

Abstract.— We computed correlations between various population estimates for Central California chinook salmon *Oncorhynchus tshawytscha* and both freshwater and marine environmental variables using methods that account for intraseries correlation in a more accurate and conservative way than those used previously. These indicated a negative influence of ENSO (El Niño-Southern Oscillation) conditions in the year during which most of these fish are caught or leave the ocean to spawn. Although freshwater environmental influences have been previously proposed on the basis of correlation analysis, and have been demonstrated using direct survival estimates based on marked fish, they were not detectable using correlation techniques that accurately account for intraseries correlation. There was also weak evidence for an influence of conditions associated with a negative upwelling index at the time chinook salmon enter the ocean. However, because these conditions are associated with high river flows in addition to oceanographic effects, these correlations may merely result from the influence of freshwater flows. To further describe oceanographic influences we computed the principal components of upwelling index, sea level height, and sea surface temperature. The first principle component, which reflected the effects of ENSO conditions in the equatorial Pacific during the previous winter, was significantly correlated with chinook salmon abundance in their final year, and marginally correlated with abundance during the first ocean summer. This work demonstrates new techniques for reducing spurious correlations and the practical difficulties involved in sorting out the multivariate influences on populations subject to remote forcing through oceanographic and meteorological conditions.

Manuscript accepted 23 January 1990.
Fishery Bulletin, U.S. 88:257-269.

Determination of Factors Affecting Recruitment of Chinook Salmon *Oncorhynchus tshawytscha* in Central California

Robert G. Kope

Department of Wildlife and Fisheries Biology
University of California, Davis, California 95616
Present address: Tiburon Laboratory, Southwest Fisheries Center
National Marine Fisheries Service, NOAA, 3150 Paradise Drive
Tiburon, California 94920

Louis W. Botsford

Department of Wildlife and Fisheries Biology
University of California, Davis, California 95616

Understanding the influences of environment on survival and abundance of chinook salmon *Oncorhynchus tshawytscha* is necessary for management of both fisheries and surface water in central California. The salmon fisheries are managed by allocating predicted pre-season abundance between catch and spawning escapement, and flow rates in central California rivers are currently managed to allow adequate flows for spawning and rearing of chinook salmon. Better understanding of environmental influences on salmon populations could improve the ability to forecast pre-season abundance and more clearly define the impacts of water management on salmon abundance.

Chinook salmon spawn in freshwater, but spend most of their lives in the ocean. In California's Central Valley, there are four distinct runs of chinook salmon named for the timing of their spawning migrations: fall, late-fall, winter, and spring. Typically over 90% of the spawning salmon are from the fall run, and over 80% spawn in the Sacramento River and its tributaries (USFWS 1987). Fall run chinook salmon migrate upstream July through November, and spawn October through January.

Eggs incubate in the gravel October through March, and young fish rear in the streams and migrate downstream December through June (USFWS 1987). Most fish spawn at age 3, with some spawning at ages 2 and 4, and a few fish at age 5 (Dettman et al. 1986, Reisenbichler 1986, Kope 1987). The precocious 2-year-old spawners are primarily males and are called "jacks." While in the ocean, Central Valley chinook salmon are harvested by commercial and recreational troll fisheries. Catches in both fisheries are dominated by 3-year-old fish (Denega 1973, Kope 1987).

In addition to natural production, several hatcheries and spawning facilities produce fish to enhance the fisheries and mitigate for losses of spawning and rearing habitat resulting from water development projects (Fig. 1). The contribution of hatchery production to spawning runs has increased in recent years, and has been estimated to be approximately 15% of the total run in the upper Sacramento River (Reisenbichler 1986), 78% of the run in the Feather River, and 87% of the total in the American River (Dettman and Kelley 1986).

Numerous studies have examined relationships between environmental

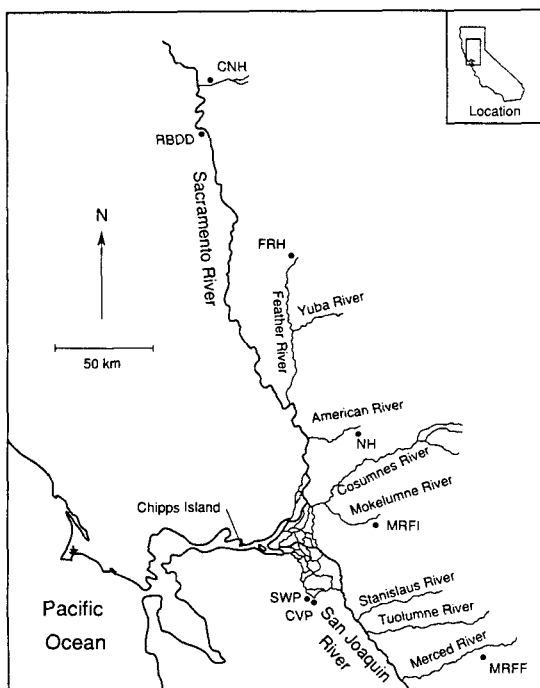


Figure 1

Chinook salmon spawning streams and fish facilities of California's Central Valley. CNH = Coleman National Hatchery; RBDD = Red Bluff Diversion Dam; FRH = Feather River Hatchery; NH = Nimbus Hatchery; MRFI = Mokelumne River Fish Installation; MRFF = Merced River Fish Facility; SWP = State Water Project pumping plant; CVP = Central Valley Project pumping plant.

variables and recruitment or abundance of Pacific salmonids through correlation analysis. Many of these studies have focused on chinook salmon (e.g., Van Hying 1973, Barton 1980), and a few have dealt with the stock of chinook salmon that spawns in California's Central Valley. Most of these studies have detected environmental influences on recruitment; but in the case of Central Valley chinook salmon, reasonably long time-series of recruitment data have been lacking. Some analysts have therefore used estimates of spawning escapement as a proxy for past recruitment (Dettman et al. 1986, Dettman and Kelley 1986, Reisenbichler 1986, USFWS 1987). In general, these studies have reported positive correlations with flow variables and negative correlations with temperature during the period when the spawners were migrating downstream as smolts. Because of a negative correlation between flow variables and temperatures (Dettman et al. 1986), it is impossible to distinguish between effects of temperature and effects of flow using existing data.

Stevens and Miller (1983) used two time-series of smolt estimates based on smolt catches in the delta (Fig. 1), and showed a positive correlation with flows in the previous winter. The most convincing studies used estimates of mortality based on the difference in survival between tagged fish released above the delta and tagged fish released below the delta to show a positive influence of flow rates in the delta and negative influences of temperature and diversions (Kjelson and Brandes 1989, Kjelson et al. 1981, USFWS 1987, Dettman et al. 1986).

