Pergamon

Progress in Oceanography 53 (2002) 283–305

Progress in Oceanography

www.elsevier.com/locate/pocean

Patterns of co-variability among California Current chinook salmon, coho salmon, Dungeness crab, and physical oceanographic conditions

L.W. Botsford *, C.A. Lawrence

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616 USA

Abstract

One of the primary motivations for the GLOBEC NEP program was the apparent inverse relationship between the increase in salmon populations in the Gulf of Alaska since the mid-1970s and concurrent declines in salmon populations in the California Current. The increase in abundance of some salmon species in the Gulf of Alaska can be plausibly explained based on mechanisms involving changes in physical structure, biological productivity, and salmon survival. To assess concurrent changes in salmon populations in the California Current and their possible physical and biological bases we examined temporal and spatial patterns of co-variability between biological variables and physical descriptors along the coasts of Washington, Oregon and California, from 1950 to 1990. The biological variables were catch records of coho salmon, chinook salmon and an ecologically related species, Dungeness crab. The physical variables were sea surface temperature, sea surface height (SSH) and the upwelling index (UWI). We found that while California Current coho salmon declined uniformly in the mid-1970s, consistent with the proposed inverse relationship, chinook salmon did not. All three species appear to be driven by the dominant mode of co-variability in the three physical variables, an indicator of warm/cool water conditions, but in different ways. In general, warm conditions have a negative effect on salmon at the age of ocean entry and spawning return, and Dungeness crab during the larval stage, while cool conditions have a positive effect. Differences in spatio-temporal variability between the two salmon species suggest they may respond to ocean conditions differently: coho salmon vary synchronously along the coast on annual time scales, while chinook salmon vary on slightly longer time scales in a specific spatial pattern. Dungeness crab vary on 10-year time scales, synchronously along the coast, except for the most southern areas (central California) where populations collapsed in the late 1950s. The dominant, warm/cool mode of physical co-variability, which drives these populations regionally, is related to basin-scale indices; it appeared to follow these indices in the 1950s and 1975–1990, but differs from them1960–1975, in ways that may be biologically important. © 2002 Elsevier Science Ltd. All rights reserved.

---

* Corresponding author.
E-mail address: lwbotsford@ucdavis.edu (L.W. Botsford).

PII: S0079-6611(02)00034-4

Contents

1. Introduction

The GLOBEC North East Pacific program is an observational, modeling and retrospective study initiated to study physical and biological ocean variability on decadal, to sub-annual time scales. A specific emphasis of the program is the opposite biological impacts of the regime shift in physical conditions in the mid-1970s indicated by the increase in salmon catches in the Gulf of Alaska (GOA), and concurrent decreases in salmon catches and endangered salmon populations in the California Current System (CCS) (i.e. off Washington, Oregon and California). The changes in catches of some salmon species in the GOA have been amply demonstrated (e.g. Beamish & Bouillon, 1993; Francis & Hare, 1994; Francis, Hare, Hollowed, & Wooster, 1998), and there are plausible links between physical changes in the atmosphere and ocean and consequent biological productivity. Changes in mixed layer depth (Polovina, Mitchum, & Evans, 1995; Polovina et al., 1994) may have led to increases in chlorophyll levels (Venrick, McGowan, Cayan, & Hayward, 1987), which in turn have probably resulted in the observed increase in zooplankton (Brodeur, Frost, Hare, Francis, & Ingraham, 1996). However, similar links between physics and biology are not as clear in the CCS.

