CYCLIC COVARIATION IN THE CALIFORNIA KING SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, SILVER SALMON, *O. KISUTCH*, AND DUNGENESS CRAB, *CANCER MAGISTER*, FISHERIES

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ABSTRACT

There are apparent cyclic fluctuations in the catch record of both northern and central California salmon fisheries. They are of the same period and strength as well-known cycles in crab catch but of different phase. Statistical characteristics of this covariation, as reflected in estimates of auto- and cross-correlation functions, change following the decline of the central California Dungeness crab fishery. Analysis of a likely cause of this phenomenon, a greater delay in switching of effort from crab to salmon during years of high crab catch, indicates that this mechanism is not present. Phase differences between salmon and crab cycles imply constraints on remaining potential causes, but a cause of the cyclic covariation has not been established.

Regular patterns in fishery catch records reflect underlying mechanisms that can provide the basis for broader understanding, better prediction, and consequently better management of the fishery. Cyclic fluctuations in the northern California Dungeness crab catch have been a topic of research for the past 10 yr. We document here cyclic fluctuations in the northern California salmon catch (Fig. 1) of the same frequency but different phase.

Coastwide fluctuations in Dungeness crab catch were originally attributed to oceanographic causes (Anonymous 1965). Peterson (1973) demonstrated a statistical relationship between coastal upwelling and crab catch. Botsford and Wickham (1975) concluded from estimates of the appropriate cross- and auto-correlation functions that, while crab catch was indeed cyclic and upwelling was correlated with crab catch after a lag of 1 or 2 yr, upwelling itself was not cyclic, hence was not the source of the cycles. Botsford and Wickham (1978) later showed that interage, density-dependent mortality could be the cause of the observed cycles, and derived new stability results that indicated size-selective fishing could decrease population stability, and thereby increase the propensity for cyclic fluctuations. They cited two known potential interage, density-dependent mechanisms, cannibalism and an egg-predator worm, and are conducting field samples of these. On the basis of a disparity between the period of observed cycles and the period of cycles produced by a model that included cannibalism, McKelvey et al. (1980) claimed that cannibalism could not cause the cycles. Botsford (1981) pointed out that the observed disparity was not new, but had been noted by Botsford and Wickham (1978), and critically analyzed the reasoning used by McKelvey et al. (1980) in drawing a new conclusion. In summary, the cause of cycles in the northern California Dungeness crab

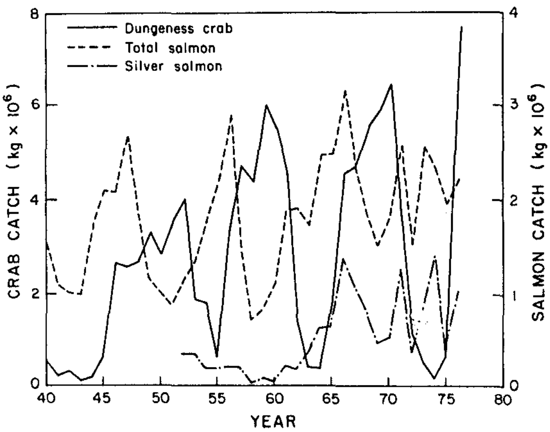

FIGURE 1.—Total landings (kg) in the northern California crab and salmon fisheries for the years 1940-76.

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catch record is still not known and research in this area is continuing.

In contrast to the considerable research attention attracted by cyclic fluctuations in crab catch, fluctuations in the salmon catch record have, to our knowledge, not been previously identified as cyclic. Yet, as seen in Figure 1, these apparently periodic fluctuations in salmon catch have a peak amplitude of about ±0.5 of the mean value. While abundance is predicted each year as part of the management process, these predictions have not taken advantage of this regular pattern that accounts for about two-thirds of the peak catch. An understanding of the underlying cause of cycles in salmon catch has great potential for improved predictive ability and better salmon management.

There are many possible causes of the observed similar cycles in the salmon and crab fisheries. There may be a direct biological interaction between the two species that by itself gives rise to cycles. Alternatively, one may vary cyclically and a direct biological interaction may cause the other to follow it. As another class of possibilities the two processes need not necessarily be directly related but may both be under the influence of a third process (e.g., environmental factors). A third class of possible causes of the observed covariation is some sort of economic linkage between the two fisheries. Since many fishermen fish both species, abundance and effort in one could affect effort in the other.

METHODS AND DATA

Our approach to eliminating unlikely causes of the observed covariation from the many possible causes is based on interpretation of estimated auto- and cross-correlation functions (also called correlograms). This statistical technique has been useful in interpretation of cycles in wildlife populations (Moran 1949; Finerty 1980) and is a recommended initial step in time series analysis (Jenkins and Watts 1968; Box and Jenkins 1970). However, there are few useful results on statistical significance of estimated correlation functions. We use a simple form of a method described by Bartlett (1946). If individual points in a time series are independent and identically distributed, an estimate of the correlation between them is Gaussian with mean zero and variance $1/N$ where N is the total number of samples on which the estimate is based. In the following analysis we show 5% error limits on plots of correlation functions. The occurrence of values of correlation greater in magnitude than this limit more frequently than 1 in 20 indicates a "nonrandom" process. This approach is somewhat limited in that it focuses on single points rather than the pattern of the estimated correlation function as a whole.