In contrast to those of freshwater, potential marine influences on Central Valley chinook stocks have not been explored. Oceanographic conditions off the California coast vary dramatically providing potentially important interannual differences in predators, prey, transport, and ocean temperature during the marine phase of chinook salmon life. The normal pattern of circulation in the northeastern Pacific involves northwesterly winds of varying strength along the coast of California in the spring and summer months which reinforce the geostrophic flow of the California Current and transport surface waters offshore (Mysak 1986, Hickey 1989). This causes varying degrees of upwelling of deeper water and longshore advection of subarctic water along the coast of California and Oregon, which are associated with colder temperatures and depressed sea level heights. The amount of upwelling is estimated by an upwelling index based on winds computed from measured atmospheric pressure gradients (Bakun 1975). Occasional El Niño-Southern Oscillation (ENSO) events, characterized by a warming of equatorial Pacific waters, have a dramatic effect on California coastal waters. These effects may result from either coastal trapped waves which propagate poleward from the Equator, or an atmospheric teleconnection between the Equator and midlatitudes (Emery and Hamilton 1985, Mysak 1986). The former would cause higher sea surface temperatures and sea level heights, but would not necessarily affect Bakun's upwelling index (Enfield and Allen 1980, Emery and Hamilton 1985, Mysak 1986). The latter involves an increase in strength of the Aleutian low-pressure system and a weakening of the north Pacific high-pressure system. Changes in the atmospheric pressure gradients, associated with ENSO events, weaken the northerly winds which results in less upwelling, warmer sea temperatures, higher sea level, and a lower upwelling index (Norton 1987, Mysak 1986). ENSO events and anomalous strengthening of the Aleutian low pressure system may occur at the same time, but each also occurs alone (Emery and Hamilton 1985, Mysak 1986).

Marine and freshwater influences on California Central Valley chinook salmon could be confounded. Large-scale oceanographic and meteorological conditions in

the Pacific have been related to precipitation in California, which could in turn influence flow rates. Markham and McLain (1977) found a positive correlation between California rainfall and sea surface temperature off the coast of Washington. However, rainfall in California is only weakly related statistically to equatorial conditions associated with ENSO events (Douglas and Englehart 1981, Cayan and Peterson 1989, Redmond 1988).

Environmental influences on fish populations are often explored by computing correlations between environmental and population time-series; however, these are computed and the significance of resulting correlations are evaluated in a variety of ways. In attempting to detect environmental influences by computing correlations, the probability of obtaining a significant result is often artificially inflated by two problems: (1) intraseries correlation and (2) multiple tests (cf. Walters and Collie 1988). The latter arises from the fact that many environmental series can be tested for correlation with the population series; hence the probability of falsely identifying a significant relationship is greater than the probability level of each test. Methods exist for dealing with both problems, but we focus on the former here [see Hollowed et al. (1987) and Drinkwater and Myers (1987), for examples of dealing with the latter]. The former, intraseries correlation, is a lack of statistical independence of observations, which implies that the true number of degrees of freedom that should be used in determining the significance of a computed correlation is less than the number of points in the series. There are two steps that can be taken to deal with this problem: (1) removing as much of the intraseries correlation as possible, and (2) accounting for the remaining correlation in the computation of confidence limits.

Removal of intraseries correlation can be accomplished by arbitrarily "pre-whitening" the series (i.e., filtering the series so that correlation between adjacent points is removed) (Box and Jenkins 1976, Fogarty 1988), but is more directly justified when there is a physical basis for doing so and the new series represents a meaningful quantity. In the case of an abundance or catch series, one can compute a recruitment time-series from the original series using deconvolution (Kope and Botsford 1988). Deconvolution is a procedure based on the observation that catch or abundance is a sum over age-classes which is essentially a weighted sum over past recruitment (i.e., a moving average), in which the weighting factors are the (assumed constant) probabilities of survival to each age. If the abundance or catch series is established using a size limit, rather than an age limit, the numbers at each age that are larger than the size limit must also be accounted for in the weighting factors. Deconvolution inverts this summing process to give recruitment

in terms of catches or abundances. Deconvolution provides two advantages over using the catch or abundance series without deconvolution: (1) it removes the intraseries correlation due to summing ages in abundance or catch data, and hence provides more conservative estimates of the significance of correlations between recruitment and the environment; and (2) it yields an estimate of recruitment from the abundance or catch data, hence it can also increase the magnitude of estimated correlation coefficients. However, deconvolution cannot yield an exact value of recruitment when noise is present in the abundance or catch data. The error present in the recruitment estimates depends on the error present in the catch or abundance series and on the stability of the deconvolution (Kope and Botsford 1988). Thus, there is a trade-off between the two advantages of removing the effects of multiple age-classes and the disadvantage of amplifying errors that depends on the stability of the deconvolution and the magnitude of measurement errors in abundance. Consequently, deconvolution may not always be useful.

Intraseries correlation is accounted for in the computation of confidence limits by estimating the variance of the computed correlation coefficient in a way that accounts for the intraseries correlation. This often involves using one of the many approximations to an expression originally due to Bartlett (1946) (Box and Jenkins 1976, Chelton 1984, Botsford 1986). This approach is functionally equivalent to adjusting the number of degrees of freedom using a variation of the expression originally due to Bayley and Hammersley (1946) (Sutcliffe et al. 1976, Drinkwater and Myers 1987). We use another method for dealing with this problem that leads to an actual probability of detection that is closer to the specified probability than other methods (Kope and Botsford 1988, Botsford and Wainwright unpubl.).

In spite of the fact that greater intraseries correlation artificially inflates the probability of detecting a significant relationship, some researchers have added intraseries correlation to the time-series before computing correlations. For example, in the freshwater chinook salmon studies cited above, Dettman et al. (1986) and Reisenbichler (1986) used 2-year moving averages of both spawning escapement and environmental variables in an effort to reduce the effects of age structure in the spawning escapement data. Hollowed et al. (1987) used five-point moving averages in their analysis of recruitment patterns in the northeast Pacific. Because the effects of intraseries correlation were not accounted for in either of these studies, the use of moving averages would decrease the probability of detecting real correlations and increase the probability of spurious correlation (Kope and Botsford 1988). Others have used moving averages before computing

correlations, but then have attempted to account for increased intraseries correlation [cf. Drinkwater and Myers (1987), who use a modified form of the Bayley and Hammersley (1946) approach].

The goals of the study reported here are to explore potential environmental influences on chinook salmon populations in California's Central Valley, and to demonstrate the effective use of some recently developed methods of correlation analysis that are more realistic and conservative than those used previously. We identify potential oceanographic environmental influences on these populations and show that the freshwater influences, which were established by direct survival estimates (USFWS 1987, Kjelson and Brandes 1989), are not detectable from correlation analysis of the available environmental and population data.

