

## IDENTIFYING INTERACTIONS AMONG SALMON POPULATIONS FROM OBSERVED DYNAMICS

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**Abstract.** A simple direct correlation analysis of individual counts between different populations often fails to characterize the true nature of population interactions; however, the most common data type available for population studies is count data, and one of the most important objectives in population and community ecology is to identify interactions among populations. Here, I examine the dynamics of the spawning abundance of fall-run chinook salmon spawning within the California Central Valley and the Klamath Basin, California, and the Columbia River Basin, Oregon. I analyzed multiple time series from each watershed using a multivariate time-series technique called maximum autocorrelation factor analysis. This technique was used for finding common underlying trends in escapement abundance within each watershed. These trends were further investigated to identify potential resource-mediated interactions among the three groups of salmon. Each group is affected by multiple trends that are likely to be affected by environmental factors. In addition, some of the trends are coherent with each other, and the differences in population dynamics originate from variations in the relative importance of these trends among the three watershed groups.

**Key words:** California Central Valley; Columbia River; fall-run chinook salmon; Klamath River; minimum/maximum autocorrelation analysis; multivariate time-series analysis; *Oncorhynchus tshawytscha*; resource-mediated population interactions.

### INTRODUCTION

Populations often directly or indirectly interact with each other. For example, populations may interact through competition and predator–prey relationships or simply respond synchronously to fluctuating environmental factors. However, current analytical methods struggle to identify the interactions among populations. This is partly because populations are affected by multiple factors: some are unique to individual populations and others are common to all populations although the relative importance of the factors may differ among the populations. One implication of this type of complexity in population dynamics is that a simple direct correlation analysis of individual counts often fails to characterize the true nature of the population interactions. Despite this limitation, the most common data type available for population studies is count data, and one of the most important objectives in population and community ecology is to identify interactions among populations.

This dilemma is exemplified in the attempt to understand the environment-mediated indirect interactions among chinook salmon (*Oncorhynchus tshawytscha*) populations that spawn within major watersheds

in California and Oregon, USA. Chinook salmon are anadromous fish, and throughout their life history their vital parameters (survival, growth, development, and reproduction) are affected by multiple environmental conditions in both river and ocean environments (e.g., Kope and Botsford 1990, Myers et al. 1998, Wells et al. 2006). Some of the factors, such as the rate of coastal upwelling, may exhibit synchronous fluctuations at these distant locations, thereby potentially producing coherent trends among the watershed groups. On the other hand, other environmental signals, such as river flow rate, may be unique to each watershed. This situation complicates any investigation of the relationships among salmon at different locations.

Despite this difficulty, there is a strong incentive to understand how one group of salmon fluctuates relative to others. At present, it is difficult for ocean fisheries to target fish based on their watershed identities; as a result, a management decision for one watershed inevitably affects the other groups. For example, a recent decline in the abundance of fall-run chinook salmon within the Klamath Basin, California, led to the near-complete closure of chinook salmon commercial fisheries off the coasts of California and Oregon in 2006. The closure was necessary despite the fact that fall-run chinook salmon that spawn within the Columbia River Basin, Oregon, and the California Central Valley were thought to be sufficiently abundant to permit harvest (PFMC 2006). This was because they comingle with the Klamath stock in the ocean. For 2007, the Klamath

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stock is forecast to be relatively abundant, but the California Central Valley stock is forecast to fall below its historical levels (PFMC 2007). This situation illuminates the complexity of the simultaneous management of multiple stocks. Information on how the dynamics of populations are related to one another is expected to guide future management decisions and research directions.

Here I use a technique known as maximum autocorrelation factor analysis (MAFA; Solow 1994) to investigate the relationships among different salmon groups. MAFA extracts smooth trends from multivariate time series. The premise of this study was that fall-run chinook salmon spawning within the California Central Valley, the Klamath Basin, and the Columbia River Basin are affected by similar types of environmental factors, and that analyzing how these factors are related to each other would lead to a better understanding of the relationships among these groups of fish. While the type of interactions investigated in this study are the resource-mediated indirect interactions among populations of the same species in different locations, the fact that MAFA is insensitive to the type of the interactions means that the same technique can be used to investigate other types of interactions such as more direct competition or consumer–resource interactions.