If samples in each series are not independent, the significance of both cross- and auto-correlation functions will be overestimated (Granger and Newbold 1974). A suggested solution to this problem in estimating cross-correlations is to prewhiten (i.e., remove correlation between samples) each series by fitting an ARMA model (Box and Jenkins 1970) to the series, then compute cross-correlations between the residuals. We have not taken this approach for two reasons: 1) Computed correlations based on the residuals actually underestimate significance of results (Box and Pierce 1970; Durbin 1970) and 2) prewhitening may actually remove correlations of real interest. With regard to the latter, some auto-correlation within each series exists because of known physical processes (e.g., the fact that catch is the result of fishing several age classes causes intraseries correlation). Removal of this intraseries correlation would reduce the chance of detecting real interseries correlation (e.g., correlation stemming from a causal mechanism that involved catch). Removal of intraseries correlation on the basis of known physical mechanisms will provide more meaningful results; however, it will require further studies of effort dynamics and life histories in both the salmon and crab fisheries. In the meantime, as a simple exploration of the possibility of "spurious" results, we also present correlograms computed from first-differenced data (first-differencing is the process of replacing the data point x_t at time t with the difference $x_t - x_{t-1}$). First-differencing reduces intraseries correlation and has been shown to greatly reduce the incidence of spurious interseries correlation (Granger and Newbold 1974). Correlation results of first-differenced data can be interpreted as the correlation between changes in each series. Also, in all correlations presented, a linear trend has been removed from the series.

Salmon data for these analyses are from monthly catch records collected and published by the California Department of Fish and Game (1954-78). The northern California salmon catch consists of landings at Crescent City, Eureka, and Fort Bragg. The central California catch is from

San Francisco and Monterey. The unit of salmon catch is kilograms of dressed fish with heads on.

Crab catch (kilograms) was summarized by season rather than calendar year so that a season's catch includes catch from November and December of the previous year. The geographic breakdown of crab catch was the same as the salmon catch. Seasonal distribution of crab catch and effort was available only from 1952 to 1976[4] for a northern California region which included an average of 93% of the total northern California catch. In addition to crab catch data, we have also used recent estimates of preseason legal abundance (Methot and Botsford 1982). These estimates were computed from the decline in catch-per-unit-effort within each season according to the Leslie method. Gotshall (1978) also estimated preseason legal abundance for the years 1967-72 using the Leslie method. His results for those years are essentially the same as those used here. McKelvey et al. (1980) also estimated preseason legal abundance, but used a method that depended on the estimated total number of pots in the fishery and annual catch. Since the relationship between these variables can change from year to year in this fishery, we did not use their estimates.

We present first the statistical characteristics of cyclic fluctuations in the northern California salmon and crab catch records as reflected in estimates of their auto- and cross-correlation functions. We then examine characteristics of each of the two salmon species in the fishery. The northern California salmon fishery is composed of king (or chinook) salmon, *Oncorhynchus tshawytscha*, which originate primarily in coastal rivers of northern California and Oregon, and silver (or coho) salmon, *O. kisutch*, which originated primarily in coastal rivers of northern California and Oregon in the 1950's, but depend increasingly on hatchery production in Oregon in the 1960's and 1970's (Pacific Fisheries Management Council 1978).

We then compare the characteristics of the northern California fishery to the central California fishery which differs in two respects: 1) It includes a period of protracted decline in the crab fishery and 2) it involves salmon stocks that originated in the Sacramento and San Joaquin River systems (Pacific Fisheries Management Council 1978). The central California crab fishery declined near 1960 and has remained at a low level since then. Putative causes of this decline and continued low level include an increase in sea temperature (Wild 1980), a predatory worm (Wickham 1979), and an increase in individual growth rate (Botsford 1981). We compare characteristics of the northern California fisheries with the central California fishery both before and after the decline.

We then examine a specific potential cause of the observed covariation. The most obvious and perhaps the most parsimonious explanation of the observed covariation in catch records is switching behavior of fishermen. The proposed hypothesis is simply that, during years of high crab abundance, more fishermen continue to fish for crab rather than beginning to fish for salmon when the salmon season opens. The legal crab season opened in December and continued at least through June in the years of interest. The salmon season opened in April or May, depending on year and species. Although most of the crab catch is landed early in the season, crab and salmon seasons do overlap, thus providing an opportunity to switch. The possibility that this mechanism is responsible for the observed behavior is examined here from three points of view: 1) A comparison of catch during overlapping and nonoverlapping segments of the salmon season, 2) analysis of changes in mean date of the salmon catch, and 3) calculation of the relationship between salmon catch and crab catch per delivery during May and June.

