Environmental influences on North Pacific salmon abundance and marine fish recruitment

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Abstract

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I investigated common patterns in North Pacific salmon abundance and marine fish recruitment and environmental drivers of these patterns. In Chapter 1 I identified patterns of covariation in the abundance of regional groups of wild pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) from 34 population groups from Asia and western North America using multivariate analysis. The most prominent pattern of abundance variation was dominated by the Alaskan population groups and greater abundance was related to warm sea surface temperatures in the eastern Bering Sea and Gulf of Alaska. The second dominant pattern captured a dipole between North American and Asian salmon population groups that was associated with an intense, large-scale Aleutian Low. This highlights the existence of basin-wide covariations in wild salmon abundance that are associated with spatially coherent and regionally distinct patterns in North Pacific climate. In Chapter 2 I tested the hypothesis that synchronous Northeast Pacific marine fish recruitment is due to a shared susceptibility to environmental variability. For 52 marine fish stocks in the Eastern Bering Sea and Aleutian Islands, Gulf of Alaska (GOA), and California Current (CC) ecosystems, I tested for synchrony in stock-recruitment residuals within each ecosystem. Based on evidence of synchrony, I used Bayesian hierarchical models to model stock-recruitment residuals for groups of stocks with similar life histories as a linear function of environmental covariates. Within the GOA several stocks had a similar strong relationship with Northeast Pacific sea surface height. In the CC many stocks had a strong relationship with San Francisco sea level, experiencing higher recruitment during periods of high sea level and low upwelling the year before spawning and low sea level and high upwelling the year of spawning. Although for most stocks these models explained only a small portion of the variance in the stock-recruitment residuals, there was a consistent relationship among stocks within the ecosystems to the covariates. Future research should utilize these common responses to environmental variables across stocks to improve identification of environmental processes important to variability in abundance and productivity of fish.

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Introduction

Many fish stocks show large variations in their abundance and productivity. These patterns of variation may take many different forms, such as cycles of low and high abundance or episodes of extreme abundance (Caddy and Gulland 1983, Spencer and Collie 1997). There is a long running debate regarding whether fishing effort or the environment drives these fluctuations (Thompson 1937, Burkenroad 1948). For many fish stocks fishing pressure does not explain a large portion of the variability (Myers et al. 1994, Gilbert 1997, Vert-pre et al. 2013). For these stocks, investigation of environmental influences may be necessary to identify the processes driving these patterns (Walters and Collie 1988).

There are a multitude of environmental processes that may influence fish stocks, so identifying the important processes is often challenging. Fish may be directly affected by changes in the physical environment through variability in growth, reproduction, survival, and distribution and indirectly affected through changes in food availability and quality and predation (Roessig et al. 2004, Perry et al. 2005, Drinkwater et al. 2010). For example, temperature affects reproduction through changes including gonadal development, maturity, and egg size in some species (Drinkwater et al. 2010). Other species in the ecosystem that interact with directly affected species (e.g., predator, prey) may exhibit a lagged response to a shift in the physical environment (Drinkwater et al. 2010). Fish are especially susceptible to environmental influences during their early lives (Hjort 1914, Cushing 1982). Examination of the environmental processes affecting fish stocks during these life stages may be especially important to identify the environmental drivers of abundance and productivity.

Identifying environmental influences on the abundance and productivity of marine resources is especially important to improving resource management. In the U.S., under the Sustainable Fisheries Act, ecosystem-based management has been identified as an important guiding principle for national ocean policy. This policy considers ecosystem effects such as the impact of seasonal weather, climate variability, and climate change on vital rates, predation, competition, and prey availability (NMFS1999). Recent research has concentrated on the incorporation of environmental covariates into fisheries stock assessment to account for both interannual variability around a mean level of productivity and regime shifts in the mean level of productivity (Maunder and Watters 2003, Deriso et al. 2008, A'mar et al. 2009, Schirripa et al. 2009, Ianelli et al. 2011a). Increased knowledge of the effects of environmental factors on the productivity of marine fish stocks will contribute to management through improved stock assessment and forecasting. Understanding drivers of productivity may also help in deciding if declines in productivity are due to environmental conditions or fishing, which contributes to the success of management plans (Vert-pre et al. 2013). Incorporating this knowledge of environmental influences on marine species into the management of marine resources is an important goal to attain.

Retrospective analyses of biological and physical data from across the North Pacific have contributed to the identification of both large- and local-scale environmental processes important to variations in the abundance and productivity of fish stocks of the North Pacific (e.g., Hare and Francis 1995, Hare and Mantua 2000, Litzow and Mueter 2009). Further analysis of variations in the abundance and productivity of North Pacific fish stocks may aide in identifying the important environmental processes driving these variations.

In my first chapter I examine the patterns of variation in North Pacific salmon abundance. I identify covariation in salmon abundance across stock groups spanning the North Pacific Rim that are related to environmental variables. While these large-scale patterns in salmon abundance may be well related to ocean indices that integrate many atmospheric and oceanographic processes (Stenseth et al. 2003), it is important to also identify local processes impacting these salmon stocks, especially during their early marine life stages when they are most susceptible to these processes.

In my second chapter I further study common environmental influences on fish stocks to identify environmental drivers of Northeast Pacific marine fish recruitment using Bayesian hierarchical models. Within the Eastern Bering Sea and Aleutian Islands, Gulf of Alaska, and California Current ecosystems, I evaluate the presence of synchrony in stock-recruitment residuals between stocks and identify groups of stocks with similar susceptibility to environmental influences during their early lives. These stocks may be especially susceptible to environmental influences during early life periods, so recruitment may be best related to local environmental processes experienced during these life stages. Since many stocks have similar early life histories, processes simultaneously impacting several stocks during these stages may create recruitment synchrony. This synchrony may aid in identifying the processes important to recruitment across stocks.

The methods I utilize draw strength from the common influences of environmental processes on many marine organisms throughout ecosystems and ocean basins. These and other methods that utilize this shared information may help in identifying environmental influences on marine species. Examining many populations simultaneously may be especially valuable because spurious correlations, a common problem in identifying environment drivers, are less likely

(Myers 1998). My research emphasizes the benefit of considering information from many fish stocks and environmental scales when attempting to identify environmental drivers of variability in fish abundance and productivity.

Chapter 1: Oceanographic influences on patterns in North Pacific salmon abundance

Abstract

Previous analyses of salmon abundance from the Northeast Pacific have identified common patterns associated with large-scale environmental patterns, such as the Pacific Decadal Oscillation (PDO), but few studies have incorporated data from around the North Pacific Rim. I objectively identified patterns of covariation in the abundance of regional groups of wild pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) from 34 population groups from Asia and western North America. I also used composite analysis to identify patterns of sea surface temperature (SST) and sea level pressure (SLP) variations that covary with the major patterns of salmon abundance variations. I used principal component analysis (PCA), non-metric multidimensional scaling (NMDS), and dynamic factor analysis (DFA) to identify the major temporal patterns in the salmon abundance time series and their regional expression. Each of these 3 methods identified similar patterns of salmon abundance variations, indicating they are robust. The most prominent pattern of abundance variation was dominated by Alaskan sockeye, pink, and chum salmon regional population groups. This Alaska pattern exhibited a positive shift in the mid-1970s and was correlated with several environmental variables including the Pacific Decadal Oscillation (PDO) index, with warm (cold) periods in the Gulf of Alaska and eastern Bering Sea corresponding with high (low) abundance years. However, the SST anomalies associated with the Alaska salmon pattern were much more confined to the eastern Bering Sea and Gulf of Alaska than the basin scale SST signatures of the PDO pattern. If environmental conditions related to SST in this region are causing changes in this salmon production pattern, the recent cool period may be a harbinger of declining salmon abundance for many pink, chum, and sockeye salmon stocks in Alaska and northern British Columbia. The second salmon abundance pattern captured a dipole between North American and Asian salmon population groups that was associated with an intense, large-scale Aleutian Low. The third salmon abundance pattern was associated with increased abundance of most Russian and western Gulf of Alaska population groups and corresponded with negative winter SLP anomalies in the Northeast Pacific. I show that warmer than average SSTs in the regions of the natal rivers during the early ocean period correspond with increased Alaska salmon abundance associated with the first pattern, increased Asian salmon abundance associated with the second pattern, and increased western Gulf of Alaska salmon abundance associated with the third pattern, but mildly cooler than average SSTs corresponding to increased abundance of Russian salmon abundance associated with the third pattern. These results add to a large body of evidence indicating the importance of early marine environmental conditions to overall survival and abundance. To my knowledge, this is the first analysis that identifies regional patterns of covariation in salmon abundance around the entire North Pacific Rim, and it highlights the existence of basin-wide covariations in wild salmon abundance that are associated with spatially coherent and regionally distinct patterns in North Pacific climate.

Introduction

Climate can have large impacts on the abundance and distribution of marine species. Marine species may be directly affected by environmental changes through variability in growth, reproduction, survival, and distribution and indirectly affected through changes in top-down and bottom-up trophic interactions (Roessig et al. 2004, Perry et al. 2005, Drinkwater et al. 2010). Retrospective analyses of biological and physical data from across the North Pacific have contributed to the identification of both large- and local-scale environmental processes important to trends and variations in the productivity of marine ecosystems of the North Pacific (e.g., Hare and Francis 1995, Hare and Mantua 2000, Litzow and Mueter 2009).

Patterns in North Pacific salmon production have been particularly well studied because Pacific salmon support major commercial, subsistence, and recreational fisheries around the North Pacific Rim, and historical catch and escapement estimates are available for many population groups over multiple decades and across broad geographic regions. Analysis of catches of pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) in the United States, Canada, Japan, and Russia for 1925-1989 indicated a common production pattern among species throughout the North Pacific (Beamish and Bouillon 1993). Multi-decadal variations in this basin-scale pattern of salmon production was related to variations in the intensity of the Aleutian Low atmospheric pressure system (Beamish and Bouillon 1993). Large scale covariation of Pacific salmon production has also been related to physical forcing through the Pacific Decadal Oscillation (PDO), the dominant pattern of North Pacific sea surface temperature (SST) variability that is also linked with variations in the Aleutian Low (Mantua et al. 1997, Hare et al. 1999).

Environmental conditions during marine life stages, especially early marine periods, are important to the survival of salmon. Early marine growth of juvenile salmon during their first summer at sea influences survival during late fall and winter, so prey availability and quality during this critical period is related to adult salmon abundance (Moss et al. 2005, Farley et al.

2007a, Cross et al. 2008). Marine food-web conditions during this period may be shaped by the physical environment over several years and correlated with large-scale environmental indices.

Regional differences in relationships between salmon production and environmental variability have also been identified. Several studies have shown positive covariation in productivity among Northeast Pacific pink, chum, and sockeye salmon stocks across scales of several hundred kilometers, but not on larger scales, using age-specific spawner and recruit abundance data collected at the stock level (Peterman et al. 1998, Pyper et al. 2001, 2002, Eggers and Irvine 2007, Mueter et al. 2007). Moreover, positive coastal SST anomalies were associated with increased productivity of pink, chum, and sockeye salmon in Alaska, and decreased productivity for stocks of these species in Washington and British Columbia (Mueter et al. 2002).

Ruggerone et al. (2010) assembled catch and spawner abundance estimates for pink, chum, and sockeye salmon from across the North Pacific. They used these estimates to evaluate trends in abundance and density-dependent interactions between wild and hatchery salmon at sea, but did not examine patterns of covariation among and between the different population groups and species of salmon. Further analysis of these data can aid in understanding regional and large-scale patterns of salmon abundance within the North Pacific. Because of the large size of this data set, identifying the patterns across regions and species is not a trivial exercise. Ordination techniques allow the variance in a large number of variables to be represented in a smaller number of dimensions with a minimal loss of information.

I applied ordination techniques to 34 regional salmon abundance time series from Ruggerone et al. (2010) to identify patterns of salmon production and associated environmental patterns of the North Pacific. I hypothesize that a small number of common patterns will account for a significant portion of the total variance of North Pacific salmon abundance, and that these patterns are associated with basin-scale patterns of climate variation. This hypothesis is tested using the regional pink, chum, and sockeye salmon abundance data compiled by Ruggerone et al. (2010) and gridded historical observations of SST and atmospheric sea level pressure (SLP). Pink, chum, and sockeye salmon made up an average of 89% of the total commercial salmon catch in the North Pacific by weight over the 1925 to 2003 period, so they represent most of the salmon within North Pacific ecosystems (Eggers et al. 2005). The large geographic span of these data allow for identification of regional influences of large-scale environmental patterns. I expect that the common patterns in abundance will be related to environmental variability during the marine stages, especially the early marine stages, due to an overlap in habitat occupied across these regional salmon groups and large-scale environmental influences similarly impacting the regional environmental conditions.

Methods

Data

I obtained estimates of wild Pacific salmon abundance from 1952-2005 based on catch and escapement data assembled by Ruggerone et al. (2010). These data were available for pink, chum, and sockeye salmon in 12 regional stock groups from eastern Asia to western North America (Figure 1.1). These abundance estimates may provide a better index of productivity than catch data alone because they are less influenced by such factors as changes in fishing effort and harvest policies, although salmon catch and abundance patterns have shown high correlation (Eggers and Irvine 2007). I aligned salmon abundance time series by the mean year of ocean entry, a period of high mortality during which year-class strength is thought to be primarily determined, by lagging the time series by the difference between the mean time of ocean entry and return (Beamish and Mahnken 2001). I assumed the following mean times between the year of ocean entry and year of return: 1 year for pink salmon, 3 years for chum salmon, and 2 years for sockeye salmon. After aligning all time series for all species, I ultimately used ocean entry years 1951-2002 in this analysis.

The multivariate analyses were carried out using standardized salmon abundance time series by regional group (34 total) for the period 1951-2002. I standardized the log-transformed abundance time series for each regional population group to have a mean of 0 and a standard deviation of 1. Pink salmon have a strict two-year life cycle, which creates genetically distinct populations in even and odd years. Because of this life history, for some regions large differences in even and odd year pink salmon spawner abundance was observed. To reduce the signal of this two-year cycle in the time series, pink salmon even and odd year abundance values were standardized independently, then recombined into a single continuous annual time series within each population group region. I considered the even and odd year pink salmon regional groups as a single time series because of their overlap in regional environmental processes that impact abundance.

I compiled environmental indices for the North Pacific to investigate their relationships with the salmon abundance trends identified in the analyses. Local- and large-scale indices were used to investigate environmental effects across a range of geographic scales. I included a total of 17 environmental indices in this analysis (Table 1.1). In addition to these time series, I used gridded SST and SLP data across the North Pacific to investigate the spatial relationship of the patterns in salmon abundance with environmental variability. Monthly values of NOAA Extended Reconstructed SST at a 2º × 2º spatial resolution and NCEP Reanalysis SLP at a 2.5º ×

2.5º spatial resolution were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their web site at http://www.esrl.noaa.gov/psd/ (Kalnay et al. 1996, Smith et al. 2008). I calculated extended winter (October-March, for year corresponding to January) and summer (April-September) averages of these data for the North Pacific Ocean for mapping to allow for investigation of environmental drivers of biological patterns.

Ordination methods

Several ordination methods have been previously employed to identify common patterns in marine productivity. Principal component analysis (PCA) is an ordination technique that reduces the number of variables in a dataset into a fewer number of dimensions that are linear combinations of the original variables. PCA has been previously used in identification of the patterns in Northeast Pacific salmon catch data (Hare and Mantua 2000, Litzow and Mueter 2009). Non-metric multidimensional scaling (NMDS) is an ordination technique that is robust to non-linear relationships (Minchin 1987). Dynamic factor analysis (DFA) is a dimension-reduction technique designed specifically for time series data that models multiple time series in terms of their common trends and additional explanatory variables (Zuur et al. 2003a). DFA has been used recently in several applications to estimate common trends in fisheries time series (Zuur et al. 2003b, Zuur and Pierce 2004, Erzini 2005, Devine and Haedrich 2011). I used these three techniques to identify temporal patterns in North Pacific salmon abundance and evaluate their relationship with the marine environment.

Principal component analysis

PCA concentrates most of the variance in a large dataset into a smaller number of easily interpreted patterns that are a linear combination of the original dataset. The principal components (PCs, also called scores) give the temporal variability in the dataset. The eigenvectors (also called loadings) describe the weights by which the individual salmon abundance time series are multiplied in calculation of the PCs. Positive loadings indicate the time series has a positive correlation with the PC and negative loadings indicate a negative correlation. The eigenvalues indicate the amount of variance explained by each PC.

The first few PCs explained most of the variance of the dataset and were used to describe the major patterns of variability. The statistical significance of the first ten PCs was used to determine the appropriate number of PCs to examine based on two commonly used methods, the broken stick model and a Monte Carlo permutation test of significance with 1,000 permutations (Legendre and Legendre 1998). Overlap in the sampling error of the eigenvalues indicates the patterns described by the PCs are potentially mixed and non-interpretable. I calculated the sampling errors of the PCs using the formula of North et al. (1982) to ensure non-overlap of the PCs examined.

To identify environmental variables related to the patterns in salmon abundance, I calculated the Pearson correlation coefficients and the corresponding statistical significance for the PCs and the environmental variables.

Non-metric multidimensional scaling

NMDS attempts to arrange objects in a low-dimensional space such that the distances in the ordination space are close to the ranked distances of the original dataset. The configuration of the points within the ordination space is iteratively adjusted to improve the correspondence with the ranked distances of the original dataset until no improvement in the fit is observed. The NMDS axes (also called scores) give the temporal variability in the dataset. The loadings indicate the correlation of the individual salmon abundance time series with the NMDS axes. I used Euclidean distance, which follows the equation

(1.1) $D(y_1, y_2) = \sqrt{\sum_{t=1}^{p} (y_{1,t} - y_{2,t})^2}$

where the distance between salmon abundance time series y_1 and y_2 ($D(y_1, y_2)$) is a function of the squared difference between the time series at time t summed over the p years of data (Legendre and Legendre 1998).

In NMDS the number of dimensions, or axes, of the ordination must be specified. The stress, a goodness-of-fit criterion that measures the discrepancy between the distance in ordination space and the distances of the original dataset, was used to determine the appropriate number of dimensions for the ordination. The stress decreases with an increase in the number of dimensions and a value of 20% or less is considered interpretable (Clarke 1993).

I also calculated the Pearson correlation coefficients and the corresponding statistical significance for the NMDS axes and the environmental variables.

Dynamic factor analysis

I used DFA to model the shared trends in abundance among the stocks as a linear combination of common trends and the effect of environmental drivers. DFA allows the common patterns among N time series to be characterized with many fewer M trends. Following Zuur et al. (2003b), the DFA model can be written as

(1.2) $\alpha_t = \alpha_{t-1} + f_t$, where $f_t \sim N(0, Q)$, and

(1.3) $y_t = Z\alpha_t + Dx_t + e_t$, where $e_t \sim N(0, R)$.

The N x 1 vector of data observed at time t (y_t) are modeled as a linear combination of the M x 1 vector of latent trends (α_t), P x 1 vector of explanatory variables (x_t), and observation (sampling) errors (e_t). The matrices Z and D contain the stock-specific loadings on the trends and explanatory effects, respectively. These loadings can be compared to determine which common trends explain the abundance variability for a particular region and which regions have shared abundance variability. The matrices Q and R are the variance-covariance matrices for the process and observation errors, respectively.

Although DFA and PCA are similar, there are some important distinctions. In PCA the trends must be straight lines that are orthogonal to each other but in DFA the trends are smooth random walks that can take many shapes. DFA also allows for a variety of forms of the covariance between time series (R) to account for interactions between stock groups.

Three forms of the observation error variance-covariance matrix R were tested: a diagonal matrix with equal variance and zero covariance, a diagonal matrix with unequal variance and zero covariance, and a non-diagonal matrix with equal variance and equal covariance. Using a diagonal matrix R can lead to common trends that are only related to a few response variables (Zuur et al. 2003b). For that reason, the variance-covariance matrix that included non-zero covariance was also considered, in which the off-diagonal elements of the variance-covariance matrix represents joint information in the regional salmon abundance time series that cannot be explained with other terms (Zuur et al. 2003b).

Indices of the PDO and North Pacific Gyre Oscillation (NPGO) were included in the DFA models as explanatory variables. Annual (October-September, for year corresponding to January) indices of the PDO and NPGO were calculated based on monthly indices available on the internet (PDO: http://jisao.washington.edu/pdo/PDO.latest; NPGO: http://www.o3d.org/npgo/npgo.php). Models that included one, both, and neither of these explanatory variables were tested.

Common trends (*M*) of one to six were investigated for each of the model forms. The small-sample Akaike information criterion (AIC_C) was used as a measure of goodness-of-fit to compare the models (Hurvich and Tsai 1989). Other model diagnostics, including examination of the residuals, model fits, trends, and factor loadings, were also used in model evaluation and selection. Minimizing the number of trends used in analysis was also important to ease interpretation. The DFA trends for the best model chosen were examined for correlation with the environmental variables.

Physical variable mapping

Compositing, or superposed epoch analysis, is a method commonly used in climate science to identify environmental conditions associated with events, such as explosive volcanic eruptions or an El Niño-Southern Oscillation (ENSO) event onset (Portman and Gutzler 1996). In compositing, the data are separated into categories or time periods (epochs) and the mean conditions for the different categories are compared. This method makes no assumptions of linearity and is good at separating small signals from noise. For compositing, the years corresponding to the highest one-third and lowest one-third of the PCs, NMDS axes, and DFA trends were identified. Mean extended winter (October-March, for year corresponding to January) and summer (April-September) SST and SLP maps for these years were plotted as composite anomalies from the mean values over the time period of analysis (1951-2002). These maps were visually inspected to identify patterns in the physical environment related to the patterns of salmon abundance.

Software

All statistical analyses was completed in R software, version 2.15.2 (R Development Core Team 2012a). PCA was implemented in the stats package, version 2.15.2 (R Development Core Team 2012a). NMDS was implemented in the vegan package, version 1.17-6 (Oksanen et al. 2011). DFA was implemented in the MARSS package, version 3.2 (Holmes et al. 2013).

Results

Principal component analysis

I limited my focus to the first three PCs because they were significant based on both the broken stick model and Monte Carlo permutation tests. Also, the sampling error of the first PC does not overlap with any other PCs. While the sampling error of the second and third PCs overlap, the sampling error of the third PC only marginally overlaps with that of the fourth PC (Figure 1.2). Therefore, these patterns should not be mixed with higher order PCs (North et al. 1982). The first three axes respectively account for 25, 12, and 10% of the total variance of the data, together accounting for 47% of the total variance (Figure 1.2).

The PCs showed extended periods of low and high scores (Figure 1.3). The first PC (PC1) shifted from low to high scores in the mid-1970s. The second PC (PC2) had low scores in the mid-1970s to the late-1980s, with moderate and high scores in the remaining periods. The third PC (PC3) had high scores through the early-1960s, followed by low scores through the mid-1970s and moderate scores in the remaining time period.

Most of the western North American (WNA) population groups had positive loadings on PC1, with several groups exhibiting very strong loadings (Figure 1.4). Cook Inlet pink and chum salmon were the only WNA groups that had negative loadings on PC1. Composite maps of SST and SLP anomalies conditioned on low PC1 values were associated with cooler SSTs in the coastal waters of Russia and the Bering Sea and higher winter SLPs over the Aleutian Islands (Figure 1.5). High PC1 values were associated with warmer coastal temperatures through much of the North Pacific and lower winter SLP over the Aleutian Islands. SST anomalies were especially strong in the far eastern Bering Sea in winter, for both the highest and lowest PC1 composites, and this sub-regional SST anomaly expression is also evident in summer but with weaker SST anomalies. PC1 was significantly correlated with many of the environmental variables investigated (Table 1.2).

Most eastern Asian (EA) population groups had positive loadings on PC2, while WNA population groups tended to have negative loadings (Figure 1.6). Low PC2 values were associated with cooler temperatures around Japan and the central North Pacific, warmer temperatures in the eastern Bering Sea and central Gulf of Alaska, and negative winter SLP anomalies over the north Pacific (Figure 1.7). High values were associated with warmer temperatures throughout much of the North Pacific, especially the coastal waters of the Northwest Pacific. PC2 did not have a significant correlation with any of the environmental indices investigated (Table 1.2).

Most Russian and western Gulf of Alaska (Southern AK Peninsula, Kodiak, Cook Inlet, and Prince William Sound) stock groups had positive loadings on PC3, with pink and chum stocks having stronger loadings (Figure 1.8). Low values of PC3 were associated with cooler coastal SSTs in the Northeast Pacific, especially in the Gulf of Alaska in summer, while high values were associated with warmer SSTs in the Gulf of Alaska and along British Columbia, Washington and Japan, cooler winter SSTs in the Bering Sea and along Russia, warmer SSTs off the coast of Japan in winter, and negative winter SLP anomalies in the Northeast Pacific (Figure

1.9). PC3 had a significant negative correlation with summer upwelling off Washington (UPWA; *r*=-0.34; *p*=0.014; Table 1.2).

The first three PCs had very high correlations with the corresponding NMDS axes and DFA trends (Table 1.3). Limited NMDS and DFA results are presented, but they are consistent with the PCA results except where noted.

Non-metric multidimensional scaling

Three dimensions were used to optimize clarity of interpretation while maintaining reliably interpretable results of the NMDS analysis and to be consistent with the number of PCs analyzed. The three-dimensional NMDS resulted in a stress of 13%, which is below 20% so the results can be considered reliable (Clarke 1993). The linear fit of the distances in ordination space to the distances of the original dataset had an R^2 value of 0.88, also indicating the ordination provides a reliable interpretation of the original dataset.

Similar to the PCA results, the NMDS axes exhibited extended periods of low and high scores (Figure 1.10). The second axis had a longer period of low scores than PC2, from the mid-1960s to the late-1980s, and was negatively correlated with summer upwelling off Washington (UPWA; *r*=-0.38; *p*=0.0056; Table 1.2). The third axis was associated with weaker SST and SLP anomalies than PC3.

Dynamic factor analysis

The model with the lowest AIC_C value had four trends and a diagonal variance-covariance matrix *R*. However, for ease of interpretation, a model with three trends and a variance-covariance matrix *R* of unequal variance and zero covariance was used as the final model. While the three trend model had an AIC_C value 26 AIC_C units greater than that of the four trend model, the trends of these models were highly correlated and the trends of the three trend model were consistently highly correlated with those of the other models tested (Figure 1.11). This indicates the robustness of these three trends across the different DFA models tested. Examination of the residuals, model fits, trends, and factor loadings indicated adequate model fit. All models with other forms of the variance-covariance matrix tested results in an increase in AIC_C from the models with a diagonal variance-covariance matrix of unequal variance and zero covariance for an equal number of trends.

The only models that included covariates that were superior to the models without covariates (with an equivalent number of trends and variance-covariance matrix) were the models with only the PDO index as an explanatory variable and one and two common trends. These models had an AIC_C value much greater (at least 160 AICc units) than the chosen model. For this reason, a model with environmental covariates was not chosen.