#### DATA

The present analysis is based on the annual counts of spawning adults (escapements) of fall-run chinook salmon. As described, for example, in Groot and Margolis (1991) and Quinn (2005), fall-run chinook salmon return from the ocean to their natal rivers for spawning during the fall months. The age at maturity of chinook salmon in California and Oregon varies between two and six years, but they typically return to their natal stream at age 3, 4, or 5; this variation occurs within individual tributaries. After spawning, the adults die. Their offspring emerge from the gravel during winter and spring, and after rearing for a short period in freshwater, they migrate to the ocean. They remain at sea until they begin their upstream spawning migration.

I use the term “population” to describe the group of individuals of the same species that spawn within each basin and have the same upstream migration season; the term “subpopulation” is used to describe a group of individuals within a population that spawn at the same location within a basin, such as the same tributary. These definitions reflect a general knowledge of the spatiotemporal locations of individuals and groupings used in stock assessments. However, there are also alternative definitions that are based on other characteristics of salmon such as migration frequencies and genetics (e.g., Myers et al. 1998, Hill et al. 2002, Quinn 2005).

The data used in this analysis include the escapement counts of individuals that are older than age 2. The abundance of spawning adults was estimated at five

locations within the California Central Valley, six locations within the Klamath Basin, and four locations within the Columbia River (Fig. 1); hereafter, these populations are called the Central Valley population, Klamath population, and Columbia population, respectively. The escapements have been estimated using various methods, including redd (nest) counts, mark–recapture of carcasses, and direct counts using weirs (KRTAT 2001–2007); these data are available from the Pacific Fishery Management Council (*available online*).<sup>2</sup>

At most of the study locations, the escapements primarily include naturally spawning adults; however, data from Bogus Creek (Klamath population) are known to include a large number of individuals that strayed from a nearby hatchery, and data from Spring Creek and lower river hatcheries (Columbia population) are mostly counts of hatchery-reared salmon (PFMC 2007). A preliminary analysis suggested that the dynamics of hatchery-reared salmon share similar factors found in the naturally spawning salmon, but the weights on the factors are different between them. Therefore, the three time series affected by hatcheries were included to supplement the time series of naturally spawning salmon.

#### METHOD

The main technique used in the present analysis is MAFA (Solow 1994). Although the technique is not new, it has rarely been used. Therefore, I first provide a synopsis of the method, followed by a description of the procedure employed in the present study.

##### *Maximum autocorrelation factor analysis (MAFA)*

MAFA is a statistical technique used for finding smooth trends from multivariate time series (Solow 1994). The technique identifies weighted linear combinations of time series to express new variables (Appendix). Mathematically, the technique is very similar to principal component analysis (PCA), which finds the weighted linear combination of multivariate data based on their variance (e.g., Johnson and Wichern 1992). MAFA departs from PCA in that MAFA finds the new variables based on their lag-one autocorrelations; in other words, the first factor, which is called the first maximum autocorrelation factor (MAF), is the weighted linear combination of the original data with the highest lag-one autocorrelation. The second MAF, another weighted linear combination, is uncorrelated with (orthogonal to) the first MAF and has the second highest lag-one autocorrelation. The third MAF, again a weighted linear combination, is uncorrelated with the first and second MAFs and has the third highest lag-one autocorrelation, and so on.

For data consisting of  $n$  time series, as many as  $n$  independent (uncorrelated) MAFs can be obtained. The

<sup>2</sup> (<http://www.pcouncil.org>)