Data and methods

Environmental data were obtained from four sources. Average monthly streamflow data were obtained from published USGS records for gauging stations at Verona on the upper Sacramento River, Nicholas on the Feather River, and Fair Oaks on the American River. Flow and diversion data for the Sacramento-San Joaquin delta were obtained from the California Department of Water Resources DAYFLOW hydrological model. Data on sea surface temperature at the Farallon Islands, southern oscillation index, and tidal height at San Francisco (37.48 N 122.22 W) were obtained from D. Cayan (Scripps Inst. Oceanography, La Jolla, CA 92037), and calculated coastal upwelling index at lat. 39°N (Bakun 1975) was obtained from A. Bakun (Pacific Fish. Environ. Group, Natl. Mar. Fish. Serv., NOAA, Monterey, CA 93940).

Population data were taken from the recreational fishery, the commercial fishery, and spawner estimates. We used spawner data from the upper Sacramento River, the Feather River, the Yuba River, and the American River. In the available data, adults had been separated from jacks on the basis of length. Fish less than 60.7 cm fork length were taken to be jacks and larger fish were counted as adults. For the period 1970-86, spawning stock estimates were obtained from Pacific Fishery Management Council (PFMC) reports. For the years 1962-69, total fall-run spawners were taken from Fry and Petrovich (1970), and adult spawners were estimated by multiplying the total estimate of fall-run spawners in each stream by the fraction of carcasses classified as adults in the spawning stock surveys. In addition to abundance indices from individual streams, total adult spawners for the entire Central Valley were estimated by multiplying the fraction of adults reported in all spawning stock surveys each

year by the number of spawners in all runs for all rivers combined.

Commercial and sport catch south of Point Arena were obtained from PFMC reports for the years 1971-86, and from L.B. Boydston (Calif. Dep. Fish Game, Region II, Rancho Cordova, CA 95670, unpubl. data) for the years 1962-70. Commercial effort, measured in thousands of landings, and sport effort, measured in thousands of angler days, were obtained or calculated from the same sources. Fishing effort was used to calculate catch-per-unit-effort (CPUE) in an attempt to remove some of the effects of variable fishing effort from the catch data.

Recruitment of year-classes at the beginning of the commercial fishing season in their second year of life was estimated by deconvolution of the abundance indices using the procedure described in Kope and Botsford (1988). This involved calculating the contribution of recruitment in each year to the abundance indices in subsequent years using an age-structured catch and escapement model with population parameters estimated by separable virtual population analysis of marked hatchery fish (Kope 1987). In addition to the recruitment estimates obtained by deconvolution of the individual abundance series, we estimated recruitment by deconvolving the combined abundance series. This combined deconvolution was obtained by adding together commercial catch, sport catch, and total spawning escapement for each year, and deconvolving the combined abundance series (Kope and Botsford 1988).

Examination of the different recruitment estimates revealed that the deconvolved spawner series contained a great deal of high-frequency noise which resulted from the marginal stability of the deconvolutions of spawner indices. Because of differences in the relative contribution of each age-class, the deconvolution of total spawners was inherently much less stable than the deconvolution of adult spawners (Kope and Botsford 1988). Because recruitment estimates from spawners (adults and jacks) and adult spawners were highly correlated with one another (hence probably represent the same signal, and the deconvolved adult spawners contain less introduced error), only deconvolved adult spawners were used as recruitment estimates derived from spawning escapement.

No attempt was made to separate natural production from hatchery fish in the spawning escapement. Because of the large contribution of hatchery fish to the spawning runs (cf., Reisenbichler 1986, Dettman and Kelley 1986) and the straying of hatchery fish (Hallock and Reisenbichler 1979, Sholes and Hallock 1979), accurate estimation of the natural component of the runs was not possible.

Before computing correlations with environmental data, we tested for an influence of density on the pop-

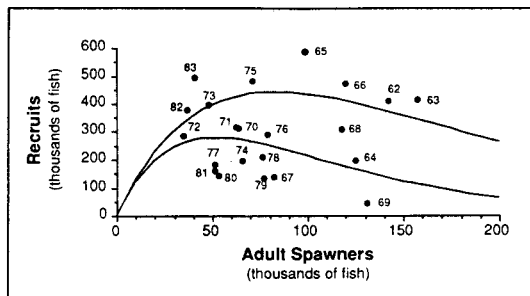


Figure 2

Chinook salmon stock-recruitment curves for the main stem of the Sacramento River. Upper curve was fitted to the data for brood years 1962-66 and the lower curve was fitted to 1967-83.

ulation series. Stock-recruitment relationships for the Sacramento, Feather, and American Rivers were examined by plotting recruitment against spawning stock, and fitting Ricker stock-recruitment curves to the data by the standard linear-regression method. This approach can result in substantial biases in the estimates of stock-recruitment parameters that result from the correlation between recruitment and subsequent spawning stock (Walters 1985, Kope 1988). However, because we use stock-recruitment curves only as a visual aid in interpreting the stock-recruitment data, potential bias was not evaluated.

To examine possible relationships between recruitment and the environment, correlations were computed between time-series of recruitment and quarterly averages of the environmental variables at all lags that had potential biological meaning. These quarterly averages are referred to as: winter, January-March; spring, April-June; summer, July-September; fall, October-December. Correlations with individual stream flows were computed at lags that corresponded to the winter, and to spring while the fish were resident in the streams as fry or migrating downstream. Correlations with delta flows and diversions were computed for the spring while the fish were migrating to sea, and correlations with oceanographic variables were computed from the spring in the year that fish migrated to sea through the summer 2 years later when most fish mature and leave the ocean to spawn. Correlations involving abundance indices (i.e., catch and spawning escapement series) were computed at lags that assumed the indices consisted primarily of 3-year-old fish.

Variability on all time scales can contribute to the variance of time-series and to the magnitude of calculated correlation coefficients. However, variability on greater than annual time scales involves intraseries correlation, which implies the effective number of

degrees of freedom is less than the number of years in the series. Linear trends in the time-series reflect variability on time scales that: (a) can easily be removed by detrending, and (b) are not detectable with existing data. We have removed linear trends from our time-series because they may obscure a relationship on faster time scales.