Similar to the PCA and NMDS results, the DFA trends had periods of low and high values except the transitions were less abrupt (Figure 1.11). The first DFA trend had a positive shift, but it was more gradual, beginning in the mid-1970s and increasing through the late-1980s. Several eastern and western Kamchatka groups had positive loadings on this trend, which was not observed in the PCA or NMDS results. The second trend had low values through the early-1980s, when there was a shift to high trend values. Trend 2 tended to have opposite loadings for the EA and WNA regions, but this pattern was less clear than in the PCA results because a few EA populations (western Kamchatka pinks salmon, eastern Kamchatka chum salmon) had positive loadings, similar to the WNA regions. High values of trend 2 were associated with warmer temperatures throughout much of the North Pacific, especially the eastern Bering Sea and the Sea of Okhotsk. The third trend showed an extended period of low values in late-1960s to the late 1980s, with moderate values in the remaining period. This trend had few strong loadings in WNA and weak SST and SLP anomalies in the Gulf of Alaska, indicating this trend mostly captured variations in EA salmon population groups.

Discussion

I used three different multivariate analysis methods to identify common patterns in North Pacific pink, chum, and sockeye salmon abundance. My analysis identified a leading pattern exhibited by many of the population groups in WNA and a second pattern that captures a dipole between many EA and WNA population groups. Identifying these patterns of salmon abundance may help in understanding environmental drivers of salmon abundance and improve management of salmon stocks throughout the North Pacific through the perspective gained by examination of the large-scale salmon abundance patterns throughout this region.

The dominant patterns and trends in salmon abundance were robust to the three different analysis methods used in this study. NMDS is more robust to capturing nonlinearities in the relationship between variables than methods such as PCA and DFA. The consistency between these methods indicates a limited influence of nonlinearities in the data. While the results of the PCA and NMDS were very similar, the DFA results differed in a few important ways. DFA, which is especially designed for use with time series data, identified trends that had greater autocorrelation than the patterns identified by PCA and NMDS. This pattern is due to the lag-one autocorrelation that is part of the modeling of the trends in DFA (Equation 1.2). The second DFA trend also showed a weaker east-west dipole pattern than the PCA and NMDS results, indicating further analysis of this pattern may be warranted. The DFA models tested also included PDO and NPGO indices as covariates, but a model without these covariates was chosen as the best model.

The poor fits of the models with these environmental covariates may be due to the high correlation of the abundance time series with these covariates for only a small portion of the population groups.

The first major pattern in the salmon abundance data captures variability in many WNA population groups, especially those from Alaska. While the time series for this pattern is correlated with the PDO index, the composite SST anomaly patterns conditioned on the highest and lowest values of PC1 feature concentrated SST anomalies in the eastern Bering Sea and northern Gulf of Alaska, but no features of note across the broader subarctic North Pacific where the PDO SST pattern has much of its signature. This pattern also had high correlations with several other indices, including the MEI and ALPI, indicating it may be related to a regional expression of these large-scale environmental patterns. While it may be tempting to interpret the positive linear trend of this pattern as being related to global increases in SST, the change in SST associated with this pattern is closely related to low-frequency, oscillatory temperature changes in the SST of the North Pacific, captured in part by the PDO. The Gulf of Alaska and eastern Bering Sea winter SST conditions associated with this pattern have actually cooler conditions than the long-term (1900-2012) mean in several recent years (2008, 2009, 2012; Figure 1.12). If environmental conditions related to SST in this region are causing changes in this salmon production pattern, the recent cool period may be a harbinger of declining salmon abundance for many pink, chum, and sockeye salmon stocks in Alaska and northern British Columbia.

The time series tracking the first salmon abundance pattern also showed a positive shift in the mid-1970s, which corresponds to a widely recognized regime shift across several Northeast Pacific ecosystems (Hare and Mantua 2000). Previous studies have shown that the increase in productivity and abundance of the WNA salmon stocks in the late-1970s coincides with an increase in productivity of plankton and many marine fish species, supporting the idea of an increase in pelagic marine production during this time period (Francis et al. 1998, Anderson and Piatt 1999). Positive values of the PDO that occurred in the period after this shift have also been associated with earlier spring ice-breakup and warmer summer water temperatures in a southwestern Alaska lake, conditions which relate to greater summer zooplankton abundance and juvenile sockeye salmon growth (Schindler et al. 2005). Large-scale climate patterns, such as those associated with the PDO, impact both the freshwater and marine environments that salmon experience, and likely influence salmon productivity in multiple habitats and life stages.

Warmer coastal ocean temperatures in much of the North Pacific, especially during winter months in the eastern Bering Sea, were associated with positive values of the first pattern. Previous research of WNA salmon stocks has also found warm anomalies in coastal temperatures are associated with increased survival rates for Alaskan stocks and decreased survival rates in Washington and British Columbia stocks (Mueter et al. 2002). While these findings for Alaskan stocks are consistent with the relationships identified in this study, we found the Washington and British Columbia stocks were similarly associated with warmer temperature anomalies, although less extreme anomalies were observed in these southern regions. This difference may be due to the limited number of stock groups in the southern region included in this analysis.

The negative sea level pressure anomalies over the Aleutian Islands are associated with positive values of the first PC and correspond to an intensified Aleutian Low. Beamish and Bouillon (1993) and Hare and Francis (1995) previously found an intense Aleutian Low to be associated with the variations in North Pacific salmon catches. An intense winter Aleutian low is associated with warm periods of the PDO and tends to result in increased wind forcing and precipitation, which enhances counterclockwise circulation in the Gulf of Alaska, increased upwelling in the interior Gulf of Alaska and central subarctic North Pacific, and increased upper ocean stratification and warm water advection into the Northeast Pacific (Bakun 1996). Increased precipitation and coastal runoff in southeast and southcentral Alaska also favors development of stronger and more widespread surface fronts that likely increase the concentration of nutrients and plankton that can contribute to higher food concentrations for juvenile salmon. Enhanced enrichment also results from the increased upwelling in the interior of the gyre and within eddies that tend to be produced by the intensified Alaskan Stream (Bakun 1996). Because all of these processes are linked, changes in temperature or winds associated with biological productivity may be associated with many oceanographic processes during intense Aleutian Low periods (Bakun 1996). Therefore, it is not surprising that the first PC was highly correlated with many of the environmental variables investigated. The strong loadings of many of the WNA population groups on this pattern indicate these environmental processes may be more regional and not influential in the Northwest Pacific where EA salmon stocks spend their early marine life.

While Beamish and Bouillon (1993) focused on one common pattern in catch of salmon across the United States, Canada, Japan, and Russia, my analysis indicates a secondary pattern of variability exists as an east-west dipole in salmon abundance between some of the WNA and EA population groups. The opposite responses may be due to large-scale climatic influences that simultaneously affect the North Pacific but have opposite effects on local-scale marine conditions in the Northwest and Northeast Pacific, respectively. For example, the warm phase of the PDO corresponds to warming in the Northeast Pacific but cooling in the Northwest Pacific

(Mantua et al. 1997). This indicates varying and possibly opposite responses to large-scale environmental forcing by salmon stocks on the two sides of the North Pacific. Additionally, periods of high recruitment for the EA population groups were associated with warmer SST in the Northwest Pacific, indicating these stocks may experience higher survival during warm periods similar to Alaskan stocks (Mueter et al. 2002). The negative winter SLP anomalies associated with negative values of this pattern were concentrated in the central North Pacific but the cooler than average SSTs around Japan may be due to an increased influence of subpolar waters that extend farther south along the coast of Japan under these conditions (Seager et al. 2001).

The opposite responses by the WNA and EA population groups captured by PC2 may also indicate a role for density dependent interactions between eastern and western populations that arises during later life stages when EA and WNA salmon have overlapping distributions in the subarctic North Pacific and Bering Sea (Ruggerone et al. 2003, Myers et al. 2007). However, the stocks that Ruggerone et al. (2003) identified to have especially strong competition were eastern Kamchatka pink salmon and Bristol Bay sockeye salmon (within the western Alaska group here), which have weak loadings on this pattern. Other EA and WNA stocks do overlap in their distributions and competition between adults is likely important to their growth and survival.

The third pattern of salmon abundance captures covariation in several Russian and western Gulf of Alaska population groups. High abundance for these population groups was related to warmer than average summer temperatures in the Gulf of Alaska but cooler than average winter temperatures in the Bering Sea and Sea of Okhotsk. The SLP anomalies associated with this pattern were concentrated in the Northeast Pacific, which may have a strong influence on the environment experienced by the western Gulf of Alaska stocks that had high loadings on this pattern.

Warmer temperatures in the region of the natal rivers of the population groups, the habitat in which they spend their early marine stages, were generally positively related to recruitment for the stocks that had strong loadings on the three dominant abundance patterns. This is consistent with previous findings for Alaskan (Mueter et al. 2002) and Japanese (Seo et al. 2010) salmon stocks. Only for the third pattern was high abundance related to cooler temperatures in the region of the natal rivers of the Russian stock groups. Incorporation of additional southern population groups may have indicated differing responses of those populations due to differing conditions favorable to growth and survival in northern and southern ends of a species range and oceanographic variability across the range (Mueter et al. 2002). Future analysis including populations covering a greater latitudinal range is important to identifying potentially differing responses to environmental variables.

I also included in my analysis other local environmental indicators. Gulf of Alaska freshwater runoff was not strongly related to the patterns identified, but the WNA upwelling indices did show moderate correlations with several of the salmon abundance trends. Investigation of additional local-scale environmental indicators may reveal how the large-scale patterns relate to the local conditions experienced by these regional groups for a more mechanistic understanding of environmental drivers of the common patterns in North Pacific salmon abundance.

My analysis focused on variability in marine productivity, but variations in freshwater productivity may also contribute to regional-scale abundance trends. Changes in rainfall and freshwater runoff, which affect the freshwater environment, may be captured by the environmental indices included in this analysis, as changes in surface air, stream and lake temperatures are correlated with regional patterns of SST variation (Rogers 2010). Consideration of other metrics tracking variations in the freshwater environment may also be important to consider when comparing patterns in regional salmon abundance trends.

Although pink, chum, and sockeye salmon have different life histories, they are similarly exposed to many environmental influences in their early marine life. I hypothesize that shared exposure in the early marine period is the mechanistic link supporting the observed covariations in abundance across these species and regions. In an analysis of the between-species correlation in stock-recruitment residuals of pink, chum, and sockeye salmon stocks, correlations of pink and chum salmon were much stronger than sockeye salmon with either pink or chum salmon (Pyper et al. 2005, Mueter et al. 2007). In my analysis, pink and chum salmon tended to have stronger positive loadings on the third pattern than sockeye salmon, but overall there was not greater correspondence in the loadings for any subset of species. Research focused on juvenile salmon distribution in the eastern Bering Sea found sockeye salmon were distributed offshore, chum salmon were distributed inshore, and pink salmon were distributed offshore and nearshore during odd years and further offshore during even years (Farley et al. 2007b). Variation in the early marine habitat utilized by these species may account for the varying productivity trends due to differences in local prey availability. There may also be competition between these species, with Japanese chum salmon found to switch to lower quality prey in years of high pink salmon abundance (Tadokoro et al. 1996).

While I investigated atmospheric and oceanographic variability through the lens of salmon abundance patterns, other factors may be important for salmon abundance that were not considered here. For example, overfishing may contribute to low production unrelated to environmental variability. I did not account for influences of spawner abundance through stock-recruit relationships because of the regional scale of the data, but this is likely an important factor in the abundance of returning salmon that has been looked at in other analyses (Peterman et al. 1998, Pyper et al. 2001, 2002, Mueter et al. 2007). In an analysis of southwestern Alaska salmon abundance over the past 500 years, Rogers et al. (2013) found that the abundance for most stocks was dominated by centennial-scale variation and there was not synchrony between stocks before commercial fisheries began, indicating the decadal-scale variability of the last century may be related to stronger anthropogenic influences. Due to the short record since commercial fishing began, centennial-scale variability is not detectable from my analysis. The biocomplexity of the salmon stocks within a region, which may be reduced due to fishing and other anthropogenic influences, may also contribute to changes in the variability in salmon abundance over the past decade (Johnson and Schindler 2012).

Increases in hatchery production in the 1970s could have increased density dependent effects in nearshore and offshore marine habitats, impacting the productivity and abundance of wild salmon population groups included in this analysis (Myers et al. 2004, Ruggerone et al. 2010, Kaeriyama et al. 2012). For example, the Cook Inlet pink and chum salmon were the only WNA groups that had negative loadings on the first PC. The opposite pattern exhibited by the salmon stocks in this region may be due to local conditions in Cook Inlet, possibly affected by an increase in hatchery salmon production during this period (Hilborn and Eggers 2000).

Regime shifts in the ecosystems of the North Pacific have been widely recognized in the literature, and the major patterns of variability identified in my analysis indicated extended periods of low and high abundance across the North Pacific salmon stocks. Regime shifts occur when the characteristic behavior of a natural phenomenon (e.g., abundance, recruitment, SST) spanning a decade or more changes abruptly, within a year or two (Bakun 2005). In the North Pacific, sustained changes in the productivity or abundance of dozens of marine fish populations in the decades before and after 1977 has been widely recognized as an example of a marine ecosystem regime shift (Hare and Mantua 2000). Due to the typically short length of the physical time series available, the dynamics of interdecadal climate variations are often indistinguishable from red noise and cyclic patterns of variability (Rudnick and Davis 2003, Overland et al. 2006, Newman 2007). The dominant pattern of salmon abundance identified in my analysis exhibited a shift in the mid-1970s and the second dominant pattern exhibited a shift in the late-1980's, which is consistent with previous regime shift analyses for the North Pacific (Hare and Mantua 2000). Future analyses should further investigate the presence and drivers of non-linear dynamics in North Pacific salmon abundance.

My analysis of North Pacific salmon abundance identified the leading pattern exhibited by many of the stocks in Alaska, similar to patterns identified in previous analysis of Northeast Pacific salmon catch and abundance, and a second pattern with opposite expression in many EA and WNA population groups. To my knowledge this is the first analysis that identifies regional patterns of covariation in salmon abundance around the Pacific Rim, and it highlights the existence of basin-wide covariations in wild salmon abundance that are associated with spatially coherent patterns in North Pacific climate.

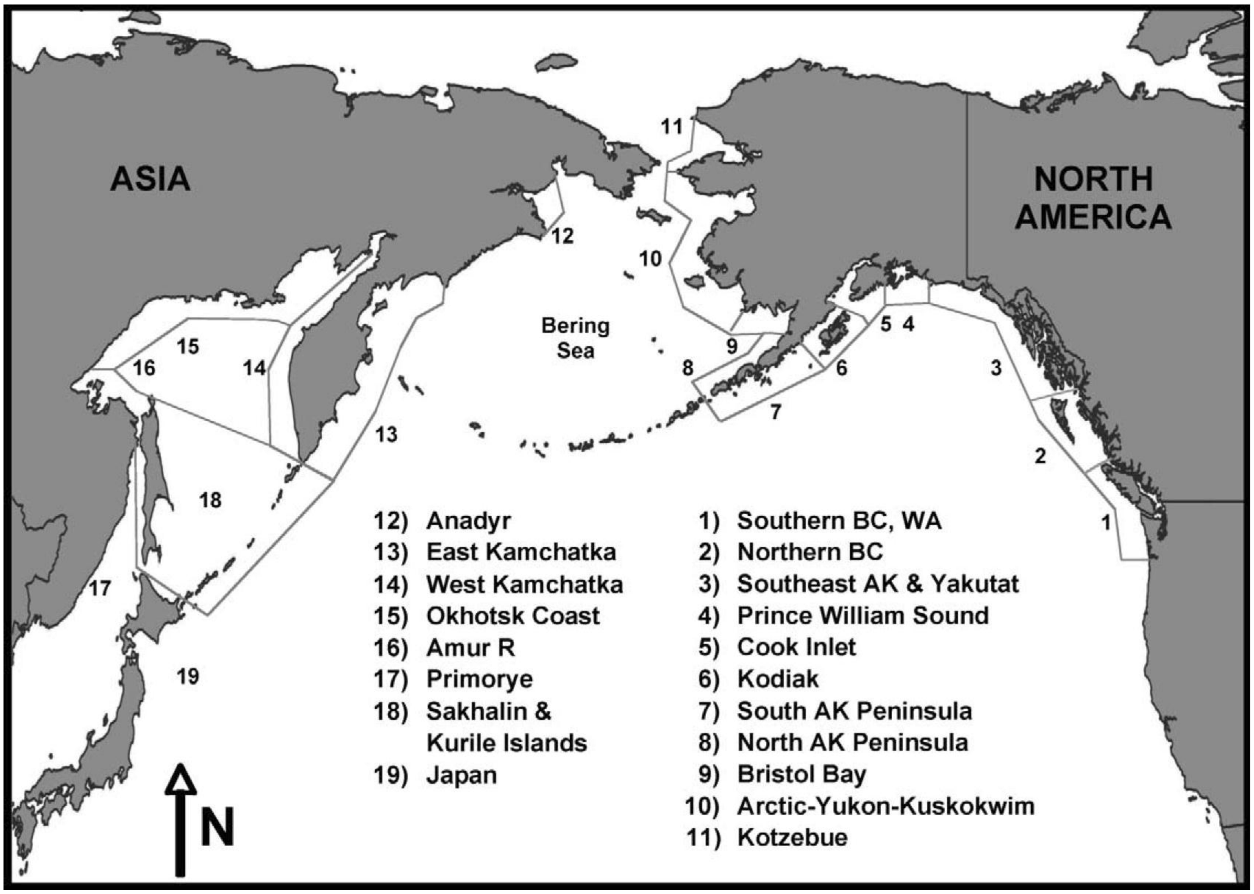

Figure 1.1: Approximate geographic locations of the regional stocks groups. The western Alaska stock group includes areas 8-11 and the Russian mainland and islands stock group includes areas 12 and 15-18 (figure from Ruggerone et al. 2010).

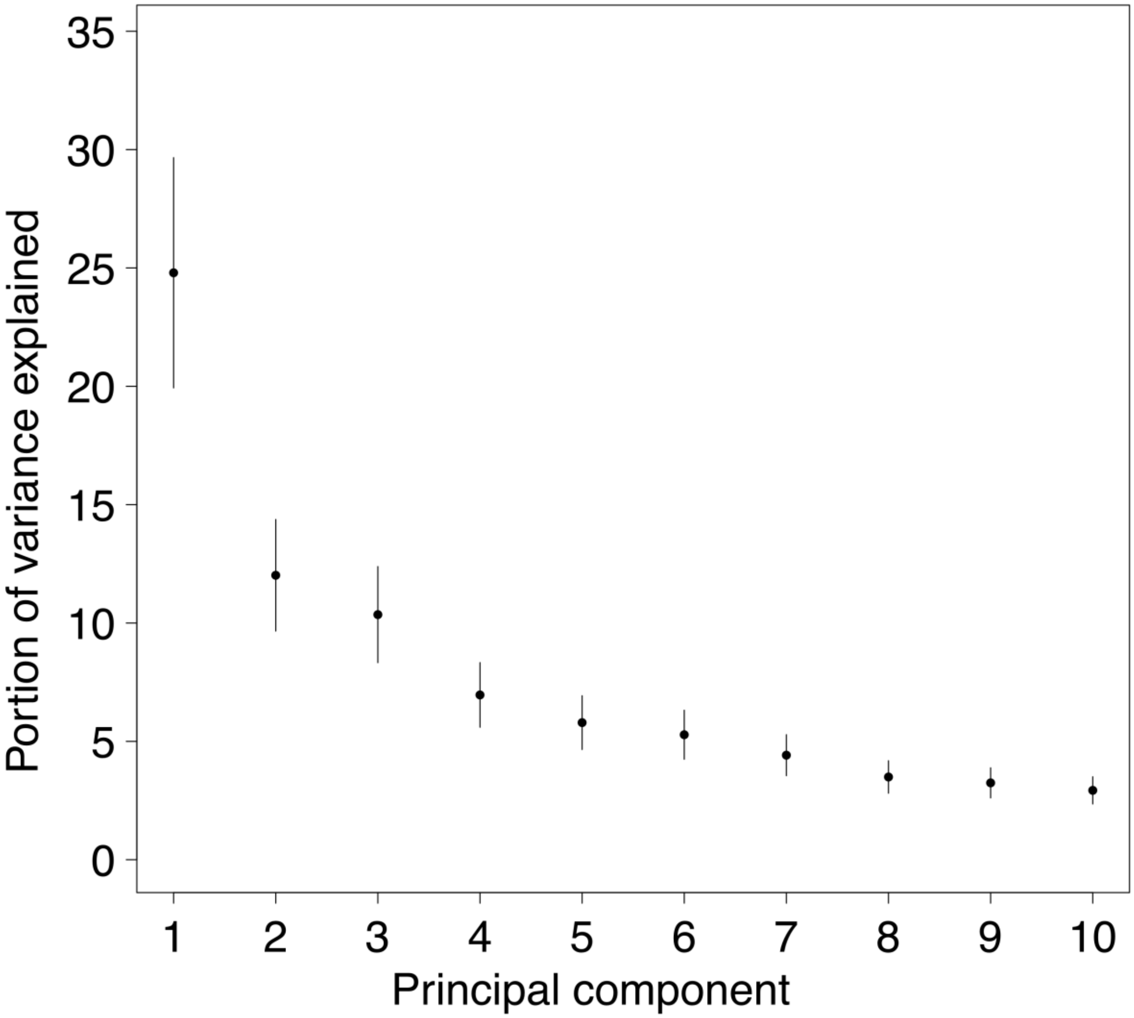

Figure 1.2: Plot of the portion of total variance explained by the first ten principal components from principal component analysis. The sampling error bars were computed using the formula of North et al. (1982).

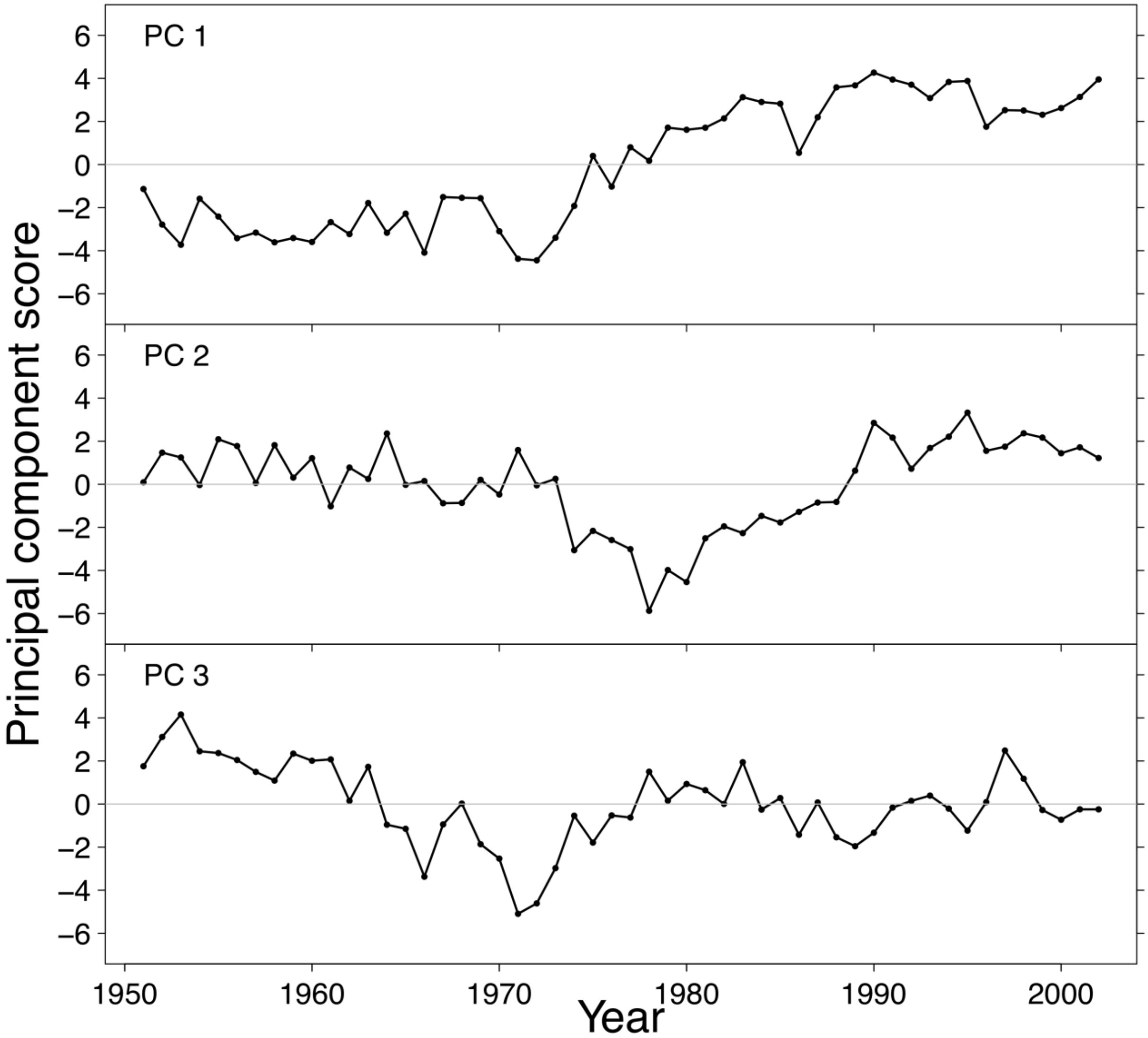

Figure 1.3: Plot of the first three principal components (PCs) from principal component analysis of the salmon abundance data.