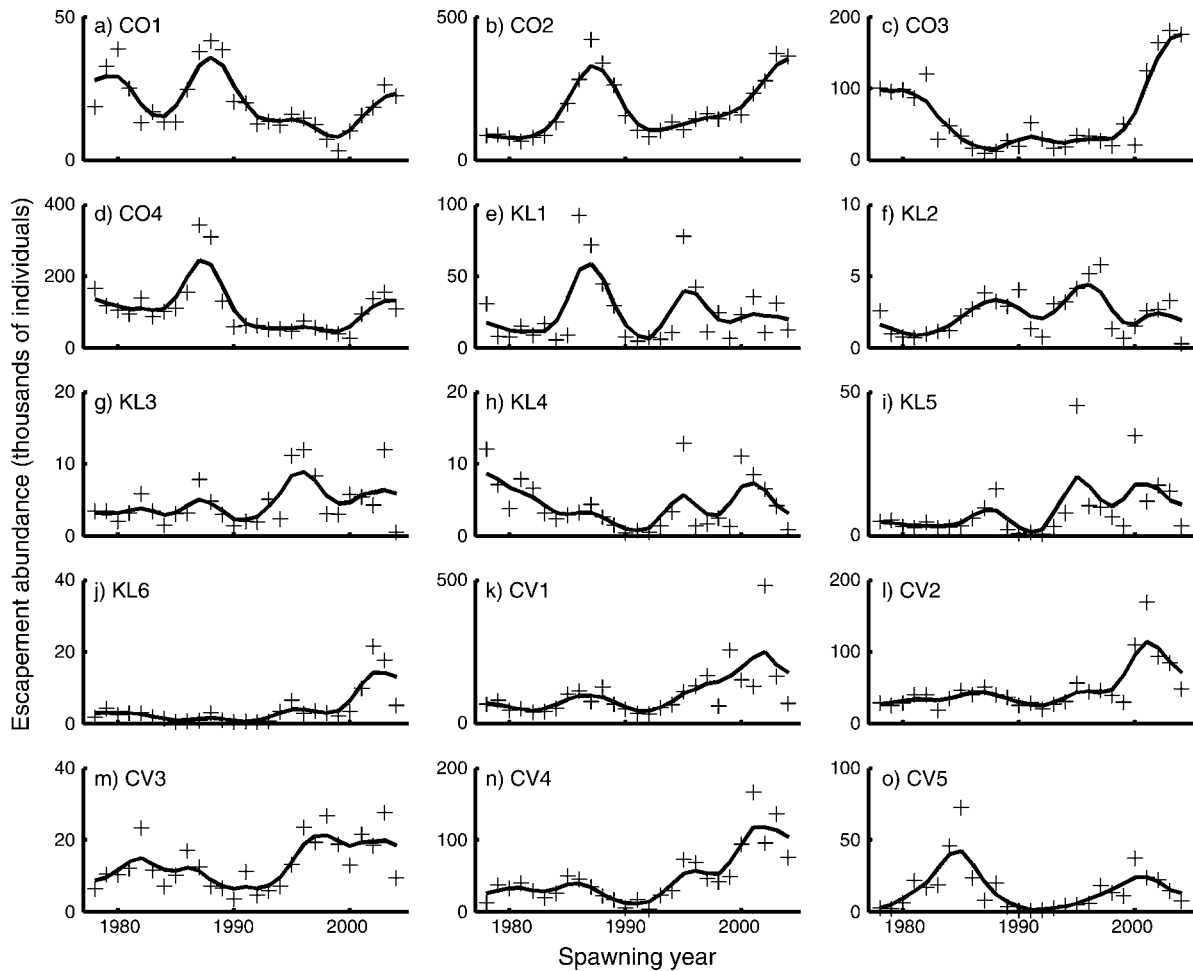


FIG. 1. Escapements of fall-run chinook salmon (*Oncorhynchus tshawytscha*): (a–d) Columbia population (Oregon, USA), (e–j) Klamath population (California, USA), and (k–o) Central Valley population (California, USA). Individual panels show data for: (a) CO1, Columbia River lower river wild, (b) CO2, Columbia river upriver bright, (c) CO3, Spring Creek Hatchery, (d) CO4, Columbia River lower river hatcheries, (e) KL1, Trinity River, (f) KL2, Salmon River, (g) KL3, Scott River, (h) KL4, Shasta River, (i) KL5, Bogus Creek, (j) KL6, Klamath River, (k) CV1, upper Sacramento River, (l) CV2, Feather River, (m) CV3, Yuba River, (n) CV4, American River, and (o) CV5, San Joaquin River. In each panel, symbols represent the raw data, and a smooth curve indicates a twice-applied three-point moving average. (See *Method: Specific procedures*.)

MAFs with significantly positive lag-one autocorrelations are often retained for further analysis. Because a positive lag-one autocorrelation indicates a smoothly changing trend (Diggle 1990), the significant MAFs are the smooth trends that exist in the original time series. Further rationale for the use of MAFA in population studies is provided in the *Discussion*.