Intraseries correlation due to variability on intermediate time scales was accounted for in evaluating the significance of computed correlation coefficients. The variance of computed crosscorrelation coefficients can be approximated by

$$\text{Var} [r_{xy}(t)] \approx \frac{1}{n} \sum_{i=1-n}^{n-1} \left(1 - \frac{|i|}{n}\right) \rho_{xx}(i) \rho_{yy}(i) \quad (1)$$

where n is the number of data pairs, $\rho_{xx}(i)$ and $\rho_{yy}(i)$ are the autocorrelation functions of the two time-series variables at lag i , and $r_{xy}(t)$ is the computed cross-correlation coefficient between the two time-series at lag t (Botsford and Wainwright unpubl., Kope and Botsford 1988). When no intraseries correlation is present, this expression simplifies to

$$\text{Var} [r_{xy}(t)] \approx \frac{1}{n} \quad (2)$$

Because the real values of the autocorrelation functions of time-series variables are unknown, and computed autocorrelation coefficients must be used instead, expression (1) can sometimes produce variance estimates smaller than expression (2). However, expression (2) places a lower bound on the possible variance of computed crosscorrelation coefficients because it approximates the variance in the best possible case, when no intraseries correlation is present. We estimated the significance of computed crosscorrelation coefficients by assuming a normal distribution with variance given by the greater of expressions (1) and (2). This strategy has performed the best in giving appropriate rejection rates in Monte Carlo simulations for independent random series with varying degrees of intraseries correlation (Botsford and Wainwright, unpubl. data).

Results

Exploration of possible density-dependence revealed no clear relationships that could be removed prior to examining the influence of environmental variables. The stock-recruitment relationship for the upper Sacramento River appears to show a decrease in the equilibrium stock size that coincides with the closure of Red Bluff Diversion Dam in 1966 (Fig. 2). This supports the

Table 1

Correlations of chinook salmon population estimates with freshwater flow variables in the Sacramento Valley, California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Feather River adult spawners	Delta diversions	1st spring	0.456**
Feather River recruits (deconvolved adult spawners)	Delta diversions	1st spring	0.424**
Total adult spawners	Delta inflow	1st spring	0.402*
	Delta outflow	1st spring	0.393*

* $p < 0.10$, ** $p < 0.05$

Table 2

Correlations with combined California Central Valley fall-run chinook salmon spawning stock indices. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Total adults	UPW	1st spring	-0.542***
		1st summer	-0.444*
	SST	3rd spring	-0.427**
		3rd summer	-0.593***
Recruits (deconvolved adults)	SLH	3rd summer	-0.425**
	SST	3rd summer	-0.541***

* $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$

argument that the decrease in recruitment is a direct consequence of the dam rather than the result of gradual habitat degradation or increasing fishing pressure (Hallock et al. 1982, Hallock 1983). A similar effect had been observed by Reisenbichler (1986) but he found that the spawning runs resulting from the 1964, 1965, and 1966 brood years were intermediate between the stock-recruit curves associated with the time periods before and after these years. With our deconvolved recruitment estimates, the 1964 brood year appears to have been abnormally low, but 1965 and 1966 appear comparable with earlier years. Data for the Feather River and the American River do not fit stock-recruitment curves as well as the Sacramento River data. Our data include few years before the damming of the Feather River and none for the American River before the construction of Nimbus Dam. On both of these rivers, the hatchery contribution to the spawning escapement is large, hence lack of a clear stock-recruitment relationship is not surprising.

To assess the influence of the freshwater environment on Sacramento Valley stocks, we computed cor-

relations between population variables and environmental variables on three rivers—the Sacramento, the Feather, and the American—as well as the total of these three, and relevant environmental variables. Population variables were total spawners, adult spawners, jacks, and recruitment estimated by deconvolution of adult spawners. We thus tested for environmental effects on all spawners, as well as differential effects on jacks and adults, and recruitment to the adult spawner population. Environmental variables were the flow of each river, total diversions of flow in the Sacramento-San Joaquin Delta, diversions as a percentage of flow, delta inflow, and delta outflow. We present all correlations that were significant at the 0.1 level using the standard uncorrelated series test, and annotate with asterisks the significance of each of these according to the more conservative test that allows for intraseries correlation.

The results (Table 1) provide no evidence for an influence of the freshwater environment on numbers of total spawners, jacks, adults, or adult recruits to these stocks. In fact, the number of correlations significant

Table 3

Correlations between chinook salmon recruitment estimates from ocean abundance indices and environmental variables in Central California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Commercial catch	UPW	1st fall	0.397*
	SLH	1st fall	-0.415**
	SST	2nd spring 3rd summer	-0.437* -0.503**
Recreational catch	SST	1st spring	0.711*
		1st summer	0.484**
		2nd winter	0.578
Commercial CPUE	UPW	1st spring	-0.607
		1st summer	-0.448
Recreational CPUE	SST	1st spring	0.583
		2nd winter	0.500
	UPW	1st spring	-0.453
		2nd winter	-0.357
Recruits (deconvolved commercial catch)	UPW	1st spring	-0.460**
	SST	3rd spring	-0.335
Recruits (deconvolved recreational catch)	SST	1st spring	0.353*
Recruits (combined deconvolution)	UPW	1st spring	-0.476**
	SST	3rd summer	-0.538**

* $p < 0.10$, ** $p < 0.05$

at the 0.1 level is half the number expected if all series were independent (i.e., 4 versus 8 out of 80), and the only correlations significant at the 0.05 level using the conservative test—a positive effect of diversions on Feather River fish—has no apparent physical or biological explanation, because diversions during downstream migration would be expected to have a negative effect on survival. We consider this one a spurious correlation. Lack of correlation with delta diversions and total delta outflow may be due in part to the fact that hatcheries on the Feather and American Rivers have released most of their smolts below the delta since the mid-1970s.

Marine influences on spawners were assessed by computing correlations between the same population variables and upwelling index, sea level height, and sea surface temperature. The resulting correlations (Table 2) are significant at the 0.05 level only for adult spawners and recruitment to the adult spawner population. They show a negative influence of conditions associated with ENSO events (i.e., higher ocean temperatures, higher sea levels) in the third spring and summer, immediately before the adults enter the rivers to spawn.

There is also a positive correlation with upwelling index in the first spring and summer, during which smolts migrate downriver, through the delta, and enter the ocean.

We also tested for marine and freshwater influences on catch data from both the commercial and the recreational fishery. We attempted to remove the effects of fluctuations in effort from the catch by computing commercial catch-per-unit-effort and recreational catch-per-unit-effort using the marginal effort data. We computed recruitment estimates from deconvolution of each of these. There is a substantial number of correlations significant at the 0.1 level using the standard test, but none reflect freshwater influences (Table 3). Of the correlations that are significant at the 0.05 level, two are with temperature in the third summer, and the remaining four are in the first marine year, three of them being with upwelling index and the other with sea level height. None of the catch-per-unit-effort variables were significantly correlated with any of the environmental variables using the conservative test.

These results indicate that oceanographic conditions during the first and third years of life may influence

Table 4

Autocorrelations of the Southern Oscillation Index (SOI) and crosscorrelations between SOI and oceanographic variables off Central California. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature, PC = principal component. Underlined correlations correspond to an influence of previous SOI on winter oceanographic conditions off California.