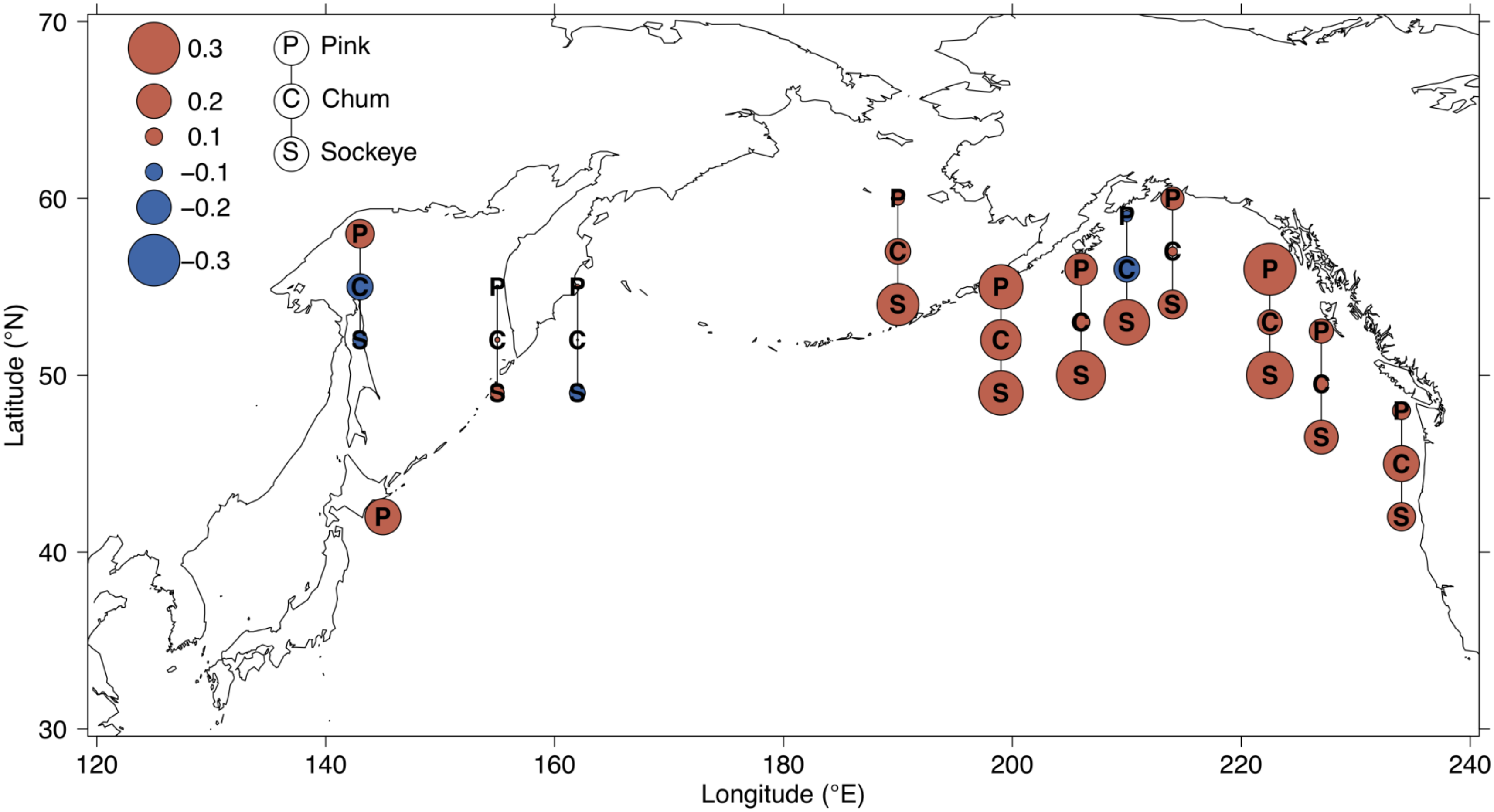

Figure 1.4: Loadings on the first principal component. The size of the circle is proportional to the magnitude of the loading. Positive values are red and negative values are blue. The species is indicated by the letter (P, pink; C, chum; S, sockeye). The locations correspond to the region of the salmon abundance data.

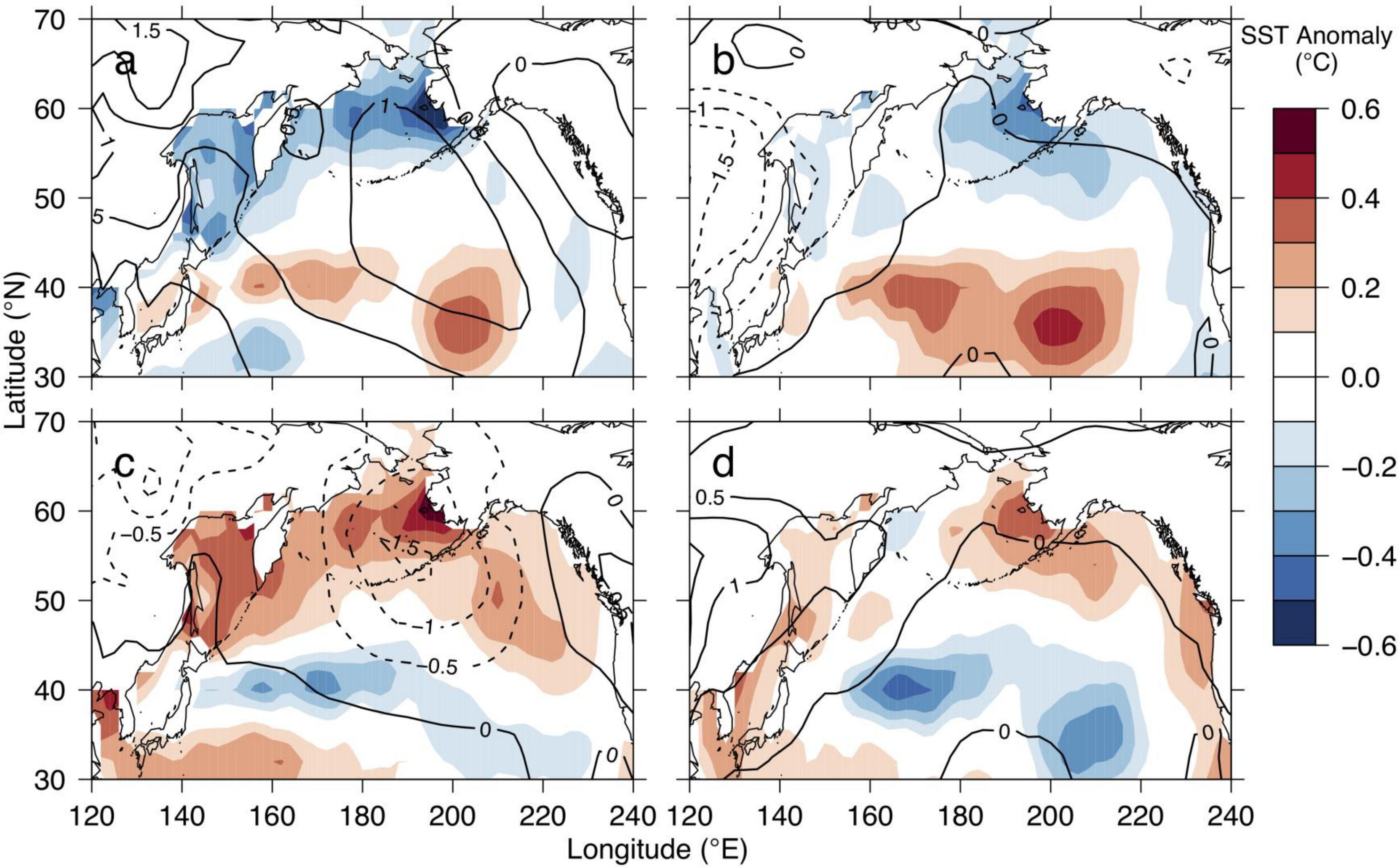

Figure 1.5: Composite maps of the winter (October-March, for year corresponding to January; a, c) and summer (April-September; b, d) sea surface temperature (SST; ºC) anomalies from the mean (1951-2002) for years corresponding to the lowest one-third (a, b) and highest one-third (c, d) of principal component one scores. Contour lines show sea level pressure anomalies from the mean (mb), with dashed lines indicating negative anomalies and solid lines indicated zero or positive anomalies.

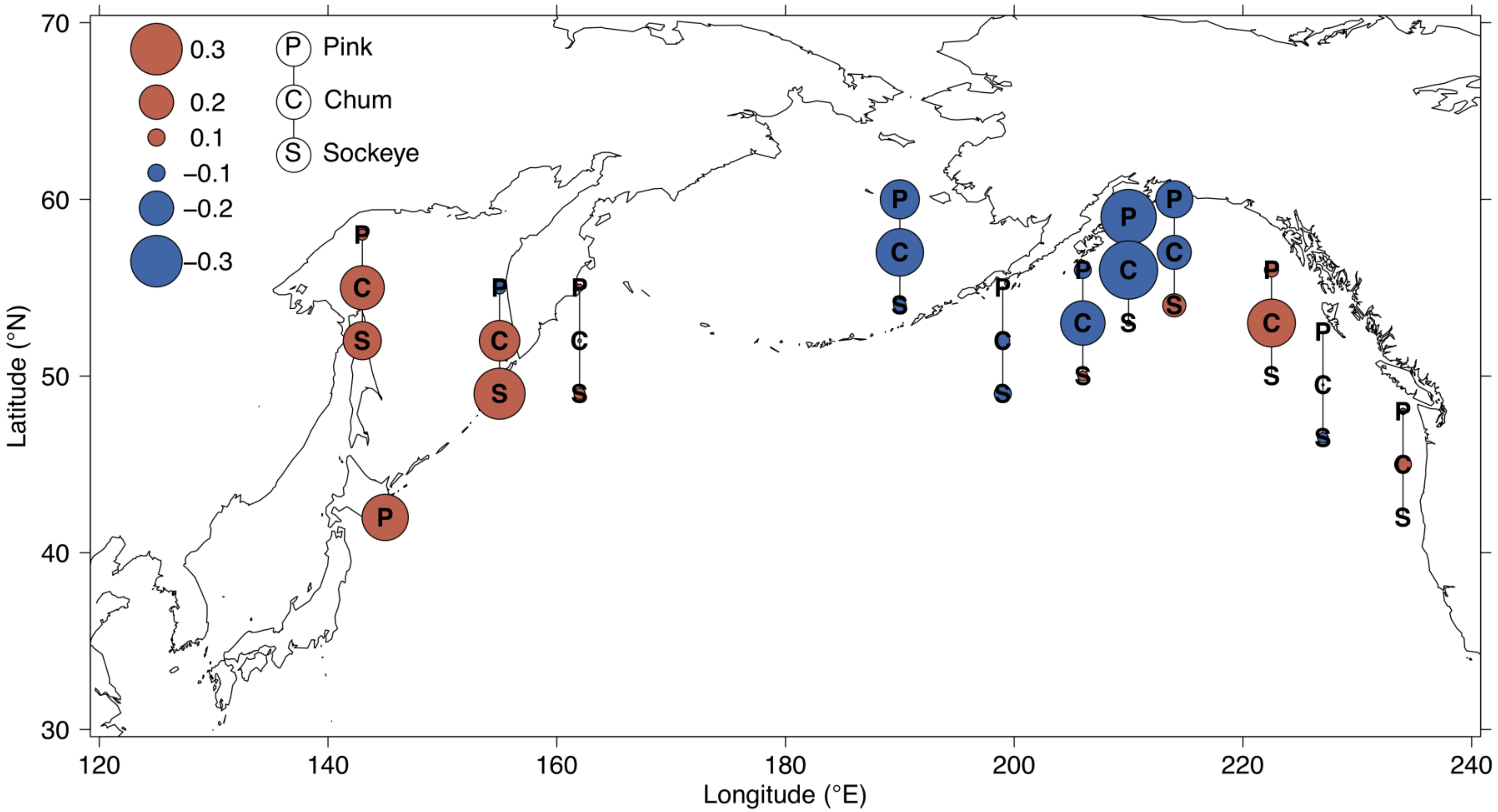

Figure 1.6: Loadings on the second principal component. The size of the circle is proportional to the magnitude of the loading. Positive values are red and negative values are blue. The species is indicated by the letter (P, pink; C, chum; S, sockeye). The locations correspond to the region of the salmon abundance data.

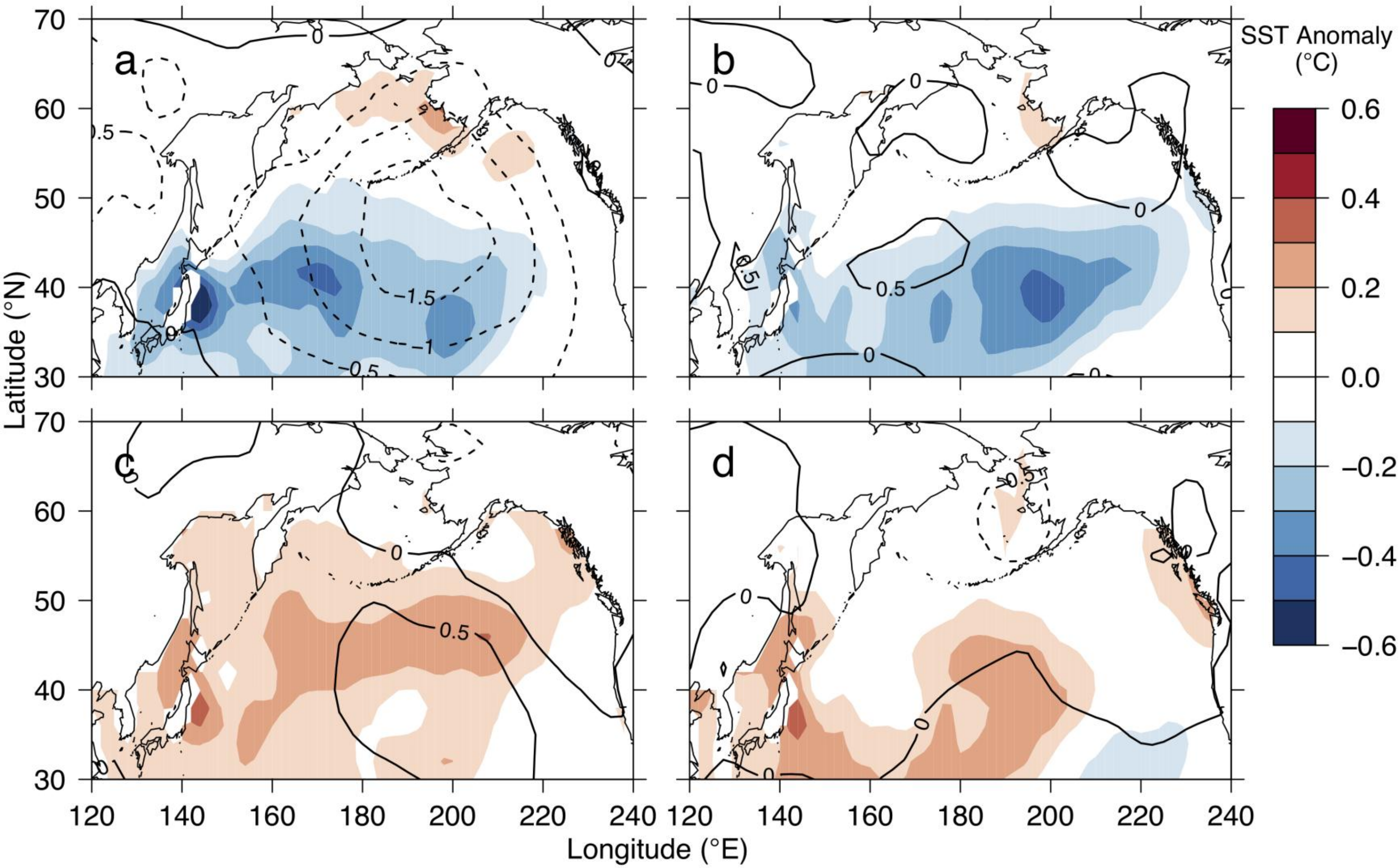

Figure 1.7: Composite maps of the winter (October-March, for year corresponding to January; a, c) and summer (April-September; b, d) sea surface temperature (SST; ºC) anomalies from the mean (1951-2002) for years corresponding to the lowest one-third (a, b) and highest one-third (c, d) of principal component two scores. Contour lines show sea level pressure anomalies from the mean (mb), with dashed lines indicating negative anomalies and solid lines indicated zero or positive anomalies.

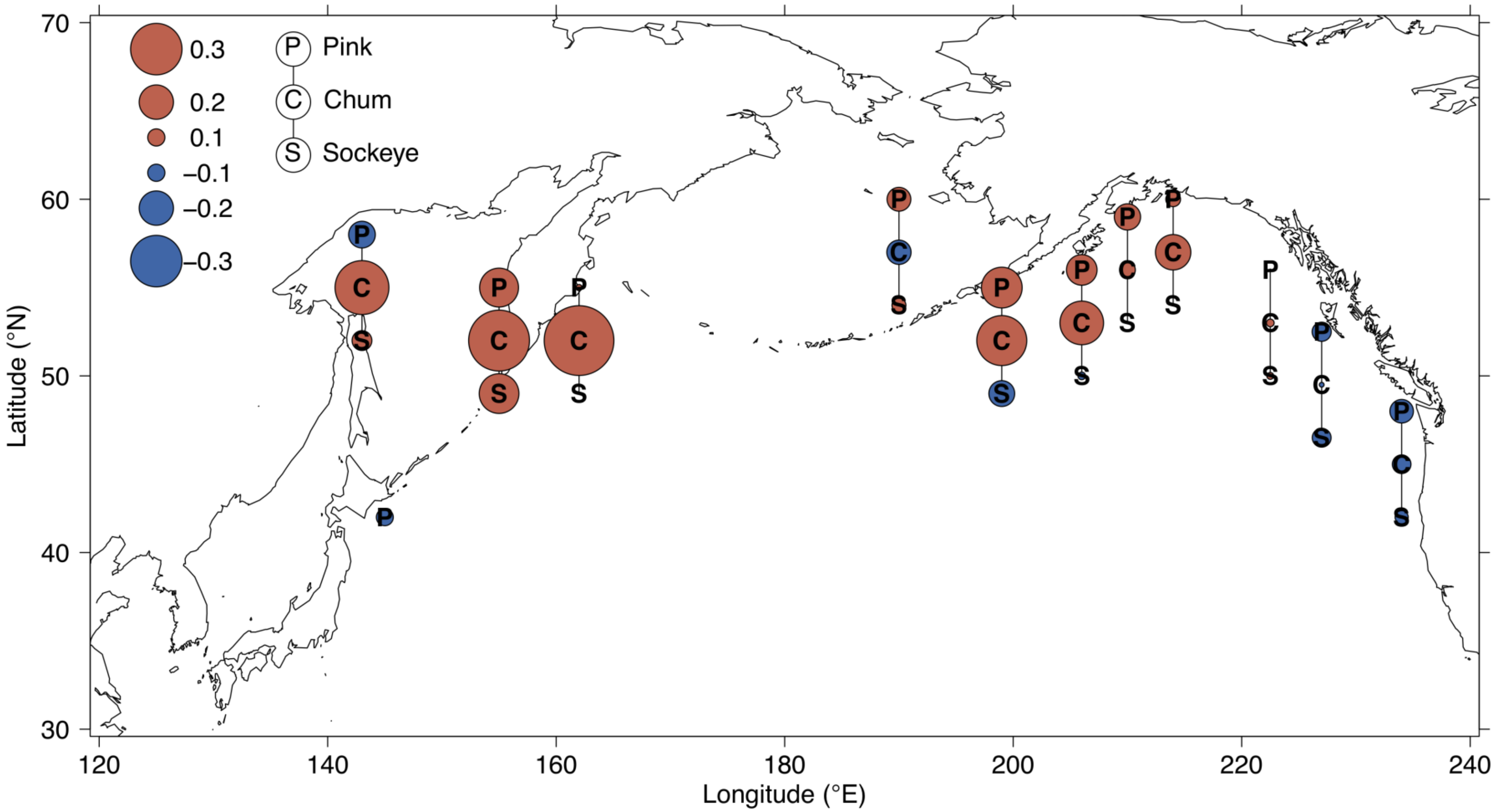

Figure 1.8: Loadings on the third principal component. The size of the circle is proportional to the magnitude of the loading. Positive values are red and negative values are blue. The species is indicated by the letter (P, pink; C, chum; S, sockeye). The locations correspond to the region of the salmon abundance data.

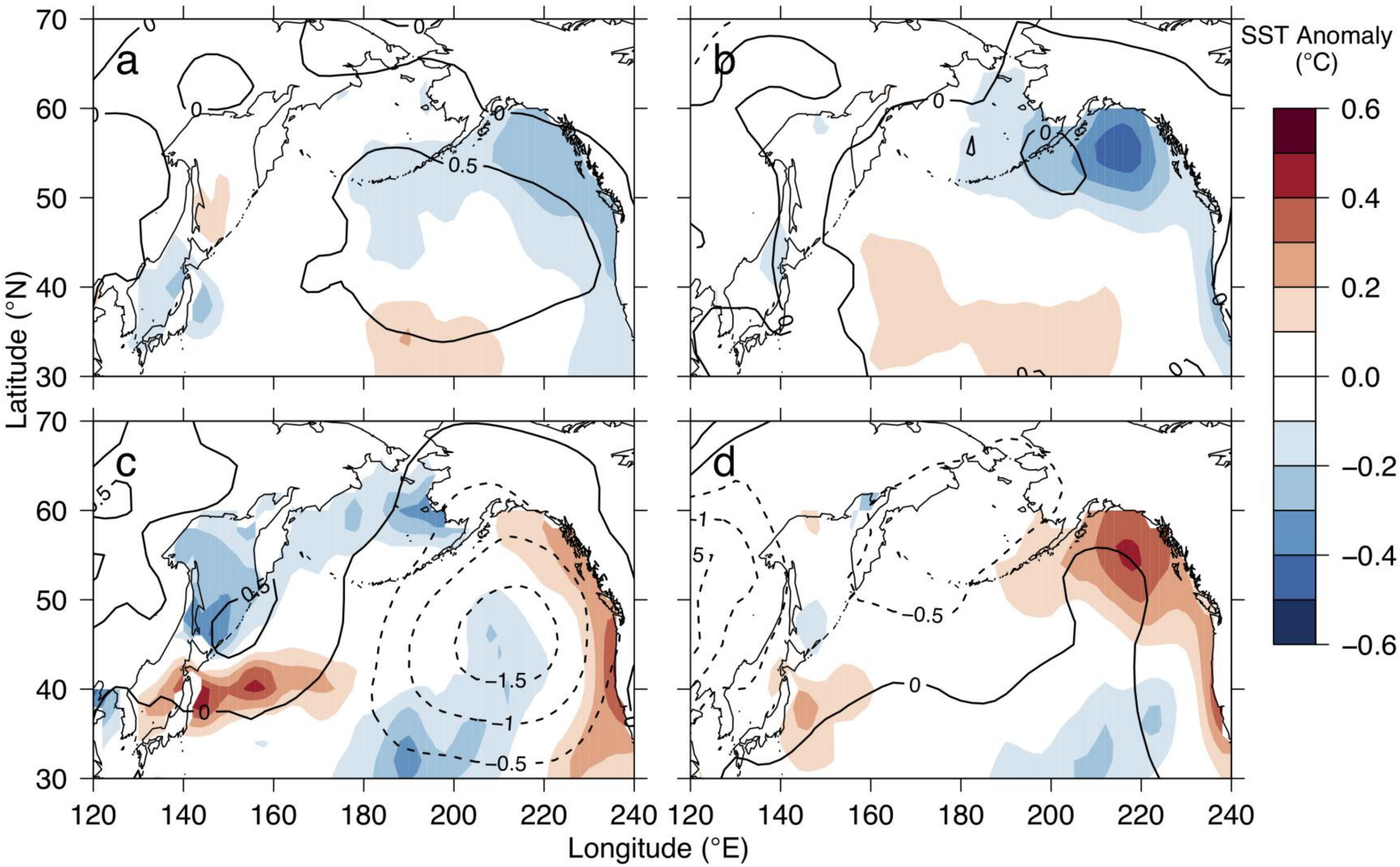

Figure 1.9: Composite maps of the winter (October-March, for year corresponding to January; a, c) and summer (April-September; b, d) sea surface temperature (SST; ºC) anomalies from the mean (1951-2002) for years corresponding to the lowest one-third (a, b) and highest one-third (c, d) of principal component three scores. Contour lines show sea level pressure anomalies from the mean (mb), with dashed lines indicating negative anomalies and solid lines indicated zero or positive anomalies.

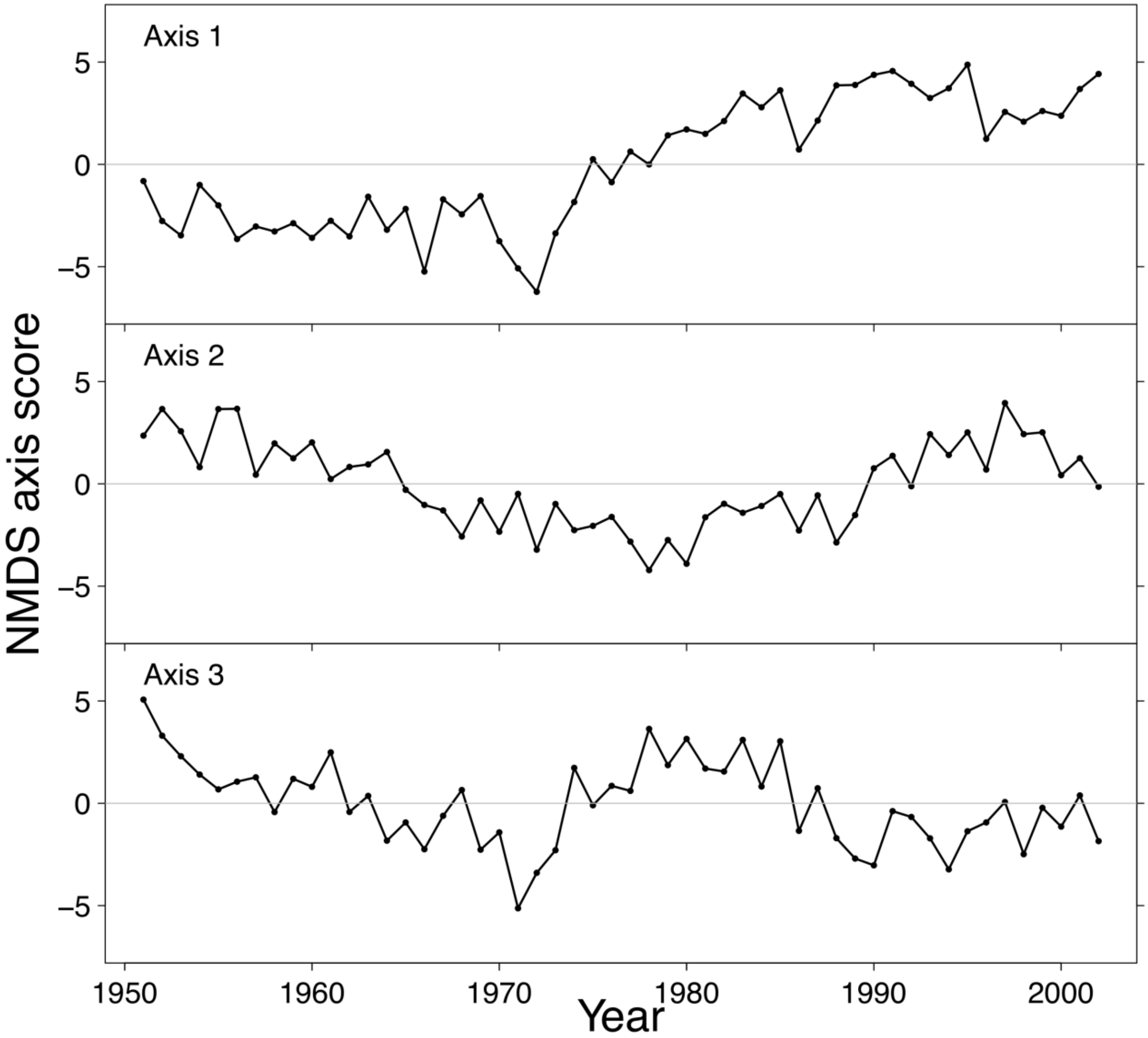

Figure 1.10: Plot of the three axes from non-metric multidimensional scaling (NMDS) of the salmon abundance data.

