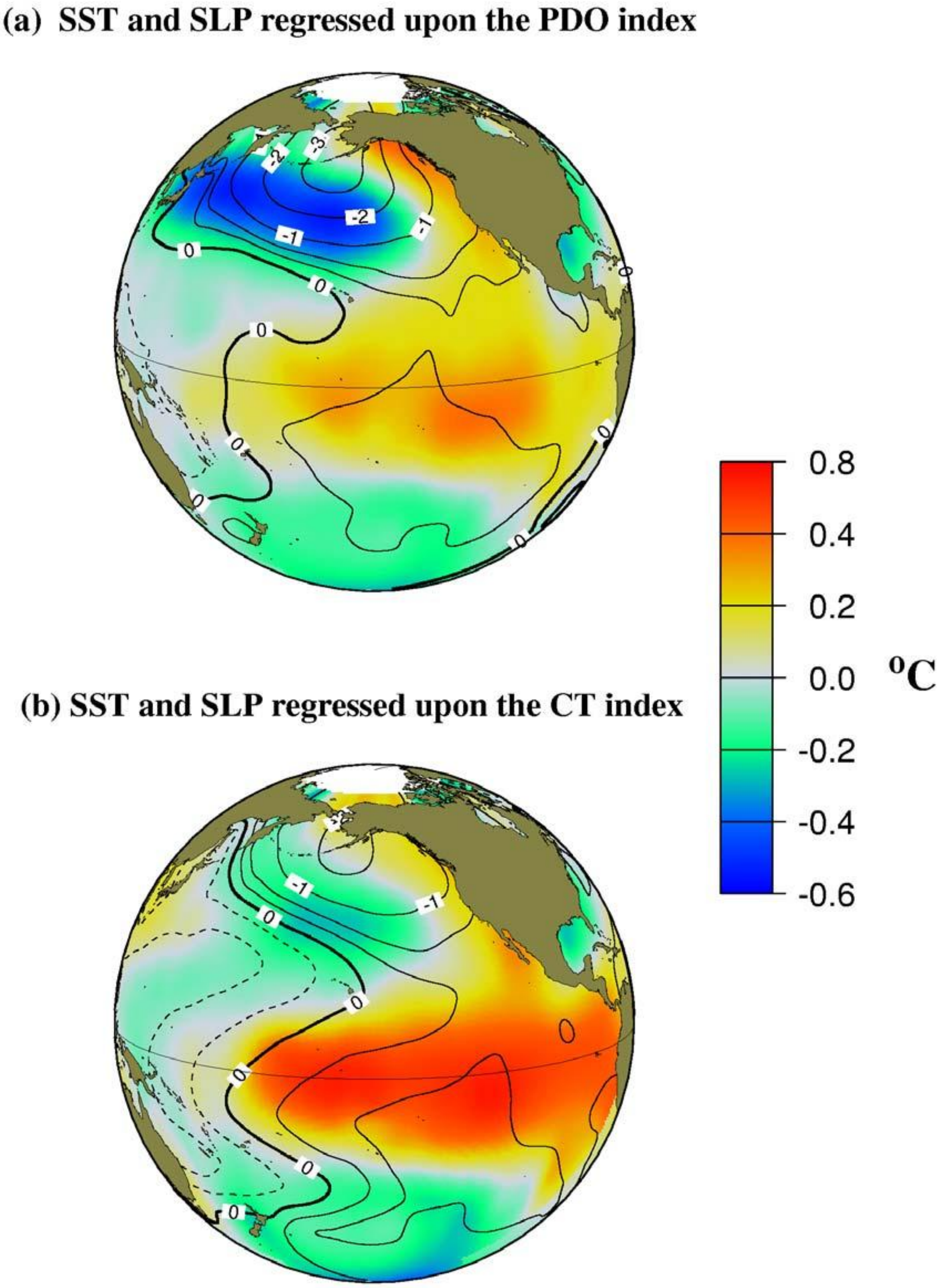


Figure 4. Annual mean normalized Pacific basin climate indices derived from SST data. Bars have been shaded such that positive values are black and negative values are grey.


(a) SST and SLP regressed upon the PDO index

(b) SST and SLP regressed upon the CT index

Figure 5. Winter mean (November-March) COADS SST regressed upon (a) the winter mean PDO index, and (b) the winter mean CT index for the period of record 1900-1992. Contour interval is 0.1˚C. Positive (negative) contours are solid (dashed). Reproduced from Zhang et al. (1996).

We include the BCSST index[1] (which is a regional measure of SST anomalies from shore stations between the Queen Charlotte Islands in British Columbia, Canada, and Neah Bay in Washington State) because it represents coastal marine climate variability in the center of the Northeast Pacific salmon's range. A more comprehensive discussion of the climate indices and related patterns is presented in Section 4.

A selection of regional climate data is examined in this document as well. In Figure 6, we show annual water year (October through September), streamflow indices from the Gulf of Alaska and the Pacific Northwest, wintertime surface air temperatures from the Gulf of Alaska, and coastal SST from Scripps Pier in southern California.

2.2. Analysis strategy

To objectively identify recurring patterns of climate variability in the North Pacific, a PC/EOF analysis of gridded SST data, poleward of 20ºN in the Pacific Basin, was done (compare analysis with Zhang et al. 1996). We used the covariance matrix from monthly SST anomalies provided by the Climatic Research Unit, University of East Anglica, for the period of record 1900 to April 1996 (Folland and Parker 1990, 1995). The analysis produced the PDO index shown in Figure 4.

To objectively identify linear relationships between our climate indices and salmon catch data, we follow a four-step procedure. The end products of this analysis are patterns of regional and species-specific salmon catch variability with time-varying indices. Each pattern explains relatively large fractions of the total variance in the salmon-catch data set.

First, we compute lag-correlations between each of the 47 salmon-catch records and each of the three climate indices. Before the lag-correlations are computed, each time series is prewhitened following Katz (1988).[2] This part of the analysis was done for two reasons. First, to gain insights into which part of each species' life history (e.g., early versus late in the ocean phase where the relationships with climate appear). The second reason is to provide guidance for building a data matrix to be used in the PC/EOF analysis. The time lags (number of years),

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[1] BCSST index is a composite of nine individual SST time series from coastal British Columbia, Canada, and Washington State. These stations are at: Amphitrite Point, Departure Bay, Race Rock, Langara Island, Kains Island, McInnes Island, Entrance Island, and Pine Island, in British Columbia (B.C.), Canada; Neah Bay, in the NW corner of Washington State. The time series from B.C. was obtained from the Institute of Ocean Sciences in Sidney, B.C., Canada, while that for the Neah Bay was obtained from the Scripps Institute of Oceanography in La Jolla, CA.

[2] The presence of strong autocorrelations in time series, which is a common property of environmental data sets, can introduce spurious cross-correlations at numerous time lags. Prior to computing the lag-correlations between the catch and climate time series, we removed the 1-year autocorrelation. An exception was made with the pink salmon catch records because they exhibit a clear peak in autocorrelation at 2-year lags, thus, we removed the 2-year autocorrelation from these catch records (see Hare 1996 for a more detailed discussion of problems introduced by autocorrelations in environmental data).

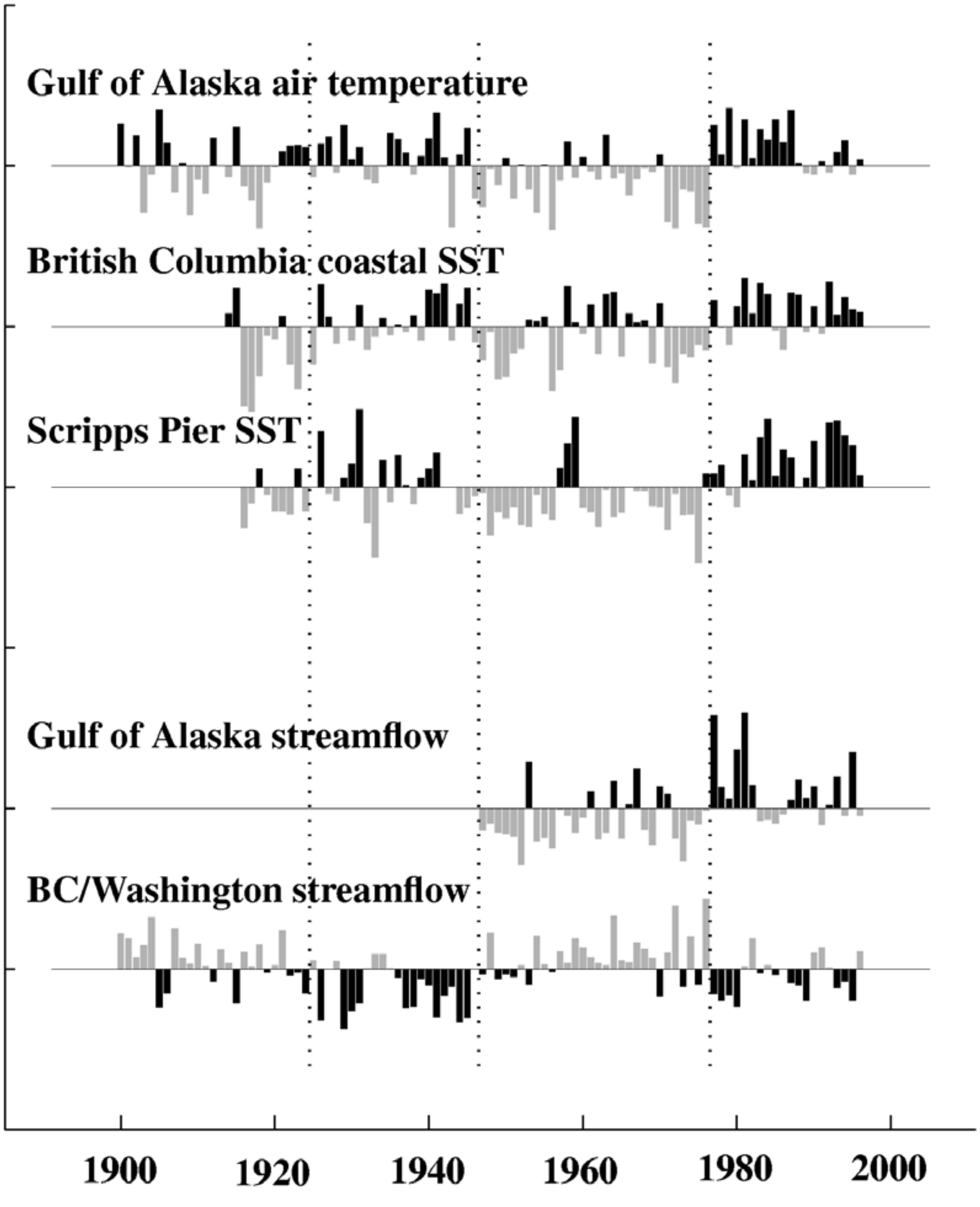

Figure 6. Selected regional climate time series with PDO signatures. Dotted-vertical lines are drawn to mark the PDO reversal times in 1925, 1947, and 1977.

for which there are statistically significant cross-correlations between the prewhitened climate and salmon time series, are recorded. From these time lags, frequency distributions for significant catch-climate lags stratified by species, are constructed (shown in Fig. 7, and discussed in Section 4.1).