RESULTS

Northern California Total Catch

Estimates of the auto-correlation function for both total northern California Dungeness crab landings and total northern California salmon landings for the years 1940 to 1976 are of the form that would arise from cyclic processes of period 9 or 10 yr (Fig. 2). They both fall to a significant negative value of correlation then rise to a significant positive value of correlation.[5] The auto-correlation of crab abundance is not shown

[4]Annual Market Crab-Statewide Reports, California Department of Fish and Game, 1952-77.

[5]Estimates of the same functions for the time period 1952 to 1976 imply that crab is more cyclic (dropping to 0.7 then increasing to 0.8) while salmon is less cyclic (dropping to -0.3 then increasing to 0.4). In this analysis, as in the raw data (Fig. 1), salmon catch appears to be more cyclic in earlier rather than later years, while the crab catch appears to be more cyclic in later years.

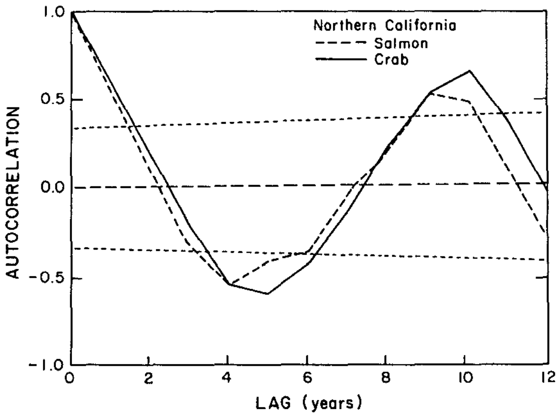

FIGURE 2.—An estimate of the autocorrelation functions for northern California total salmon and crab catch data (Fig. 1). Dotted lines are 0.05 error limits (see text).

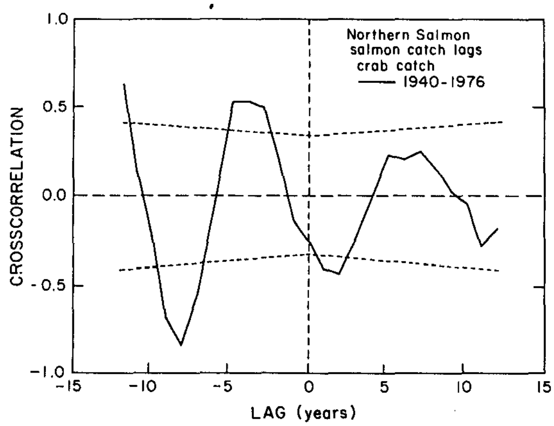

FIGURE 3.—An estimate of the cross-correlation function between northern California total salmon and crab catch data (Fig. 1). A positive lag corresponds to salmon following crab.

but is essentially the same as the auto-correlation of catch (i.e., decreases to significant negative values at 4 and 5 yr, then increases to significant positive values at 10 yr).

The auto-correlation functions computed from first-differenced crab and salmon catch series have the same form but are lower in absolute values. The first negative peak is just barely significant in both, whereas the positive peak of about 10 yr is significant only for the crab catch series.

An estimate of the cross-correlation between total northern California salmon and crab catch is of the form that would arise from two cyclic, covarying processes with a period of 9 or 10 yr and a constant lag of about 4 yr (salmon leading crab) (Fig. 3). Decreasing amplitude of the correlation function with increasing lag is caused by the increasing amplitude of crab catch. The implications of Figure 3 are that crab catch is negatively correlated with salmon catch 1 or 2 yr later and salmon catch is positively correlated with crab catch 3, 4, and 5 yr later.

The same cross-correlation computed for the years for which crab abundance estimates are available (1952-76) is essentially the same as Figure 3. The cross-correlation computed using preseason abundance instead of catch also is quite similar. First-differencing all three cross-correlation functions reduces the amplitude of the function somewhat. The correlation at positive lag is no longer significant and correlation at negative lag is significant only at a lag of −5 yr (except for first-differenced preseason abundance which is not quite significant). The values of cross-correlation for the various versions of these time series are summarized in Table 1.

Northern California Catch by Salmon Species

Because of differences in life history between the two species and the fact that increasing numbers of silver salmon originate in hatcheries, comparison of the relative contributions of each species to the cyclic covariation with crab could provide a clue to the underlying cause. Neither of the estimated auto-correlation functions for king and silver salmon appear as cyclic as the auto-correlation of combined salmon catch (Fig. 4). From this figure king salmon appears somewhat

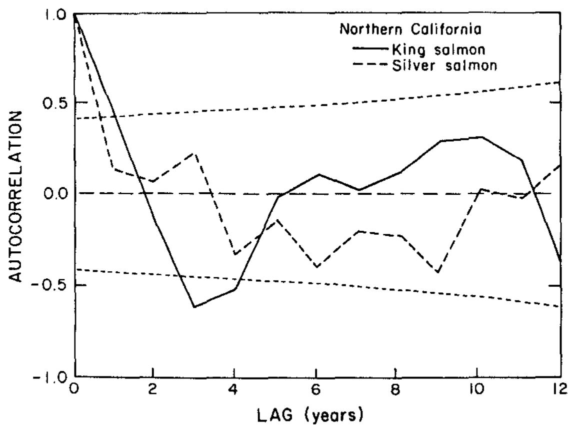

FIGURE 4.—An estimate of the autocorrelation functions for northern California king salmon and silver salmon catch data (Fig. 1) for the years 1952-76.