Maximum autocorrelation factors can be found by simple calculations. The method is described by Solow (1994), and the Appendix describes some important statistics associated with MAFA. Furthermore, the MATLAB (MathWorks 2001) code used to calculate MAFs is provided in the Supplement to this paper. This code is more general than the method described in Solow (1994), in that it can also find the maximum autocorrelation factors based on a time lag of greater than one. Although I do not use the analysis with a higher lag in

the present study, I suspect that in future studies it may prove useful in extracting specific types of trends, such as cyclic trends, from multivariate time series. I term the analysis with a higher lag a “generalized autocorrelation factor analysis.”

#### *Specific procedure*

To gain some insight into the way in which raw subpopulation data may be related to each other, I first calculated pairwise correlations between subpopulation time series. Then, treating the correlations as a similarity measure, multidimensional scaling (MDS; e.g., Johnson and Wichern 1992) was used to visualize the relationship among the time series. MDS can be thought of as a technique to plot a map of objects based on their pairwise distances rather than their coordinates. The objects that are close to each other are clustered on the map,

and vice versa. In the present analysis, the value of “one minus the correlation between the time series” was used as the distance measure. Therefore, objects (i.e., subpopulation time series) that are more strongly correlated with each other are placed closer together on “the map.”

To extract smooth trends from subpopulation data within each basin, MAFA was applied separately to the time series from each basin. Because the primary interest lies in the trends in the time series rather than the degree of variability, each time series was standardized before applying MAFA by subtracting its mean and dividing by its standard deviation. Those MAFs with a significant positive lag-one autocorrelation were then retained for subsequent analysis. The test of the significance of lag-one autocorrelation was based on the one-tail Bartlett test (Diggle 1990) with the significance level  $\alpha$  of 0.1. The conservative  $\alpha$  value was used because signals with a smaller lag-one autocorrelation can also reflect environmental signals (see *Discussion*). This process was repeated for the data from the other basins. Finally, to find the associations between the MAFs from different basins, pairwise correlations were calculated between the significant MAFs.

## RESULTS

### *Multidimensional scaling of subpopulation dynamics*

Multidimensional scaling of the correlations among the subpopulation time series (Fig. 2) reveals that the subpopulation dynamics within each population tend to be clustered together. The exceptions to this trend are the subpopulations in the Klamath River (Klamath population; Fig. 1j) and Spring Creek (Columbia population; Fig. 1c), both of which exhibit similarities with the dynamics of the Central Valley subpopulations. Without further analysis, one might conclude that the escapement trends in the Klamath River and Spring Creek are unique within the basin and are similar to those observed in the Central Valley population.

### *Maximum autocorrelation factor analysis*

MAFA reveals that the escapements within each basin are affected by three significant smooth trends (Fig. 3). The trends are denoted by MAF A1, A2, and A3 for the Columbia Basin in order of decreasing lag-one autocorrelation. Similarly, the three trends in the Klamath Basin and the Central Valley are denoted by MAF B1, B2, and B3, and MAF C1, C2, and C3, respectively. The lag-one autocorrelations of these trends are shown in Table 1. The three MAFs from each basin show potential underlying trends exhibited by a corresponding population.

The loadings on these factors are shown in Fig. 4. These loadings are the coefficients on the scaled MAFs (Appendix), and indicate how much variability in the scaled subpopulation data is explained by each scaled MAF. Here, I consider that if a loading is greater in magnitude than 0.32, then the factor is deemed to affect

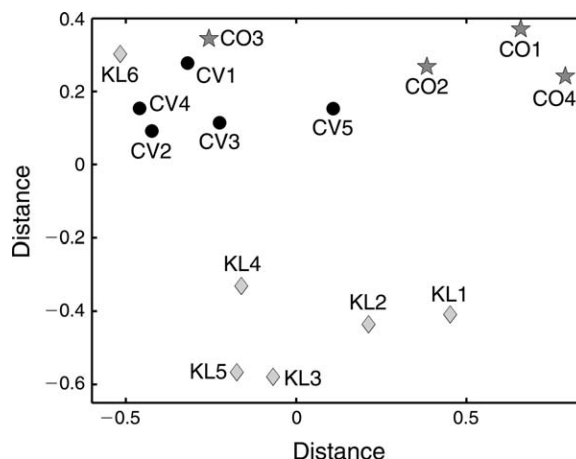


FIG. 2. Multidimensional scaling of correlations among escapement time series of fall-run chinook salmon (gray stars, Columbia Basin; light gray diamonds, Klamath Basin; black circles, California Central Valley). See Fig. 1 for the description of abbreviations. Values are unitless because they have been scaled.

the subpopulation dynamics. If a loading is greater in magnitude than 0.71, then the effect is considered to be strong. These values (0.32 and 0.71) correspond to ~10% and 50%, respectively, of the variability in the subpopulation dynamics explained by the MAF (Appendix).