In the next step, we create a data matrix composed of the 47 selectively-lagged catch records. The appropriate time lags for each species are determined by the peaks in the histograms of statistically significant lag-correlations.

In step three, we compute a population-weighted covariance matrix. The weighting amounts to a normalization of each group of catch time series, by region, such that each of the 10 fishery areas has the same total variance. Within each region, the variance for each species is weighted by its fractional contributions to the annual mean catch in that region.

In the final step, we apply a PC/EOF analysis to the population-weighted covariance matrix. The products of the PC/EOF analysis are a set of objectively derived orthogonal principal components (PCs), or expansion-coefficient time series and corresponding loading vectors. Each PC is a time series that describes the time varying amplitude of the associated loading vector. In a less formal analysis presented in Section 5, we examine three case studies, which exemplify nonlinear complex responses of salmon populations to environmental forcing, of which climate is a part.

3. A Retrospective Look at North Pacific Climate Variability

Previous work has demonstrated that climate fluctuations captured by the BCSST, CT, and PDO indices are important to marine ecosystems along the Pacific Coast of the Americas. For example, coastal SST variability represented by the BCSST index has been implicated as an important environmental forcing on nearshore marine ecosystems in the Northeast Pacific (e.g., Wooster and Fluharty 1985, Mysak 1986). Tropical SST variations marked by the CT index have been identified as a factor in pelagic fish population change in the eastern tropical Pacific (Barber and Chavez 1983, Sharp and McClain 1993). Large-scale SST fluctuations projecting onto the PDO have been linked to variability in large marine ecosystems of the Northeast Pacific and Bering Sea (Hollowed and Wooster 1992, Beamish and Boullion 1993, Francis and Hare 1994, Hare and Francis 1995, Beamish et al. al. 1995, Hare 1996, Mantua et al. 1997). In the remainder of this Section, we discuss the characteristics of the climate patterns associated with the three SST indices shown in Figure 4.

At the top of Figure 4 is the PDO index which represents the time history of the dominant pattern of North Pacific SST variability for the period of record from 1900 to April 1996. The PDO has experienced strong interdecadal fluctuations over the past century, with mostly positive values from the mid-1920s to the mid-1940s, negative values from the mid-1940s to 1976, and positive values since 1977. In this century interdecadal fluctuations in this index have closely paralleled those in the dominant pattern of North Pacific SLP (Hare 1996, Latif and Barnett 1996, Zhang 1996, Zhang et al. 1996). Thus, the PDO represents a large-scale, coherent ocean-atmosphere interaction at preferentially interdecadal time scales.

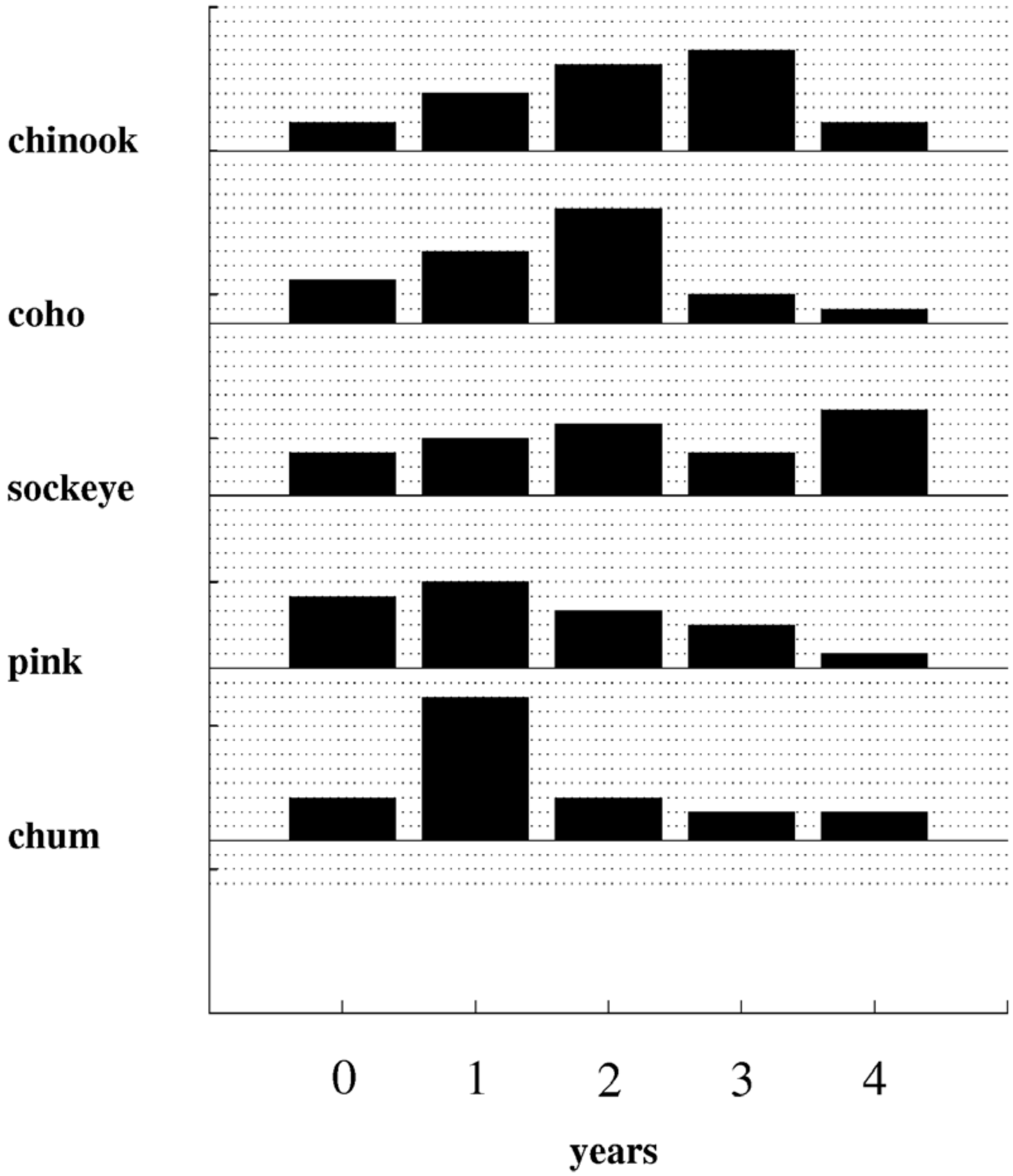

Figure 7. Histograms of statistically significant catch-climate lag-correlation, in years.

Shown at the bottom of Figure 4 is the CT index, which represents the time history of the dominant pattern of tropical Pacific SST variability. Over the past century, the CT index has varied mostly at interannual time scales and is highly correlated with an index for the leading pattern of SLP variability in the tropical Pacific. The CT index is a commonly used oceanic indicator for the well-known ENSO[3], which involves large-scale, ocean-atmosphere interactions.

Shown in the middle of Figure 4 is the BCSST index. The BCSST index has exhibited regime-like behavior that parallels behavior in the PDO for much of the common period record. Exceptions are clearly evident during the 1958 to 1962 and 1988 to 1992 periods of record when the PDO was weak or negative but BCSST was positive. Time variability in BCSST appears to contain a mix of the lower- and higher-frequency variability that is contained in the PDO and CT indices, respectively.

By regressing records of gridded wintertime SST and SLP data upon the PDO index, spatial patterns typically associated with a positive unit standard deviation of the PDO are generated (Fig. 5a). The largest PDO-related SST anomalies are found in the central North Pacific Ocean, where a broad pool of cooler-than-average surface water has been centered for much of the past 20 years. The peak amplitude of the SST regression coefficients in the cold pool are on the order of -0.5ºC. The narrow belt of warmer-than-average SST that, in the past 2 decades, has prevailed in the near shore waters along the West Coast of the Americas, is also a distinctive feature of this pattern and is consistent with the relatively strong positive correlations between the PDO and BCSST indices. The SLP anomalies (not shown) that are typical of the positive PDO are characterized by basin-scale negative anomalies between 20ºN and 60ºN. The peak amplitude of the mid-latitude wintertime SLP signature is about 4 *mb*, which represents an intensification of the climatological-mean Aleutian Low. This SLP pattern is very similar to the dominant pattern of wintertime North Pacific SLP variability (Hare and Francis 1995).

Shown in Figure 5b are the SST fields regressed upon the CT index. The map in Figure 5b shows anomalies typically associated with a unit standard deviation ENSO pattern. Comparing Figure 5a with 5b, it is evident that the tropical PDO spatial signatures are in many ways, reminiscent of canonical warm-phase ENSO SST anomalies (Rasmussen and Carpenter 1982). However, the PDO amplitudes in the tropical fields are weaker than those obtained by regressing the surface fields upon the CT index. Likewise, the PDO regression amplitudes in the Northern Hemisphere extratropics are stronger than those obtained from regressions upon the CT index (Zhang et al. 1996), both in the interior North Pacific and along the coastal strip of the Northeast Pacific.

Over the past century, the CT, BCSST, and PDO indices are positively correlated at statistically significant levels (see Table 1). With a linear multiple regression, using the CT and PDO indices as predictors, one can explain 44% of the variance in the BCSST index for the period of record between 1925 and 1993. Using the PDO index alone to model BCSST

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[3] Note that the essence of ENSO is thought to be contained within the tropical latitudes of the Pacific Basin (see Battisti and Sarachik 1995 for a comprehensive review on understanding and predicting ENSO), while that of the PDO remains an area of active research.

variability, one can predict about 40% of the variance. Using the CT index alone explains about 20% of the BCSST variance.

Table 1. Correlation coefficients between the PDO, BCSST, and CT indices.

	PDO	**BCSST**	**CT**
PDO	----	.65	.43
BCSST	----	----	.40
CT	----	----	----

There is little evidence that the BCSST region is the locus for a strong, ocean-atmosphere interaction important to larger scales of Pacific climate variability. In our view, BCSST is best understood to vary in response to the PDO, tropical ENSO, and other patterns of Pacific climate variability.

For example, the tropical ENSO is known to influence Northeast Pacific SST via two pathways. First, by so-called atmospheric teleconnections (Wallace and Gutzler 1981) and second, via coastally trapped, poleward-propagating, internal ocean waves (Gill 1982).

ENSO-related changes in tropical precipitation excite changes in the wintertime atmospheric circulation over the mid-latitude North Pacific (Bjerknes 1969, Julian and Chervin 1978, Horel and Wallace 1981, Hoskins and Karoly 1981). It is the teleconnected change in extratropical surface winds that ultimately force changes in North Pacific ocean temperatures through air-sea fluxes of heat and momentum (Namias 1969, Miller et al. 1994, Miller 1996).

ENSO-related changes in tropical winds can influence Northeast Pacific SST, via the generation of coastally trapped, upper-ocean disturbances in the equatorial Pacific (Enfield and Allen 1980, Chelton and Davis 1982). Results of empirical, theoretical, and numerical modeling studies suggest that the oceanic connections between variability in the tropical ENSO and mid-latitude coastal waters of the eastern Pacific are most robust equatorward of San Francisco. Poleward of San Francisco, coastal SST and sea-level variability are primarily driven by atmospheric forcing in the North Pacific (Chelton and Davis 1982, Parres-Sierra and O'Brien 1989, Miller et al. 1994).