TABLE 1.—Cross-correlation between salmon catch and crab catch. Positive lags correspond to salmon following crab. Correlations are calculated from detrended original series (O) and from detrended, first-differenced series (F). Tabulated values are multiplied by 100 and are underlined if significant at the 5% level.

Region	Years	Variables			Lag −9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	7	8	9
North	40-76	Crab	Salmon	O	-68	-84	-55	-02	53	53	49	19	-14	-25	-41	-44	-25	00	22	20	24	15	02
				F	-40	-59	-26	00	49	17	28	01	-20	03	-16	-25	-05	08	30	-08	17	-01	-10
North	52-76	Crab	Salmon	O	-72	-90	-62	03	69	60	61	20	-18	-30	-46	-42	-13	19	43	33	29	09	-09
				F	-50	-55	-33	08	57	14	39	-06	-24	06	-24	-28	-05	07	40	-03	19	-04	-17
North	52-76	Crab[1]	Salmon	O	-59	-83	-64	-02	66	45	58	21	-16	-20	-40	-48	-15	16	35	35	20	09	-09
				F	-25	-45	-34	06	50	07	39	-08	-21	17	-16	-38	-01	09	24	09	-01	08	-15
North	52-76	Crab	Salmon[2]	O	-48	-71	-49	-04	42	51	77	19	-35	-32	-52	-39	-01	17	48	40	40	-06	-36
				F	-29	-42	-13	03	19	17	51	-08	-38	14	-23	-23	18	-12	31	-06	35	-14	-31
North	52-76	Crab	Salmon[3]	O	-68	-77	-54	07	67	49	34	15	-03	-20	-29	-32	-18	16	28	19	15	16	11
				F	-48	-44	-37	09	67	05	13	-01	-02	-04	-16	-21	-22	21	32	01	-02	06	01
North	52-76	Crab	King	O	-69	-80	-45	18	62	60	50	-04	-11	-36	-45	-26	03	31	43	22	08	-10	-15
				F	-45	-45	-19	17	49	31	27	-31	08	-12	-35	-14	-01	11	39	-04	05	-15	-05
North	52-76	Crab	Silver	O	-30	-47	-47	-21	34	22	38	42	-17	-02	-17	-38	-29	-10	15	27	41	30	05
				F	-21	-29	-27	-09	26	-17	26	28	-44	22	06	-24	-06	-03	14	-00	22	12	-20
Central	40-61	Crab	Salmon	O			-25	-19	16	64	81	33	-11	-66	-50	-05	09	26	34	27	-00		
				F			-01	-09	18	15	12	16	06	-59	-18	33	18	24	-07	10	-13		
Central	62-76	Crab	Salmon	O					92	-06	-47	-53	-29	24	-01	08	10	38	28				
				F					95	-40	-28	-25	-09	45	-10	08	-12	07	20				

[1]Abundance.
[2]Early season.
[3]Late season.

cyclic while silver salmon is less so. The latter may be due to the shorter time record for silver salmon. First-differencing decreases the value of the peak of negative correlation in king salmon to an insignificant level but the pattern is preserved.

Estimates of cross-correlation between crab catch and catch of each salmon species appear similar to the correlation between crab catch and total salmon catch (Fig. 5). Again, the observed characteristics seem to be stronger in the king salmon rather than the silver salmon records. First-differencing of the crab and salmon series reduces correlation values so that the positive correlation at a negative lag remains significant for king salmon only (Table 1).

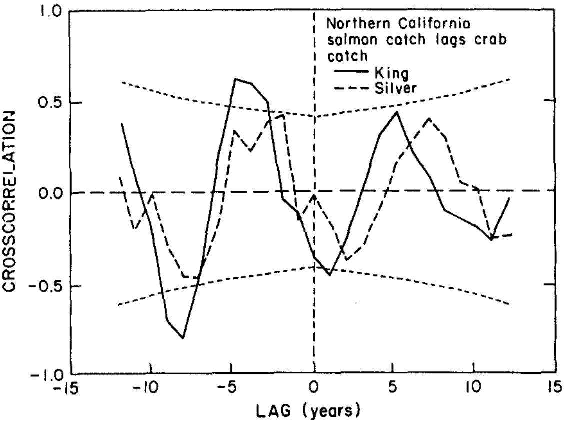

FIGURE 5.—An estimate of the cross-correlation function between northern California crab catch and king salmon and silver salmon for the years 1952-76.