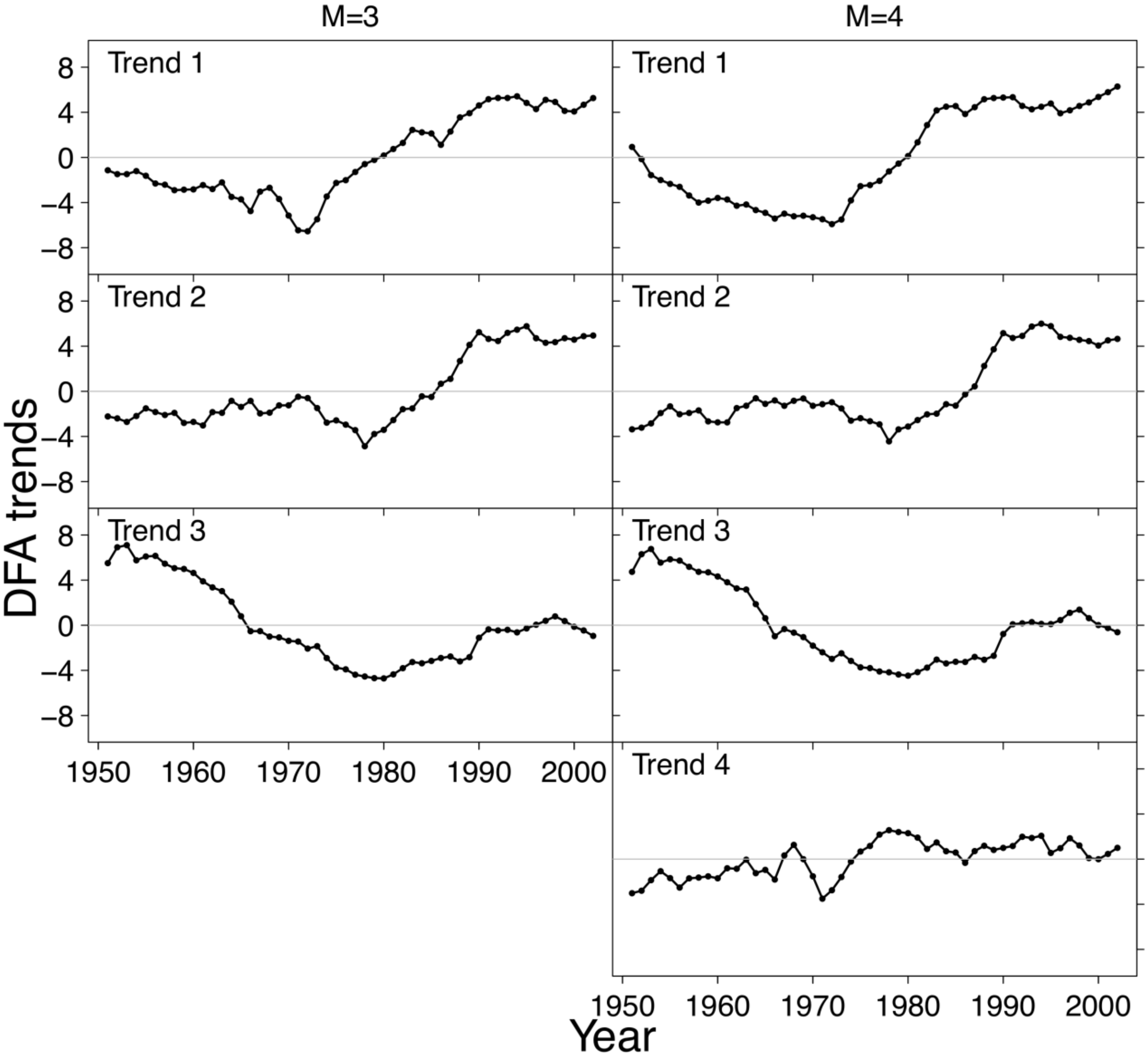

Figure 1.11: Plot of the trends from dynamic factor analysis (DFA) of the salmon abundance data for the chosen model (left, M=3) and for the best model based on AIC$_C$ model selection (right, M=4). The trends identified by the two models were highly correlated.

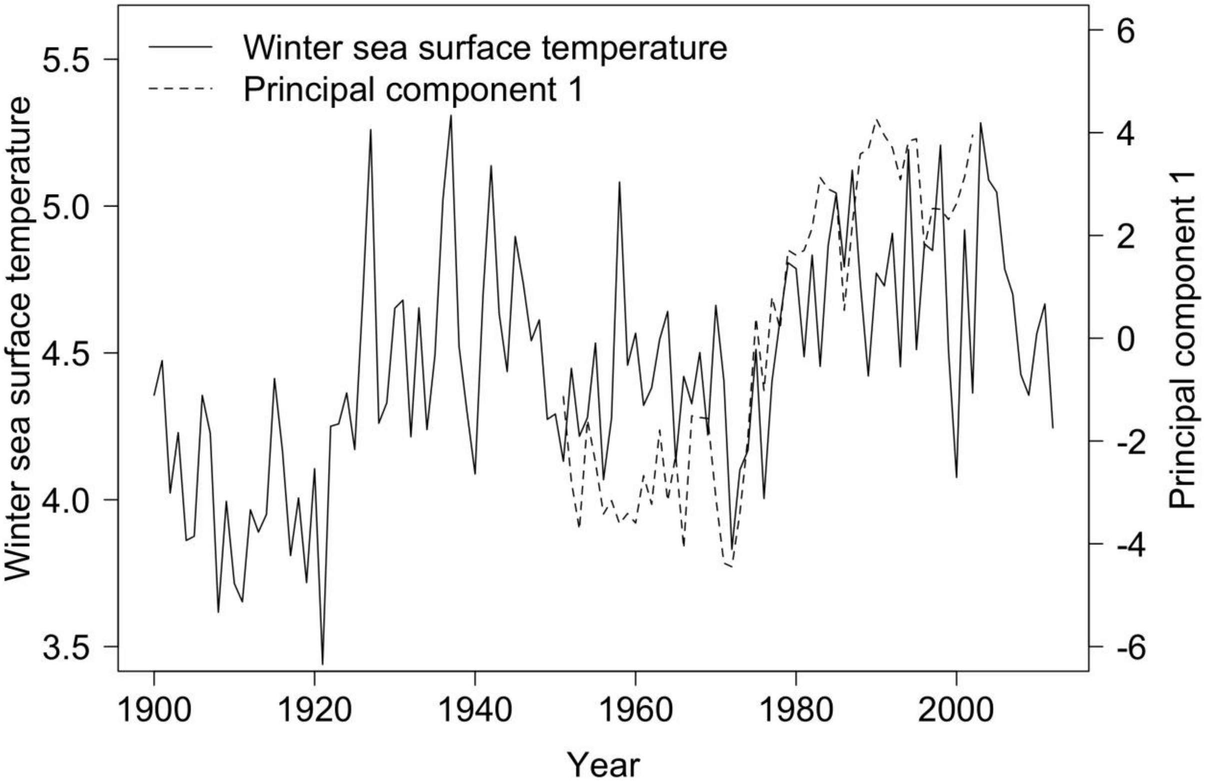

Figure 1.12: Plot of the mean winter (October-March, for year corresponding to January) sea surface temperature in the Gulf of Alaska and eastern Bering Sea (50-60°N 180-220°E) and principal component one from principal component analysis of the salmon abundance data.

Table 1.1: Description of environmental time series used in analyses. Indices spanning two years are assigned to the year corresponding to January.

Abb.	Name	Description	Data source	Reference
AO	Arctic Oscillation Index	Dominant pattern of sea level pressure variability north of 20°N in winter (Jan-Mar)	NOAA Climate Prediction Center	Thomson and Gower 1998
MEIW	Multivariate El Nino-Southern Oscillation Winter Index	Dominant pattern of variability of six observed variables over the tropical Pacific in winter (Oct-Mar)	NOAA Earth System Research Laboratory	Wolter and Timlin 1998
MEIS	Multivariate El Nino-Southern Oscillation Summer Index	Dominant pattern of variability of six observed variables over the tropical Pacific in summer (Apr-Sep)	NOAA Earth System Research Laboratory	Wolter and Timlin 1998
NPGOW	North Pacific Gyre Oscillation Winter Index	Second dominant pattern of sea surface height variability in the Northeast Pacific in winter (Oct-Mar)	Emanuele Di Lorenzo, Georgia Institute of Technology	Di Lorenzo et al. 2008
NPGOS	North Pacific Gyre Oscillation Summer Index	Second dominant pattern of sea surface height variability in the Northeast Pacific in summer (Apr-Sep)	Emanuele Di Lorenzo, Georgia Institute of Technology	Di Lorenzo et al. 2008
PDOW	Pacific Decadal Oscillation Winter Index	Dominant pattern of North Pacific SST variability north of 20°N in winter (Oct-Mar)	University of Washington, Joint Institute for the Study of the Atmosphere and Ocean	Mantua et al. 1997
PDOS	Pacific Decadal Oscillation Summer Index	Dominant pattern of North Pacific SST variability north of 20°N in summer (Apr-Sep)	University of Washington, Joint Institute for the Study of the Atmosphere and Ocean	Mantua et al. 1997
EPNP	East Pacific-North Pacific Index	Teleconnection index with positive phase associated with a southward shift and intensification of the Pacific jet stream measured in summer (Apr-Sep)	NOAA Climate Prediction Center	Barnston and Livezey 1987
ALPI	Aleutian Low Pressure Index	Index of the relative intensity of the Aleutian Low pressure system in winter (Dec-Mar)	Fisheries and Oceans Canada	Beamish et al. 1997
NPHPI	North Pacific High Pressure Index	Index of NCEP Reanalysis seal level pressure at 30-42.5°N, 135-180°W in summer (Apr-Sep)	NOAA Earth System Research Laboratory	Kalnay et al. 1996

Table 1.1 (continued)

Abb.	Name	Description	Data source	Reference
FRS	Gulf of Alaska Summer Freshwater Runoff	Freshwater runoff for a location near Seward, Alaska during summer months (Jun-Nov) of high discharge	Tom Royer, Old Dominion University	Royer et al. 2001
FRW	Gulf of Alaska Winter Freshwater Runoff	Freshwater runoff for a location near Seward, Alaska during winter months (Dec-May) of low discharge	Tom Royer, Old Dominion University	Royer et al. 2001
IRI	Eastern Bering Sea Ice Retreat Index	Number of days after Mar 15 that the average ice concentration is >10% in a 2° x 2° box (56-58°N, and 163-165°W) on the eastern Bering Sea shelf	NOAA Fisheries-Oceanography Coordinated Investigations	NA
UPSCAK	Southcentral Alaska Coastal Upwelling Index	Index of upwelling at 60°N 149°W in spring-summer (Mar-Aug)	NOAA Pacific Fisheries Environmental Laboratory	Bakun 1973
UPSEAK	Southeast Alaska Coastal Upwelling Index	Index of upwelling at 57°N 137°W in spring-summer (Mar-Aug)	NOAA Pacific Fisheries Environmental Laboratory	Bakun 1973
UPBC	British Columbia Coastal Upwelling Index	Index of upwelling at 51°N 131°W in spring-summer (Mar-Aug)	NOAA Pacific Fisheries Environmental Laboratory	Bakun 1973
UPWA	Washington Coastal Upwelling Index	Index of upwelling at 48°N 125°W in spring-summer (Mar-Aug)	NOAA Pacific Fisheries Environmental Laboratory	Bakun 1973

Table 1.2: Pearson correlation coefficients (*r*) for the correlation of the environmental time series with the principal components (PC), non-metric multidimensional scaling (NMDS) axes, and dynamic factor analysis (DFA) trends. Subscripts indicate the principal component, axis, or trend number. Environmental time series are abbreviated as in Table 1.1. An asterisk (*) indicates a significant correlation ($p<0.05$).

	PC_1	PC_2	PC_3	$NMDS_1$	$NMDS_2$	$NMDS_3$	DFA_1	DFA_2	DFA_3
AO	0.39*	0.21	-0.11	0.39*	0.06	-0.27	0.41*	0.46*	-0.13
MEIW	0.24	-0.01	0.08	0.24	-0.05	-0.06	0.23	0.13	-0.14
MEIS	0.39*	-0.05	0.16	0.37*	0	0.07	0.41*	0.26	-0.2
MEIA	0.37*	-0.03	0.14	0.36*	-0.03	0	0.37*	0.22	-0.19
NPGOW	0.07	-0.12	0.01	0.08	-0.14	0.1	0.05	-0.03	-0.07
NPGOS	0.06	-0.06	-0.07	0.07	-0.09	-0.03	0.04	0.02	-0.12
NPGOA	0.07	-0.09	-0.03	0.08	-0.12	0.04	0.05	-0.01	-0.1
PDOW	0.44*	-0.25	0.09	0.42*	-0.23	0.05	0.37*	0.13	-0.39*
PDOS	0.52*	-0.16	0.17	0.52*	-0.1	0.1	0.51*	0.27	-0.34*
PDOA	0.55*	-0.24	0.14	0.53*	-0.19	0.08	0.5*	0.23	-0.41*
EPNP	-0.03	0.1	-0.03	-0.03	0.08	-0.12	0.03	0.1	0.1
ALPI	0.35*	-0.18	0.19	0.36*	-0.17	0.13	0.35*	0.13	-0.25
NPHPI	-0.1	-0.12	-0.01	-0.1	-0.09	0.04	-0.17	-0.22	-0.07
FRS	0.21	0.2	0.12	0.23	0.26	0.03	0.31*	0.28*	0.06
FRW	0.22	0.07	0.21	0.22	0.05	-0.01	0.27	0.16	0.02
IRI	0.14	0.11	-0.22	0.23	0.14	0	0.07	0.09	0.04
UPSCAK	-0.36*	0.04	0	-0.36*	0.1	-0.06	-0.35*	-0.23	0.22
UPSEAK	-0.31*	0.07	0.09	-0.29*	0.09	-0.05	-0.26	-0.19	0.3*
UPBC	-0.14	0.08	-0.09	-0.13	0	-0.11	-0.14	-0.03	0.13
UPWA	0.1	-0.25	-0.34*	0.08	-0.38*	-0.09	-0.08	-0.08	-0.36*

Table 1.3: Pearson correlation coefficients (*r*) for the correlations between the principal components (PC), non-metric multidimensional scaling (NMDS) axes, and dynamic factor analysis (DFA) trends. Subscripts indicate the principal component, axis, or trend number. An asterisk (*) indicates a significant correlation ($p<0.05$).

	PC_1	PC_2	PC_3	$NMDS_1$	$NMDS_2$	$NMDS_3$	DFA_1	DFA_2
PC_1								
PC_2	0							
PC_3	0	0						
$NMDS_1$	0.99*	0.02	0.07					
$NMDS_2$	-0.06	0.8*	0.5*	0				
$NMDS_3$	-0.05	-0.52*	0.72*	0	0			
DFA_1	0.93*	0.25	0.21	0.93*	0.25	-0.05		
DFA_2	0.69*	0.64*	-0.21	0.67*	0.35*	-0.55*	0.8*	
DFA_3	-0.52*	0.58*	0.57*	-0.46*	0.77*	0.17	-0.22	-0.11

Chapter 2: Bayesian hierarchical analysis of environmental influences on Northeast Pacific marine fish recruitment

Abstract

Based on previous observations of synchrony in recruitment of Northeast Pacific marine fish, I tested the hypothesis that synchronous recruitment is due to a shared susceptibility to environmental variability. For 52 marine fish stocks in three ecosystems of the Northeast Pacific, the Eastern Bering Sea and Aleutian Islands (BSAI), Gulf of Alaska (GOA), and California Current (CC), I tested for synchrony in stock-recruitment residuals within each ecosystem. I tested for the occurrence of years with anomalous proportions of strong and weak year-classes and significant distributions of correlations of stock-recruitment residuals between stocks. Based on evidence of synchrony from these analyses, I used Bayesian hierarchical models to model recruitment for groups of stocks within each ecosystem as a linear function of environmental covariates. The stocks were grouped based on the processes thought to be most important to recruitment and the parameters for individual stocks were informed by group-level distributions. Several principal components (PCs) from principal component analysis (PCA) of environmental variables within each ecosystem were tested as covariates of recruitment in these models. Within the GOA, the best model chosen included the first two PCs from a PCA of Northeast Pacific sea surface height data as covariates and there was a consistent response within one group to these covariates. In the CC the best model chosen included the first two PCs from a PCA of San Francisco sea level height data as covariates. There was a consistent response across many CC stocks to the second PC, which related to higher recruitment during periods of high sea level and low upwelling the year before spawning and low sea level and high upwelling the year of spawning. In the BSAI the best model included PCs from a PCA of several environmental

variables. Although only a small portion of the variance in the stock-recruitment residuals was explained by these environmental covariates for many of the stocks, there was a consistent relationship among stocks within the ecosystems to the covariates, supporting my hypothesis. Future research should use these common influences of environmental covariates on several stocks to improve identification of environmental processes important to recruitment for marine fish stocks.

Introduction

Fishing and the environment influence the abundance and productivity of marine fish stocks. Recruitment is especially variable and is impacted by fluctuations in spawner abundance, egg production, and survival during early life stages (Hjort 1914, Cushing 1982). Spawner abundance often accounts for only a small portion of the variability in recruitment (Myers et al. 1994, Gilbert 1997). For these stocks, investigation of environmental influences on egg production and survival during early life stages is necessary to identify the processes important to recruitment and provide accurate recruitment predictions (Walters and Collie 1988).

Incorporating environmental influences is an important goal for management of marine resources, but the prevalence of spurious environmental-recruitment correlations that do not remain robust over time makes understanding and forecasting recruitment dynamics challenging (Myers 1998). Recent research has concentrated on the incorporation of environmental covariates into fisheries stock assessment to account for both interannual variability around a mean level of productivity and regime shifts in the mean level of productivity (Maunder and Watters 2003, Deriso et al. 2008, A'mar et al. 2009). Increased knowledge of the effects of environmental influences on the productivity of marine fish stocks will contribute to management through improved stock assessments that incorporate these factors. Understanding causes of recruitment changes may also help in deciding if recruitment declines are due to environmental conditions or reduced abundance, which contributes to the success of management plans. An initial step is to identify these influences on productivity for stocks for which this has not yet been identified (Jensen et al. 2012). Examining many populations simultaneously may be especially valuable because spurious correlations are less likely (Myers 1998).

In the Northeast Pacific Ocean, physical influences on the biological community have been well documented. Large-scale patterns of environmental variability and regime shifts in the biological communities have been observed in this region (Hare and Mantua 2000). These large-scale patterns consist of community-wide shifts in abundance and recruitment coinciding with fluctuations in basin-scale environmental indicators. At smaller spatial scales, synchrony of extreme fish recruitment events has been observed within the ecosystems of the Northeast Pacific (Hollowed et al. 1987). Positive correlations in recruitment among taxonomically related stocks and negative correlations between these groups have also been found (Hollowed et al. 1987). These findings indicate that further analysis of Northeast Pacific marine fish stocks may allow for identification of patterns of recruitment variability shared by groups of related stocks and environmental influences causing this variability.

My analysis builds on previous work by investigating synchrony in Northeast Pacific marine fish recruitment. I will also link synchronous recruitment to environmental variables to test the hypothesis that synchronous recruitment is due to a shared susceptibility to environmental variability. While there are currently a few well-studied Northeast Pacific fish stocks for which we have some understanding of environmental influences on recruitment, there are many more species for which understanding is limited but estimates of recruitment are available. Modeling environmental influences on recruitment for groups of stocks will help to inform the relationship.

Bayesian hierarchal modeling is advantageous for this analysis of environmental influences on recruitment for groups of related fish stocks because it utilizes information from all stocks within a group to improve the parameter estimation for stocks with weaker data, generally providing more reliable parameter estimates with lower response variability (Gelman and Hill 2007, Helser et al. 2007). In this hierarchal structure, coefficients are estimated for individual stocks but assumed to be drawn from a distribution described by a group-level mean and variance. This method assumes dependence among parameters and the parameters at all levels are estimated simultaneously so that they can inform each other. This technique has been used in several fisheries application, including estimation of the stock-recruitment relationship for Northeast Pacific rockfish (*Sebastes* spp.) (Dorn 2002, Forrest et al. 2010) and Atlantic salmon (*Salmon salar*) stocks (Michielsens and McAllister 2004), modeling pink salmon (*Oncorhynchus gorbuscha*) escapement abundance and timing (Su et al. 2001), and in an analysis of growth variability and biological covariates for Northeast Pacific rockfish (Helser et al. 2007). Analysis of fish recruitment data with this technique will allow me to identify environmental covariates for groups of stocks with similar susceptibility to environmental variability with enhanced statistical power and diminished probability of spurious correlations through the hierarchical structure. It will also allow me to test the significance of the grouping structure in the model fitting to determine if the defined groups have similar susceptibility to the environmental influences investigated.

Here I investigate recruitment synchrony and evaluate the relationships between recruitment and environmental covariates for groups of marine fish stocks for three Northeast Pacific ecosystems: Eastern Bering Sea and Aleutian Islands (BSAI), Gulf of Alaska (GOA), and California Current (CC). I model environmental effects on recruitment for each ecosystem independently based on previous analyses that have found differing response of groundfish recruitment by ecosystem (Hollowed et al. 1987, Mueter et al. 2007). I define groups of stocks with similar susceptibility to environmental variability based on their early life histories and previous studies of environmental influences on recruitment for these stocks. I hypothesize that members of these groups have synchronous recruitment dynamics and these recruitment dynamics are associated with relevant environmental driving variables. Using hierarchal models, I identify the environmental variables important to recruitment and evaluate the significance of the defined grouping structure.

Methods

Recruitment data

I compiled recruitment and spawning stock biomass (SSB) estimates from stock assessments for marine fish stocks across the Northeast Pacific. Only stocks and years for which there were reliable estimates of recruitment were used in the analysis. I included in the analysis 14 BSAI stocks, 14 GOA stocks, and 24 CC stocks (Table 2.1). For stock assessment models that included a stock-recruitment relationship in estimation of recruitment, the residuals of this relationship were also compiled and used as a spawning biomass adjusted estimate of recruitment, representing remaining environmental influences on recruitment. For stock assessments that did not include a stock-recruitment relationship in recruitment estimation, I tested three models for this relationship. The Ricker model followed the equation

(2.1) $R_{s,t} = \alpha_s SSB_{s,t} e^{-\beta_s SSB_{s,t}} e^{\epsilon}$

where $R_{s,t}$ is recruitment for stock s in year t, $SSB_{s,t}$ is SSB for stock s in year t, α_s and β_s are estimated parameters for stock s, and ϵ is the normally distributed error. The Beverton-Holt model followed the equation

(2.2) $R_{s,t} = \frac{\alpha_s SSB_{s,t}}{1+\beta_s SSB_{s,t}} e^{\epsilon}$

where the variables are as in equation (1). The mean model, in which recruitment was independent of SSB, followed the equation

(2.3) $R_{s,t} = \alpha_s e^{\epsilon}$

where the variables are as in equation (1). These three models were fit using maximum likelihood estimation and the statistically best model was chosen based on the small-sample Akaike information criterion (AICc; Hurvich and Tsai 1989). The residuals from the best model were used in this analysis as an index of recruitment and the portion of total variance explained by the best model was calculated. Of the 24 stocks that were fitted to the stock-recruitment models, the Ricker model was chosen for 7 stocks, the Beverton-Holt model was chosen for 3 stocks, and the mean model was chosen for 14 stocks (Table 2.2).

Stock grouping

To identify groups of stocks within an ecosystem with overlapping susceptibility to environmental influences, data on their life history and previously identified relationships with environmental variables were compiled. Life history information collected included the taxonomic classification, spawning mode, spawning or parturition time, egg size, larval size at transformation, larval size at hatching or release, larval size at transformation, larval habitat, pelagic stage duration, juvenile habitat, larval and juvenile predators and prey (Appendix A). I also compiled information from previous studies documenting environmental influences on recruitment for these stocks. For many stocks this information was available from stock assessment reports, the Ichthyoplankton Information System (Ichthyoplankton Information System 2010), and scientific articles and reports. I also obtained information from scientists familiar with the stocks when it was not available in the literature. However, there was still unknown or uncertain life history information for many stocks.

Using the compiled information, I identified groups of stocks with similar susceptibility to environmental variability. I solicited expert opinion for this task through a workshop to develop the grouping structure. After considering several grouping methods, I decided to group the stocks based on the environmental processes thought to be most important to successful recruitment.

I identified three primary processes important to recruitment for the BSAI stocks and grouped the stocks based on these processes (Table 2.1). The “cross-shelf transport” group included stocks that spawn on the outer continental shelf and the slope, for which inshore transport to juvenile nursery grounds is important to successful recruitment. For the stocks that spawn on the continental shelf, inshore retention and shelf productivity may be important to successful recruitment so these stocks were labeled the “retention” group. The final group consisted of stocks with high “parental investment” because of life history characteristics that allow for large larval size to withstand variation in primary production but may be more influenced by parental conditions. See Appendix B for further details regarding the grouping structures identified.

I identified four major processes important to recruitment in the GOA (Table 2.1). The “cross-shelf transport,” “retention,” and “parental investment” groups were based on similar reasoning to the definition of these groups in the BSAI. There was also a “coastal” group for stocks spawning near shore that are especially susceptible to coastal processes during early life stages.

I identified two major processes important to recruitment in the CC (Table 2.1). The “cross-shelf transport” group was based on similar reasoning to the definition of this group in the BSAI. The “moderate upwelling” stocks include those for which high recruitment has been associated with cooler water temperatures and moderate upwelling events that contribute to greater prey availability and decreased predation.

Synchrony

To examine the synchrony in extreme recruitment events across stocks within each ecosystem, I identified the years corresponding to the 25% strongest year classes and 25% weakest year classes for each stock. For years for which I had stock-recruitment data for at least half of the stocks in the ecosystem, I compared the observed distributions of strong, weak, and average year classes in each year across stocks to the expected distribution using a Chi-square test at a significance level of $\alpha=0.05$. I used a Bonferroni correction to correct for the large number of comparisons.

I also examined the correlation in stock-recruitment residuals between stocks within each ecosystem to determine if there was evidence for covariation between the stocks within the ecosystem and identify groups of stocks with strong covariation. Strong between-stock correlations were identified as Pearson correlation coefficients (r) greater than 0.40 or less than -0.40. A frequency distribution (histogram) of the Pearson correlation coefficients between the stock-recruitment residuals of all stocks within each ecosystem was used to summarize the correlations within the ecosystem. I evaluated whether the observed correlation frequency distributions differed from the expected distribution under the null hypothesis that stock-recruitment residuals for stocks within each ecosystem vary independently. If there is significant covariation the distribution of correlations may differ from the expected distribution under the null hypothesis. The mean correlation ($\bar{r}$) may differ from zero or there may be significant overdispersion with a greater variance in the observed correlations (σ_r^2) than expected (Mueter et al., 2007). Based on the methods of Pyper et al. (2001) and Mueter et al. (2007), I used a randomization procedure to obtain the expected distributions of the correlations within each ecosystem, accounting for the effects of autocorrelation. I first evaluated $\bar{r}$ to determine if it differed from the expected distribution. If this was not significant I evaluated σ_r^2 to determine if it differed from the expected distribution, since tests for overdispersion are only valid if average correlations are not different than zero (Mueter et al. 2007).

Hierarchical cluster analysis of the Euclidean distance in stock-recruitment residuals between stocks within each ecosystem was also used to identify groups of stocks with similar patterns. However, in most cases the clusters identified were not robust to the clustering technique used or there was not an identifiable life history link between stocks within clusters.