Large-scale atmospheric-circulation anomalies that impact coastal SST also generate terrestrial climate variability. Typical of positive (negative) PDO and warm (cool) ENSO years are relatively warm (cool), wet (dry) winters with high (low) water-year (October-September) stream flows in the coastal regions of the Gulf of Alaska. During those same years, the Pacific Northwest tends to experience relatively warm (cool), dry (wet) winter with low (high) snowpack and low (high) stream flows (Cayan 1996, Mantua et al. 1997).

Selected climate records from western North America highlight the widespread signatures of the PDO (Fig. 6). Interdecadal fluctuations in wintertime surface-air temperature in the Gulf of Alaska, and SST near the coast from Alaska to southern California, varies in phase with the PDO. During positive PDO years the annual, water-year discharge in the Skeena, Fraser, and Columbia Rivers is on average 8%, 8%, and 14% lower, respectively, than that during negative PDO years. In contrast, positive PDO year discharge from the Kenai River in the central Gulf of Alaska region is on average about 18% higher than that during the negative-polarity PDO years (Mantua et al. 1997).

In summary, evidence suggests that it is primarily by their North Pacific atmospheric expressions that the PDO and ENSO climate phenomena influence the terrestrial and coastal oceanic environments in which Northeast Pacific salmon live. Over the past century, interdecadal variability associated with the PDO climate pattern has dominated that associated with teleconnections to the interannual ENSO (as expressed by the CT index) in the North Pacific.

4. Climate Influences on Salmon Populations

4.1. Linear Climate-Catch Data Relationships

Following the analysis outlined in Section 2.2, we generated frequency distributions for years with significant lag-correlations between the climate indices and catch records, constructed a population-weighted catch-data covariance matrix, and then applied a PC/EOF analysis to identify coherent patterns of salmon metapopulation variability along the Pacific Coast of North America.

Histograms showing the number of statistically significant, climate-catch, lag-correlations, stratified by year, lag and species, are shown in Figure 7. For this part of the analysis, we collected the significant lag-correlations from all 10 regions for each species where they exist. The histogram for chinook salmon shows statistically significant correlations at lags of 2 and 3 years, with a few significant correlations occurring at 0-, 1-, and 4-year lags as well. For coho salmon, the peak in the histogram occurs at 2 years, and there are significant lags at 0, 1, 2, and 4 years. Two- and 4-year lags emerge as the peaks in the histogram for lag-correlations between sockeye salmon catch and climate indices[4]. The histograms for pink salmon and chum salmon show that the most frequent significant correlations with the three climate indices occur at a 1-year lag.

Based on the results of the climate-catch lag-correlations, the following time lags were used to construct the catch-data matrix for the PC/EOF analysis: chinook salmon – 3 years, coho salmon – 2 years, sockeye salmon – 2 years, pink salmon – 1 year, and chum salmon – 1 year.

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[4] The 4-year lag appears to be related to year-class cycles in some sockeye salmon breeding populations (Burgner 1991). We follow Francis and Hare (1994) and Hare and Francis (1995) by focusing on the 2-year lag-correlation peak which points to an early ocean life-history connection between most Alaskan sockeye salmon stocks and climate variability.

For all but chum salmon, the years emerging as peaks in significant lag-correlations suggest that the climate patterns considered here are most often impacting salmon populations early in the ocean or late in the freshwater phases of their life histories (compare with Pearcy 1992, Francis and Hare 1994, Hare and Francis 1995, Hare 1996).

The leading pattern of salmon-catch variability, emerging from our statistical analysis of the selectively-lagged, salmon catch covariance matrix, explains 34% of the variance from the original data matrix (Figs. 8a, 8b). The leading principal component (PC1), or expansion-coefficient time series, is shown by the shaded bars in Figure 8a. The time variability in PC1 depicts an interdecadal vacillation with predominantly positive values from 1925 to 1942, negative values from the early 1940s to about 1976, and then positive values from 1977 through 1992. For the common period of record, the similarity between the PDO index (shown by the solid line with open circles in Fig. 8a) and PC1 is striking. PC1 is also positively correlated with the BCSST and CT indices, much more strongly with the former than the latter (Table 2).

Table 2. Correlation coefficients between catch data PC1 and climate indices.

	PDO	**BCSST**	**CT**
PC1:	0.55	0.46	0.17

The loading vector that corresponds with PC1 is shown in Figure 8b. Each weight is plotted as the correlation coefficient between PC1 and each individual catch record, and only those correlations which exceed a 95% confidence interval are plotted. This loading vector is interpreted as follows: temporally coherent and positively correlated with PC1 are catches of coho salmon and sockeye salmon in the three Alaska regions; pink salmon in central and southeast Alaska and Oregon; chum salmon in western and central Alaska, west Vancouver Island, and Puget Sound; chinook salmon in Puget Sound and central Alaska; coho salmon in Puget Sound; and sockeye salmon on west Vancouver Island. Temporally coherent but negatively correlated with PC1, are coho salmon landings on the Washington Coast, Oregon and California, and chinook salmon catches in west Vancouver Island, the Washington Coast and California.

To test the robustness of these results, the PC/EOF analysis was repeated with several modified versions of the catch data covariance matrix. In one case, the climate indices were added to the catch data, and a catch-climate data matrix was analyzed. The leading PC-loading vector pair that emerges is very similar to that shown in Figure 8b, and the variance explained was slightly greater at 36%. In another case, none of the catch records were lagged. The leading PC-loading vector pair from this version of the analysis again remained like that in Figure 8b, though the variance explained was slightly weaker at 33%. The PC from this analysis, like that in Figure 8a, is strongly auto-correlated with negative values from the mid-1920s through the mid-1940s, then negative values from the late 1940s to the late 1970s, and positive values thereafter.

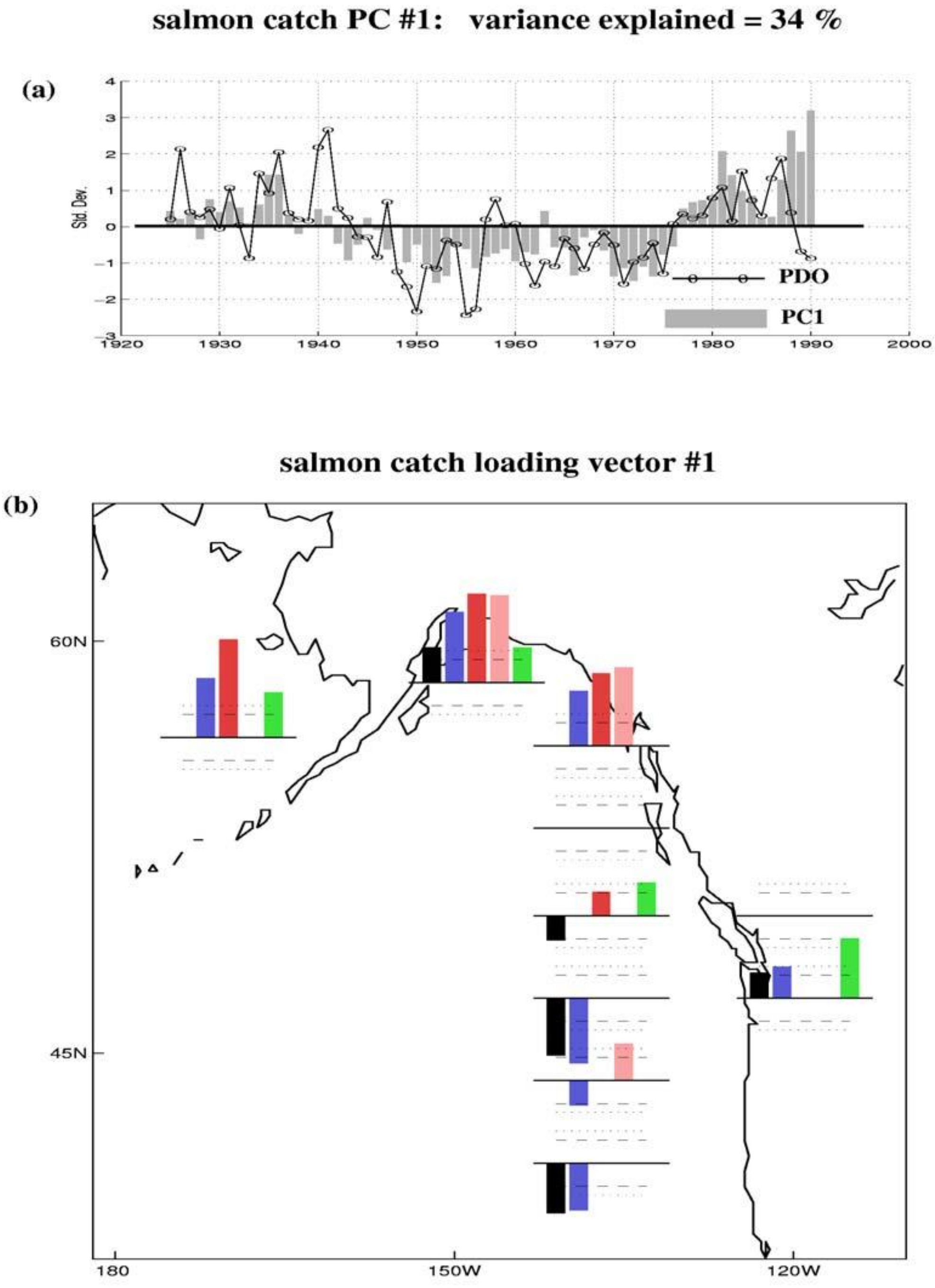


Figure 8. Results from the salmon catch PC/EOF analysis. In Panel (a) PC1 is shown with the grey shaded bars; the PDO index (from Fig. 3) is repeated with the solid line and open circles. In Panel (b) is the corresponding loading vector. Bars are plotted a correlation coefficients between PC1 and the selectivily lagged normalized time series for each catch record. The variance of the total data set explained by this PC/loading vector pair is printed in the upper right hand corner.

Based on the suite of PC/EOF analyses discussed, we are confident that the leading pattern of salmon-catch/climate variability shown in Figures 8a and 8b is robust. Clearly, the interdecadal climate variability associated with the PDO is coherent with that in many catch records, and presumably regional populations, for salmon in the Northeast Pacific.

4.2. Biophysical linkages between Pacific salmon and the PDO

Results of studies by Pearcy (1992) and Francis and Hare (1994) indicate that it is very early in the salmon's marine life history – likely just months after they enter the ocean – when many climate-related biophysical linkages to salmon populations take place. The early ocean life history also emerges as an important period in our climate versus salmon-catch lag-correlation analysis.

Recent work suggests that the marine-ecological response to the PDO-related environmental changes starts with phytoplankton and zooplankton at the base of the food chain and works its way up to top level predators like salmon (Venrick et al. 1987, Hare and Francis 1995, Roemmich and McGowan 1995, Brodeur et al. 1996, Hare 1996). This bottom-up enhancement of overall productivity appears to be closely related to upper ocean changes that are characteristic of the positive polarity of the PDO. For example, some phytoplankton-zooplankton population dynamics models are sensitive to specific upper ocean mixed-layer depths and temperatures. For the decade following the 1977 climate regime shift, such models have successfully simulated aspects of the observed increases in Gulf of Alaska productivity as a response to an observed 20% to 30% shoaling and 0.5ºC to 1ºC warming of the mixed layer (Polovina et al. 1995).