Central California Total Catch

Because of differences between the central California crab fishery (Fig. 6) and the northern California crab fishery, comparison of characteristics of covariation between salmon and crab in northern California with that in central California provides some basis for determining the underlying cause of the covariation in northern California. We can narrow the range of possible causes by determining whether the covariation under discussion here exists both before and after the decline of the crab fishery in 1961. This investigation is, however, somewhat hampered by the extremely short time series that result from bisecting these records.

For the predecline period (1940-61), the auto-

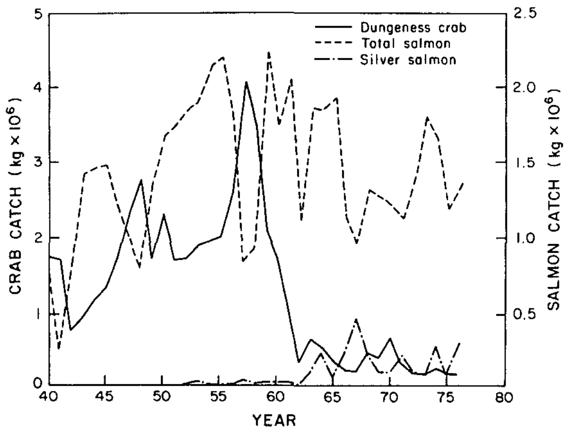

FIGURE 6.—Total landings (kg) in the central California crab and salmon fisheries for the years 1940-76.

correlation functions of salmon and crab catch are virtually the same as in northern California. Salmon and crab fall to −0.37 and −0.59, respectively, (the latter is significant at 0.05) at 4 yr, then increase to +0.43 and +0.54, respectively, (neither significant at 0.05) at 10 yr. First-differencing decreases the strength of both the positive and negative peaks of auto-correlation in both of these series. The estimated cross-correlation between salmon and crab catch in the early period is also similar to that in northern California except for a shift in the negative lag direction near zero lag (Fig. 7). The correlation at zero lag has a significant negative value in central California whereas it is not significant in northern

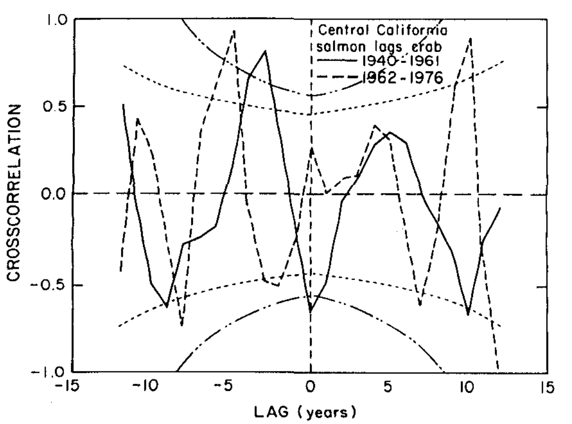

FIGURE 7.—Estimates of cross-correlation functions between central California Dungeness crab and total salmon catch, both before and after the decline in 1961. Outer significance levels apply to the period after the decline.

California. This shift would correspond to a negative relationship between crab and salmon, with salmon following crab more closely in central than in northern California. After first-differencing each series the positive correlation peak at negative lag disappears but the negative correlation at zero lag remains (Table 1).

For the postdecline period (1962-76), the auto-correlation function for crab catch appears cyclic, as it was before the decline, but the period of the cycles has apparently decreased (Fig. 8). The auto-correlation function for salmon decreases to a significant negative value at 3 yr, but shows no clear cyclic tendency for greater lags. First-differencing decreases this first peak by about 0.1 for both series. The cross-correlation estimate for the postdecline period is similar to the northern California relationship for negative lags (i.e., crab following salmon), but is not similar for zero and positive lags (Fig. 7). Both of these latter estimates are for a low number of data points, hence interpretation for large lags is risky (note that the outer significance levels in Figure 7 are for the later period correlation). After first-differencing only the positive correlation at negative lag remains significant (Table 1).

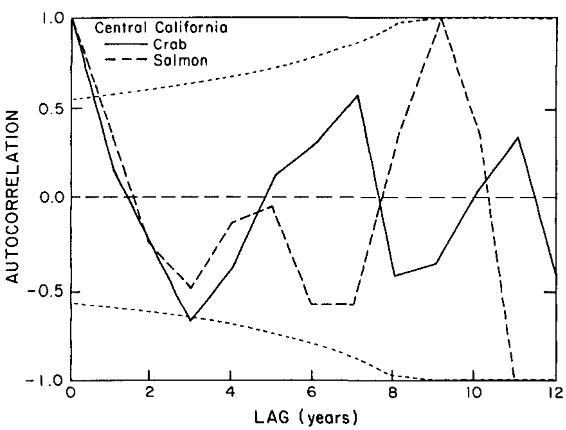

FIGURE 8.—An estimate of autocorrelation functions for central California Dungeness crab and total salmon catch for the years following the decline in crab catch (i.e., 1962-76).