	SOI	UPW	SLH	SST	1st PC
Winter SOI					
-9 mo	0.552***	0.478***	-0.205	0.000	-0.253
-6 mo	0.730***	0.261	-0.211	-0.093	-0.279
-3 mo	0.811***	0.208	-0.439**	-0.405**	-0.390*
0	1.000***	0.667***	-0.651***	-0.573***	-0.712***
3 mo	0.256	0.380*	-0.342*	-0.305	-0.449**
6 mo	0.031	-0.140	-0.270	-0.108	-0.168
9 mo	-0.110	0.231	-0.239	-0.133	0.163
12 mo	-0.131	-0.034	-0.042	-0.103	-0.078
Spring SOI					
-9 mo	0.112	0.340*	-0.102	-0.088	-0.202
-6 mo	0.115	0.113	-0.117	-0.330	-0.321
-3 mo	0.256	-0.050	-0.169	-0.165	-0.030
0	1.000***	0.393*	-0.268	-0.298	-0.414*
3 mo	0.825***	0.022	-0.297	-0.328	-0.326
6 mo	0.688***	0.246	-0.540***	-0.402**	-0.406*
9 mo	0.562***	0.424**	-0.389	-0.518***	-0.531***
12 mo	-0.224	-0.094	-0.067	-0.212	-0.129
Summer SOI					
-9 mo	-0.154	0.143	0.190	0.029	-0.070
-6 mo	0.031	-0.091	-0.037	0.007	0.092
-3 mo	0.825***	0.390*	-0.242	-0.191	-0.353
0	1.000***	0.269	-0.337*	-0.350*	-0.448**
3 mo	0.785***	0.200	-0.573***	-0.572***	-0.507***
6 mo	0.761***	0.428**	-0.433**	-0.535***	-0.544***
9 mo	0.109	0.197	-0.147	-0.337	-0.301
12 mo	-0.214	-0.256	-0.021	0.047	0.090
Fall SOI					
-9 mo	-0.110	-0.175	0.063	0.128	0.197
-6 mo	0.688***	0.426**	-0.324	-0.246	-0.406*
-3 mo	0.785***	0.305	-0.211	-0.192	-0.309
0	1.000***	0.164	-0.441**	-0.344*	-0.346
3 mo	0.835***	0.504***	-0.630***	-0.479***	-0.604***
6 mo	0.114	0.233	-0.341*	-0.314	-0.385*
9 mo	-0.152	-0.269	-0.123	0.043	0.010
12 mo	-0.072	0.263	-0.044	0.087	-0.031

* $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$

these stocks of chinook salmon. However, because the correlations are with three oceanographic variables rather than consistently with one, they are somewhat difficult to interpret in terms of a causal mechanism. To attempt to solve this problem, we sought a single indicator of variability in the coastal ocean. We computed the principal components (Harris 1975) of variability in sea surface temperature, sea level height, and upwelling index, in the hope that they would have a meaningful physical interpretation. The resulting first principal component is larger than the second and

third by about a factor of two, depending on season, and its loading is approximately equal for all three variables (positive for sea level height and ocean temperature and negative for upwelling index). Positive values of sea level height and surface temperature are consistent with the higher latitude effects of ENSO events as would be propagated by coastal trapped waves, but the negative value of upwelling index would require atmospheric teleconnection (recall the upwelling index is not a measure of actual upwelling, but an estimate based on atmospheric pressure

Table 5

Correlations between first principle component of the oceanographic variables and estimated total age-3 abundance (recreational catch + commercial catch + adult spawners) of chinook salmon in Central California.

	Season	First year	Second year	Third year
Total abundance	Winter	0.289	0.101	-0.151
	Spring	0.356*	-0.317	-0.354
	Summer	0.274	-0.139	-0.482**
	Fall	-0.115	0.114	0.080
Deconvolved total abundance	Winter	0.121	0.239	-0.139
	Spring	0.361*	-0.202	-0.319
	Summer	0.166	0.017	-0.480**
	Fall	-0.177	0.108	0.097

* $p < 0.10$; ** $p < 0.05$

differences, cf. Emery and Hamilton 1985, Mysak 1986).

To test whether the first principle component was actually related to ENSO events, we computed lagged correlations between it and the Southern Oscillation Index (SOI), a primary indicator of ENSO events (Table 4). The results show that the first principal component is highly correlated with the Southern Oscillation Index during the previous winter. Also, in all but one instance (sea level height and spring SOI) the three oceanographic variables are correlated with SOI in the previous winter in the way that would be expected from their loading in the first principle component.

To further simplify interpretation, we attempted to use a single indicator of abundance. In correlations computed thus far, no single population variable had a demonstrably stronger relationship to environmental variables tested. We therefore used the sum of commercial catch, recreational catch, and spawner estimates as a single indicator of annual population abundance. For the corresponding deconvolved estimate we use the deconvolution of this combination of these three series, the deconvolution that was previously shown to provide the best estimate of recruitment (Kope and Botsford 1988).

The results using the first principle component and the total abundance estimate (Table 5) indicate an influence of ENSO-related conditions during the summer of the third year ($\alpha \leq 0.05$) and provide weak evidence for an influence of ENSO-related conditions during the first spring ($\alpha \leq 0.10$). These relationships are reflected in both the total abundance and the estimate of recruitment to total abundance obtained through deconvolution. The estimate of total abundance is also correlated with previously identified oceanographic variables. The correlations with spring upwelling are -0.478 ($\alpha \leq 0.10$) and -0.511 ($\alpha \leq 0.01$) for total abundance and decon-

volved total abundance, respectively. The correlations with summer ocean temperature are -0.551 ($\alpha \leq 0.10$) and -0.540 ($\alpha \leq 0.05$) for total abundance and deconvolved total abundance respectively.

Discussion

The negative correlation between abundance in the third year and the first principle component of the oceanographic variables is consistent with observed effects of ENSO events on coastal oceanographic conditions and fish populations. Productivity in the California Current, as represented by zooplankton biomass, has long been known to be inversely correlated with sea surface temperature (Reid et al. 1958, Reid 1962). High productivity has traditionally been attributed to upwelling, but this explanation was recently questioned by Chelton et al. (1982) who proposed that higher zooplankton biomass resulted from increased equatorward flow in the California Current. The two proposed mechanisms are difficult to separate because conditions conducive to upwelling would also increase the strength of the California Current. However, whether colder water comes from the subarctic or from deeper coastal waters, it is higher in nutrients than the warmer surface waters, hence colder ocean temperatures in the winter and spring are associated with higher productivity in the California current (Chelton et al. 1982). Effects on productivity would be most noticeable during strong ENSO events. For example, total catch and average weight of chinook salmon landed in the commercial and sport fisheries were lower during the recent 1983 ENSO event (PFMC 1984, Pearcy et al. 1985, Johnson 1988).