Variability in the strength of wind-driven mixing of the upper ocean is also influenced by the PDO. Wind-driven mixing replenishes vital nutrients to the light- and phytoplankton-rich, near-surface waters from below the thermocline. The strength of wind-driven mixing in the upper ocean is proportional to the cube of the SLP gradient (Garwood 1979), so that small changes in the latter field may cause relatively large changes in wind stirring. We speculate that, during positive PDO winters in the Gulf of Alaska, enhanced mixing of the upper ocean may also promote increased biological productivity.

Finally, to the extent that high- or low-stream flows favor high or low survival of juvenile salmon respectively, PDO-related stream-flow variations are likely working in concert with the changes to the marine environment in regard to impacts on salmon production. For Alaska salmon, the typical positive-PDO year brings relatively warm winter air temperatures, enhanced stream flows, and ocean mixed-layer conditions favorable to high biological productivity. Generally speaking, the converse appears to be true for Pacific Northwest salmon. In the Pacific Northwest, typical positive-PDO year stream flows are anomalously low, while nearshore upper ocean conditions appear to be unfavorable for high biological productivity.

5. Nonlinear and Complex Responses of Salmon Populations to Climate: Case Studies

In Section 4 we described a pattern of regional salmon-metapopulation variability that is related to a pattern of large-scale interdecadal climate forcing. Now, we would like to look at three cases: 1) Bristol Bay sockeye salmon, 2) Prince William Sound pink salmon, and 3) Oregon Production Index (OPI) coho salmon. For these three cases, there is more detailed information than what was presented in Section 4. These cases tend to display characteristics that are particularly important to the issues which arise around potential population extinctions. Extinctions are non-linear population events and, except on very large time and space scales (e.g., ice age/interglacial cycles), they are likely to be population responses to more than climatic forcing alone. We present the following three cases to give some perspective into complex salmon population responses to environmental forcing, of which climate is a part.

5.1. Bristol Bay Sockeye salmon

The Bristol Bay (Alaska) sockeye salmon fishery is the largest sockeye salmon fishery in the world. It appears to be extremely well-managed with the major goal of management to keep escapements to the various watersheds (Fig. 9) at optimum levels. Egegik is one watershed in Bristol Bay. From the 1950s through the 1980s, it accounted for less than one-third of the total sockeye salmon production (total run) of the region. Then in the early 1990s, production suddenly exploded to where, in 1992 and 1993, it accounted for well over 50% of the total sockeye salmon production (Fig. 10, top panel). This all occurred under relatively constant long-term escapement levels (Fig. 10, bottom panel).

This seems to us to be a classic example of a rapid and unpredictable shift in the organization of an ecosystem (Bak and Chen 1991, Waldrop 1992): in this case, the entire Bristol Bay salmon production system. It appears that it is also an example of density-dependent constraints operating from the top down (Apollonio 1994) and at the ecosystem level rather than the population level (Wilson et al. 1994). If one examines the top panel Figure 10 carefully, it appears that all systems in Bristol Bay responded to the climate-driven increase in production felt throughout Alaska starting in the late 1970s (Francis and Hare 1994). It also shows that most Bristol Bay production systems, except Egegik, declined in production in the early 1980s. During this time, Egegik became the major producer, as production once increased in the late 1980s, setting the stage for the explosion in Egegik production in the early 1990s.

What this points out to us is that in complex systems, history is important. A change in the constraint structure could have occurred in the early 1980s which set the stage for the sudden outbreak at Egegik in the early 1990s. This is the essence of self-organized criticality (Bak and Chen 1991). Hare (1996) tends to further support this, when he reports estimation failure when trying to fit the most common form of a spawner-recruit model (Ricker 1954) to Egegik data. No simple model can explain the dynamics of the stock over the past several decades – in particular, the response to the 1976/1977 climate shift, coupled with the sudden outbreak at Egegik in the early 1990s.

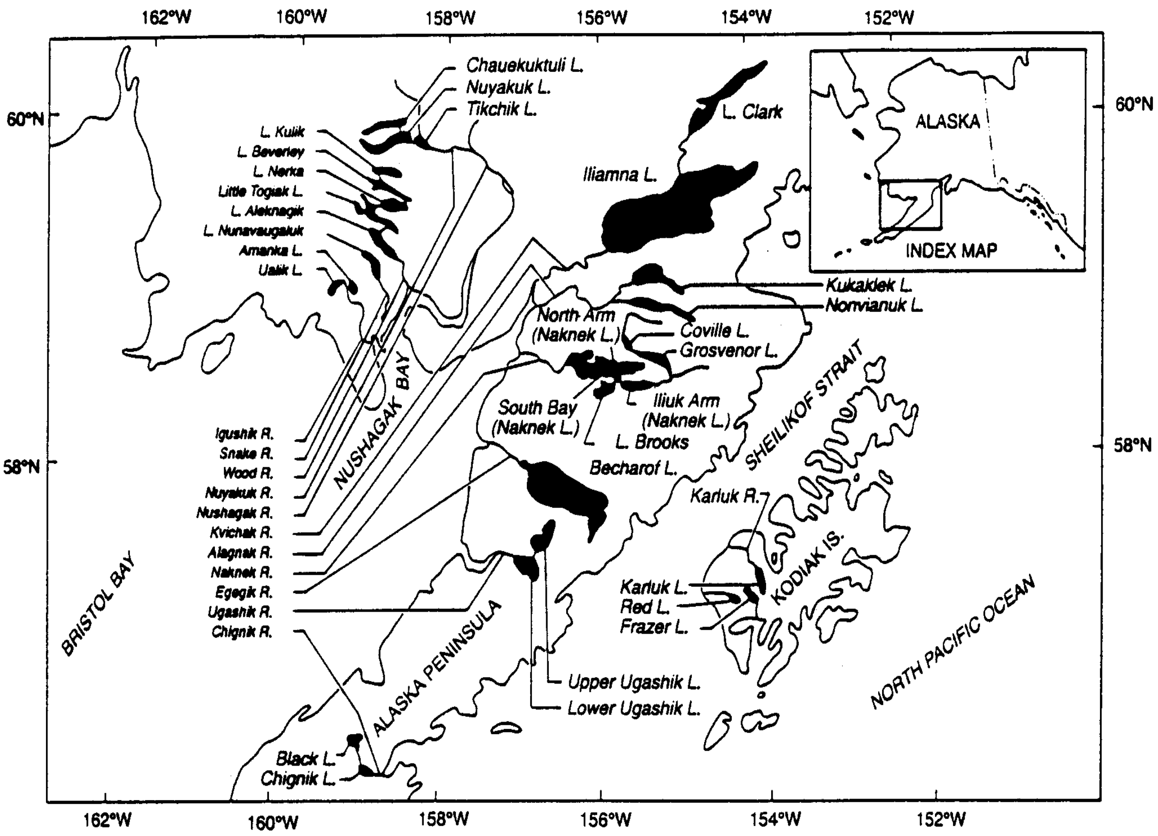


Figure 9. Sockeye salmon drainages in southwestern Alaska.

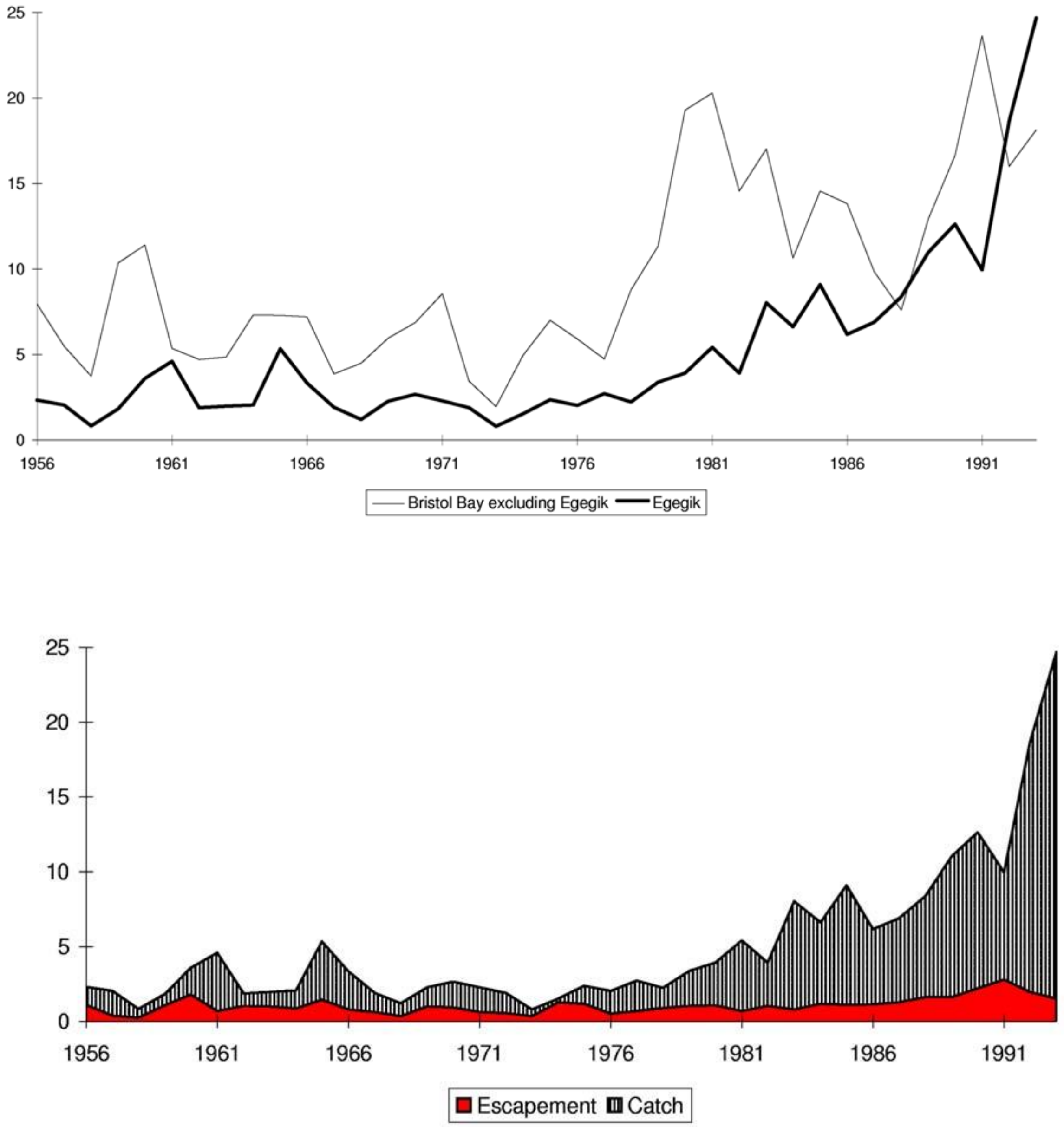


Figure 10. Top panel: Bristol Bay (excluding Egegik) and Egegik sockeye salmon total run size (millions), 1956-1993. Bottom panel: Egegik sockeye salmon escapement and catch (millions), 1956-1993.