For the Columbia population, MAF A1 strongly affects the escapements in the upper river, and MAF A2 strongly affects those in Spring Creek; however, other locations are unaffected by these two factors. MAF A3 affects the escapements in all of the locations except Spring Creek.

For the Klamath population, MAF B1 affects the escapements at all locations except the Scott River and Bogus Creek; however, those at the Trinity River and Klamath River are negatively associated with this factor. MAF B2 has an especially strong effect upon the escapements in the Klamath River; it also affects those in the Scott River and Bogus Creek. Finally, MAF B3 explains part of the trends at all locations with the exception of the Klamath River.

For the Central Valley population, MAF C1 affects the escapements at all locations except the San Joaquin River. MAF C2 strongly affects the escapements at the San Joaquin River, and to a lesser degree those at the Yuba River. MAF C3 affects the escapements at the Yuba River and San Joaquin River, but the signs of the associations are reversed between these two locations.

These results reveal that most of the subpopulations share MAF with at least one other location within the same basin and that the subpopulation dynamics reflect a mixture of these common factors. The only exception to this observation is the subpopulation at Spring Creek (Columbia population), which is only affected by a single factor that is unique within the basin; however, in

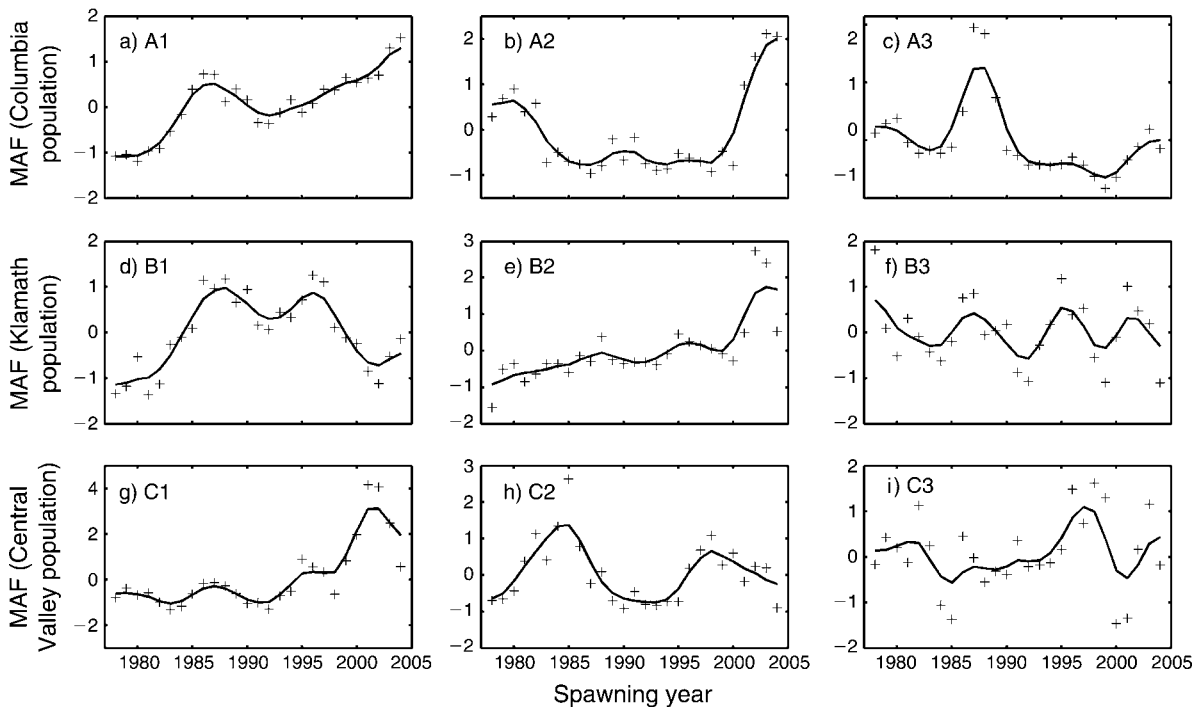


FIG. 3. Maximum autocorrelation factors (MAFs). Symbols show resultant linear combinations of original escapement data, and a smooth curve indicates a twice-applied three-point moving average. (a–c) MAF A1–A3 of the Columbia population, (d–f) MAF B1–B3 of the Klamath population, and (g–i) MAF C1–C3 of the California Central Valley population.

the following section, I will show that this exception is probably an artifact of the limited number of time series available from the Columbia River.