The weak correlation between marine environmental variables during the first summer and indices of

abundance and recruitment is of the opposite sign to that expected on the basis of these relationships between the environment and productivity. However, it is possible that because juvenile fish feed on different prey than adult fish, shifts in prey distributions in warm-water years may result in higher growth and survival rates for juveniles. Northward shifts in the distribution of larval clupeids have been documented in warm-water years (Radovich 1959, 1961), and larval anchovies were found closer to shore than usual during the 1983 ENSO (Brodeur et al. 1985). Larval clupeids are a principal prey of juvenile chinook salmon (Peterson et al. 1982, Pearcy et al. 1985). Data taken off the Oregon coast show no significant difference in feeding by first-year chinook salmon between 1983, a warm-water year, and the other years 1980–85 (Brodeur and Pearcy In press).

The results obtained here for freshwater influences during the downstream migration in the first year have greater implications for the general methodology of correlation analysis in fisheries than for the dependence of salmon survival on environment. Other direct observations—the fact that differences in survival between marked fish released above the delta and marked fish released below the delta is correlated with flow over 10 years (USFWS 1987)—provide convincing evidence for a negative effect of low flows in the delta. Our results merely underscore the potential for falsely identifying a suspected relationship using standard methods for computing correlations. A dependence of abundance on freshwater variables was not detected when intraseries correlation was removed, rather than artificially added, and when it was taken into account in computing correlation coefficients. Fortunately, for this case there have been direct measurements of survival, and we need not rely solely on correlation analysis of abundance and environmental data.

Although a freshwater effect is not detectable in correlations with these freshwater variables, it may provide a partial explanation for the weak correlation seen between population variables and oceanographic conditions during the first year. During the spring, the first principle component of oceanographic variables is highly correlated with total delta inflow—flow in the Sacramento, Feather, and American Rivers (0.687, 0.577, 0.610, and 0.631, all significant at the 0.01 level using the conservative test). Thus the correlation between the first principle component of oceanographic variables during the first spring may be due to occurrences in freshwater, rather than oceanographic influences.

The various relationships implied in the results of this study provide a view of remote forcing of the North American marine and terrestrial environment that may be of general utility in examining the effects of envi-

ronmental variability on other species. Events in the equatorial Pacific appear to drive the oceanographic and meteorological environment in the eastern North Pacific and western North America. Autocorrelations in the SOI (Table 4) indicate that the Equatorial events are spring to winter events (i.e., in column 1, seasons within any spring-to-winter period are correlated with each other, but none are correlated with seasons in any other spring-to-winter period). The rest of Table 4 indicates that these events influence conditions in our coastal ocean only in the following winter. This “winter only” aspect of this correlation is consistent with results relating an index of atmospheric pressure conditions on the west coast of North America, the Pacific North American index to events in the equatorial Pacific (Horel and Wallace 1981). Mysak (1986) attributed this “winter only” aspect of the equatorial/midlatitude teleconnection to the requirement for strong westerlies between the equator and midlatitudes in order to advect the atmospheric Rossby waves responsible for the teleconnection to the northeast. These westerlies exist only during the winter. The covariability among our three oceanographic variables (i.e., the fact that UPW is as important as SLH and SST in the loading on the first principle component) suggests an atmospheric teleconnection with equatorial ENSO rather than a wave propagating poleward from the Equator (cf. Emery and Hamilton 1985, Mysak 1986). These variables are also related to winter rainfall in central California. For example, annual rainfall in Sacramento is significantly correlated with the first principle component and the upwelling index in winter. Flows through the Sacramento-San Joaquin Delta the following spring are in turn correlated with that rainfall, as well as winter oceanographic conditions. This remote forcing on a global scale and the associated covariability of marine and terrestrial variables further confound the identification of causal mechanisms from these kinds of data.

However, even direct measures of survival versus environmental variables do not necessarily identify mechanisms unequivocally. Covariation between flow rates, diversions, and reversed flows in the lower San Joaquin River continue to obscure the true cause of lower run size in the San Joaquin River system (Kjelson and Brandes 1989, USFWS 1987).

The differences in results between standard methods and the new methods used here are a rough measure of how much more conservative they are. At the 0.10 level, for example, the more conservative method of computing the variance of the estimate of correlation coefficient yielded significant correlations roughly half as often as standard methods (Tables 1–3). These results, together with simulations that show that the combination of equations (1) and (2) yield the prescribed

false detection rates (α) (Botsford and Wainwright unpubl.), imply that this correction for intraseries correlation or a similar one should be used in correlation analysis.

Deconvolution also reduced the number of significant correlations. For example, at the 0.10 level, using the standard test, there were only 6 significant correlations with deconvolved variables, whereas there were 21 significant correlations for corresponding variables that were not deconvolved. The fact that this ratio is lower when the more conservative correlated series test is used (5 with deconvolution and 13 without) is to be expected because the test itself accounts for some of the intraseries correlation. Although the number of significant correlations is less with deconvolution, we cannot recommend its use in all situations. Deconvolution can have two positive effects on correlation analysis: (1) It can provide a better estimate of recruitment, and (2) it can reduce intraseries correlation, hence the variance of the estimate of correlation coefficient (Kope and Botsford 1988). However it can also have a negative effect. If the deconvolution is marginally stable, the abundance data is noisy, or the coefficients of the deconvolution are inaccurate, deconvolution can lead to a poorer estimate of recruitment. In the results presented here, deconvolution introduced some additional significant correlations and reduced the magnitude of existing correlations (although they remained significant at the same level). This suggests that the deconvolved series may be a poorer proxy for recruitment than the raw abundance series, and that this detracts from the removal of intraseries correlation.

The practical implication for chinook salmon managers of the correlations obtained here is primarily a recommendation of where to focus further research rather than a means of immediately achieving a dramatic improvement in management. Because these stocks are managed by annually attempting to control effort based on an attempt to predict abundance, an understanding of the factors affecting abundance is necessary. The relationship between salmon populations and oceanographic conditions during the third year has an R^2 of 0.23, and hence would not produce predictions that could substantially improve catch. It also does not hold for oceanographic conditions in the previous 3-month period, hence there is little potential for long-term prediction. However, the results do indicate two potentially useful relationships between environment and abundance. Our understanding of these relationships could possibly be improved to the point that they could be useful in management. The ability to estimate numbers at each age in catch and escapement would improve our ability to determine potential oceanographic effects as well as provide a possible predictor

of catch (i.e., 2-year olds). The current practice of differentiating jacks from older fish on the basis of size leads to considerable uncertainty that could be removed by determining age through hard parts or separation of modes in the size distributions each year. Also, the existence of a demonstrated freshwater effect implies we should attempt to remove that effect from the data before searching for an oceanographic effect. However, this is complicated by the fact that an unknown fraction of the annual catch is produced by hatchery fish that were trucked below the delta for release, and hence not exposed to that effect. Better knowledge of where and when fish are released could provide the basis for removal of the effects of variable release numbers and release strategies from the data before searching for oceanographic effects.