5.2. Prince William Sound pink salmon

Our guess is that a similar thing happened in Prince William Sound (PWS), Alaska, with very different results. The top panel of Figure 11 shows the total PWS pink salmon wild and hatchery runs (catch plus escapement) from 1960 to 1994. To be brief, in the mid-1970s, when catches and runs of pink salmon in Prince William Sound (and throughout the Gulf of Alaska) had been at an all-time low for a number of years, a group of fishermen and processors formed a nonprofit hatchery corporation with the idea of enhancing depressed levels of wild production. The hope was to create runs which would provide bountiful harvests even in years when wild runs were weak. By the mid-1980s, the consortium had created the largest man-made pink salmon run in North America. In the late 1980s, however, the wild run declined significantly, while the hatchery run stayed strong. The run (mostly hatchery fish) became so large that it outgrew its market in 1990, forcing the dumping of millions of fish, which could not be sold, and then the market crashed in 1992 and 1993.

The causes of both the rapid increase in the early to mid-1980s, the decline of the wild run in the late 1980s, and the precipitous fluctuations of the total run in the early 1990s are hotly debated issues. Candidates to take credit for the increase are the new hatchery system and the marine environment. Causes for the subsequent declines and fluctuations are the 1989 *Exxon Valdez* oil spill and its effects on both freshwater and marine habitats, overfishing, over-production by the hatcheries, and changes in the marine environment.

As was mentioned earlier, it is clear that salmon production in Alaska increased significantly starting in the late 1970s due to a climatic shift in the marine environment (Fig. 12). It is clear that there was a significant increase in wild pink salmon production in the region in the late 1970s, and that it occurred long before hatchery production had become significant (Fig. 11).

The top panel of Figure 13 shows the PWS wild pink salmon run and hatchery releases the previous year. The rapid decline in wild production in the late 1980s occurred at a time when hatchery production had become significant. This decline does not appear to be related to a reduction in overall wild pink salmon escapement (Fig. 13, bottom panel), which would result from overharvest of wild populations. As a matter of fact, the exploitation rate for wild pink salmon in PWS stayed well below that for hatchery pink salmon during the late 1980s and early 1990s. The likely cause of declines in wild pink salmon production is due to competition between wild and hatchery juveniles when they first enter the marine environment (Cooney 1993). Hatchery smolts are generally released before wild smolts migrate from their natal streams into the near shore marine environment. As a result, not only do they swamp the environment due to the recent quantities of releases, but they get a competitive jump on their wild counterparts in the timing of entry. Of course, this is just speculation but it appears to be a likely scenario.

The abrupt fluctuations in both wild and hatchery production which occurred in the early 1990s could reflect a reorganization of the system in response to what happened at approximately the same time in Bristol Bay. Prince William Sound could have been in a state of severe tension, far removed from equilibrium at that time, and manifested a significant response in the early 1990s. The balance could have been tipped by an event as significant as the *Exxon Valdez*

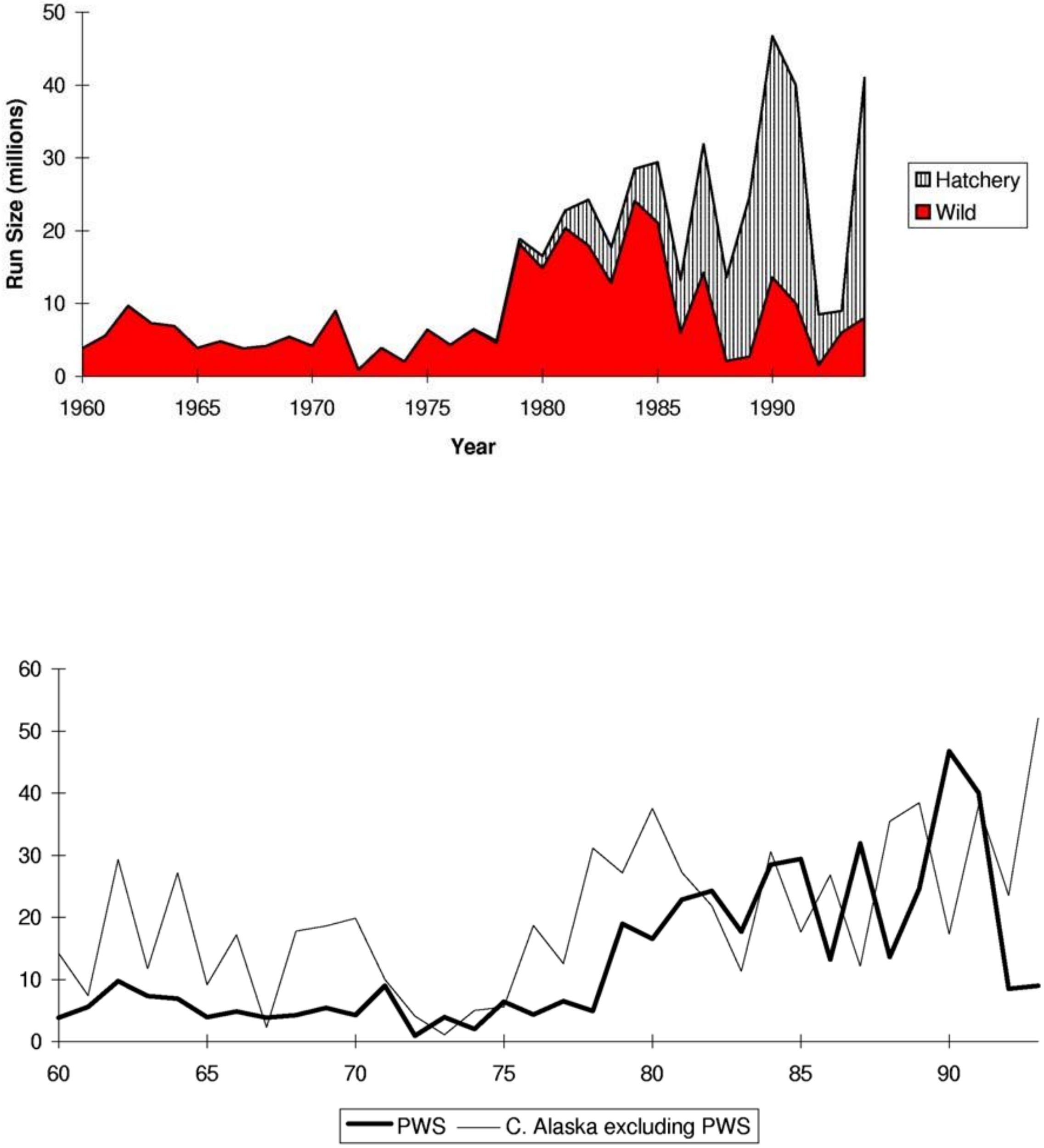


Figure 11. Top panel: Prince William Sound (PWS), Alaska, pink salmon estimated run sizes (millions), 1960-1994. Bottom panel: estimates of PWS and Central Alaska (exclusing PWS) pink salmon total run sizes (millions).

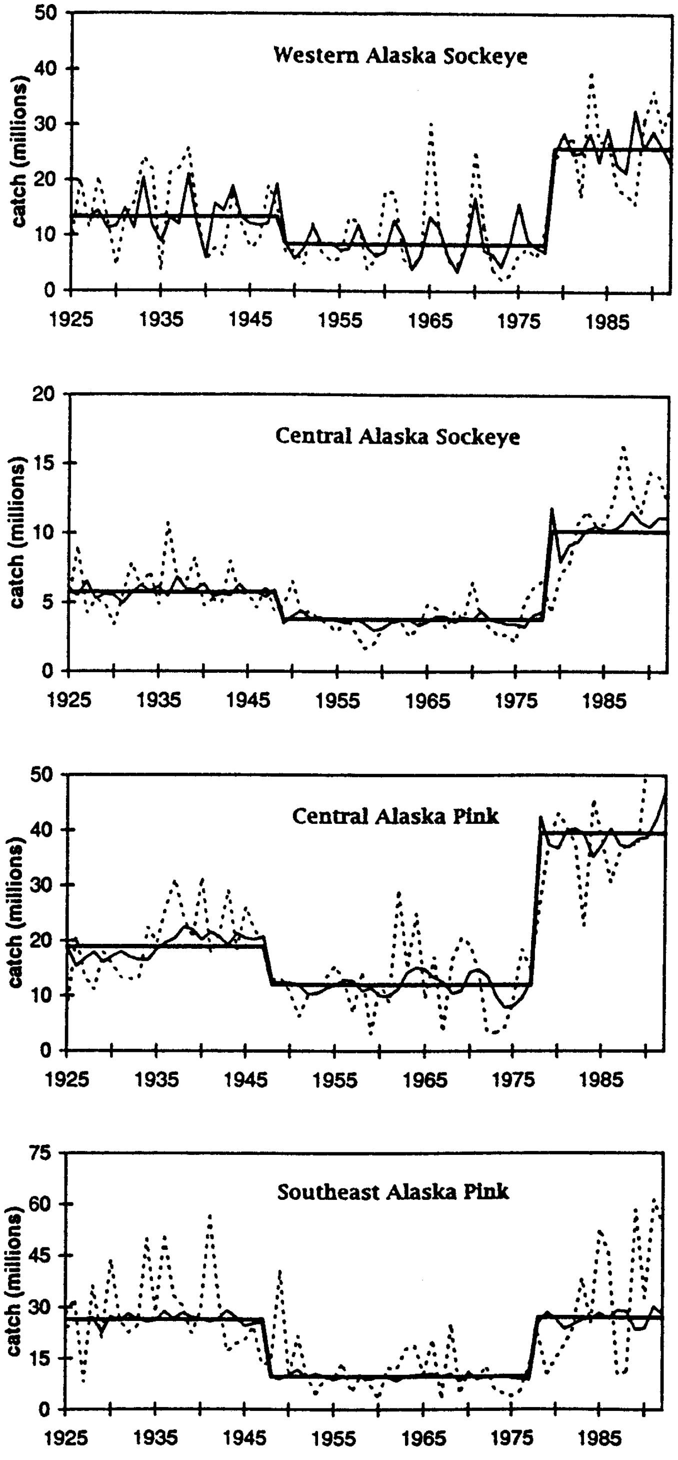
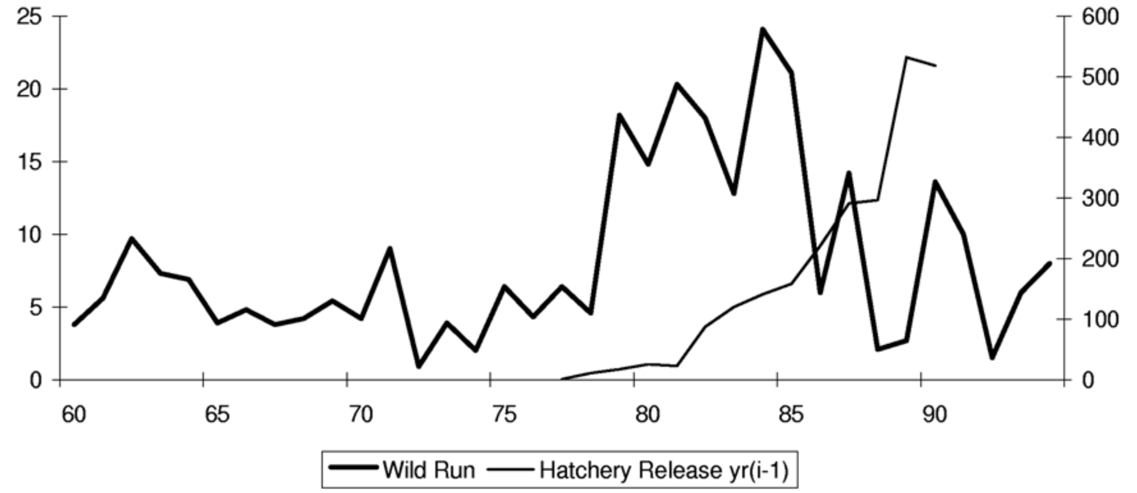


Figure 12. Time history (dashed lines), intervention model fits (thin solid lines), and estimated intervention (thick solid lines) for Alaska salmon catch time series (reproduced from Francis and Hare 1994).