Environmental variables

I compiled regional environmental variables thought to affect the recruitment for the marine fish stocks analyzed (Table 2.3). Within all three ecosystems temperature, freshwater discharge, and sea surface height data were included in the analysis. In addition, for the BSAI wind and sea ice data were included, for the GOA upwelling data were included, and for the CC upwelling and local sea level data were included. All seasonal variables were included corresponding to the year before spawning in order to capture environmental effects on spawner condition and ecosystem productivity, and the year of spawning in order to capture environmental effects during the larval and early juvenile stages. For further details regarding the environmental variables included, see Appendix C.

I used principal component analysis (PCA) to reduce the environmental variables into a smaller number of uncorrelated variables for use as predictors in the hierarchical models. For each region, I used PCA to analyze the environmental variables within each category of data (temperature, sea surface height, upwelling, wind, freshwater discharge, ice, or sea level). I also used PCA to identify covariations across all environmental variables within an ecosystem. For this, I weighted the variables so that each category of data had equal weight because some categories of data had a disproportionally large number of time series due to the nature of the data. From the PCA within each category, the first two principal components (PCs) explained greater than 50% of the variance for most (10 of 14) of the categories by region. Based on this, the first two PC for a single category of data were used as predictors in the models. Because the PCA across all of the environmental variables within an ecosystem contained more variables, additional PCs were needed to explain a high portion of the total variance. I tested models with the first two to five PCs from this PCA as predictors.

Bayesian hierarchical models

Hierarchical models are useful tools for analyzing groups of data with related parameters. This method allows for modeling the dependence among parameters through a hierarchical structure. By structuring dependence among parameters the effective number of parameters is reduced, avoiding the problem of overfitting that is often suffered by nonhierarchical models (Gelman and Hill 2007).

I used Bayesian hierarchical models to model the stock-recruitment residual time series as a function of the environmental variable PCs. The models covered the time periods that stock-recruitment residual data were available for at least one stock within the ecosystem and all of the environmental variables were available or estimated (BSAI: 1953-2008; GOA: 1958-2008; CC: 1968-2008). In the model formulation I used redundant parameterization to improve numerical convergence (Gelman and Hill 2007).

The linear models followed the equation:

$$\overline{SR_{s,t}} = \beta_{s,0} + \sum_{i=1}^{n} \beta_{s,i} PC_{i,t} \tag{2.4}$$

where $\overline{SR_{s,t}}$ is the mean stock-recruitment residual for stock s in year t, $\beta_{S,0}$ is the intercept parameter, $PC_{i,t}$ is the *i*th PC resulting from PCA on the environmental variables, $\beta_{s,i}$ is the parameter relating PC_i to the stock-recruitment residuals for stock s, and n is the total number of PCs modeled. The error was assumed to follow a normal distribution:

$$SR_{s,t} \sim N(\overline{SR_{s,t}}, \sigma_s) \tag{2.5}$$

where $SR_{s,t}$ is the predicted stock-recruitment residual and σ_s is the stock-recruitment residual variance. The number of PCs modeled (n) was two for the PCA on a single category of environmental variables and two to five for the PCA across all environmental variables in an ecosystem.

The parameters relating the PCs to the stock-recruitment residuals ($\beta_{s,i}$) were residuals from a group-level distribution:

$$\beta_{s,i} = \overline{\beta_{g,\imath}} + \eta_{\beta_{s,i}} \tag{2.6}$$

where $\overline{\beta_{g,\imath}}$ is the group-level mean for group g and $\eta_{\beta_{s,i}}$ is the residual from the group-level mean for the parameter $\beta_{s,i}$. The residuals followed a group-level distribution:

(2.7) $\eta_{\beta_{s,i}} \sim N(0, \sigma_{\overline{\beta_{g,\iota}}})$

where $\sigma_{\overline{\beta_{g,\iota}}}$ is the group-level variance in the residuals from the mean.

At the highest level the group-level parameters were drawn from an ecosystem-level distribution which followed the equation:

(2.8) $\overline{\beta_{g,\iota}} = \overline{\overline{\beta_{e,\iota}}} + \eta_{\overline{\beta_{g,\iota}}}$

where $\overline{\overline{\beta_{e,\iota}}}$ is the ecosystem-level mean for ecosystem e and $\eta_{\overline{\beta_{g,\iota}}}$ is the residual from the ecosystem-level mean for the parameter $\overline{\beta_{g,\iota}}$. The residual followed an ecosystem-level distribution:

(2.9) $\eta_{\overline{\beta_{g,\iota}}} \sim N(\overline{\eta_{\overline{\beta_{g,\iota}}}}, \sigma_{\overline{\overline{\beta_{e,\iota}}}})$

where $\overline{\eta_{\overline{\beta_{g,\iota}}}}$ is the mean residual from the ecosystem-level mean ($\overline{\overline{\beta_{e,\iota}}}$) and $\sigma_{\overline{\overline{\beta_{e,\iota}}}}$ is the ecosystem-level variance.

Because there is currently little known about the environmental influences on recruitment for many of the stocks investigated, non-informative prior distributions across the range of possible parameter values were used for most parameters in this analysis (Appendix D). Using a non-informative prior distribution decreases the weight of the prior distribution on the posterior distribution so that the likelihood primarily contributes to the posterior distribution (Gelman and Hill 2007). However, I wanted the stock-level parameters to be related within a group so I placed a mildly informative prior on their variance ($\sigma_{\overline{\beta_{g,\iota}}}$) to prevent large variation within a group. To select dispersed and reasonable initial values for the chains, they were chosen as random numbers from defined distributions (Appendix D).

I tested the models by running three chains for 200,000 iterations with a burn-in period of 100,000 and a thinning rate of 200. The total sample size was 500 for each chain and 1,500 for each model. Several diagnostics were used to evaluate model convergence. Plots of the parameter posterior density were monitored as indicators of convergence. The Geweke statistic (Geweke 1992) and the Heidelberger and Welch statistic (Heidelberger and Welch 1983) were used to monitor the chains for trends. I also monitored the effective sample size adjusted for autocorrelation, the lag-1 autocorrelation to measure the dependency of samples and insure a large enough thinning rate was used, and the correlation between model parameters.

The deviance information criterion (DIC) was used for model selection. This is calculated as the mean deviance across all simulated parameter vectors plus the effective number of parameters (Spiegelhalter et al. 2002). The increase in DIC from the lowest DIC value within an ecosystem (ΔDIC) was also calculated for comparison. Examination of the model fits and residuals were also used as diagnostic tools. For the best model chosen within each ecosystem, the relationship with the environmental variables by stock was investigated further.

I also investigated how well the models tested fit the observed stock-recruitment residual estimates for the individual stocks. The Pearson correlation coefficients between the median predicted stock-recruitment residuals for each stock and the observed stock-recruitment residual value were calculated. Correlations of at least 0.5 were considered a good model fit. I also calculated the proportion of variance in the stock-recruitment residuals explained for each stock by the best model chosen within each ecosystem.

To test the hypothesis that groups of stocks with similar processes important to recruitment respond similarly to environmental forces, I also fit hierarchical models with only one group for each ecosystem. The predictors for these models were the ones from the best model chosen with multiple groups for each ecosystem. The DIC values for the models with one group were compared to the best models chosen with groupings to determine if the models support the groupings.

Software

All analysis was completed in R version 2.14.2 (R Development Core Team 2012a). Just Another Gibbs Sampler (JAGS) was used for the Bayesian hierarchical modeling (Plummer 2011) and the R package CODA (Plummer et al. 2010) was used in analysis of the results. PCA was carried out using the stats package (R Development Core Team 2012b) and with weighting of variables in the ade4 package (Chessel et al. 2009).

Results

Synchrony

BSAI

Plots of the categorized stock-recruitment residuals for the BSAI showed limited synchrony (Figure 2.1). There were no significant deviations from the expected distribution of strong, weak, and average year classes. Without the Bonferroni correction, there was a significant portion of stocks with high recruitment in 1977 (8), especially for stocks in the retention and parental investment groups, and a significant portion with low recruitment in 1982 (8), 1994 (8), and 2004 (7).

For all the ecosystems, there were generally low to moderate correlations in stock-recruitment residuals (Figure 2.2). The mean correlation across all stocks within the BSAI was not significantly different from the expected value under the null hypothesis ($\bar{r}$=0.033; p=0.071). The variance of the observed correlations was significantly different than that expected under no covariation (σ_r^2=0.068; p=0.0090). There were generally positive correlations between stock-recruitment residuals for stocks within the cross-shelf transport ($\bar{r}$=0.081), retention ($\bar{r}$=0.044), and parental investment ($\bar{r}$=0.13) groups, although this relationship was not strong. Pacific cod had strong negative correlations with several flatfish, including arrowtooth flounder, yellowfin sole, and northern rock sole. Pacific cod had strong positive correlations with Greenland turbot and EBS walleye pollock.

GOA

Moderate synchrony across stocks was identified in GOA recruitment (Figure 2.3). The distribution of year class strength was nearly significant in 2000 (p=0.086), with strong year classes for 9 stocks in that year. There were several stocks with strong recruitment in 1998 (8) and 1999 (7), indicating a period of high recruitment in 1998-2000. These strong year classes occurred for stocks across the groups identified.

There were moderately high correlations in stock-recruitment residuals between GOA stocks within the groups identified and the observed mean across all stocks was significant ($\bar{r}$=0.11, p<0.001). There were strong positive correlations between the stocks in the cross-shelf transport ($\bar{r}$=0.38) and moderate positive correlations within the coastal ($\bar{r}$=0.49) and parental investment ($\bar{r}$=0.25) groups, but near-zero correlations within the retention group ($\bar{r}$=0.0081). Arrowtooth flounder and Dover sole were most strongly correlated (r=0.76). Walleye pollock had strong positive correlations with several flatfish, including arrowtooth flounder, Dover sole, and Pacific halibut.

CC

Moderate synchrony was identified in recruitment for the CC stocks (Figure 2.4). The distribution of year class strength was highly significant in 1999 (p<0.001), with strong year classes for 16 stocks across both groups in that year. Before the Bonferroni correction, there was a significant portion of stocks with was low recruitment in 1982 (9), 1983 (10) and 2006 (10) especially for the moderate upwelling group, and in 1986 (11) and 1992 (11), especially for the cross-shelf transport group. There was also high recruitment for 12 stocks in 2000, especially for the cross-shelf transport group.

The observed mean stock-recruitment residual correlation across all CC stocks was significant ($\bar{r}$=0.10, p<0.001). There were low positive correlations between the stocks in the cross-shelf transport ($\bar{r}$=0.17) and moderate upwelling ($\bar{r}$=0.14) groups. All of the species for which there were multiple stocks (black rockfish, cabezon, lingcod) had positive correlations between the stocks within these species.

Environmental models

BSAI

From the PCA across all the environmental variables, the five PCs explained a total of 68% of the variability in the data. The first PC explained 31% of the variance and was strongly associated with ice cover and spring SST the year of and the year before spawning (Table 2.4). The second PC explained 12% of the variance and was strongly associated with SSH PC1. The third PC also explained 12% of the variance and was associated with winter cross-shelf wind the year of spawning. The fourth PC explained 6.8% of the variance and was associated with winter cross-shelf wind the year before spawning. The fifth PC explained 5.7% of the variance and was associated with winter along-shelf wind the year before spawning.

The model with the five PCs from PCA on all of the BSAI environmental variables as covariates had the lowest DIC value (Table 2.5). This model was an improvement of at least 6.8 DIC units from all the other models tested and an improvement of at least 15 DIC units from all the models selected based on a single environmental variable category. This was chosen as the best model and the results from this model are presented.

Plots of the observed and predicted stock-recruitment residuals, and the correlation between these, were used to evaluate the model fit and determine which recruitment dynamics the model was able to explain. Several of the stocks had moderately good model fits, including arrowtooth flounder, Greenland turbot, northern rock sole, Pacific cod, and AI walleye pollock (Figure 2.5). Greenland turbot had a large portion of the variance in the stock-recruitment residuals explained by these covariates (R^2=0.51; Table 2.2). These stocks also had a strong relationship with one or more of the covariates. Greenland turbot, Pacific cod, and EBS walleye pollock had a negative relationship with PC1; flathead sole, Togiak herring, and AI walleye pollock had a positive relationship with PC3; and arrowtooth flounder and northern rock sole had a positive relationship with PC5 (Figure 2.6). The 95% credible interval for all other parameters included zero, indicating uncertainty in sign of the relationship of recruitment with the predictor.

All of the stocks within the parental investment group had low correlations between the observed and median predicted stock-recruitment residuals (Figure 2.5). The fit for northern rockfish was better with the freshwater discharge model (r=0.40). For the other stocks, the models fits were not substantially better for any of the models tested.

I found marginal evidence that the effect of environmental variables varied across groups. The model without separate groups had a DIC value 4.8 DIC units greater than that of the grouped model. The median predicted stock-recruitment residual values were more highly correlated with the observed data for all stocks except for flathead sole, AI walleye pollock and Togiak herring, which had slightly greater correlations between the observed and predicted data under the single group model.

GOA

The first two SSH PCs accounted for 17% and 12% of the total variance. The loadings indicated that PC1 was negatively correlated with SSH anomalies in the coastal waters of the Northeast Pacific and positively correlated with SSH anomalies in offshore waters (Figure 2.7). PC2 was negatively correlated with SSH anomalies in northern offshore waters of the Northeast Pacific. These PCs were strongly correlated with annual indices covering the same time period of the PDO (PC1; r=-0.82; p<0.001) and NPGO (PC2; r=0.72; p<0.001).

The best-fitting model used the first two SSH PC's as predictor variables. This model had substantial support over all other models (Table 2.5). There were relatively good fits for only a few stocks, including Pacific halibut and flathead sole (Figure 2.8; Table 2.2). Arrowtooth flounder and rex sole had a positive correlation with PC1, and flathead sole and Pacific halibut had a positive correlation with PC2 (Figure 2.9). All of the stocks in the cross-shelf transport group tended to have a positive correlation with PC1 and PC2.

The other models tested provided a better fit to the observed stock-recruitment residuals than the chosen model for a few of the stocks. For Dover sole the SST model provided a better model fit (r=0.40), and for Pacific ocean perch the SST (r=0.42) and freshwater discharge (*r*=0.45) models provided better model fits. The models that included the PCs from all the environmental variables also moderately improved the model fits for several of the stocks.

There was little evidence that the effect of environmental variables varied across groups. The model without separate groups had a DIC value only 2.5 DIC units greater than that of the grouped model. This model resulted in a moderate increase in the correlation between the observed and median predicted values for several (6) of the stocks over the grouped model.

CC

The first two San Francisco sea level PCs explained a large portion of the total variance in the data, accounting for 46% and 24% respectively. PC1 was strongly positively associated with San Francisco sea level in the spring and summer the year of spawning and the spring, summer, and fall the year before spawning (Table 2.6). PC2 was positively associated with seasonal values for the year before spawning and negatively associated with seasonal values for the year of spawning.

The model with two San Francisco sea level PCs had the lowest DIC value by at least 7.9 DIC units (Table 2.5). This model provided good fits for a few of the CC stocks, including Petrale sole and chilipepper rockfish (Figure 2.10; Table 2.2). Petrale sole and splitnose rockfish had a positive correlation with PC1 and many (15) of the stocks, across both groups, had a positive correlation with PC2.

The other models tested provided a better fit to the observed stock-recruitment residuals than the chosen model for several of the stocks. The model with the upwelling PCs as covariates provided a moderately better fit for widow rockfish (*r*=0.39) and Oregon cabezon (*r*=0.33) than the chosen model. The model with the SSH PCs improved the model fit for Washington and Oregon lingcod (*r*=0.38), CA lingcod (*r*=0.50), and English sole (*r*=0.59) stocks. The model with the SST PCs improved the model fit for Pacific hake (*r*=0.48) and greenstriped rockfish (*r*=0.53). Several of the stocks, including splitnose rockfish, English sole, Washington and Oregon lingcod, California lingcod, and greenstriped rockfish had a better model fits for the models with three to five PCs from PCA on all environmental variables. However, these models also have additional covariates than those with only two environmental covariates. Dover sole, darkblotched rockfish, sablefish, Northern California cabezon, Oregon cabezon, and Washingon and Oregon black rockfish had poor fits for all of the models examined.

There was moderate evidence that the effect of environmental variables varied across groups. The model without separate groups had a DIC value 6.4 greater than that of the grouped model. This model resulted in a moderate increase in the correlation between the observed and median predicted values for 5 of the stocks over the grouped model.

Discussion

I examined recruitment synchrony in marine fish stocks within three ecosystems of the Northeast Pacific and examined environmental variables that may drive recruitment synchrony within these ecosystems by similarly influencing recruitment for several stocks. I found moderate evidence for recruitment synchrony, both in the correlation of recruitment time series and the timing of extreme recruitment events. I also found the hierarchical models of stock-recruitment residuals predicted by a variety of regional environmental variables showed strong recruitment-environmental relationships for few of the stocks investigated and limited coherence within the defined stock groups.

The best BSAI model included PCs across all categories of environmental variables tested and the models with PCs from a single environmental variable category did much poorer.

This indicates the importance of multiple environmental processes for recruitment of the BSAI fish stocks examined here, or the correlation of several of these variables that may make it difficult to identify the process(es) affecting recruitment. Greenland turbot, Pacific cod, and EBS walleye pollock had a strong relationship with PC1, with higher recruitment in periods of increased ice cover and colder spring SST the year before and the year of spawning. Increased ice cover and subsequent late ice retreat relates to higher production of large copepods, as described by the revised Oscillating Control Hypothesis, that may serve as prey for these fish during early life stages and alternative prey for larvae predators (Hunt et al. 2011). Recruitment for many stocks within the retention group was associated with PC3, with higher recruitment in years of stronger northeasterly cross-shelf wind, or along-shelf Ekman transport to the northwest, during the winter of spawning. Previous research suggests on-shelf wind-driven advection in spring favors high recruitment of flathead sole, northern rock sole, and arrowtooth flounder (Wilderbuer et al. 2002, Wilderbuer et al. In press). Northward Ekman transport has been related to reduced cannibalism of larval and juvenile pollock due to separation from cannibalistic adults, so similar mechanisms may be important for these stocks (Mueter et al. 2006). Arrowtooth flounder and northern rock sole also had a significant relationship with PC5, which relates to stronger southeasterly along-shelf wind the year before spawning. These conditions cause Ekman transport to the northeast and coastal downwelling, which increases on-shelf nutrient fluxes over the southern Bering Sea shelf and may affect shelf ecosystem productivity (Danielson et al. 2012b). These PCs are also related to variation in several other environmental variables, so further investigation of the environment processes impacting recruitment may be important to the development of recruitment predictors.

Recruitment for many GOA stocks, especially those within the cross-shelf transport group, was strongly related the SSH variability. Positive coastal GOA SSH anomalies associated with PC1 relate to onshore transport, coastal downwelling, and an accelerated Alaska Coastal Current (ACC). These conditions may reflect enhanced onshore transport of larvae and nutrients and may also be a precursor to enhanced mesoscale eddy activity in the ACC one year later (Thomson and Gower 1998, Combes and Di Lorenzo 2007). Mesoscale eddy activity may increase cross-shelf exchange and advect deep, nitrate rich waters onto the shelf (Stabeno et al. 2004). Although there have been few studies of the impacts of mesoscale eddies on marine fish, they have been found to entrain larval fish, possibly contributing to greater survival through enhanced feeding conditions within the eddies and cross-shelf transport of larvae (Atwood et al. 2010). Offshore upwelling conditions associated with SSH PC2 are also associated with higher recruitment for the GOA cross-shelf transport group and flathead sole. These conditions relate to enhanced nutrient supplies from offshore upwelling and onshore advection, which may enhance larval feeding conditions and transport larvae inshore. El Niño-Southern Oscillation (ENSO), which is often expressed in the GOA through positive coastal SSH anomalies and enhanced eddy formation during warm ENSO events (El Niño), has previously been linked to recruitment variability of Pacific halibut in the GOA (Melsom et al. 1999, Bailey and Picquelle 2002). The synchronous high recruitment for many stocks in 1998-2000 coincides with a strong warm ENSO event (El Niño) in 1997-1998 followed by a strong cold ENSO event (La Niña) in 1998-2000. The coherence of the cross-shelf transport group in their relationship with these environmental predictors indicates these stocks are similarly affected by environmental processes linked to the two dominant modes of SSH variability. Further investigation of the local environmental processes related to SSH dynamics may be useful for identification of the mechanism responsible for GOA marine fish recruitment dynamics.

Recruitment for many CC stocks was strongly related to sea level at San Francisco, which relates to many other local environmental variables including bottom temperature and upwelling (Kruse and Huyer 1983). Several stocks had a strong positive relationship with sea level PC2, which corresponds to low sea levels the year of spawning. Schirripa and Colbert (2006) found low sea levels were associated with high CC sablefish recruitment. These conditions relate to stronger upwelling that may create enhanced primary and secondary production (King et al. 2011). This may also relate to changes in the horizontal advection of surface water and an increased occurrence of large, lipid-rich cold-water copepods (Keister et al. 2011). Overly intense upwelling conditions may also lead to high turbulence which impairs larvae’s ability to capture prey (Lasker 1981) and may reduce onshore transport, but episodes of relaxed upwelling may allow for periods of feeding and movement inshore (Johnson et al. 2001). Sea level PC2 also corresponds to positive sea level anomalies the year before spawning. These low upwelling conditions may result in lower productivity in the previous year and lower abundance of age-1 fish. This may reduce the level of competition and cannibalism, which have been suggested as important to Pacific hake recruitment (Buckley and Livingston 1997). The rockfish stocks may also have low investment in reproduction, and even skip spawning, during years of low productivity but in subsequent years invest additional energy in reproduction (Rideout et al. 2005). Many CC stocks within both groups had a positive relationship with PC2, which contradicts my initial reason for grouping the stocks based on a hypothesized varied response across these groups to upwelling conditions. I also tested PCs from regional sea surface height data from across the Northeast Pacific as predictors of recruitment within the CC, but these models provided a much poorer fit to the data than the chosen model based on coastal sea level at San Francisco. This may be because the data covered a much larger area so it did not capture the coastal sea level dynamics more closely related to upwelling conditions in the CC and coastal productivity. Coastal sea level may be a good predictor to use in future analysis of environmental influences on CC stocks because of the many factors within the ecosystem it relates to, and for identification of specific processes most important to recruitment for these stocks.

Across all of the ecosystems studied, many of the rockfish stocks with the highest maternal investment had poor model fits. Although I did account for the effects of SSB on recruitment, I did not account for other population factors that may be especially important for these stocks. For rockfish, early survival may be strongly linked with maternal effects, such as maternal age and length, which have been found to be important to fecundity, parturition date, oil globule size, growth rate, and starvation resistance for several CC rockfish species (Berkeley et al. 2004, Sogard et al. 2008). Maternal effects not captured in my analysis may be responsible for a large portion of the variability in recruitment for these stocks. Further analysis of rockfish recruitment that includes these population effects may aid in identification of environmental influences on recruitment.

Although previous studies have identified synchrony in recruitment of Northeast Pacific marine fish stocks, I found moderate synchrony within the ecosystems investigated. Hollowed et al. (1987) compared recruitment patterns for Northeast Pacific stocks without accounting for stock-recruitment relationships. They found positive correlations in recruitment among related species (groundfish, pelagic) within regions and negative correlations between species groups and regions. More recently, Mueter et al. (2007) investigated the correlation between recruitment and stock-recruitment residuals for groundfish within the GOA and BSAI and found relatively weak coherence within these ecosystems. They did identify positive correlations in recruitment between BSAI gadids (walleye pollock and Pacific cod), positive correlations between BSAI flatfishes (arrowtooth flounder, yellowfin sole, rock sole, and flathead sole), and negative correlations between BSAI gadids and flatfishes. While I identified similar correlation patterns, few of the correlations were strong ($|r|>0.40$).

The poor model fits attained for many of the stocks in the hierarchical models of environmental influences on recruitment may relate to the moderate synchrony in the stock-recruitment residuals. The grouped models were only slightly superior to the models with a single group, indicating the grouping structure used did not substantially improve the model fit. In developing the grouping structure I considered many methods, including groups based on the main geographic region within the ecosystem (Aleutian Islands or Eastern Bering Sea; western or eastern Gulf of Alaska; northern or southern California Current), taxonomic classification, bottom-up influences (timing of spawning and egg size which may affect susceptibility to first feeing mortality), and top-down influences (predators). Since these grouping methods individually did not fully capture the processes driving synchrony across stocks within the ecosystems, I decided to develop groups based on the processes thought to be most important to recruitment. This grouping method was not easily defined and development was aided by several scientists very familiar with the early life histories of these species and the ecosystems. This grouping structure may be reevaluated to find groups with greater support within these models. While I attempted to collect available early life history information from the scientific literature and scientific experts, I found many aspects of the early life history for these stocks were uncertain. Additional early life history information may aid in the development of future groupings structures that better represent the common exposure across stocks to environmental influences. Multivariate analysis of the early life history aspects of GOA marine fish species has been used to identify groups of species with similar life history patterns (Doyle and Mier 2012). While the unavailability of certain life history data for many of the stocks in this analysis limited my use of this type of multivariate analysis grouping procedure, improved early life history information may allow for this method to be used more widely in identifying shared susceptibility of stocks to environmental influences.

While I attempted to select a variety of regional environmental variables to give a comprehensive look at the environmental processes in these regions important to recruitment, all of the models tested provided poor fits for many of the stocks. While there is moderate recruitment synchrony and overlap in the early life histories of many of these stocks, it seems likely that there are many unique susceptibilities of each stock to environmental processes. Further examination of the stock-specific early life history processes may reveal more information about local environmental variables that influence recruitment for individual stocks. Increased knowledge of environmental influences on individual stocks may allow for more informed grouping and environmental variable predictors.

The recruitment and spawning stock biomass values used were estimates from stock assessment models. While I attempted to use data only from periods for which adequate information was available for estimation of recruitment within the models, changes in data collection or stock assessment model assumptions may have affected the data used in our analysis. The uncertainty in the recruitment and spawning stock biomass estimates was also not accounted for, but this may be important to consider to better understanding recruitment variability.

My analysis used linear models to identify the recruitment-environmental relationship so I was not able to identify non-linear influences on recruitment. Non-linear dynamics and phase shifts in recruitment may be important to consider in future analysis. In the North Pacific, sustained changes in the productivity or abundance of dozens of marine fish populations in the decades before and after 1977 has been widely recognized as an example of a marine ecosystem regime shift (Hare and Mantua 2000). With shifts in the ecosystem, the relationship between recruitment and environmental variables may not be constant through time, and recruitment may only be well correlated with environmental variables for a subset of the period these data are available (Bailey, 2000; Stige et al., in press). Even if there is a significant relationship between an environmental variable and recruitment, it is difficult to anticipate when this relationship might change. Zhang et al. (2010) found that accounting for environmental shifts in modeling recruitment of GOA walleye pollock improved model predictions. Future study of recruitment-environmental relationships that account for non-linearities and shifts are important to identifying drivers of recruitment dynamics.