In general, results from correlation analyses in fisheries will always contain an element of doubt and, by themselves, are probably not strong enough evidence of causal relationships that management should be based on them. Poor performance of past relationships argue for less dependence on them (Sissenwine 1984, Drinkwater and Myers 1987, Walters and Collie 1988), however, as we have shown here, there are ways of improving the reliability of correlation analyses. For example, smoothing with moving averages should be done only when the level of measurement noise warrants it, and it should always be accompanied by some means of accounting for the intraseries correlation introduced. Although we agree that the resulting statistical relationships do not, by themselves, provide a solid basis for management, we are not as pessimistic as some others (e.g., Walters and Collie 1988) regarding the utility of correlation analysis. It supplies information on patterns that allows formulation of hypotheses that can then be tested through direct means. It increases the probability of detection of relationships that might otherwise be missed. Fisheries analysts cannot afford to dismiss the opportunities it provides, but should use it only as exploratory analysis (cf. Bakun 1990, Botsford et al. 1989).

Acknowledgments

We thank L.B. Boydstun and Chuck Knutson of the California Department of Fish and Game, D. Cayan of Scripps Institution of Oceanography, and A. Bakun of the National Marine Fisheries Service for their assistance in obtaining data. This work was supported in part by the NOAA, National Sea Grant College Program, Department of Commerce, under grant number NA80AA-D-00120, Project number R/MA-16, through the California Sea Grant College Program.

Citations

- Bakun, A.**
 1975 Daily and weekly upwelling indices, west coast of North America, 1967-73. NOAA Tech. Rep. NMFS SSRF-693, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 114 p.
 1990 L'océans et la variabilité des populations marines. In Troadee, J.P. (ed.), L'homme et les écosystèmes halieutiques, p. 155-187. Inst. Français Recherche Explor. Mer, Brest, France [in French].
- Bartlett, M.S.**
 1946 On the theoretical specification and sampling properties of autocorrelated time series. J. R. Stat. Soc., B8:27-41.
- Barton, A.C.K.**
 1980 Factors influencing the life history of spring Chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Columbia River watershed from 1960 to 1977. Ph.D. diss., Oregon State Univ., Corvallis, 243 p.
- Bayley, G.V., and J.M. Hammersley**
 1946 The effective number of independent observations in an autocorrelated series. J. R. Stat. Soc., B8:184-197.
- Botsford, L.W.**
 1986 Analysis of environmental influences on population dynamics. In Vincent, T.L., Y. Cohen, W.J. Grantham, G.P. Kirkwood, and J.M. Skowronski (eds.), Modeling and management of resources under uncertainty, Vol. 72 in Lecture Notes in Biomathematics, p. 54-64. Springer-Verlag, NY.
- Botsford, L.W., D. Armstrong, and J.M. Shenker**
 1989 Oceanographic influences on the dynamics of commercially fished stocks. In Landry, M.R., and B. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 511-565. Elsevier Sci. Publ., Amsterdam.
- Box, G.E.P., and G.M. Jenkins**
 1976 Time series analysis: Forecasting and control. Holden-Day, Oakland, 575 p.
- Brodeur, R.D., and W.G. Pearcy**
 In press Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fish. Bull., U.S. 88(4).
- Brodeur, R.D., D.M. Gadomski, W.G. Pearcy, H.P. Batchelder, and C.B. Miller**
 1985 Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Estuarine Coastal Shelf Sci. 2:365-378.
- Cayan, D.R., and D.H. Peterson**
 1989 The influence of North Pacific atmospheric circulation on streamflow in the West. In Peterson, D.H. (ed.), Aspects of climate variability in the Pacific and the western Americas, p. 375-397. Geophys. Monogr. 55, Am. Geophys. Union, Wash. DC.
- Chelton, D.B.**
 1984 Commentary: Short-term climatic variability in the northeast Pacific Ocean. In Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 87-99. Oregon State Univ. Press, Corvallis.
- Chelton, D.B., P.A. Bernal, and J.A. McGowan**
 1982 Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095-1125.
- Denega, M.M.**
 1973 Age composition and growth rates of chinook salmon from northern California's salmon troll fishery. M.S. thesis, Humboldt State Univ., Arcata, CA, 56 p.
- Dettman, D.H., and D.W. Kelley**
 1986 The roles of Nimbus hatchery and Fether River hatchery and natural reproduction in maintaining the lower American River salmon run. Report to the California Department of Water Resources by D.W. Kelley & Associates, Newcastle, CA, 73 p.
- Dettman, D.H., D.W. Kelley, and W.T. Mitchell**
 1986 The influence of flow in Sacramento River salmon. Report to the California Department of Water Resources by D.W. Kelley & Associates, Newcastle, CA, 56 p.
- Douglas, A.V., and P.J. Englehart**
 1981 On a statistical relationship between autumn rainfall in the central equatorial Pacific and subsequent winter precipitation in Florida. Monthly Weather Review 109:2377-2382.
- Drinkwater, K.F., and R.A. Myers**
 1987 Testing predictions of marine fish and shellfish landings from environmental variables. Can. J. Fish. Aquat. Sci. 44: 1568-1573.
- Emery, W.J., and K. Hamilton**
 1985 Atmospheric forcing of interannual variability in the northeast Pacific Ocean: Connections with El Niño. J. Geophys. Res. 90:857-868.
- Enfield, D.B., and J.S. Allen**
 1980 On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. J. Phys. Oceanogr. 10:557-578.
- Fogarty, M.J.**
 1988 Time series models of the Maine lobster fishery: The effect of temperature. Can. J. Fish. Aquat. Sci. 45:1145-1153.
- Fry, D.H., Jr., and A. Petrovich, Jr.**
 1970 King salmon (*Oncorhynchus tshawytscha*) spawning stocks of the California Central Valley, 1963-1969. Admin. Rep. 70-11, Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 34 p.
- Hallock, R.J.**
 1983 Effect of Red Bluff Diversion Dam on chinook salmon, *Oncorhynchus tshawytscha*, fingerlings. Calif. Dep. Fish Game, Red Bluff, CA, 8 p.
- Hallock, R.J., and R.R. Reisenbichler**
 1979 Evaluation of returns of chinook salmon, *Oncorhynchus tshawytscha*, released as fingerlings at Coleman and Nimbus hatcheries and in the Sacramento River Estuary. Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 10 p.
- Hallock, R.J., D.A. Vogel, and R.R. Reisenbichler**
 1982 The effect of Red Bluff Diversion Dam on the migration of adult chinook salmon, *Oncorhynchus tshawytscha*, as indicated radio-tagged fish. Admin. Rep 82-2, Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 47 p.
- Harris, R.J.**
 1975 A primer of multivariate statistics. Acad. Press, NY, 332 p.
- Hickey, B.M.**
 1989 Patterns and processes of circulation over the Washington Continental shelf and slope. Chapter 3. In Landry, M.R., and B. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 41-115. Elsevier Sci. Publ., Amsterdam.
- Hollowed, A.B., K.M. Bailey, and W.S. Wooster**
 1987 Patterns in recruitment of marine fishes in the northeast Pacific ocean. Biol. Oceanogr. 5:99-131.
- Horel, J.D., and J.M. Wallace**
 1981 Planetary-scale atmospheric phenomena associated with the Southern Oscillation. Monthly Weather Review 109: 813-829.