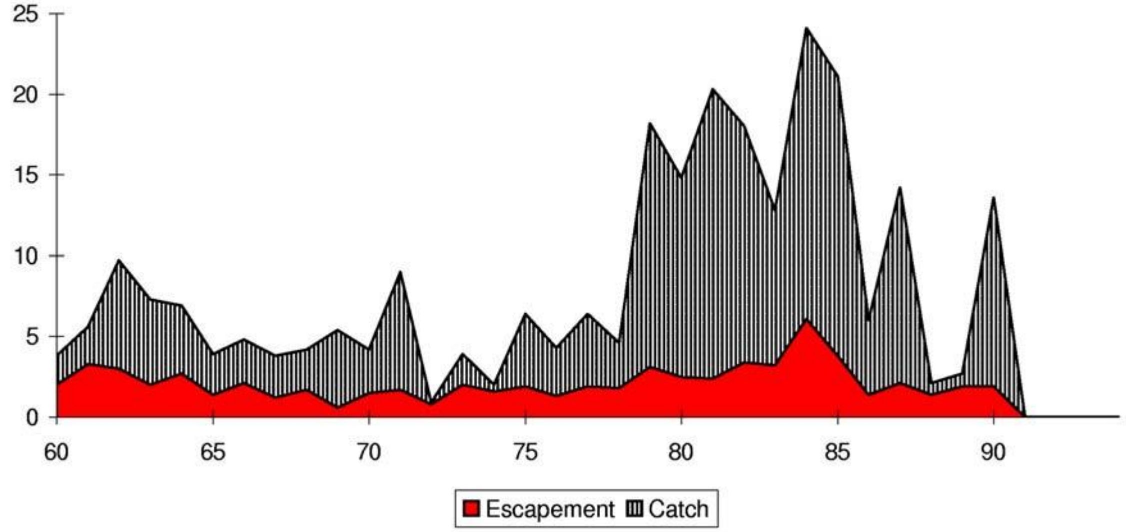


Figure 13. Top panel: Prince William Sound (PWS) wild pink salmon run in year *i* and hatchery releases in year (*i*-1) (millions), 1960-1994. Bottom panel: PWS, wild pink salmon escapement and catch (millions), 1960-1991.

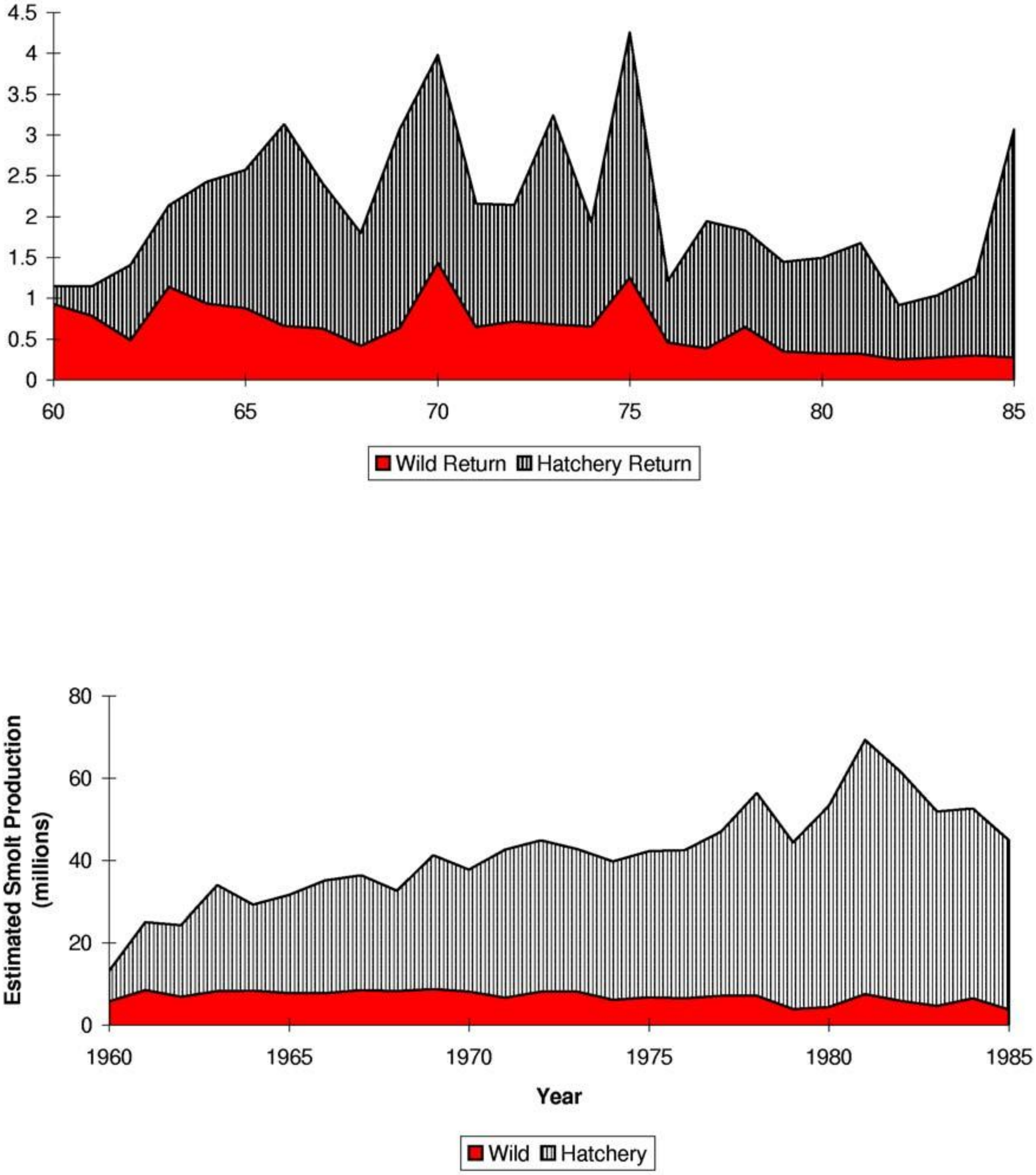


Figure 14. (Top panel) OPI coho salmon estimated run size (millions), 1960-1985. (Bottom panel) OPI coho salmon estimated total smolt production (millions), 1960-1991.

oil spill of 1989 (and its ramifications through the system), or as insignificant as a slight shift in marine climate or fishery dynamics. As Allen (1985) says, when this tension or disequilibrium reaches a certain intensity, "then many amazing and surprising things can happen."

The difference between the Prince William Sound and Bristol Bay experiences, however, comes down to one (Bristol Bay) being considered to be within the realm of normal variability around sustainable use, and the other (Prince William Sound) being considered a biological, social and economic disaster. In neither case is cause directly attributable. However, in one (Bristol Bay), human activities are clearly expected to ebb and flow with the vagaries of nature. In the other (Prince William Sound), blame is quickly passed around from one human institution to another.

5.3. Oregon production index (OPI) coho salmon

A third case involves the OPI of coho salmon. The OPI area is a portion of the Pacific coastal water bounded by Leadbetter Point, Washington, on the north and Monterey Bay, California, on the south. The top panel of Figure 14 shows coho adult salmon returns from 1960 to 1985 (Brodeur 1990, Emlen et al. 1990). The bottom panel of Figure 14 shows the corresponding increases in smolt production, all of which are due to increased hatchery output. However, it is clear that there is a point in the mid-1970s when there was an abrupt decrease in OPI coho salmon run size which persists through the end of the time series. Table 3 shows wild, hatchery and the total OPI coho salmon run size estimates (millions) for 1966 to 1975 and 1976 to 1985.

Table 3. Wild, hatchery, and total OPI coho salmon run size estimates (in millions).

	Wild	**Hatchery**	**Total**
1966–1975	0.77	2.04	2.81
1976–1985	0.36	1.23	1.59

A number of factors have been implicated in both the relatively large run sizes of the 1960s and early 1970s and the subsequent decreases in coho salmon numbers during the late 1970s and 1980s. These factors include: changes in the marine environment, compensatory and depensatory effects of increases in hatchery production, habitat loss, and overfishing. For years, the debate has been on whether the declines in both wild and total OPI coho adult salmon production are due to: 1) density-dependent factors operating early in the marine life history, which are imposed by competition between smolts (overproduction of hatchery smolts), or 2) shifts in constraints induced by the effects of large-scale climate variations in the marine environment and its productive capacity (Nickelson 1986, Emlen et al. 1990, Pearcy 1992, Francis and Brodeur 1996).

Figure 15 attempts to show how difficult it is to sort these factors out. Estimated hatchery and wild smolt-to-adult (ocean) survival rates against total smolt production by year class, are shown in the top panel of Figure 15. It is clear that as smolt production increased due to increased hatchery output, ocean survival of both wild and hatchery populations decreased. The same variables are plotted against time in the bottom panel of Figure 15. It is clear that there was a significant and abrupt decrease in ocean survival which occurred in the late 1970s and, with the exception of the 1983 year class (1985 smolt year), it has persisted to the present.

Recall that in the late 1970s, a climate-induced increase in Alaska salmon production occurred (Francis and Hare 1994). Consistent with the results of our analysis in Section 4.1 many (e.g., Francis and Sibley 1991, Hollowed and Wooster 1992) believe that climate-driven effects on biological production tend to operate in opposite directions in the California Current and Alaska Current ecosystems. As a result, corresponding to the late 1970s increase in Alaska salmon production, one would expect to see a corresponding decrease in Washington-Oregon-California salmon production (Fig. 8). The bottom line is that wild coho salmon populations in the OPI region are at very low levels, and have been petitioned to be declared endangered under the ESA (Weitkamp et al 1995).

Francis and Brodeur (1996) attempted to deal directly with this issue of compound effects on OPI coho salmon fishery production by building a simple model to explore the consequences of empirical relationships in smolt-to-adult survival:

1) between wild and hatchery fish,

2) under a range of ocean environmental (coastal upwelling) conditions believed to influence early ocean survival,

3) as a function of the total number of smolts entering the marine environment, and

4) as a function of improved freshwater spawning and rearing habitat for wild populations.

Figure 16 shows a number of the relationships that were input to the model. The top panel shows two habitat scenarios under which the model was run. Current habitat reflects the Ricker spawner-to-smolt relationship currently used by ODWF to predict wild smolt production from spawner abundance in the OPI area (P. Lawson[5]). Double Habitat reflects a modification of the Ricker relationship to reflect a doubling of the smolt production resulting from an increase of wild coho salmon spawning and rearing habitat (the Ricker b parameter was halved).