The Bayesian hierarchical models used here offer a unique method for modeling the relationship with predictors for groups of stocks in order to quantify the group level effects. The knowledge we have regarding the recruitment variability and early life histories of many stocks contributes to our understanding of the environmental influences on recruitment. The group-level parameter posterior distributions may be useful to use as prior distributions in future analyses of environmental influences on recruitment for stocks not included in this analysis that may be susceptible to similar environmental processes as the groups identified here. Other methods, such as state-space models, that can model environmental influences on several stocks as related processes may also be useful to investigate these relationships further. While few strong recruitment-environmental relationships were identified here, future research with this method may be useful in examining environmental influences for groups of fish stocks for identification of environmental covariates that may be used to support prediction of recruitment within stock assessments, improving our ability to manage these fish populations. If robust recruitment-environmental relationships remain elusive, it is wise to consider the development and implementation of management policies that are robust to high levels of recruitment uncertainty.

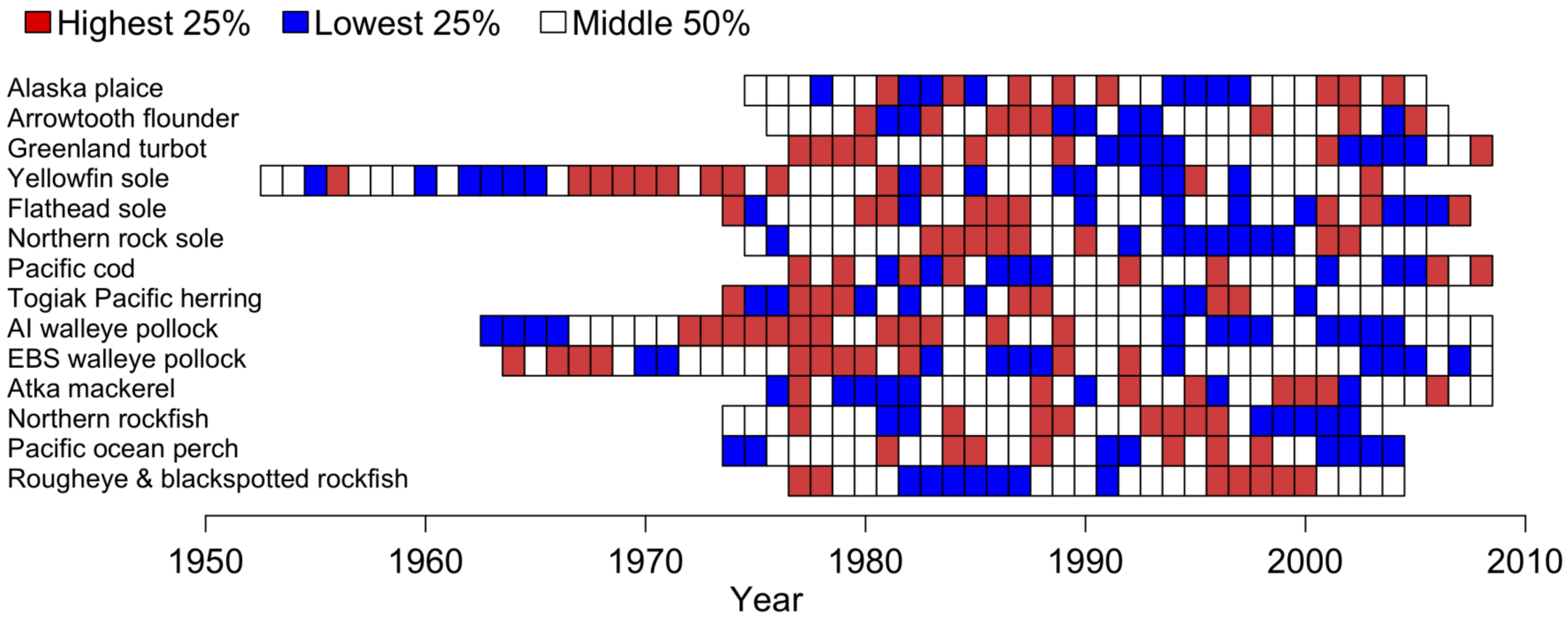

Figure 2.1: Plot of the extreme stock-recruitment residuals for the Eastern Bering Sea and Aleutian Islands stocks. The top (bottom) 25% of recruitment residuals for each stock, respectively, are shaded in red (blue).

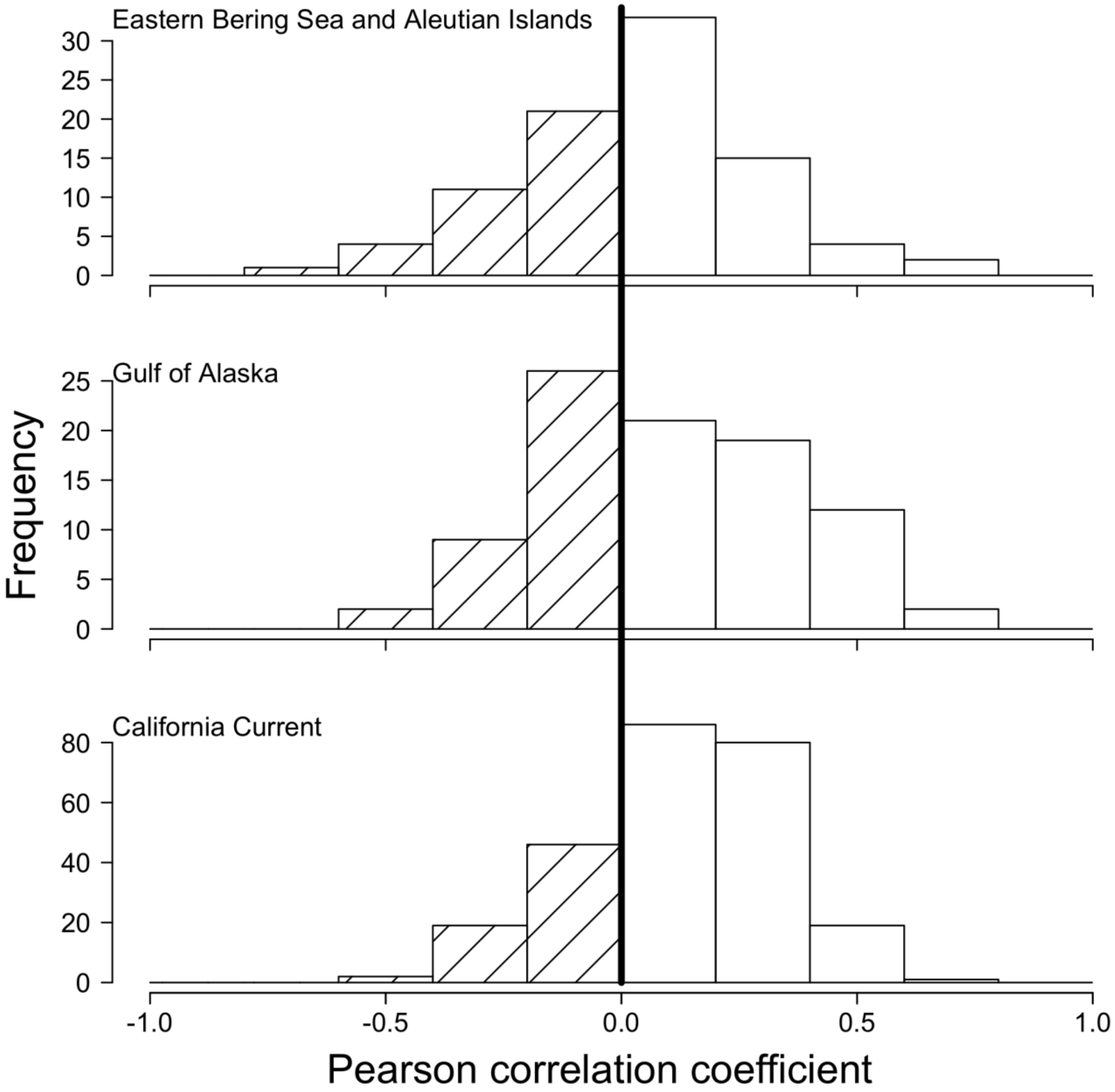

Figure 2.2: Frequency of Pearson correlation coefficients between stock-recruitment residuals for all stocks within each ecosystem.

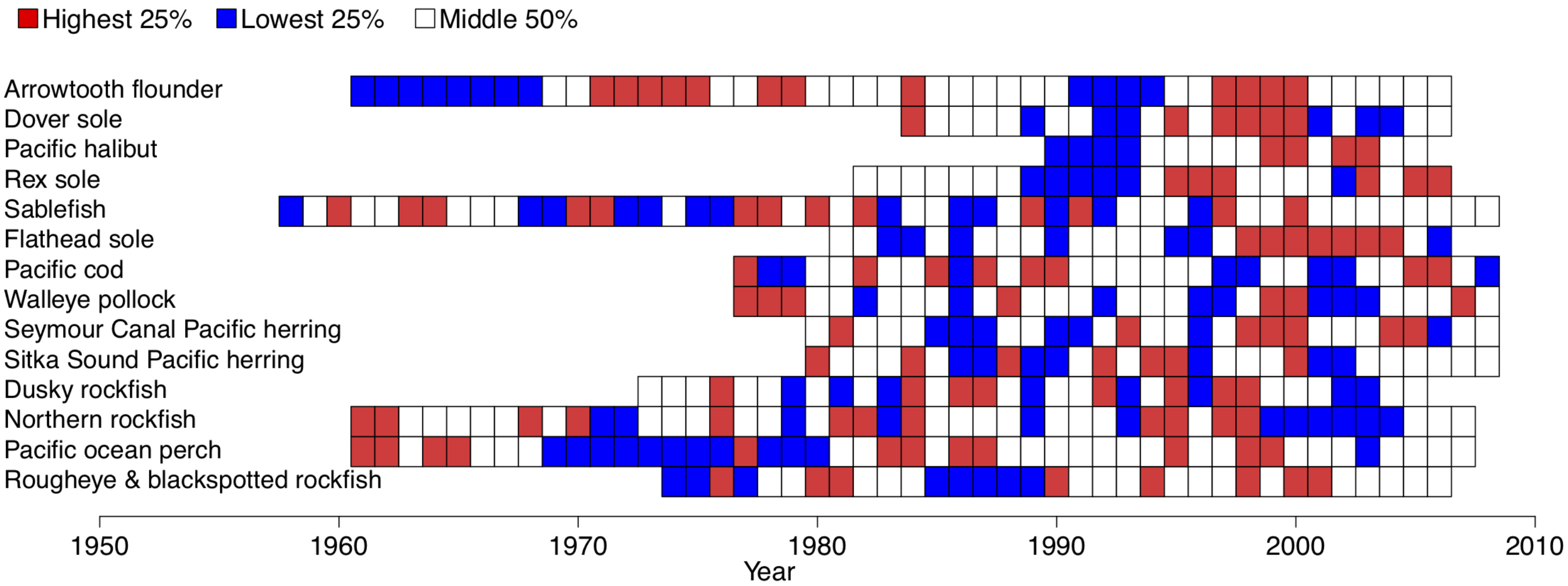

Figure 2.3: Plot of the extreme stock-recruitment residuals for the Gulf of Alaska stocks. The top (bottom) 25% of recruitment residuals for each stock, respectively, are shaded in red (blue).

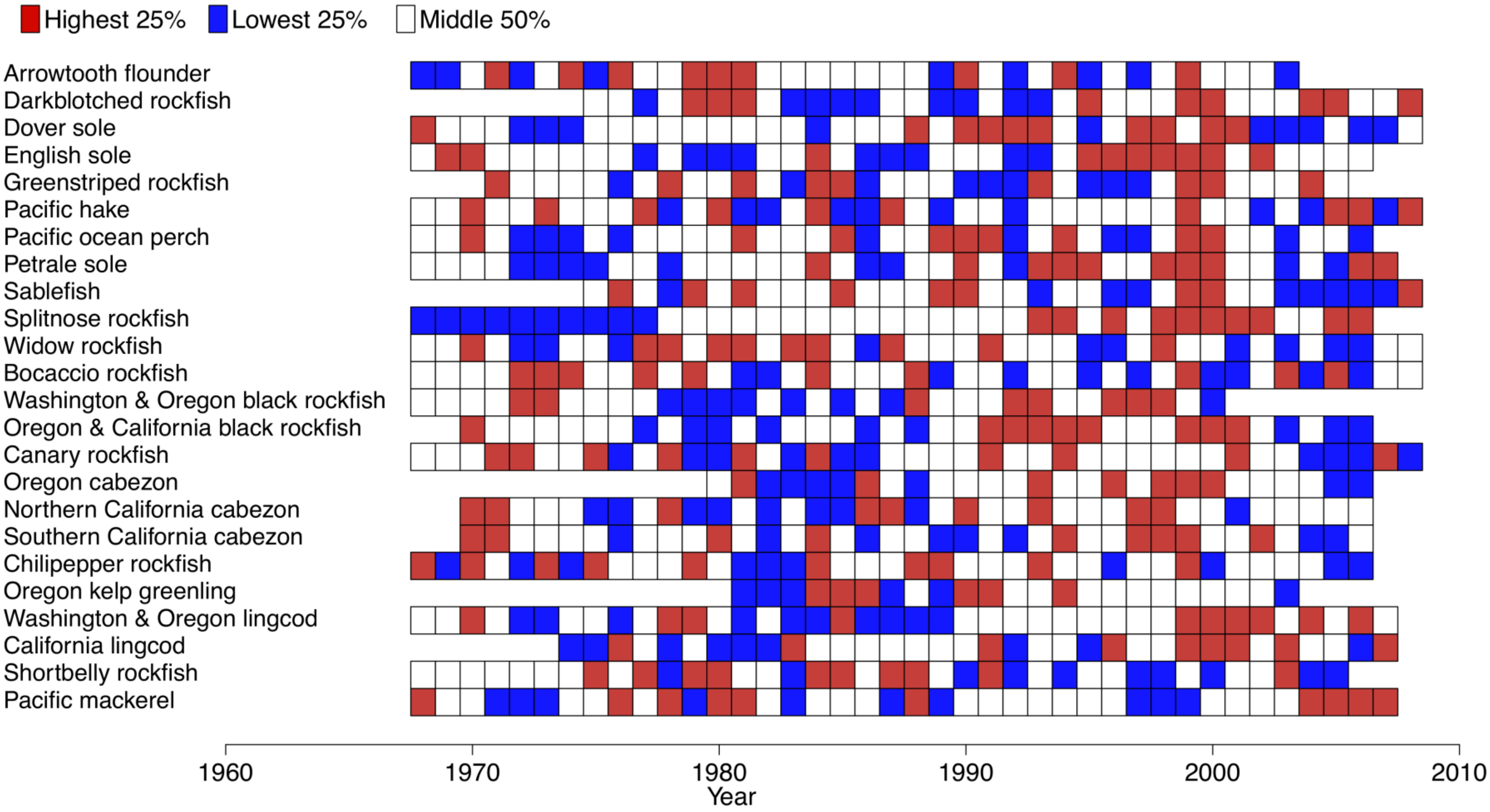

Figure 2.4: Plot of the extreme stock-recruitment residuals for the California Current stocks. The top (bottom) 25% of recruitment residuals for each stock, respectively, are shaded in red (blue).

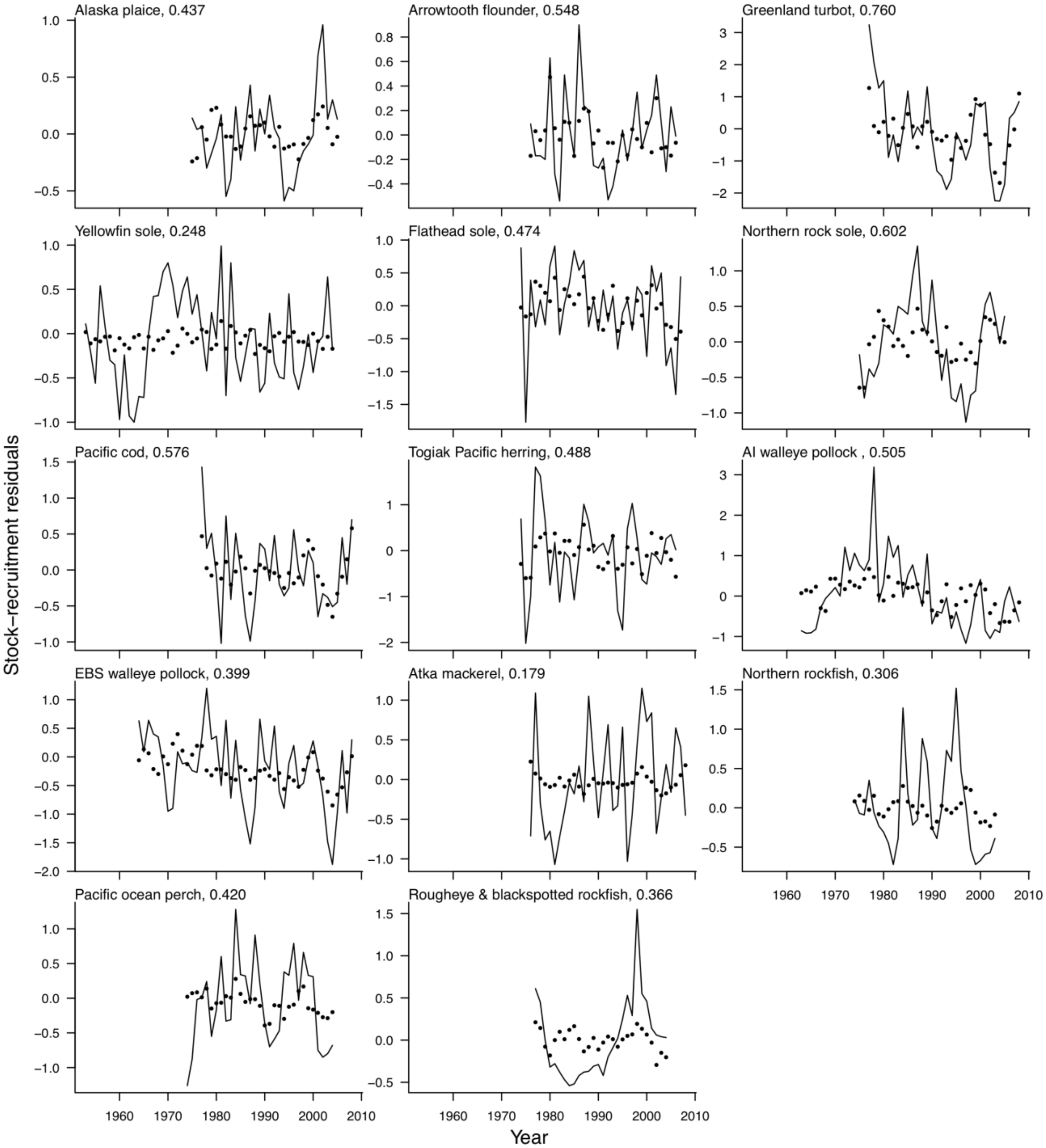

Figure 2.5: Observed (lines) and median model predicted (points) stock-recruitment residuals for the Bering Sea and Aleutian Islands stocks for the model with five principal components from principal component analysis of all environmental data included as the predictors. The Pearson correlation coefficients between the observed and median model predicted stock-recruitment residuals are also shown.

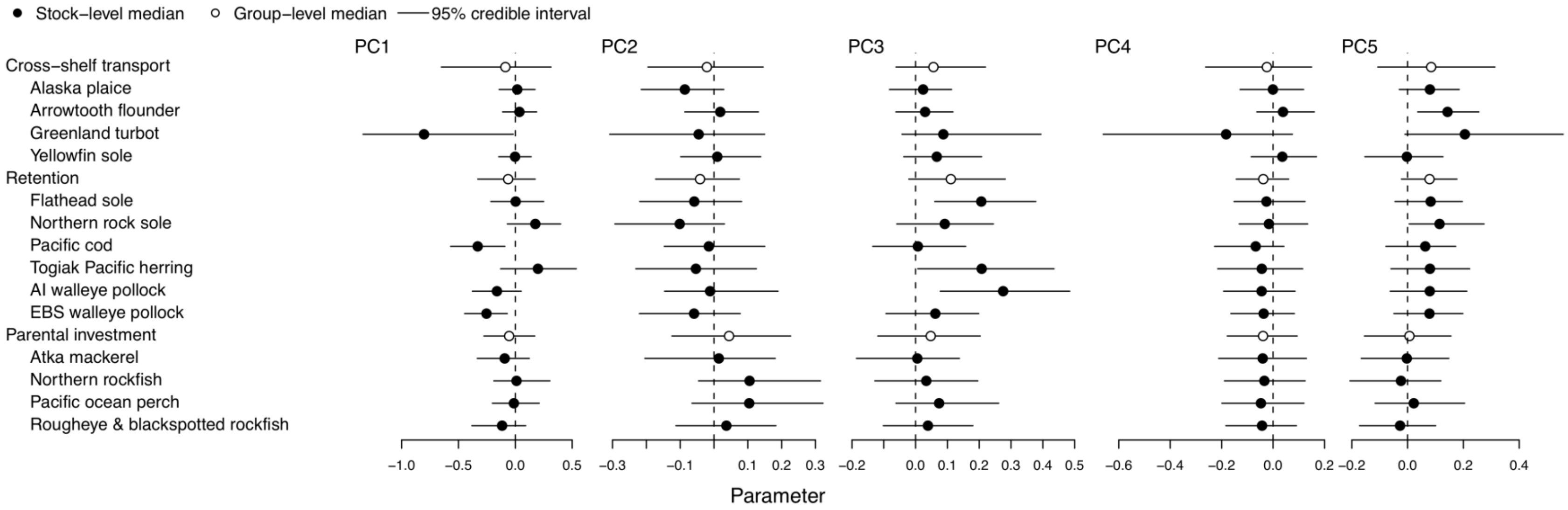

Figure 2.6: Group-level and stock-level parameter distributions for the coefficients of the five principal components (PCs) from principal component analysis of all the environmental data for the Eastern Bering Sea and Aleutian Islands stocks.

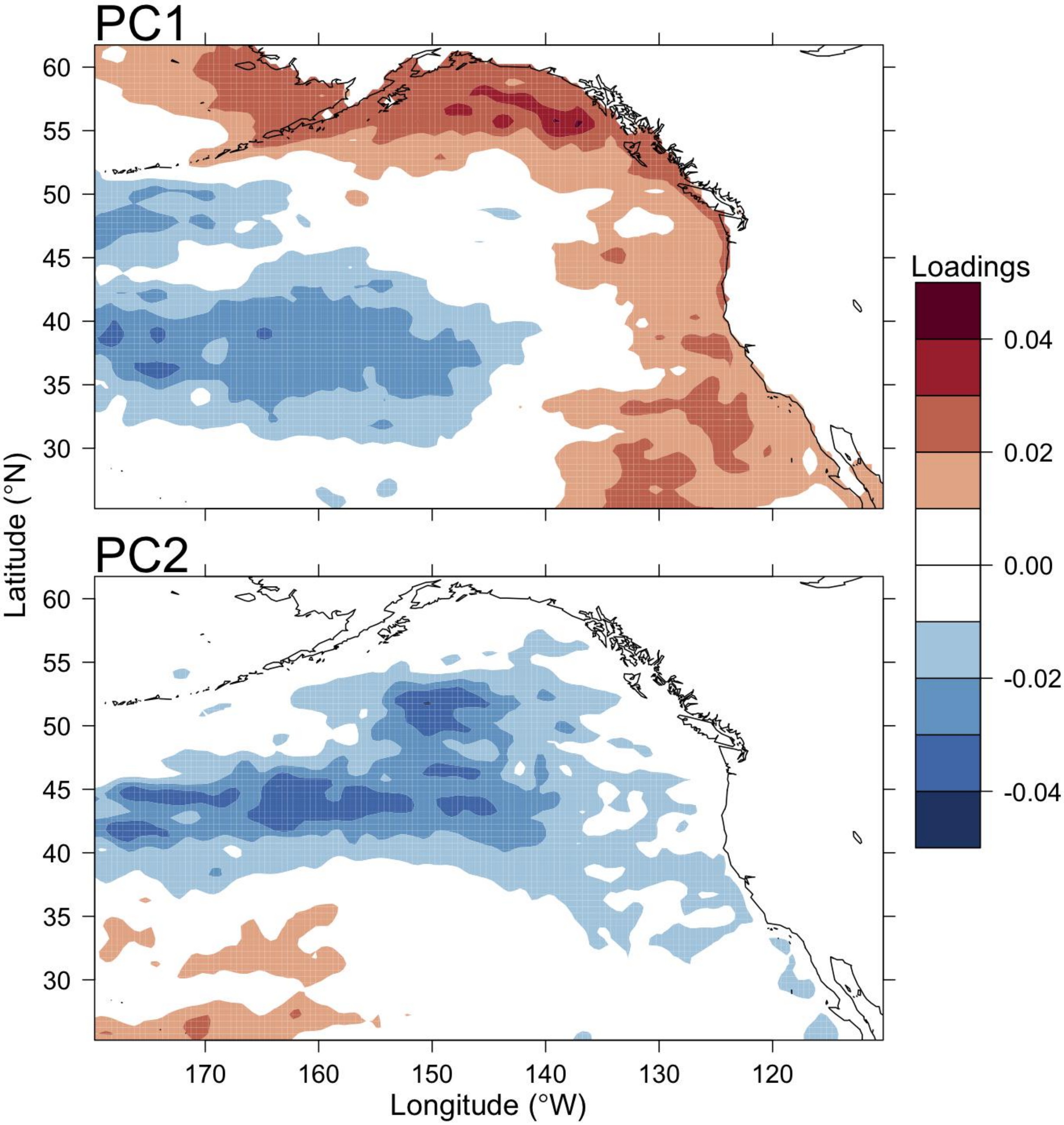

Figure 2.7: Loading of the annual (July-June, for year corresponding to January) Northeast Pacific sea surface height data on the principal components (PCs) from principal components analysis of these data.