Switching Effort Between Species

If the cyclic nature of salmon catch is caused by fishermen fishing salmon only when crab are not abundant, then cycles in salmon catch should be determined by salmon catch in the part of the season that overlaps the crab season. In other words, salmon catch should appear to be much more cyclic early in the season than late in the season. Salmon catch for the months of April through June and the period from July through September are shown in Figure 9.[6] The only readily apparent feature of this plot is the increasing trend of early season catch.

Estimates of the auto-correlation functions of early and late season salmon catch are shown in Figure 10. Neither of these appears as smoothly cyclic as the total catch. However, since they both decrease to negative values then increase to approximately the same positive value at a 10-yr lag, one does not appear more cyclic than the other.

Estimates of the cross-correlation between total crab catch and early salmon catch and between total crab catch and late salmon catch are shown in Figure 11. There is very little difference between these functions for each time period and they are quite similar to the same function for total annual catch. The only difference between the two species is a slightly more pronounced pattern of correlation for early rather than late season to the right of the origin (i.e., where salmon follows crab). After first-differencing only the positive correlation at a lag of −5 remains (Table 1).

From Figures 10 and 11 we can conclude that the cyclic nature of salmon catch is not contained entirely in the early, overlapping part of the season.

A second, though not independent, means of testing the proposed hypothetical mechanism is to examine the mean data of salmon catch. If crab abundance determined salmon catch early in the salmon season, mean date of the salmon catch would increase with crab catch. The correlation between mean date of salmon catch and total crab catch was not significant ($r = -0.022$ with linear trend subtracted from mean date of salmon catch). Thus this test also yields a negative result.

A third consequence of the proposed mecha-

[6]The same analysis as that presented here was performed with a bisecting date of 31 May rather than 30 June with no difference in the results.

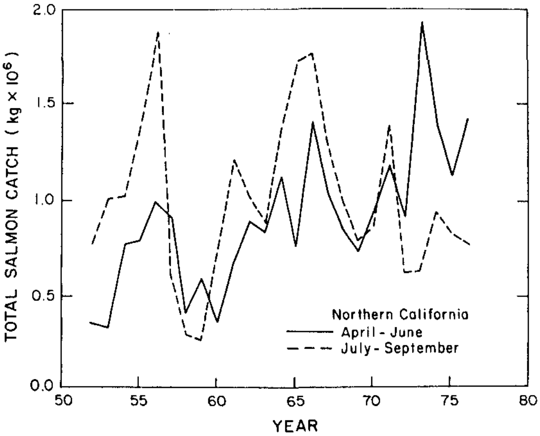

FIGURE 9.—Total salmon catch (kg) in northern California in the early part of the season (April-June) and the late part of the season (July-September) for the years 1952-76.

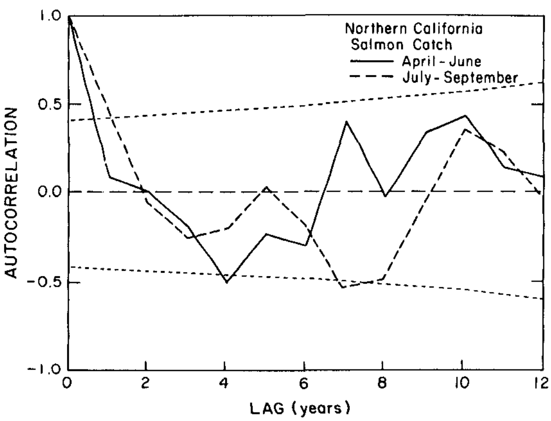

FIGURE 10.—Estimates of the autocorrelation functions for the early (April-June) and late (July-September) parts of the season.

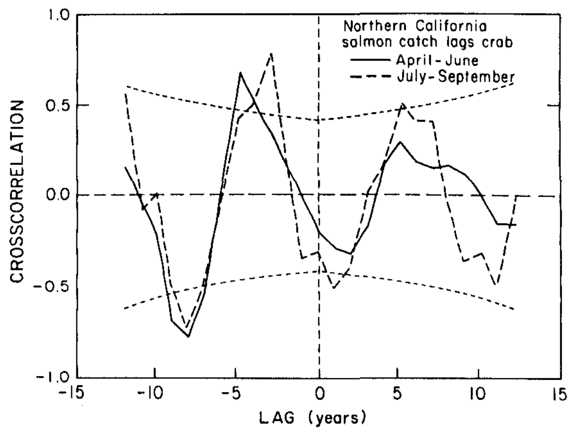

FIGURE 11.—Estimates of the cross-correlation functions between Dungeness crab catch and total salmon catch early in the season (April-June) or total salmon catch late in the season (July-September).

nism is a relationship between catch per delivery of crab and salmon catch. If fishermen continue to fish crab when crab is abundant, then there would be a relationship between catch per crab delivery and salmon effort in months of overlap between the two fisheries. This relationship would show up in salmon catch provided it was not occluded by fluctuations in salmon abundance. The value (v) per delivery of crab catch was computed for the months of May and June each year as follows:

$$v = \frac{P \cdot W}{CPI \cdot D}$$

where P = market price
W = total weight landed in the months of May and June
CPI = consumer price index
D = number of deliveries in the months of May and June.