The bottom two panels of Figure 16 show the empirical smolt-to-adult survivals used in the model. These were computed as functions of total smolts entering the marine environment in a particular year, and mean coastal-upwelling volumes (March through September) partitioned

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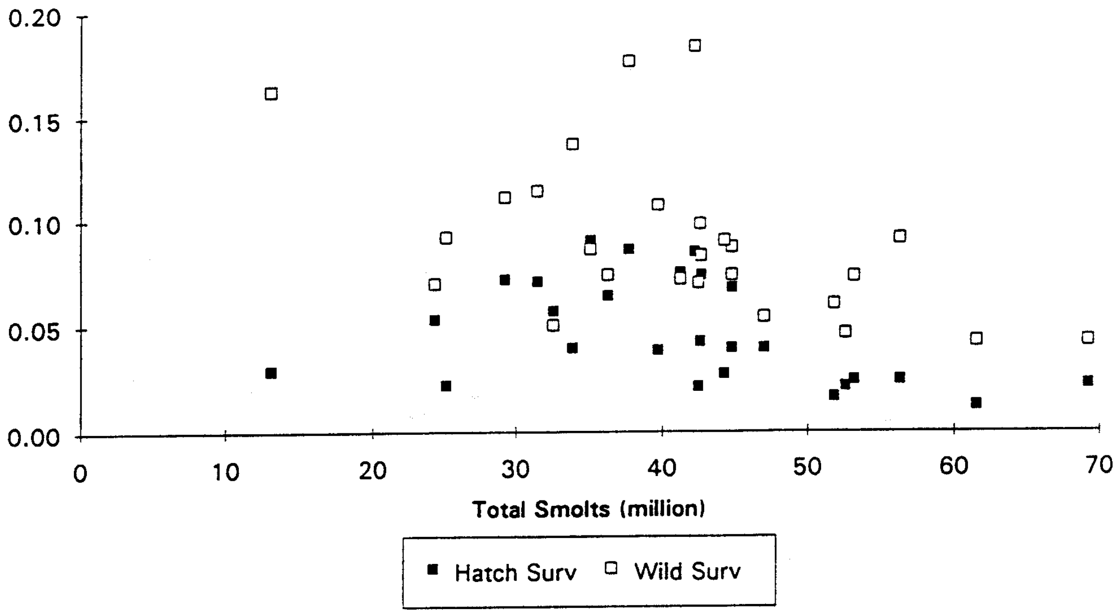
[5] P. Lawson, ODFW, Newport OR. Pers. commun. 1996.



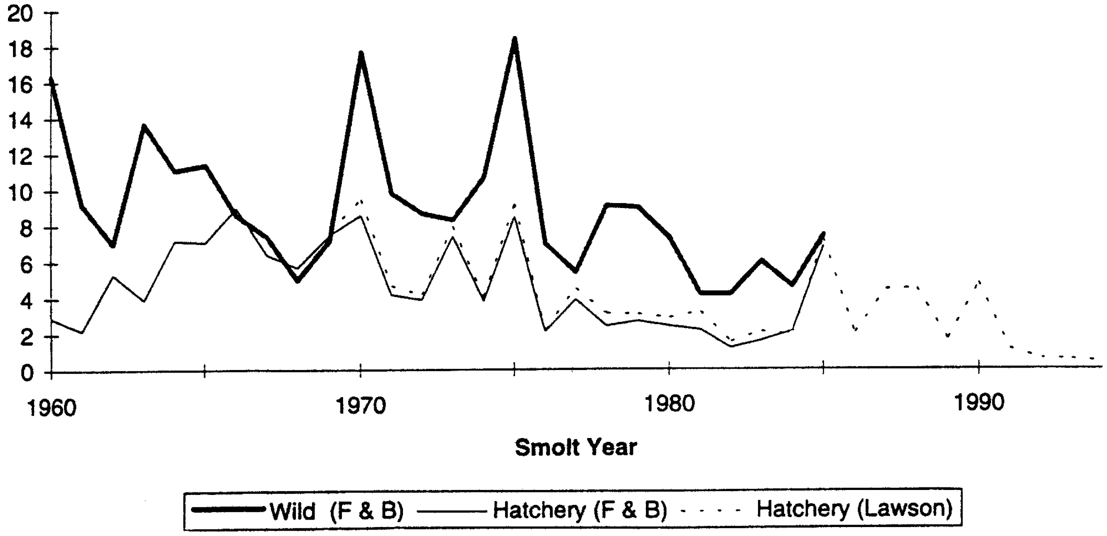


Figure 15. Top panel: OPI coho salmon wild and hatchery ocean survival versus total smolts release (millions), 1960-1985. Bottom panel: OPI coho wild and hatchery ocean survival versus year of ocean entry, 1960-1985 from Francis and Brodeur (1996, F&B). Shown with the dashed line are the official ODFW hatchery ocean survival estimates from 1970-1995 (courtesy of P. Lawson, footnote 5).

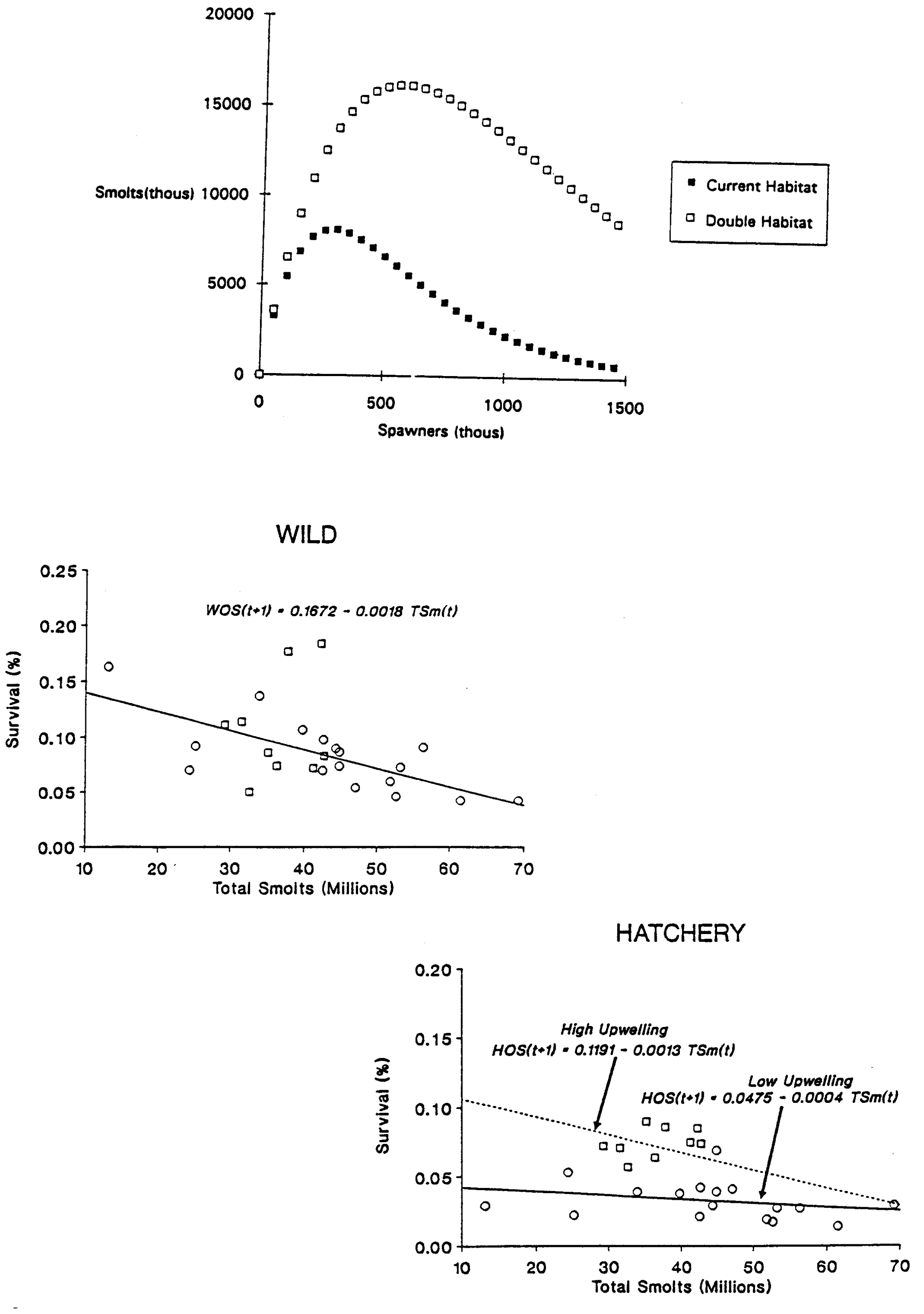


Figure 16. Top panel: OPI coho salmon spawner-to-smolt recruitment curves under current and "doubled" habitat scenarios. Middle panel: empirically derived survival of wild OPI coho salmon smolts as a function of total (wild+hatchery) smolts. Bottom panel: empirically derived survival of hatchery OPI coho salmon smolts as a function of total smolts.

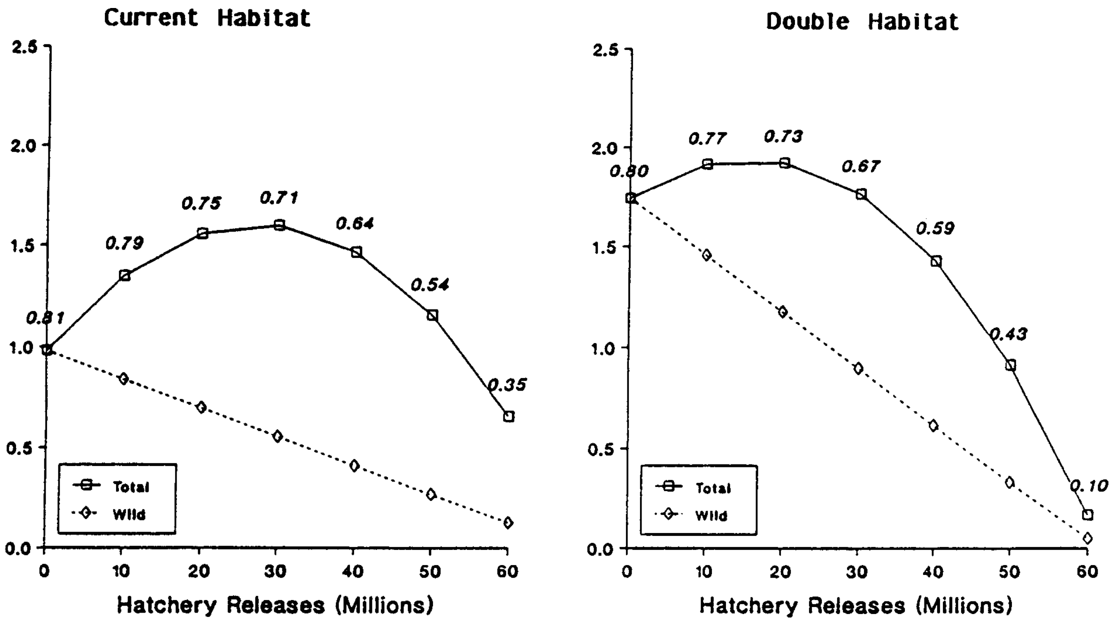


Figure 17. Model estimates for the maximum average wild and total catch (hatchery+wild) versus hatchery releases for (left panel) current habitat and (right panel) doubled habitat scenarios. Printed above each data point is the harvest rate at which those yields are obtained.

into strong and weak upwelling as defined by Nickelson (1986) for wild (middle panel) and hatchery (bottom panel) populations.