#### Associations among maximum autocorrelation factors

Pairwise correlations among the MAFs (Table 2) reveal that MAF A1 (the Columbia population), MAF B2 (the Klamath population), and MAF C1 (the Central Valley population) are strongly correlated with each other. In addition, MAF A2 is significantly correlated with MAFs B1, B2, and C1. The latter relationship suggests that MAF A2 may contain a mixture of at least two trends; this is probably an artifact resulting from the low number of time series available from the Columbia River.

The association between the dynamics of the Klamath River subpopulation and those in the California Central Valley (Fig. 2) is derived from the strong association between MAF B2 and C1. MAF B2, however, is not unique to the Klamath River subpopulation because this trend is shared by the Scott River and Bogus Creek subpopulations (Fig. 4b). The associations between the latter two time series and the subpopulation dynamics of the Central Valley population was not discovered by simple correlation analysis between the raw time series (Fig. 2), as other factors also strongly affect the Scott River and Bogus Creek subpopulations.

The association between the dynamics of the Spring Creek subpopulation of the Columbia River population

and those of the California Central Valley (Fig. 2) is derived from the association between MAFs A2 and C1. The upper river subpopulation of the Columbia population also exhibits a trend (MAF A1) that is strongly associated with MAFs B2 and C1; however, the upper river subpopulation is also loaded with MAF A3, which is not correlated with the trends found in other basins. This characteristic distinguishes the trends of the upper river subpopulation from those in other basins (Fig. 2).

#### DISCUSSION

The dynamics in the time series of individual counts (population and subpopulation data) are produced by the superimposition of multiple signals, including those associated with the environment and sampling variations. Some of the variations are shared among many time series, while others are unique to single time series or restricted to a small number of time series. Maximum autocorrelation factor analysis (MAFA) can take

TABLE 1. Lag-one autocorrelation of maximum autocorrelation factors (MAFs).

	MAF								
	A1	A2	A3	B1	B2	B3	C1	C2	C3
Lag-one autocorrelation	0.92	0.83	0.74	0.80	0.67	0.43	0.82	0.65	0.30

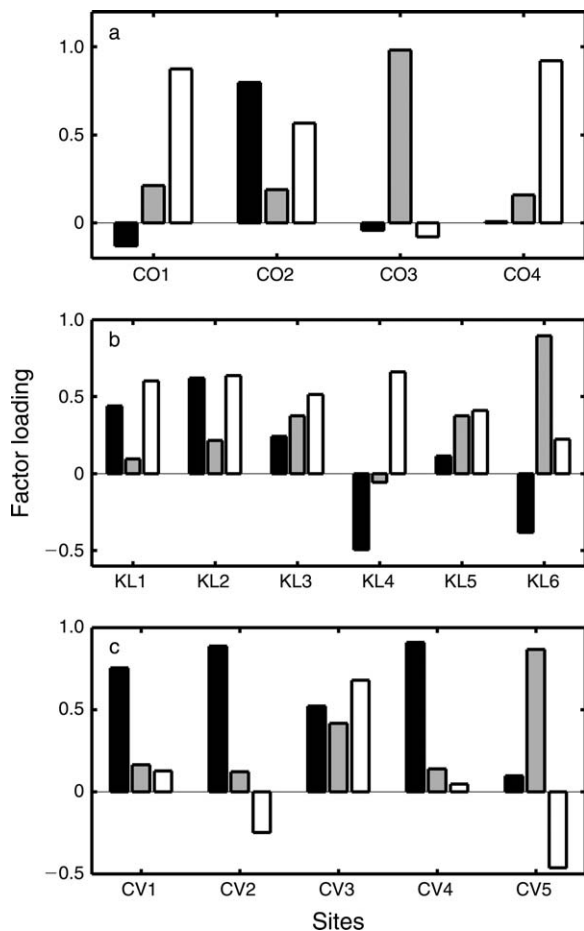


FIG. 4. Loadings of the spawning escapements on the three maximum autocorrelation factors: (a) Columbia River Basin, (b) Klamath Basin, and (c) California Central Valley. See Fig. 1 for the description of abbreviations. For each subpopulation, loadings on the first, second, and third MAFs (see Appendix) from left to right are shown. Values are unitless because they have been scaled.

advantage of this complexity and extract smooth trends from multivariate time series of individual counts.