- Johnson, S.L.**
1988 The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. *Fish. Res.* 6:105-123.
- Kjelson, M.A., and P.L. Brandes**
1989 The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California. In Levins, C.D., L.B. Holby, and M.A. Henderson (eds.), Proceedings, National workshop on the effects of habitat alteration on salmonid stocks, p. 100-115. *Can. Spec. Publ. Fish. Aquat. Sci.* 105.
- Kjelson, M.A., P.F. Raquel, and F.W. Fisher**
1981 Influences of freshwater inflow on chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin Estuary. In Cross, R.D., and D.L. Williams (eds.), Proceedings, National symposium on freshwater inflow to estuaries, p. 88-104. U.S. Fish Wildl. Serv., Office Biol. Serv. FWS/OBS-81/04.
- Kope, R.G.**
1987 Separable virtual population analysis of Pacific salmon with application to marked chinook salmon, *Oncorhynchus tshawytscha*, from California's Central Valley. *Can. J. Fish. Aquat. Sci.* 44:1213-1220.
1988 Effects of initial conditions on Monte Carlo estimates of bias in estimating stock-recruitment relationships. *Can. J. Fish. Aquat. Sci.* 45:185-187.
- Kope, R.G., and L.W. Botsford**
1988 Detection of environmental influence on recruitment using abundance data. *Can. J. Fish. Aquat. Sci.* 45:1448-1458.
- Markham, C.G., and D.R. McLain**
1977 Pacific sea-surface temperature related to rain in California. *Nature (Lond.)* 269:502-504.
- Mysak, L.A.**
1986 El Niño, interannual variability and fisheries in the north-east Pacific Ocean. *Can. J. Fish. Aquat. Sci.* 43:464-497.
- Norton, J.G.**
1987 Ocean climate influences on rockfish recruitment in the California Current. In Proceedings, International Rockfish Symposium, 20-22 Oct. 1986, Anchorage, Alaska, p. 73-98. Alaska Sea Grant Rep. 87-2, Univ. Alaska, Fairbanks.
- PFMC (Pacific Fishery Management Council)**
1984 A review of the 1983 ocean salmon fisheries and status of stocks and management goals for the 1984 salmon season off the coasts of California, Oregon, and Washington. *Pac. Fish. Manage. Council*, Portland, OR 97201, 218 p.
- Pearcy, W., J. Fisher, R. Brodeur, and S. Johnson**
1985 Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. In Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 188-204. *Wash. Sea Grant Prog.*, Univ. Wash., Seattle, 312 p.
- Peterson, W.T., R.D. Brodeur, and W.C. Pearcy**
1982 Food habits of juvenile salmon in the Oregon coastal zone, June 1979. *Fish. Bull.*, U.S. 80:841-851.
- Radovich, J.**
1959 Redistribution of fishes in the eastern North Pacific Ocean in 1957 and 1958. *Calif. Coop. Oceanic Fish. Invest. Rep.* 3:163-171.
1961 Relationships of some marine organisms of the Northeast Pacific to water temperatures, particularly during 1957 through 1959. *Calif. Dep. Fish Game, Fish. Bull.* 112, 62 p.
- Redmond, K.**
1988 Surface temperature and precipitation variations in the western U.S. and their relation to large scale circulation indices. In Fifth Workshop on Climate Variability of the Eastern North Pacific and Western North America, Pacific Grove, CA, p. 15-16. Sponsored jointly by Natl. Science Foundation, Monterey Bay Aquarium Research Inst., and the U.S. Geological Survey.
- Reid, J.L.**
1962 On the circulation, phosphate-phosphorous content and zooplankton volume in the upper part of the Pacific Ocean. *Limnol. Oceanogr.* 7:287-306.
- Reid, J.L., G.I. Roden, and J.G. Wyllie**
1958 Studies of the California Current system. *Calif. Coop. Oceanic Fish. Invest. Rep.* 5:28-57.
- Reisenbichler, R.R.**
1986 Use of spawner-recruit relations to evaluate the effect of degraded environment and increased fishing on the abundance of fall-run chinook salmon, *Oncorhynchus tshawytscha*, in several California streams. Ph.D. diss., Univ. Wash., Seattle, 175 p.
- Sholes, W.H., and R.J. Hallock**
1979 An evaluation of rearing fall-run chinook salmon, *Oncorhynchus tshawytscha*, to yearlings at Feather River Hatchery with comparison of returns from hatchery and downstream releases. *Calif. Fish Game* 65:239-255.
- Sissenwine, M.P.**
1984 Why do fish populations vary? In May, R.M. (ed.), Exploitation of marine communities, p. 59-94. Springer-Verlag, NY.
- Stevens, D.E., and L.W. Miller**
1983 Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt and delta smelt in the Sacramento-San Joaquin River system. *N. Am. J. Fish. Manage.* 3:425-437.
- Sutcliffe, W.H., Jr., R.H. Loucks, and K.F. Drinkwater**
1976 Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. *J. Fish. Res. Board Can.* 33:98-115.
- USFWS**
1987 The needs of chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary. Exhibit 31, entered by the U.S. Fish and Wildlife Service for the State Water Resources Control Board. 1987 Water Quality/Water Rights Proceeding on the San Francisco Bay/Sacramento-San Joaquin Delta. Bay-Delta Project, U.S. Fish. Wildl. Serv., Stockton, CA 95205, 179 p.
- Van Hynning, J.M.**
1973 Factors affecting the abundance of fall chinook salmon in the Columbia River. *Oreg. Fish Comm. Res. Rep.* 4, 87 p.
- Walters, C.J.**
1985 Bias in the estimation of functional relationships. *Can. J. Fish. Aquat. Sci.* 42:147-149.
- Walters, C.J., and J.S. Collie**
1988 Is research on environmental factors useful to fisheries management? *Can. J. Fish. Aquat. Sci.* 45:1848-1854.