Figure 17 shows one set of model results which clearly illustrates the findings of the study. The two panels show estimates of maximum average wild catches and associated total (hatchery + wild) catches plotted against fixed levels of hatchery releases under both current and doubling of wild spawning and rearing habitat. The model was run under a time-varying pattern of ocean environmental conditions meant to reflect what was observed over the 1960 to 1981 period of record. Above each point is the harvest rate at which those yields of wild coho salmon adults are obtained. This example illustrates the apparent constraint on the production potential of wild salmon populations posed by high-levels of hatchery release, apparently similar to the Prince William Sound situation discussed previously. Two important conclusions arose from this study:

1) The levels of OPI-coho salmon hatchery releases in the late 1970s and early 1980s, which were 40-to-50 million per year, were significantly in excess of those necessary to maximize the total catch or realize increases in wild adult fishery production.

2) The more one increases wild spawning and rearing potential, the more one must reduce hatchery production in order to realize that potential in terms of wild adult salmon.

This modeling study was clearly at the metapopulation level. As Francis and Hare (1996) have pointed out, the connection between large-scale climate forcing and Pacific Northwest salmon production may relate more to interdecadal time-scale changes in the structure of the mixed-layer of the coastal ocean, than to variability in the winds that drive the coastal upwelling process. However, no matter how one represents these processes, the implications for individual breeding populations at risk seem to us to be even more acute than these model results reflect.

6. Discussion

How do the case studies relate to the issue of potential extinctions of salmonid populations? Mundy (1997) states: “What the currently prosperous salmon populations have, that the failed populations do not, is adequate habitat. In all cases where harvest of salmon apparently has been sustained indefinitely, there are two common elements; maintenance of adequate habitat, and the eventual implementation of rational limits on harvest.”

One can argue that all three cases have relatively rational limits on harvest, although debate might arise in the case of OPI coho salmon. What really distinguishes the three cases is habitat. Bristol Bay is essentially pristine. Prince William Sound is relatively pristine from the physical point of view. However, the existence of massive populations of hatchery juveniles and adults likely have had a serious impact on the productive capacities of the wild pink salmon populations of the region. In this case, artificially-produced populations of pink salmon become part of the habitat for wild populations.

OPI coho salmon have experienced a quadruple whammy. First, OPI coho salmon spawning and rearing habitat is largely damaged and/or lost (Fig. 18). Second, the region has experienced a significant increase in hatchery salmon production. Third, unfavorable marine and terrestrial environmental conditions have persisted in the region for most of the past two decades. Fourth, as both the wild and hatchery populations and fisheries have declined, the fraction of the catch harvested out of the region (called interceptions) has greatly increased (Fig. 19) The end product has been disaster not only for the populations themselves but also for the fisheries which depend upon them for their sustenance.

7. Conclusions

The results of our analyses demonstrate clear linear relationships between naturally occurring and large-scale changes to the physical environment and a number of salmon populations in the Northeast Pacific. Of particular interest to the issue of climatic influences on salmon extinctions, interdecadal environmental fluctuations, associated with the Pacific Interdecadal Oscillation (PDO), appear to have significantly reduced the ecosystem(s) carrying capacity for West Coast coho salmon since the 1977 regime shift. The overall productivity of salmon in Alaska has dramatically increased during this same time period in response to PDO-related climate changes. Our results agree with those of previous studies that identify the first few months of the salmon's ocean life as the period of critical climatic influences on survival, which in turn, suggests that coastal and estuarine environments are key areas of biophysical interaction.

It seems likely that the polarity of the PDO climate pattern will continue to change at interdecadal time scales as it has over (at least) the past century. If and when that happens, West Coast coho salmon will once again experience favorable climatic conditions while Alaska salmon will be faced with poor marine and terrestrial climate conditions. However, wild West Coast coho salmon will continue to face the problems caused by the legacy of human land use, hatchery and harvest practices.

In summary, what are the lessons to be learned regarding the effects of climate on the extinction of salmon populations?

1) Climate alone is not likely to tip the balance. However, climate variability clearly has the capacity to amplify the risk and likelihood of extinction when superimposed upon salmonid ecosystems under extreme stress from humans.

2) Since climate effects on salmon seem to be much more significant at interdecadal than annual time scales, and since interdecadal time-scale climate change can only be recognized in hindsight, the effects of climate need to be hard wired into fishery management policy (e.g., different management strategies and algorithms may be required for different climatic regimes).

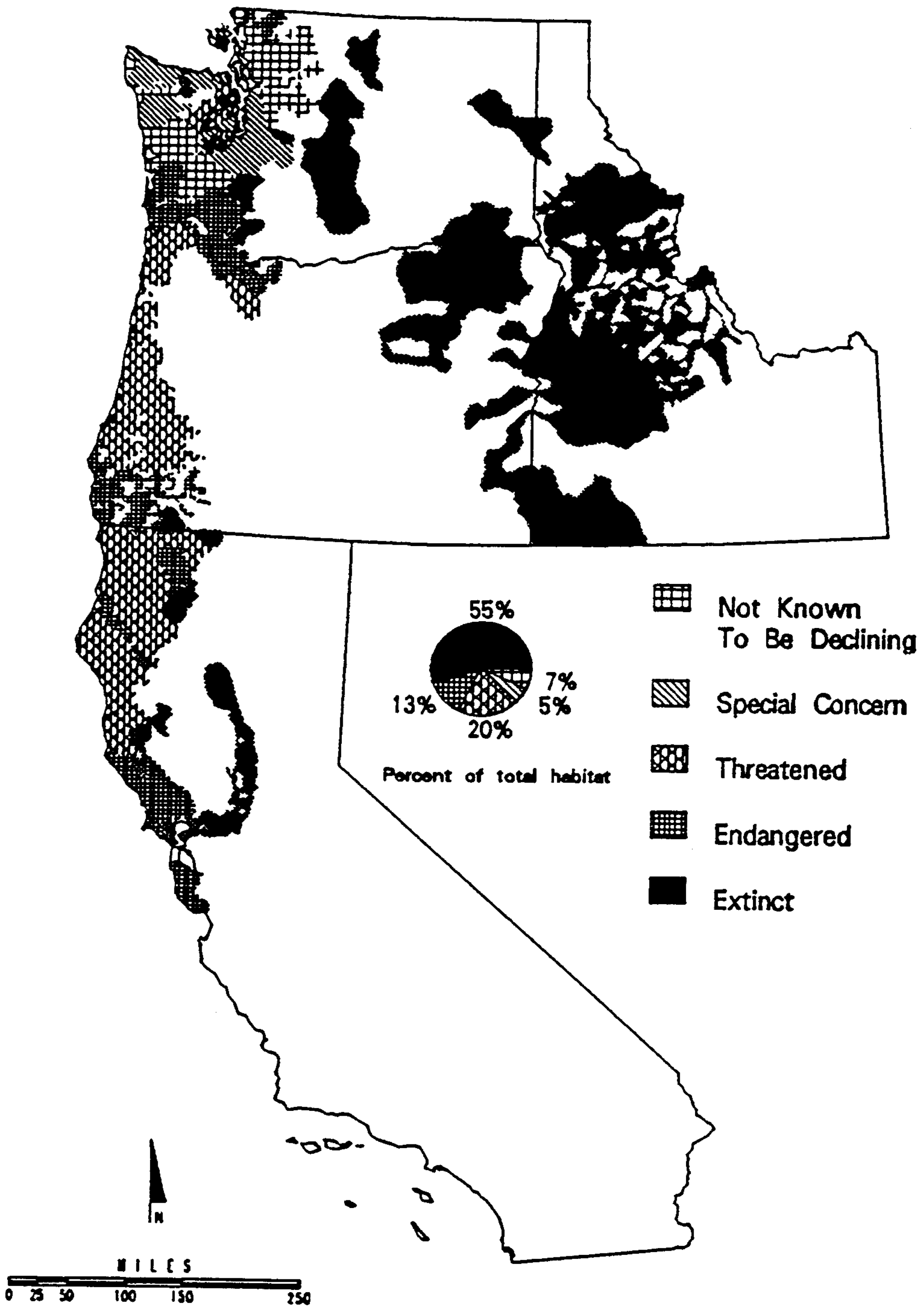


Figure 18. Status of coho salmon in the Pacific Northwest and California (reproduced from The Wilderness Society 1993).

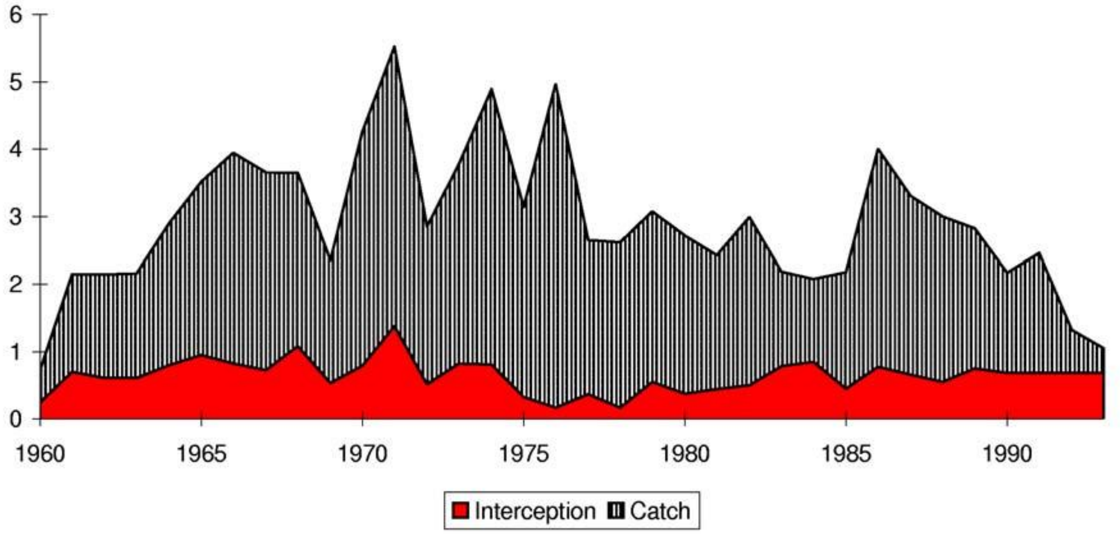


Figure 19. Washington-Oregon-California coho salmon fishery interceptions and in-area catches (million), 1960-1994.

3) Climate-related negative impacts on salmon production at the regional scale likely have much more severe implications for individual breeding populations than for metapopulations as a whole. Clearly, this has been the case for thousands of years. However, combining the effects of human activities with climate fluctuations likely amplifies a number of these negative influences.

It is also important to note that human activities have not only altered the salmon's terrestrial and estuarine environments, but they have also contributed to the envelope of climate variability by rapidly increasing the concentrations of radiatively important gases in the atmosphere. At present, our analysis of the climate record for the Pacific Basin suggests that anthropogenic climate change, if it is occurring, has been swamped by natural variability in this century. However, anthropogenic changes to the Earth's radiation budget are expected to lead to rapid changes to the climate system over the next few decades and centuries. Can Pacific salmon adapt to new climatic regimes?

It is our opinion that salmon populations in regions with healthy habitat will probably survive as long as the time scale of environmental change does not exceed their rate of adaptation. On the other hand, those populations that are presently stressed by occupying healthy, marginal or fragmented habitat, will most likely face more acute threats of extinction with the additional burden of significant anthropogenic climate changes.

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