Subpopulation time series within each of the three populations contain three smooth trends. The trends from different populations (MAF A1 in the Columbia population, MAF B2 in the Klamath population, and MAF C1 in the Central Valley population; Fig. 3, Table 2) are strongly associated with each other, suggesting that a common environmental condition affects all three populations; however, the original subpopulation time series loaded with these factors (Fig. 4) did not necessarily show clear direct correlations with each other because they were also affected by other factors that are not strongly correlated among the populations. A general conclusion from this result is that simple correlation analysis between individual counts may not reveal the true nature of associations between them. This

issue can be overcome using a more detailed analysis such as the one presented here.

These results can assist prediction of the relative escapement abundances of the three populations. I suspect that this type of information, along with further improvements in the technology used to rapidly determine the population identity of fish caught at sea, will become important tools in the future management of these populations.

In addition to factors that are strongly correlated with each other, the three analyzed populations are also affected by factors that are not strongly correlated; however, although MAFs A3, B3, and C3 do not show statistically significant correlations with each other (Table 2), their peaks and troughs show some similarities (Fig. 3). This observation is also true of MAFs B1 and C3. I speculate that further research may prove that these factors actually represent similar types of environmental conditions at different locations. If this is the case, then the underlying factors of the three populations are very similar to each other, and the factor that actually separates them is the relative importance of these factors among the populations.

The results from the present study suggest that the dynamics of the three populations exhibit some similarities. One of explanations for the synchronous trends is that they are caused by coherent fisheries along the coast of California and Oregon. The escapement abundance (i.e., the magnitude) is strongly affected by the fisheries; however, the trends (i.e., relative abundance over time) are often not affected because in most years the fish are harvested in numbers proportional to the estimated total abundance for that year for the basin. Therefore, I suspect the environmental factors are probably the cause. A study has recently been initiated to determine the associations between the trends and various environmental variables. The results of the present study are expected to aid the future analysis by giving some indication of the potential relationships of the factors among the three populations.

TABLE 2. Correlation between maximum autocorrelation factors (MAFs) of three different Chinook salmon (*Oncorhynchus tshawytscha*) populations in Oregon and California, USA.

Population	Klamath population			Central Valley population		
	B1	B2	B3	C1	C2	C3
Columbia						
A1	0.39	0.62†	-0.07	0.55†	0.10	-0.03
A2	-0.64†	0.52†	0.02	0.51†	-0.17	0.09
A3	0.25	0.01	0.27	-0.12	-0.11	-0.13
Klamath						
B1	1.00	0.00	0.00	-0.22	-0.05	0.06
B2	0.00	1.00	0.00	0.75†	-0.01	0.21
B3	0.00	0.00	1.00	0.31	-0.10	-0.09

† Significant correlation at  $\alpha = 0.05$ .

Solow (1994) discusses two attributes that make MAFA particularly appropriate in population analysis. First, MAFA takes advantage of the fact that the data are collected in sequence. This contrasts with other techniques, such as principal component analysis and usual factor analysis, which ignore the order in which data are collected. Second, MAFA maximizes the signal:noise ratio of the time series. Population data are often noisy because they include sampling errors. MAFA is a general approach to the extraction of signals from multivariate time-series data, making it appropriate for the analysis of population time-series data.