For the years 1952 to 1976 there is no significant relationship between salmon catch during May and June and value of each crab delivery (r = 0.31).

DISCUSSION

Interpretation of the correlation functions computed here is somewhat subjective. Since, as described earlier, significance levels do not hold rigorously, they can be interpreted only in a relative sense. Correlations from the first-differenced data can supplement interpretations of the raw (except for detrending) data. First-differencing removes intraseries correlation, hence emphasizes changes between adjacent points in a series. Cross-correlations computed from first-differenced series are more sensitive to the timing of changes, and less sensitive to sustained high and low values. The lag between recurring changes in specific directions in each series must remain constant in order to produce a high cross-correlation. Significant correlations that do not remain high following first-differencing should not necessarily be regarded as spurious, rather they may stem from variables that are highly autocorrelated (e.g., abundance or catch as compared with age-class sizes). On the other hand significant correlations that remain high following first-differencing probably stem from variables with less intraseries correlation.

Computed cross- and auto-correlations support the existence of cyclic covariation between crab and salmon catch in northern California. The fact that the negative correlation at a lag of +2 (Fig. 3) is no longer significant after first-differencing (Table 1) implies that it probably arose from the extended periods of high constant crab catch and low constant salmon catch (Fig. 1).

These same characteristics appear to be present when each salmon species is considered individually. They are, however, weaker in the king salmon and weaker still in silver salmon. The shorter length of the silver salmon time series may be responsible for the latter.

The analysis of central California data is more informative, although it too is constrained by shorter series. Early catch records in central California resemble northern California records in some respects. The auto-correlations of both salmon and crab are the same and the cross-correlation function has the same general shape except that the peak at negative lag is at −3 yr and the peak at positive lag in northern California is at a lag of zero (Figs. 3, 7). This negative correlation at 0 lag is quite apparent in Figure 6. The most striking departure from the northern California situation is the substantial decline of the positive peak at negative lag and the persistence of the negative peak at 0 lag following first-differencing (Table 1). This implies that changes in crab and salmon that are in the same direction are less regular than changes in the opposite direction.

Following the decline in crab catch in central California the auto-correlation functions show weaker cycles of shorter period for the crab and the existence of a cyclic pattern for salmon is questionable. The cross-correlation function is similar to the predecline case but shifted to more negative lags. This could occur, for example, if two cyclic processes retained their shape but were shifted in time with respect to each other. After first-differencing the positive peak at negative lags persists yet the negative peak is diminished in magnitude by half. The postdecline period is similar to northern California in this respect but differs in having a negative correlation at a lag of −2.

The observed differences in lag value of points of significant correlation raise the question of whether the northern California crab or salmon fishery lags its central California counterpart. The cross-correlation between northern California and central California salmon catch for the period 1940 to 1976 has a significant positive peak at +1 and +2 yr that remains significant at +1 yr after first-differencing. The same characteristics are present, though less strong, when the predecline and postdecline periods are considered individually. This lag of 1 or 2 yr between northern California and central California salmon catch is commensurate with the shift in the point of negative correlation for the predecline situation (Fig. 7). The cross-correlation between crab catches at the two locations does not show significant results nor do higher correlations persist after first-differencing.

We can consider the implications of observed correlations for three classes of possible mechanisms. The first class of mechanisms involves cyclic environmental factors which independently drive the cycles in each species. Differences in life history between the two species could be responsible for the phase difference between the two cyclic processes. In the second class of mechanisms, one species is cyclic because of environmental factors or an endogenous mechanism within the population and the second species is cyclic because of some linkage to the first species. The third possibility requires neither species to be inherently cyclic. Rather, a biological interaction between the two species results in cyclic behavior in both (e.g., as in a classical predator-prey system). The computed correlation functions place constraints on specific timing of the mechanisms in each of these classes. These can be compared with known life history characteristics and suspected interactions to eliminate some possibilities.

The life histories of the two species follow similar temporal patterns. The eggs of Dungeness crab and fall-run king salmon hatch in midwinter. The pelagic crab larvae drift for several months then settle as first crabs during April and May. The salmon fry remain in streams for several months then enter the ocean in late spring through summer. Some adult crabs enter the fishery 3 yr after hatching but most are caught at age 4. King salmon first enter the fishery about 2½ yr after hatching, and most are caught at 3½ yr and some are caught 4½ yr after hatching.

That there was no significant positive cross-correlation between the two catch records at 0 lag indicates that a cyclic environmental factor which drives the cycle of one species through an effect on one age-class cannot also affect the same age-class of the other species. This implies, for example, no direct interaction between the 0 age classes of the two species. This is to be expected since most crab larvae have settled before salmon smolts begin entering the nearshore pelagic environment.

The positive cross-correlation, which indicates that good (bad) salmon catches are followed 3 to 5 yr later by good (bad) crab catches, may be a result of a cyclic environmental factor which affects early salmon survival in 1 yr and similarly affects larval crab survival 3 to 5 yr later. This environmental factor need not affect exactly the same age class in both species. For example, a positive effect on growth and survival of maturing salmon in their penultimate year at sea and a simultaneous positive effect on ovary development in female crab could increase salmon catch in the following year and crab catch 4 to 6 yr later through increased egg production in the following year.