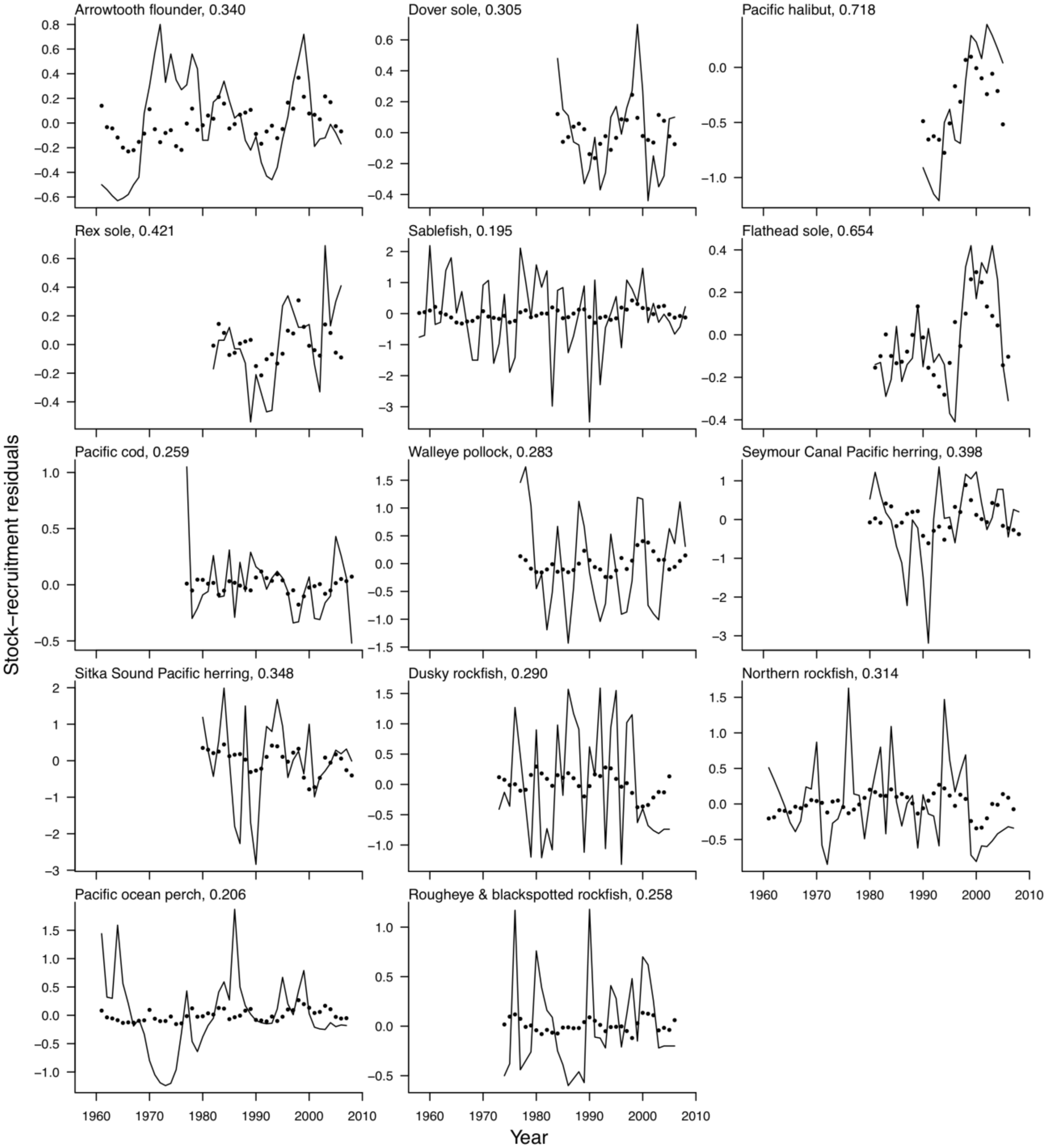

Figure 2.8: Observed (lines) and median model predicted (points) stock-recruitment residuals for the Gulf of Alaska stocks for the model with the first two axes from principal component analysis of sea surface height data as the predictors. The Pearson correlation coefficients between the observed and median model predicted stock-recruitment residuals are also shown.

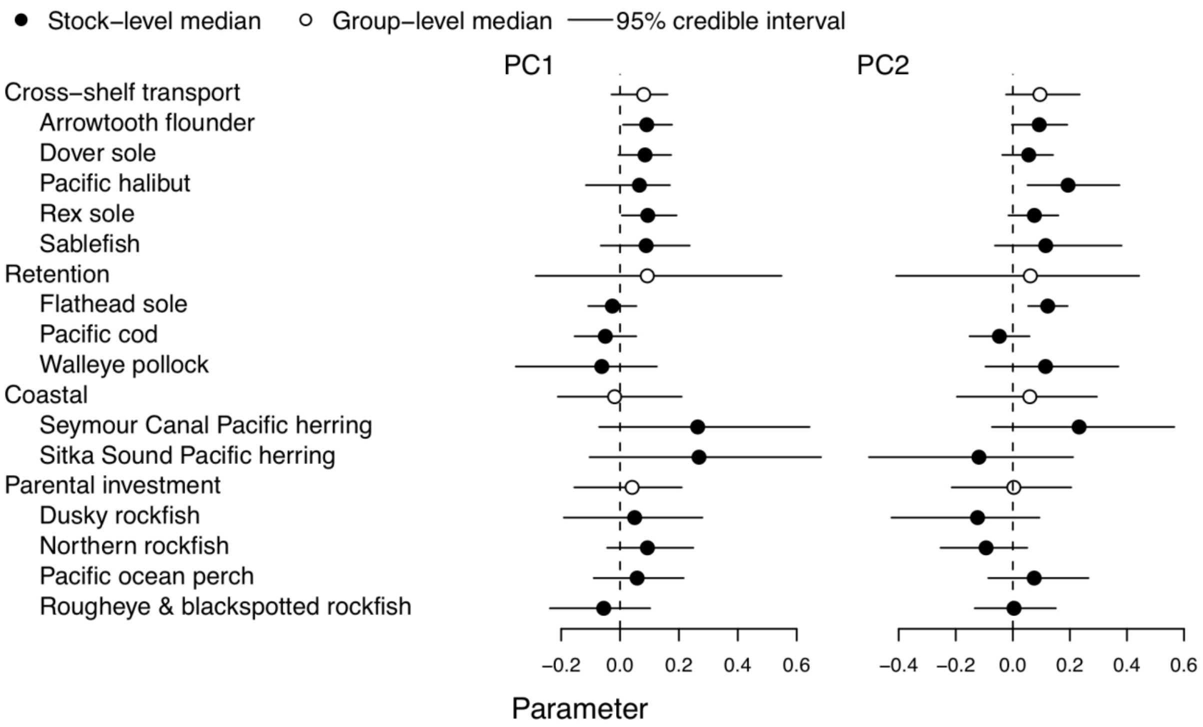

Figure 2.9: Group-level and stock-level parameter distributions for the coefficients of the two principal components (PCs) from principal component analysis of Northeast Pacific sea surface height data for the Gulf of Alaska stocks.

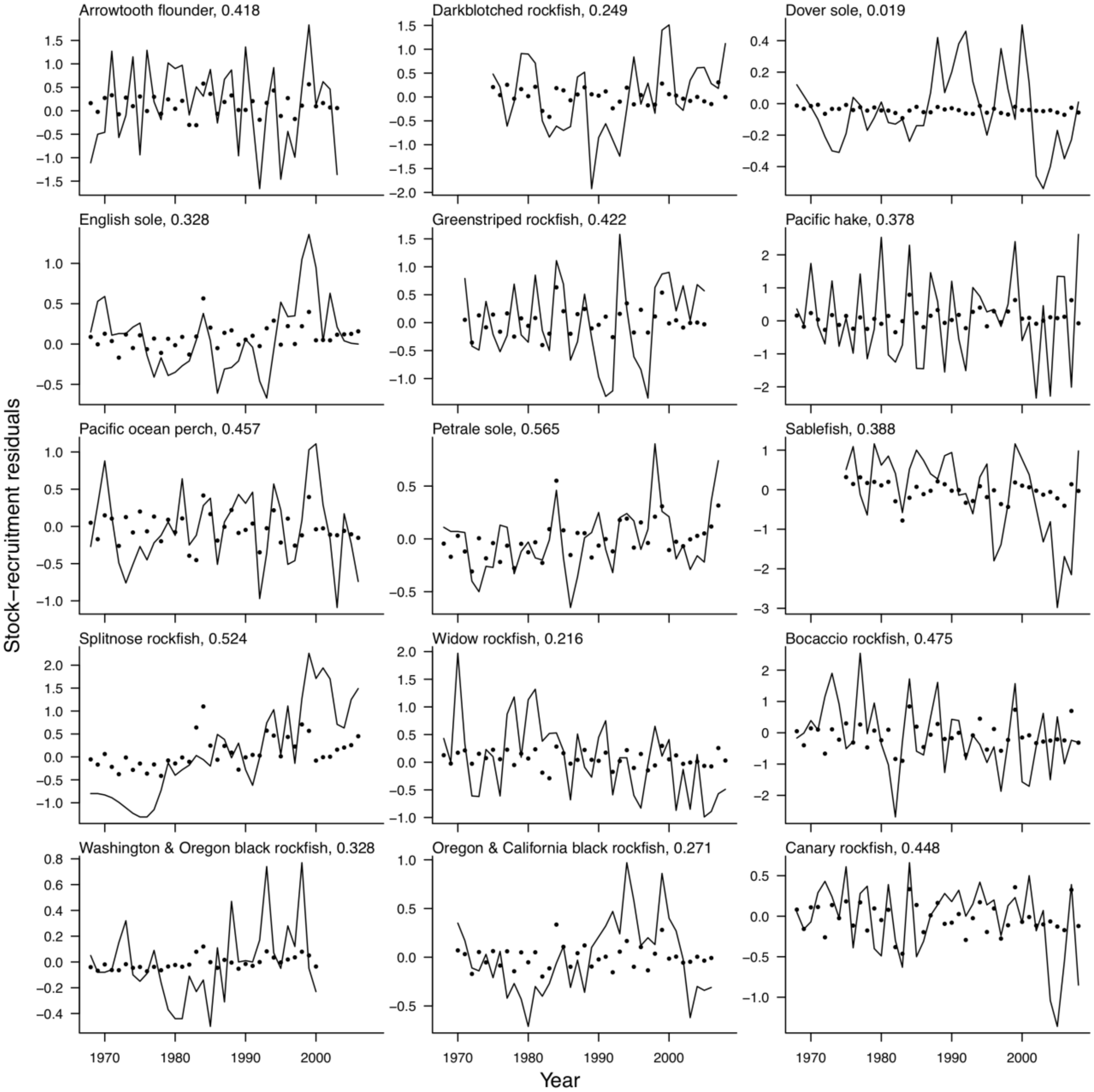

Figure 2.10: Observed (lines) and median model predicted (points) stock-recruitment residuals for the California Current stocks for the model with the first two axes from principal component analysis of sea surface height data as the predictors. The Pearson correlation coefficients between the observed and median model predicted stock-recruitment residuals are also shown.

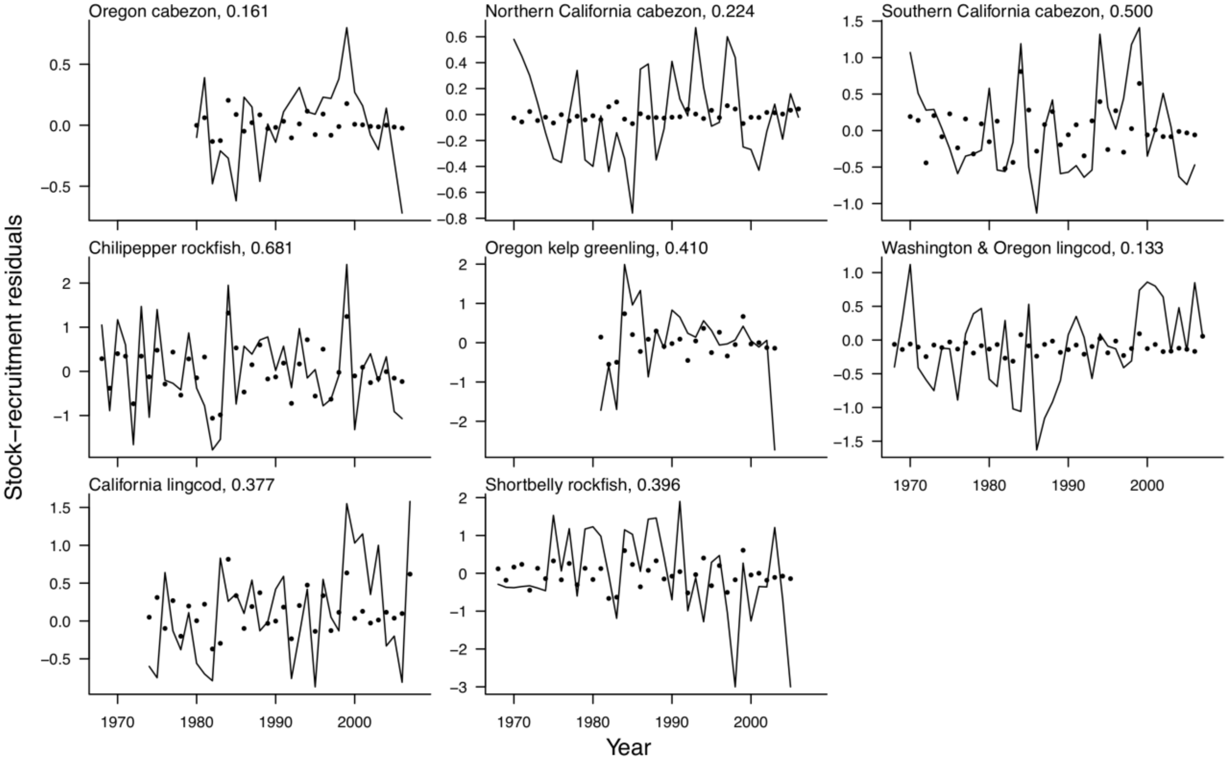

Figure 2.10 (continued)

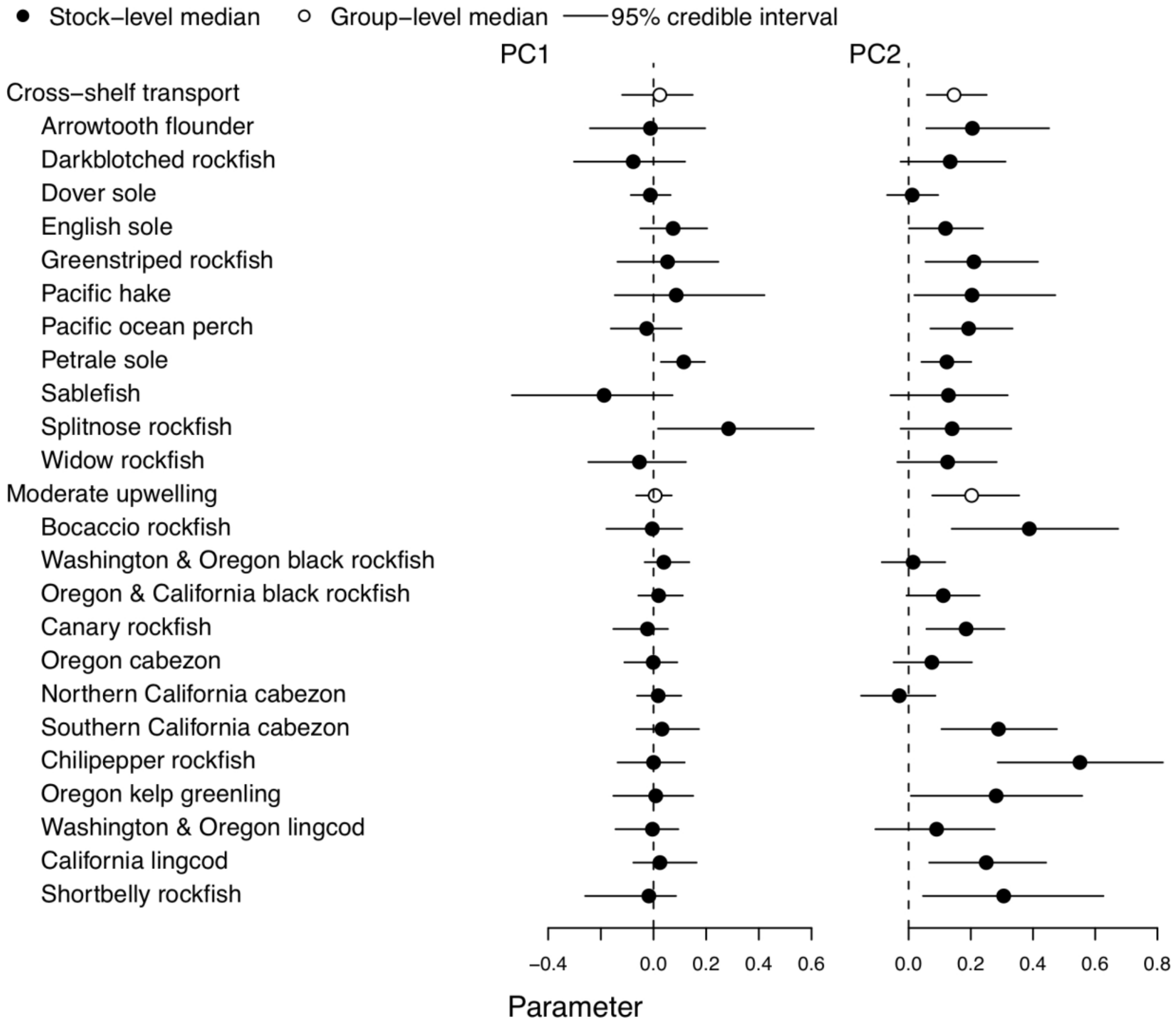

Figure 2.11: Group-level and stock-level parameter distributions for the coefficients of the two principal components (PCs) from principal component analysis of the San Francisco sea level data for the California Current stocks.

Table 2.1: Stocks included in the analysis by ecosystem (Eco.; BSAI, Eastern Bering Sea and Aleutian Islands; GOA, Gulf of Alaska; CC, California Current), the grouping structure used, and the data source.

Eco.	Group	Stock name	Scientific name	Source
BSAI	Cross-shelf transport	Alaska plaice	*Pleuronectes quadrituberculatus*	Wilderbuer et al. 2010c
		Arrowtooth flounder	*Atheresthes stomias*	Wilderbuer et al. 2010a
		Greenland turbot	*Reinhardtius hippoglossoides*	Ianelli et al. 2011c
		Yellowfin sole	*Limanda aspera*	Wilderbuer et al. 2010b
	Retention	Flathead sole	*Hippoglossoides elassodon*	Stockhausen et al. 2010
		Northern rock sole	*Lepidopsetta polyxystra*	Wilderbuer and Nichol 2010
		Pacific cod	*Gadus macrocephalus*	Thompson et al. 2010a
		Togiak Pacific herring	*Clupea pallasii*	G. Buck, personal communication
		AI walleye pollock	*Theragra calcogramma*	Barbeaux et al. 2011
		EBS walleye pollock	*Theragra calcogramma*	Ianelli et al. 2011b
	Parental investment	Atka mackerel	*Pleurogrammus monopterygius*	Lowe et al. 2010
		Northern rockfish	*Sebastes polyspinis*	Spencer and Ianelli 2010b
		Pacific ocean perch	*Sebastes alutus*	Spencer and Ianelli 2010a
		Rougheye & blackspotted rockfish	*Sebastes aleutianus*	Spencer and Rooper 2010
GOA	Cross-shelf transport	Arrowtooth flounder	*Atheresthes stomias*	Turnock 2010
		Dover sole	*Microstomus pacificus*	Stockhausen 2010a
		Pacific halibut	*Hippoglossus stenolepis*	Hare 2010
		Rex sole	*Glyptocephalus zachirus*	Stockhausen 2010c
		Sablefish	*Anoplopoma fimbria*	Hanselman et al. 2010b
	Retention	Flathead sole	*Hippoglossoides elassodon*	Stockhausen 2010b
		Pacific cod	*Gadus macrocephalus*	Thompson et al. 2010b
		Walleye pollock	*Theragra calcogramma*	Dorn et al. 2010
	Coastal	Seymour Canal Pacific herring	*Clupea pallasii*	S. Dressel, personal communication
		Sitka Sound Pacific herring	*Clupea pallasii*	S. Dressel, personal communication
	Parental investment	Dusky rockfish	*Sebastes variabilis*	Lunsford et al. 2010
		Northern rockfish	*Sebastes polyspinis*	Heifetz et al. 2010
		Pacific ocean perch	*Sebastes alutus*	Hanselman et al. 2010a
		Rougheye & blackspotted rockfish	*Sebastes aleutianus*	Shotwell et al. 2010

Table 2.1 (continued)

Eco.	Group	Stock name	Scientific name	Source
CC	Cross-shelf transport	Arrowtooth flounder	*Atheresthes stomias*	Kaplan and Helser 2007
		Darkblotched rockfish	*Sebastes crameri*	Stephens et al. 2011
		Dover sole	*Microstomus pacificus*	Hicks and Wetzel 2011
		English sole	*Parophrys vetulus*	Stewart 2007
		Greenstriped rockfish	*Sebastes elongatus*	Hicks et al. 2011
		Pacific hake	*Merluccius productus*	Stewart et al. 2011a
		Pacific ocean perch	*Sebastes alutus*	Hamel and Ono 2011
		Petrale sole	*Eopsetta jordani*	Haltuch et al. 2011
		Sablefish	*Anoplopoma fimbria*	Stewart et al. 2011b
		Splitnose rockfish	*Sebastes diploproa*	Gertseva et al. 2009
		Widow rockfish	*Sebastes entomelas*	He et al. 2011
	Moderate upwelling	Bocaccio rockfish	*Sebastes paucispinis*	Field et al. 2009
		Washington & Oregon black rockfish	*Sebastes melanops*	Wallace et al. 2006
		Oregon & California black rockfish	*Sebastes melanops*	Sampson 2007
		Canary rockfish	*Sebastes pinnager*	Wallace and Cope 2011
		Oregon cabezon	*Scorpaenichthys marmoratus*	Cope and Key 2009
		Northern California cabezon	*Scorpaenichthys marmoratus*	Cope and Key 2009
		Southern California cabezon	*Scorpaenichthys marmoratus*	Cope and Key 2009
		Chilipepper rockfish	*Sebastes goodei*	Field 2007
		Oregon kelp greenling	*Hexagrammos decagrammus*	Cope and MacCall 2005
		Washington & Oregon lingcod	*Ophiodon elongatus*	Hamel et al. 2009
		California lingcod	*Ophiodon elongatus*	Hamel et al. 2009
		Shortbelly rockfish	*Sebastes jordani*	Field et al. 2007

Table 2.2: For all stocks included in the analysis by ecosystem (Eco.; BSAI, Eastern Bering Sea and Aleutian Islands; GOA, Gulf of Alaska; CC, California Current), the stock-recruitment model chosen (SR: R, Ricker; BH, Beverton-Holt; M, Mean; SA, stock assessment stock-recruitment model), the portion of variance in the recruitment data explained by the chosen stock-recruitment relationship (SR R^2), and the portion of remaining variance in the stock-recruitment residuals explained by the environmental covariates from the Bayesian hierarchical model median predicted values (Env. R^2).

Eco.	Stock name	SR	SR R^2	Env. R^2
BSAI	Alaska plaice	R	0.09	0.19
	Arrowtooth flounder	BH	0.49	0.30
	Greenland turbot	M	0.00	0.51
	Yellowfin sole	M	0.00	0.05
	Flathead sole	M	0.00	0.22
	Northern rock sole	BH	0.12	0.34
	Pacific cod	M	0.00	0.32
	Togiak Pacific herring	M	0.00	0.22
	AI walleye pollock	SA	SA	0.24
	EBS walleye pollock	SA	SA	0.16
	Atka mackerel	M	0.00	0.03
	Northern rockfish	M	0.00	0.09
	Pacific ocean perch	M	0.00	0.15
	Rougheye & blackspotted rockfish	R	0.26	0.12
GOA	Arrowtooth flounder	R	0.59	0.12
	Dover sole	R	0.29	0.09
	Pacific halibut	M	0.00	0.47
	Rex sole	R	0.23	0.18
	Sablefish	M	0.00	0.03
	Flathead sole	M	0.00	0.43
	Pacific cod	M	0.00	0.06
	Walleye pollock	R	0.21	0.07
	Seymour Canal Pacific herring	SA	SA	0.15
	Sitka Sound Pacific herring	SA	SA	0.12
	Dusky rockfish	M	0.00	0.07
	Northern rockfish	R	0.23	0.09
	Pacific ocean perch	BH	0.06	0.04
	Rougheye & blackspotted rockfish	M	0.00	0.05

Table 2.2 (continued)

Eco.	Stock name	SR	SR R^2	Env. R^2
CC	Arrowtooth flounder	SA	SA	0.14
	Darkblotched rockfish	SA	SA	0.06
	Dover sole	SA	SA	0.00
	English sole	SA	SA	0.11
	Greenstriped rockfish	SA	SA	0.16
	Pacific hake	SA	SA	0.11
	Pacific ocean perch	SA	SA	0.20
	Petrale sole	SA	SA	0.32
	Sablefish	SA	SA	0.13
	Splitnose rockfish	SA	SA	0.24
	Widow rockfish	SA	SA	0.05
	Bocaccio rockfish	SA	SA	0.21
	Washington & Oregon black rockfish	SA	SA	0.08
	Oregon & California black rockfish	SA	SA	0.07
	Canary rockfish	SA	SA	0.20
	Oregon cabezon	SA	SA	0.02
	Northern California cabezon	SA	SA	0.04
	Southern California cabezon	SA	SA	0.25
	Chilipepper rockfish	SA	SA	0.44
	Oregon kelp greenling	SA	SA	0.16
	Washington & Oregon lingcod	SA	SA	0.02
	California lingcod	SA	SA	0.14
	Shortbelly rockfish	SA	SA	0.14

Table 2.3: Physical variables included in the analysis by ecosystem (BSAI, Eastern Bering Sea and Aleutian Islands; GOA, Gulf of Alaska; CC, California Current; SST, sea surface temperature; SSH, sea surface height; SODA, simple ocean data assimilation; CUI, cumulative upwelling index- summation of daily mean upwelling indices at each location starting on).