In addition to these attributes, I consider two other factors that justify the use of MAFA in population studies. First, the signals of environmental fluctuations are generally not just white noise; they contain structures. For example, commonly used environmental indices such as the North Atlantic Oscillation Index and Pacific Decadal Oscillation Index, which have been shown to be associated with population trends in many organisms (e.g., Hare et al. 1999, Fujiwara and Caswell 2001, Hallett et al. 2004) have a significant positive lag-one autocorrelation (see Fujiwara 2008). Thus, summarizing the population data based on a lag-one autocorrelation increases the chance of detecting such environmental signals in population data. Second, the life history strategy of organisms can also act as a smoothing mechanism that induces a positive lag-one autocorrelation in population time series. For example, the chinook salmon counts included two or more cohorts; consequently, an environmental condition in a given year affects the population counts over two or more years unless the effect occurred during the short period around the upstream spawning migration period. As a result, even if the relevant environmental fluctuation did not contain a significant lag-one autocorrelation, the life history strategy of the organisms would have induced a positive lag-one autocorrelation; this enhances the ability to extract the environmental signals from population time-series data using MAFA.

An obvious alternative approach to MAFA is canonical correlation analysis (CCA; e.g., Johnson and Wichern 1992). As with MAFA, CCA finds the weighted linear combinations of the variables in each of the two groups of variables; however, CCA differs from MAFA in that it finds the linear combinations within each of the two groups simultaneously based on correlations between the complementary linear combinations from the two groups (e.g., Johnson and Wichern 1992). One disadvantage of CCA is that it tends to overfit the statistical model to the data, especially when many time series are included in the analysis. This problem is analogous to the tendency to overfit a model to data in multiple regression analysis when many independent variables are included. Thus, the results of CCA need to be interpreted with caution.

The results obtained from MAFA also need to be interpreted carefully because, for example, MAFA does

not necessarily separate all signals from the multivariate time-series data. This is especially true when the underlying factors that affect a population are also correlated with each other or if a limited number of time series are available. I suspect that MAF 2 from the Columbia population is an example of this phenomenon; however, MAFA remain useful in that it can isolate other independent signals from the data if any exist. On the other hand, when a large number of variables are included in the analysis, many significant factors are found. This makes the interpretation of the results complicated. This was the case with the preliminary analysis in which spawning escapement time series from all three basins are included in a single MAFA. Currently, there is no guideline for appropriate number of variables to be included or the minimum length of time series required for the analysis, except the number of variables cannot exceed the length of the time series. However, I suspect the data requirements for MAFA are very similar to those for PCA because the two methods are mathematically very similar.

Another caveat regarding the use of MAFA is that it may fail to separate signals that do not have a significant lag-one autocorrelation. This is especially true in the case that the life history strategy of the organisms does not enhance a lag-one autocorrelation. For example, if coho salmon (*O. kisutch*), which have a fixed age at maturation, are affected only by environmental factors that do not have a significant lag-one autocorrelation, it would be difficult to isolate the environmental signals from their population dynamics using MAFA. The final caveat regarding MAFA is the issue concerning correlations between autocorrelated time series (Pyper and Peterman 1998). When two time series are autocorrelated, it increases the chance of finding a spurious correlation between them; consequently, the correlation analysis between autocorrelated variables should be interpreted cautiously.

In the present study, MAFA was used to identify associations between populations of the same species by taking advantage of multivariate time-series data available for each population; however, there are ways in which this approach might be extended. For example, it may be possible to use MAFA to analyze data when only a single time series is available from each population but data are available from multiple populations of possibly different species. In such a case, I would suggest applying MAFA to the time series by treating the data from different populations as a single set of multivariate time series. In this way, the loadings from single MAFA can then be examined to find their associations. When a large number of time series are available from different populations, I suggest classifying them into logical subgroups. This type of analysis would be useful when analyzing interactions among populations within a community, such as the data available from a marine reserve or fishery data of multiple species within the same region. In such studies,

consumer–resource interactions and more direct competition might appear as negative associations between time series.

The analysis presented in this paper summarized the data based on a positive lag-one autocorrelation; however, as suggested by Solow (1994), it is conceivable that in some studies the negative lag-one autocorrelation may be of interest. For example, a negative lag-one autocorrelation may be indicative of overcompensatory density dependence. Similarly, MAFA with autocorrelation in lags of higher than one time unit (generalized autocorrelation factor analysis) may be useful in certain studies.

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#### APPENDIX

Descriptions of maximum autocorrelation factor analysis and associated statistics (*Ecological Archives* E089-001-A1).

#### SUPPLEMENT

MATLAB source codes used to calculate maximum autocorrelation factors (*Ecological Archives* E089-001-S1).