Salmon have been observed to prey heavily on pelagic crab megalopae (Orcutt 1978). If this mechanism is considered as increased larval crab mortality when salmon are abundant, it does not fit the conditions implied by the correlations. However, if abundant crab megalopae lead to a good crab year class while increasing the growth and survival of adult salmon, then the observed cross-correlation would result. A mechanism by which salmon were more available to the fishery during years of high crab larval abundance could also cause the observed covariation.

The negative cross-correlation indicates that good (bad) crab catches are followed 1 to 2 yr later by bad (good) salmon catches. That this does not persist following first-differencing is commensurate with it being a result of fluctuation in an auto-correlated series (e.g., abundance) rather than a less auto-correlated series (e.g., recruitment). The mechanism which is a priori the most likely cause of this observation was the one investigated in detail in this paper: the cycle in salmon catch is actually a cycle in fishing effort for salmon and that this cycle is driven by the highly cyclic crab catch.

The conclusion resulting from analyses of the hypothesis of behavioral switching by fishermen is that an immediate response to crab abundance is not a likely cause. The strongest evidence for this was the comparison of the cyclic nature of early with late season salmon catch. The other two analyses are less powerful because both the availability of salmon and the variation in weather conducive to salmon fishing introduce variability in April and May salmon catch. The conclusion drawn from the comparison of early versus late season catch, however, rests on observing the cyclic nature in the late season catch regardless of its cause.

While we have concluded that an immediate behavioral response is not a likely cause, other related possibilities remain. The observed covariation could be caused by an inherently cyclic crab fishery and a negative response of effort in salmon throughout the salmon season (rather than solely in the months of overlap). Further elucidation of the economic question awaits results of an ongoing study of microeconomic behavior of fishermen.

Consideration of the life histories of the species and the timing of events implied by the lags in correlation admits the possibility of direct interaction and dependence of both cycles on environmental factors. Oceanographic conditions have been suggested as causes of fluctuations in other fisheries. Wild (1980) recently proposed that a change in sea surface temperature in the late 1950's reflects a change in the marine environment that is responsible for the decline in the central California Dungeness crab fishery. He also suggested that changes in sea surface temperature were related to fluctuations in the northern California crab catch record. However the actual values of correlation between these processes are not significant. Southward et al. (1975) presented data on cyclic fluctuations in sea temperature and covarying changes in fish population parameters over the past 50 yr in the English Channel.

Though the observed changes in lags and sensitivity to first-differencing may not be related to the causal mechanism, the nature of the covariation between salmon and crab catch does appear to have changed following the decline in central California crab landings. This change is not explained by fishermen switching between species, but could stem from Wild's (1980) proposed change in oceanographic conditions. The decrease in the period of the cycles in crab abundance following the decline is of some interest with regard to the issue of the cause of the decline itself. One of the possible causes of a decrease in period of the cycles is an increase in individual growth rate. This increase in growth rate is a necessary component of one of the potential causes of the decline (Botsford 1981) but is difficult to demonstrate because of the paucity of samples before the decline.

Possible effects of internal population dynamics on the observed behavior are worthy of examination. An interage, density-dependent mechanism has been cited as a potential cause of the cycles in crab abundance (Botsford and Wickham 1978, 1979). A similar mechanism could be operating on salmon abundance if the several stocks in the fishery were in synchrony. Peterman (1978) found positive correlations in smolt-to-adult survivorship between several groups of Pacific salmon populations. Populations that are not density-dependent but reproduce only in their final year have also long been known to fluctuate in a cyclic fashion (Bernardelli 1941; Leslie 1945). However, the period of the cycles is equal to the age of reproduction rather than twice the mean age of reproduction as it is in the stock-dependent recruitment case (Ricker 1954; Botsford and Wickham 1978).

The methods used here could prove useful in other fisheries problems. While time-series techniques have been applied to fishery problems, the primary goal has been a final model of the fishery rather than a search for causal relationships. The latter approach, the one taken here, has the advantage of leading to models that are based on known causal mechanisms rather than correlations of unknown causal mechanisms. Since the nature of these mechanisms could change significantly (possibly because of a change in fishing policy itself), a policy that is cognizant of them will fare better than one that relies on a statistical description from the past.

Another analytical time-series technique that we have not used here is the computation of causality as defined by Granger (1969). His special definition of causality is based on whether addition of data from past time on one variable decreases the error with which another variable can be predicted. The investigations performed here are in the same spirit but do not result in a single quantitative measure of causality.

While we have demonstrated here a potentially important statistical relationship, we have not uncovered the underlying cause. The ultimate cause, however, is worth pursuing. Its discovery and quantitative description could put salmon and crab management on a firmer basis by supplying greater predictive ability. Management could then respond to abundance on a firmer, predictive basis rather than a trial-and-error basis.

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