Eco.	Variable	Description	Citation	Data source
BSAI	Ice cover index	Average ice concentration at 56-58°N 163-165°W for Jan 1-May 31; values before 1979 were estimated as a linear function of SST	NA	http://www.beringclimate.noaa.gov/
	Kuskokwim River Discharge	Discharge from the Kuskokwim River at Crooked Creek, AK during the winter months of low discharge (Nov-Apr) and summer months of high discharge (May-Oct)	NA	http://waterdata.usgs.gov/nwis
	Cross-Shelf Wind	Winter (Oct-Apr) cross-shelf wind at 60°N 170°W from NCEP/NCAR Reanalysis; positive values correspond to SE Ekman transport along the shelf	Kalnay et al., 1996	http://www.esrl.noaa.gov/psd/
	Along-Shelf Wind	Winter (Oct-Apr) along-shelf wind at 60°N 170°W from NCEP/NCAR Reanalysis; positive values correspond to NE Ekman transport onto the shelf	Kalnay et al., 1996	http://www.esrl.noaa.gov/psd/
	SST	SST from NOAA Extended Reconstructed SST for winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec) at 60°N 170°W	Smith et al. 2008	http://www.esrl.noaa.gov/psd/
	SSH	First two principal components from principal component analysis of Jul-Jun SSH data from SODA at 52-65°N 158-198°W	Carton and Giese 2008	http://apdrc.soest.hawaii.edu/dods/public_data/SODA
GOA	Upwelling	Summer (Mar-Aug) upwelling in southeast AK (57°N 137°W) and southcentral AK (60°N 149°W)	Bakun 1973	http://www.pfeg.noaa.gov/
	SST	SST from NOAA Extended Reconstructed SST for winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec) in southeast AK (57°N 137°W) and southcentral AK (60°N 149°W)	Smith et al. 2008	http://www.esrl.noaa.gov/psd/
	Freshwater Discharge	Freshwater discharge for a location near Seward, Alaska during winter months of low discharge (Jan-Jul) and summer months of high discharge (Aug-Dec)	Royer et al. 2001	Tom Royer, Old Dominion University
	SSH	First two principal components from principal component analysis of Jul-Jun SSH data from SODA at 25-62°N 110-180°W	Carton and Giese 2008	http://apdrc.soest.hawaii.edu/dods/public_data/SODA

Table 2.3 (continued)

Eco.	Variable	Description	Citation	Data source
CC	Spring Transition Index	The date (Julian day) on which the CUI reaches its minimum value for WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Bakun 1973, Bograd et al. 2009	http://www.pfeg.noaa.gov/
	Upwelling Season End Date Index	The date on which the CUI reaches its maximum value for WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Bakun 1973, Bograd et al. 2009	http://www.pfeg.noaa.gov/
	Length of Upwelling Season Index	The total number of days between the observed start date (Spring Transition Index) and the observed end date (dated of maximum CUI) of the upwelling season for WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Bakun 1973, Bograd et al. 2009	http://www.pfeg.noaa.gov/
	Total Upwelling Magnitude Index	The total CUI integrated from the observed spring transition date (Spring Transition Index) to the observed end date of the upwelling season for WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Bakun 1973, Bograd et al. 2009	http://www.pfeg.noaa.gov/
	Total Downwelling Magnitude Index	The total CUI integrated from the observed end date of the upwelling season (Upwelling Season End Date Index) to the observed spring transition date (Spring Transition Index) the following year for WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Bakun 1973, Bograd et al. 2009	http://www.pfeg.noaa.gov/
	SST	SST from NOAA Extended Reconstructed SST for winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec) in WA (48°N 125°W), OR (42°N 125°W), and CA (36°N 122°W)	Smith et al. 2008	http://www.esrl.noaa.gov/psd/
	Columbia River Discharge	Discharge from the Columbia River at The Dalles, OR during the winter months of low discharge (Aug-Mar) and summer months of high discharge (Apr-Jul)	NA	http://waterdata.usgs.gov/nwis
	San Francisco Sea Level	Sea level at San Francisco, CA for winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec)	NA	http://tidesandcurrents.noaa.gov/
	SSH	First two principal components from principal component analysis of Jul-Jun SSH data from SODA at 25-62°N 110-180°W	Carton and Giese 2008	http://apdrc.soest.hawaii.edu/dods/public_data/SODA

Table 2.4: Loading of the Eastern Bering Sea and Aleutian Islands environmental variables on the principal components (PCs) from principal component analysis, calculated as the correlation between the original variables and the PCs. Variables for the year before spawning (t-1) and the year of spawning (t) were included (SST, sea surface temperature; SSH, sea surface height). Strong loadings (|*r*|>0.4) are in bold. Also shown is the variance explained by the PCs.

Variable	PC1 (31%)	PC2 (12%)	PC3 (12%)	PC4 (6.8%)	PC5 (5.7%)
Ice cover index (t-1)	**-0.76**	-0.31	**0.49**	0.07	-0.15
Ice cover index (t)	**-0.86**	0.19	-0.21	-0.07	0.23
Winter Kuskokwim River discharge (t-1)	0.35	0.21	-0.38	0.17	-0.20
Summer Kuskokwim River discharge (t-1)	-0.22	-0.21	-0.17	**0.62**	-0.24
Winter Kuskokwim River discharge (t)	**0.46**	-0.26	-0.16	0.05	-0.37
Summer Kuskokwim River discharge (t)	-0.20	**-0.44**	-0.23	-0.03	0.09
Winter cross-shelf wind (t)	-0.19	-0.25	**-0.60**	-0.38	-0.34
Winter along-shelf wind (t)	**0.58**	-0.34	0.24	-0.29	-0.11
Winter cross-shelf wind (t-1)	-0.23	-0.10	-0.20	**0.70**	-0.20
Winter along-shelf wind (t-1)	**0.53**	0.05	-0.35	0.32	**0.55**
Winter SST (t-1)	**0.54**	0.23	**-0.46**	0.18	0.24
Spring SST (t-1)	**0.69**	0.18	-0.40	-0.16	0.04
Summer SST (t-1)	**0.51**	0.16	-0.34	-0.16	-0.17
Fall SST (t-1)	**0.67**	0.19	-0.21	-0.06	-0.16
Winter SST (t)	**0.67**	-0.13	-0.03	-0.27	-0.31
Spring SST (t)	**0.78**	-0.18	0.23	0.16	-0.04
Summer SST (t)	**0.57**	-0.19	-0.08	0.23	-0.12
Fall SST (t)	**0.64**	0.06	-0.03	0.11	-0.22
SSH PC1	-0.14	**-0.83**	**-0.41**	-0.07	0.18
SSH PC2	**0.67**	-0.33	**0.47**	0.08	0.24

Table 2.5: Model selection results for the Eastern Bering Sea and Aleutian Islands (BSAI), Gulf of Alaska (GOA), and California Current (CC) ecosystems. Results are shown as the mean deviance, the effective number of parameters (pD), the deviance information criterion (DIC), and the increase in DIC from the lowest within each ecosystem (ΔDIC). The values for the best model chosen within each ecosystem are in bold.

Eco.	Model	Mean deviance	pD	DIC	ΔDIC
BSAI	**All 5**	**847.8**	**41.1**	**888.9**	**0.0**
	All 5 one group	860.6	33.1	893.7	4.8
	All 3	863.9	31.8	895.7	6.9
	All 4	863.5	36.1	899.5	10.7
	Freshwater runoff	878.3	25.8	904.1	15.3
	SST	880.2	26.1	906.3	17.5
	All 2	882.1	26.6	908.6	19.8
	SSH	883.8	26.0	909.8	21.0
	Ice	895.0	25.4	920.4	31.6
	Wind	901.7	24.1	925.8	36.9
GOA	**SSH**	**805.5**	**26.9**	**832.3**	**0.0**
	SSH one group	811.1	23.8	834.8	2.5
	All 2	819.7	26.9	846.5	14.2
	All 5	807.0	40.1	847.2	14.9
	All 3	815.7	31.9	847.6	15.3
	All 4	813.1	36.4	849.5	17.2
	SST	836.4	24.5	860.8	28.5
	Freshwater discharge	838.7	24.4	863.1	30.8
	Upwelling	850.6	22.7	873.4	41.0
CC	**San Francisco sea level**	**1506.2**	**40.4**	**1546.6**	**0.0**
	San Francisco sea level one group	1514.0	39.1	1553.0	6.4
	All 5	1498.4	55.6	1554.0	7.4
	All 4	1509.0	50.3	1559.4	12.7
	All 3	1546.2	41.9	1588.2	41.6
	SST	1552.7	37.9	1590.6	43.9
	SSH	1574.8	36.0	1610.8	64.1
	Upwelling	1604.0	33.1	1637.0	90.4
	All 2	1604.7	33.2	1638.0	91.3
	Freshwater discharge	1616.5	31.2	1647.6	101.0

Table 2.6: Loading of the California Current San Francisco sea level data on the principal components (PCs) from principal component analysis, calculated as the correlation between the original variables and the PCs. Variables for the year before spawning (t-1) and the year of spawning (t) were included. Strong loadings (|*r*|>0.4) are in bold. Also shown is the variance explained by the PCs.

Season	PC1 (46%)	PC2 (24%)
Winter (t-1)	**0.53**	**0.57**
Spring (t-1)	**0.70**	**0.59**
Summer (t-1)	**0.73**	**0.52**
Fall (t-1)	**0.75**	0.15
Winter (t)	**0.64**	**-0.41**
Spring (t)	**0.74**	**-0.50**
Summer (t)	**0.80**	-0.38
Fall (t)	**0.44**	**-0.62**

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Appendix A: Life history information

Life history information compiled for stock by ecosystem (Eco.; BSAI, Eastern Bering Sea and Aleutian Islands; GOA, Gulf of Alaska; CC, California Current), including the peak spawning or parturition months, spawning mode (pl, pelagic; dm, demersal; ns, nest; vi, viviparous/ovoviviparous), spawning area (sl, slope; sh, shelf; in, inshore; off, offshore), egg size (mm), larval size at hatching/parturition (mm), larval size at transformation to juvenile stage (mm), pelagic duration (months), and juvenile area (sh, shelf; in, inshore). NA indicates the information was not available.

Eco.	Stock name	Spawning months	Spawning mode	Spawning area	Egg size	Larval size hatching	Larval size transformation	Pelagic duration	Juvenile area
BSAI	Alaska plaice	Apr-May	pl	sh	1.9	5.9	10.7	2.5	in
	Arrowtooth flounder	Dec-Mar	pl	sl	1.8	4.4	29.3	4.0	in
	Greenland turbot	Dec-Jan	pl	sl	4.3	13.0	55.0	8.0	sh
	Yellowfin sole	May-Aug	pl	sh	0.8	2.7	16.0	2.5	in
	Flathead sole	Mar-Apr	pl	sh	3.3	6.1	19.5	NA	in
	Northern rock sole	Dec-Mar	dm	sl	1.0	3.8	16.8	2.5	in
	Pacific cod	Jan-May	dm	sh	1.0	3.5	30.0	NA	in
	Togiak Pacific herring	May	dm	in	1.5	6.6	30.5	2.5	in
	AI walleye pollock	Feb-Mar	pl	sh	1.4	3.5	35.0	2.0	sh
	EBS walleye pollock	Mar-May	pl	sh	1.4	3.5	35.0	2.0	sh
	Atka mackerel	Sep	ns	sh	2.7	8.0	35.0	6.0	sh
	Northern rockfish	Mar-Apr	vi	sl	NA	NA	NA	NA	sh
	Pacific ocean perch	Feb-May	vi	sl	NA	NA	NA	12.0	sh
	Rougheye & blackspotted rockfish	Feb-Apr	vi	sl	NA	4.7	NA	NA	sh
GOA	Arrowtooth flounder	Jan-Feb	pl	sl	1.8	4.4	29.3	4.0	in
	Dover sole	May	pl	sl	2.4	6.0	20.0	21.0	sh
	Pacific halibut	Nov-Mar	pl	sl	3.4	8.2	19.4	NA	in
	Rex sole	Apr-May	pl	sl	2.0	5.0	60.5	12.0	sh
	Sablefish	Mar	pl	sl	2.0	5.5	37.0	4.0	in
	Flathead sole	May	pl	sh	3.3	6.1	19.5	NA	in
	Pacific cod	Mar	dm	sh	1.0	3.5	30.0	NA	in
	Walleye pollock	Mar	pl	sh	1.4	3.5	35.0	2.0	sh
	Seymour Canal Pacific herring	May	dm	in	1.5	6.6	30.5	2.5	in
	Sitka Sound Pacific herring	mid Mar-Apr	dm	in	1.5	6.6	30.5	2.5	in
	Dusky rockfish	Apr	vi	sh	NA	NA	NA	NA	in
	Northern rockfish	Apr-Jun	vi	sl	NA	NA	NA	NA	sh
	Pacific ocean perch	Apr-May	vi	sl	NA	NA	NA	12.0	sh
	Rougheye & blackspotted rockfish	Feb-June	vi	sl	NA	4.7	NA	NA	sh

Eco.	Stock name	Spawning months	Spawning mode	Spawning area	Egg size	Larval size hatching	Larval size transformation	Pelagic duration	Juvenile area
CC	Arrowtooth flounder	Sept-Mar	pl	off	1.8	4.4	29.3	4.0	sh
	Darkblotched rockfish	Nov-Mar	vi	off	NA	5.7	18.5	6.0	sh
	Dover sole	Dec-Feb	pl	off	2.4	6.0	20.0	12.0	sh
	English sole	Jan-Mar	pl	off	0.9	2.6	17.5	2.0	in
	Greenstriped rockfish	Apr-July	vi	off	NA	5.0	NA	4.0	sh
	Pacific hake	Jan-Mar	pl	off	1.1	2.4	32.5	5.0	in
	Pacific ocean perch	Jan-Mar	vi	off	NA	NA	NA	12.0	sh
	Petrale sole	Dec-Feb	pl	off	1.2	2.8	20.0	6.0	sh
	Sablefish	Jan-Feb	pl	off	2.1	6.0	NA	3.0	in
	Splitnose rockfish	Feb-July	vi	off	NA	5.2	NA	12.0	sh
	Widow rockfish	Feb	vi	off	NA	4.8	26.2	5.0	in
	Bocaccio rockfish	Jan-Feb	vi	off	NA	4.5	15.0	3.5	in
	Washington & Oregon black rockfish	Jan-May	vi	in	NA	4.0	28.5	5.0	in
	Oregon & California black rockfish	Jan-May	vi	in	NA	4.0	28.5	5.0	in
	Canary rockfish	Jan-Feb	vi	off	NA	3.8	15.6	3.5	in
	Oregon cabezon	Jan-Feb	ns	in	1.7	5.0	14.0	3.5	in
	Northern California cabezon	Jan-Feb	ns	in	1.7	5.0	14.0	3.5	in
	Southern California cabezon	Jan-Feb	ns	in	1.7	5.0	14.0	3.5	in
	Chilipepper rockfish	Dec-Feb	vi	off	NA	5.2	22.0	3.5	in
	Oregon kelp greenling	Dec-Feb	vi	off	NA	5.2	22.0	3.5	in
	Washington & Oregon lingcod	Jan-Mar	ns	in	2.7	8.5	30.0	3.0	in
	California lingcod	Jan-Mar	ns	in	2.7	8.5	30.0	3.0	in
	Shortbelly rockfish	Feb	vi	off	NA	5.4	28.5	3.0	in

Appendix B: Stock groupings

BSAI

I identified three primary processes important to recruitment for the BSAI stocks and grouped the stocks based on these processes. For the stocks that spawn on the outer continental shelf and the slope, including Alaska plaice, arrowtooth flounder, Greenland turbot, and yellowfin sole, inshore transport to juvenile nursery grounds is important to successful recruitment (Wilderbuer et al. 2002, Sohn 2009, Duffy-Anderson et al. 2010, Duffy-Anderson et al. 2011). These stocks were identified as the "cross-shelf transport" group. For the stocks that spawn on the continental shelf, inshore retention and productivity may be import to successful recruitment. The flathead sole, northern rock sole, Pacific cod, Togiak Pacific herring, Aleutian Islands (AI) walleye pollock, and Eastern Bering Sea (EBS) walleye pollock stocks were part of the "retention" group. For walleye pollock, for which cannibalism of larvae and juveniles is reduced when they are transported inshore away from the adult population, advective processes may be especially important (Wespestad 2000, Mueter et al. 2006). Changes in the timing of the spring bloom, regulated by the timing of ice retreat, have also been important to the survival of larvae and juvenile walleye pollock in the Eastern Bering Sea and may similarly affect the early survival of other shelf spawning fish species (Mueter et al. 2006, Hunt et al. 2011). The rockfish stocks, including northern rockfish, Pacific ocean perch, and rougheye and blackspotted rockfish, are ovoviviparous and have high maternal investment in their young. Egg development for rockfish may also be dependent on environmental conditions in the period before parturition, especially for younger fish, as has been shown for Pacific ocean perch (Hannah and Parker 2007).

Similarly, Atka mackerel are nest spawners with male guarding of the nests. These rockfish and Atka mackerel stocks were grouped based on their high “parental investment” because of life history characteristics that allow for large larval size to withstand variation in primary production but may be more influenced by parental conditions.

GOA

I identified four major processes important to recruitment in the GOA. The “cross-shelf transport” group included arrowtooth flounder, Pacific halibut, rex sole, dover sole, and sablefish. These stocks spawn along the continental slope and pelagic larvae spend time in offshore waters, but transport to juvenile nursery grounds is important to survival. Previous research indicates the importance of inshore transport to recruitment for sablefish (Sigler et al. 2001), arrowtooth flounder and Pacific halibut (Bailey and Picquelle 2002, Bailey et al. 2008), and dover sole and rex sole (Abookire and Bailey 2007, Bailey et al. 2008). For the stocks that spawn on the continental shelf, including Pacific cod, walleye pollock, and flathead sole, retention of the larvae in inshore waters is important to successful recruitment (Porter 2005, Doyle et al. 2009). These stocks were identified as the “retention” group. Because of the small egg size of Pacific cod and walleye pollock, lower trophic level productivity and timing may also be especially important to survival for these stocks. The rockfish stocks of the GOA, dusky rockfish, northern rockfish, Pacific ocean perch, and rougheye and blackspotted rockfish, are ovoviviparous so they were grouped based on their high “parental investment.” Pacific herring spawn near shore and are especially susceptible to coastal processes during early life stages, so the Seymour Canal and Sitka sound Pacific herring stocks were grouped as “coastal.”

CC

I divided stocks into two groups within the CC for modeling. The “cross-shelf transport” group contained stocks that spawn on the outer continental shelf or slope and larvae must be transported inshore to juvenile nursery habitat. Because of the influence of strong upwelling events on onshore transport, high recruitment for these stocks may also be associated with low upwelling conditions during the period of cross-shelf movement. The stocks in this group included arrowtooth flounder, darkblotched rockfish, dover sole, English sole, greenstriped rockfish, Pacific hake, Pacific ocean perch, petrale sole, sablefish, splitnose rockfish, and widow rockfish. Previous research has supported this relationship with onshore transport for arrowtooth flounder (Doyle et al. 2009), greenstriped rockfish (Johnson et al. 2001), widow rockfish (Norton 1986), Pacific hake (Bailey 1981, King et al. 2011), dover sole (King et al. 2011), petrale sole (Castillo 1992), English sole (Boehlert and Mundy 1987), and sablefish (Schirripa and Colbert 2006). Studies of Pacific ocean perch (Hannah and Parker 2007) and English sole (Hayman and Tyler 1980) also suggest that pre-spawning environmental conditions affect recruitment through influences on egg condition and spawning timing. For other stocks within the CC, high recruitment has been associated with cooler water temperatures and moderate upwelling events that contribute to greater prey availability and decreased predation. The stocks grouped as “moderate upwelling” were bocaccio rockfish, Washington and Oregon black rockfish, Oregon and California black rockfish, canary rockfish, Oregon cabezon, Northern California cabezon, Southern California cabezon, chilipepper rockfish, Oregon kelp greenling, Washington & Oregon lingcod, California lingcod, and shortbelly rockfish. These environmental conditions have been related to high settlement and recruitment for cabezon (Wilson et al. 2008), bocaccio rockfish (Tolimieri and Levin 2005), black rockfish (Wilson et al. 2008, Woodson et al. 2012), shortbelly rockfish (Yoklavich et al. 1996), and chilipepper rockfish (Norton 1986).

Appendix C: Environmental variables

BSAI

Within the BSAI, five categories of environmental variables were included: wind, sea ice, temperature, sea surface height, and freshwater discharge.

Circulation on the eastern Bering Sea shelf is strongly dependent on wind direction and may affect the transport of nutrients and larval fish across the shelf (Danielson et al. 2012a). Monthly zonal and meridional wind at 60°N 170°W from NCEP Reanalysis were provided by NOAA/OAR/ESRL PSD (Kalnay et al. 1996). Extended winter (October-March) averages of cross-shelf wind, corresponding to along-shelf Ekman transport, and along-shelf wind, corresponding to cross-shelf Ekman transport, were calculated as indices of wind-driven transport.

Sea ice is a large driver of ecosystem dynamics in the Bering Sea so an index of the average ice concentration at 56-58°N 163-165°W for January 1 to May 31 was used as an environmental predictor for the BSAI (Wyllie-Echeverria and Ohtani 1999). This index was only available for 1979-2010, so to extend this index I developed a linear model to predict the ice index based on NOAA Extended Reconstructed Sea Surface Temperature (SST), provided by the NOAA/OAR/ESRL PSD, over the same time period and area (Smith et al. 2008). This model accounted for a large portion of variability in the data (R^2=0.60), so it was used to estimate the ice index for 1958-1978.

Because temperature is important to many physiological processes and lower trophic level productivity, seasonal (January-March, April-June, July-September, October-December) averages of monthly NOAA Extended Reconstructed SST at 60°N 170°W were used as an index of SST (Smith et al. 2008).

Monthly values of SSH at 52-65°N 158-198°W from the simple ocean data assimilation (SODA) were obtained from the Asia-Pacific Data-Research Center (Carton and Giese 2008). Annual averages (July-June), covering the pre-spawning through the spawning period, were calculated and the first two principal components (PCs) from principal component analysis (PCA) of these data were used as environmental variables.

Freshwater discharge for the Kuskokwim River, a principal source of terrestrial freshwater onto the Bering Sea shelf that has a large impact over the southern and central parts of the eastern Bering Sea, was used as an index of freshwater discharge (Mathis et al. 2011). The total discharge from the Kuskokwim River at Crooked Creek, AK during the winter months of low discharge (November-April) and summer months of high discharge (May-October) was calculated from monthly discharge data provided by the U.S. Geological Survey.

GOA

Within the GOA, four categories of environmental variables were included: upwelling, temperature, freshwater discharge, and sea surface height.

The GOA is predominately a coastal downwelling system, but during summer periods coastal upwelling occurs during periods with relaxed winds, resulting in onshore transport of nutrient rich waters (Stabeno et al. 2004). Mean indices of upwelling during the summer months of relaxed downwelling (March-August) for southeast Alaska (57°N 137°W) and southcentral Alaska (60°N 149°W) were calculated based on monthly Bakun upwelling indices provided by the Pacific Fisheries Environmental Laboratory.

Temperature is important to physiological processes and it has been related to larval fish abundance and recruitment in the GOA (e.g., Ciannelli et al. 2005, Doyle et al. 2009). Seasonal (January-March, April-June, July-September, October-December) averages of monthly NOAA Extended Reconstructed SST in southeast AK (57°N 137°W) and southcentral AK (60°N 149°W) were used as indices of SST (Smith et al. 2008).

Freshwater discharge drives the Alaska Coastal Current (ACC) and is important to coastal circulation in the GOA (Royer 1979, Stabeno et al. 2004). It also contributes nutrients necessary for phytoplankton production, which is especially important during the summer months of high discharge when the shelf nutrients are otherwise depleted (Stabeno et al. 2004). Estimates of total freshwater discharge for a location near Seward, Alaska during winter months of low discharge (January-July) and summer months of high discharge (August-December) were used as indices of freshwater discharge in the GOA (Royer et al. 2001, Royer and Grosch 2007).

SSH data may also serve as an index of ecosystem variability. The second PC from PCA of Northeast Pacific SSH, defined as the North Pacific Gyre Oscillation (NPGO), is significantly correlated with fluctuations in salinity, nutrients, and chlorophyll within this region (Di Lorenzo et al. 2008). Large eddy features in the GOA, which may increase cross-shelf exchange and advect deep, nitrate rich waters onto the shelf, may also be captured in SSH variability (Stabeno et al. 2004). Monthly values of SSH at 25-62°N 110-180°W from SODA were used to calculate annual averages (July-June), covering the pre-spawning through the spawning period. The first two PCs from PCA of these data were used as environmental variables. Because the SSH PCs were expected to be related to the PDO and NPGO, I calculated the correlations of the PCs with annual (July-June) averages of these indices, with the degrees of freedom adjusted for autocorrelation using the method of Peterman et al. (1998). Monthly values of the NPGO index were obtained from http://www.o3d.org/npgo/npgo.php and monthly values of the PDO index were obtained from http://jisao.washington.edu/pdo/PDO.latest.

CC

Within the CC, five categories of environmental variables were included: upwelling, temperature, freshwater discharge, sea surface height, and local sea level.

The CC is one of the major coastal upwelling regions of the world. The phenology of coastal upwelling is especially important because many marine species within the CC have life histories adapted to the timing and intensity of upwelling within the ecosystem. Bograd et al. (2009) defined five indices of the phenology of coastal upwelling in the CC: spring transition index, upwelling season end date index, length of the upwelling season index, total upwelling magnitude index, and total downwelling magnitude index. These definitions were used to calculate these indices based on daily Bakun upwelling index data provided by the Pacific Fisheries Environmental Laboratory for locations in Washington (48°N 125°W), Oregon (42°N 125°W), and California (36°N 122°W).

Temperature, often related to upwelling which brings cold, deep water to the surface, is also an important environmental variable relating to factors such as the shifts in the zooplankton community (Keister et al. 2011). Seasonal (January-March, April-June, July-September, October-December) averages of monthly NOAA Extended Reconstructed SST in Washington (48°N 125°W), Oregon (42°N 125°W), and California (36°N 122°W) were used as indices of SST (Smith et al. 2008).

Freshwater discharge contributes nutrients to coastal ecosystems and contributes to the development of fronts, which have been linked to recruitment variability of marine fishes in the in CC (Bakun 1996, Woodson et al. 2012). Furthermore, salinity variations due to Columbia River discharge have been associated with petrale sole recruitment (Castillo 1992). The total discharge from the Columbia River at The Dalles, Oregon during the winter months of low discharge (August-March) and summer months of high discharge (April-July) was calculated from monthly discharge data provided by the U.S. Geological Survey and used as an index of freshwater discharge in the CC.

Regional patterns in SSH have been linked to ecosystem variability in the CC, for example the correlation of the NPGO with fluctuations in salinity, nutrients, and chlorophyll (Di Lorenzo et al. 2008). Monthly values of SSH at 25-62°N 110-180°W from SODA were used to calculate annual averages (July-June), covering the pre-spawning through the spawning period. The first two PCs from PCA of these data were used as environmental variables.

Local sea level indices may also serve as a good predictor of near-bottom ocean temperature along the shelf (Kruse and Huyer 1983) and has been significantly related with recruitment of sablefish in the CC (Schirripa and Colbert 2006). Seasonal (January-March, April-June, July-September, October-December) averages of sea level data at San Francisco, California, based on monthly data obtained from the NOAA Center for Operational Oceanographic Products and Services, were calculated and used as environmental variables.

Appendix D: Bayesian hierarchical models

The prior distributions used for the parameters not drawn from group level distributions were:

(D.1) $\beta_{s,0} \sim U(-100,100)$

(D.2) $\sigma_s \sim U(0,100)$

(D.3) $\frac{1}{\sigma_{\overline{\beta_{g,i}}}} \sim \Gamma(0.5,0.5)$

(D.4) $\overline{\overline{\beta_{e,i}}} \sim N(0,1000000)$

(D.5) $\sigma_{\overline{\overline{\beta_{e,i}}}} \sim U(0,100)$

(D.6) $\overline{\eta_{\overline{\beta_{g,i}}}} \sim N(0,1000000)$

To select dispersed and reasonable initial value for the chains, they were chosen to as random numbers from the following distributions:

(D.7) $\beta_{s,0} \sim U(-0.5,0.5)$

(D.8) $\sigma_s \sim U(0,1)$

(D.9) $\eta_{\beta_{s,i}} \sim U(0,1)$

(D.10) $\sigma_{\overline{\beta_{g,i}}} \sim U(0.1,1)$

(D.11) $\overline{\overline{\beta_{e,i}}} \sim U(0,1)$

(D.12) $\sigma_{\overline{\overline{\beta_{e,i}}}} \sim U(0,1)$

(D.13) $\eta_{\overline{\beta_{g,i}}} \sim U(0,1)$

(D.14) $\overline{\eta_{\overline{\beta_{g,i}}}} \sim U(0,1)$