There have been changes in the CCS, in physical oceanographic conditions, zooplankton and salmon, but the effects of a shift in physical regime on CCS salmon have not been described as comprehensively as in the GOA. The proposed inverse relationship between biological production in the CCS and the GOA is based on hypothesized interannual change in the relative distribution of the West Wind Drift into these two current systems (Chelton, Bernal, & McGowan, 1982; Francis et al., 1998). This hypothesis, based on the coherence of sea surface height (SSH) along western North America (Chelton & Davis, 1982), was proposed to explain the source for the low salinity water observed in the CCS during cool years. More recently, Strub and James (2000) have noted other potential sources for that water. Also, the intensification of the Aleutian low pressure system in the mid-1970s appears to have caused a weakening of the Alaska Gyre, rather than a spin-up as might have been expected (Lagerloef, 1995), indicating this mechanism is less likely. While there have been long-term, decadal-scale physical changes in the California Current temperature and sea level (Roemmich, 1989), there does not seem to have been a decline in mass transport of water from the north in the southern part of the CCS in the mid-1970s (McGowan, Cayan, & Dorman, 1998; McGowan, Chelton, & Conversi, 1996). Rather the effect of long-term change at those latitudes appears to be a deepening of the mixed layer, resulting in fewer nutrients in the euphotic zone (McGowan et al.,1996; McGowan et al., 1998; Miller, 1996). Comparison of temperature and salinity on the central California coast before and after the mid-1970s indicates warmer, fresher water in the later period, consistent with the regime shift (Pennington & Chavez, 2000). There has been a decline in zooplankton productivity in southern California (Roemmich & McGowan, 1995), but there was not a clear, sharp drop in the mid-1970s. There is an inverse correlation between spring zooplankton abundance more than 60 km offshore in southern California and at Station P in the GOA from 1957 to 1980 (Brodeur et al., 1996). However, identification of this relationship has influenced more by data from the late 1950s than by the data from the mid-1970s.

The evidence for an inverse relationship between salmon abundance in the GOA and the CCS is based primarily on visual comparisons of graphs, and is often merely a comment associated with a demonstration of changes in GOA. More careful and critical scrutiny is required as research interest shifts from suggesting that there may be such an effect, to trying to establish the underlying mechanisms. Francis and Sibley (1991) noted in plots of catches that the high catches of CCS coho salmon appear visually to correspond to the low catches of GOA pink salmon, and vice versa, on decadal time scales. Subsequent analyses of changes in GOA salmon catches have been focused on pink, chum and sockeye, species that are not dominant in Washington, Oregon and California (e.g. Beamish & Bouillon, 1993). Hare and Francis (1995) showed that intervention analysis with changes in the mean placed in 1949 and 1979 led to better fits of time series models to Alaska sockeye and pink salmon data. The years 1949 and 1979 were determined from intervention analysis of the North Pacific Index and Kodiak Island air temperature data (Francis & Hare, 1994). Mantua, Hare, Zhang, Wallace and Francis (1997) showed that placing changes at these times, and in 1925, in time series models of the Pacific Decadal Oscillation (PDO) improved their fit significantly, but the same procedure did not improve the fit of the Southern Oscillation Index (SOI). To relate these shifts to catch records from the GOA and the CCS (i.e. CCS coho salmon and Columbia River spring chinook salmon), they appealed to visual interpretation of time series of catches and climate indices with the shift times identified, noting that the CCS comparisons were not as compelling as the GOA series. Hare, Mantua and Francis (1999) interpreted the loadings from the leading empirical orthogonal function (EOF) of catch records from 1925 to 1997 for five salmon species in seven regions along the coast from Alaska to California as indicating that there was an inverse relationship between the CCS and the GOA. In computing this EOF, the catch records were weighted so that each location was of equal magnitude (i.e. the combined variance of coho and chinook salmon in California equaled the combined variance of the five species at the more northern locations). This EOF explained 34% of the variance, and loadings in the CCS were predominantly of the opposite sign to those in the GOA but were not uniformly strong over space. The magnitude of all of the loadings was approximately uniformly distributed between 0.0 and 0.9, while half of the loadings in the CCS were less than 0.3. Thus, there is not strong statistical evidence for inverse co-variability between the GOA and the CCS salmon; the evidence consists of visual comparisons of graphs and interpretation of EOF loadings in which the differences are not very distinct.

There have also been investigations of environmental effects on the two primary CCS salmon species at specific locations on interannual scales (see reviews in Botsford, Armstrong, & Shenker, 1989; Pearcy, 1992). The most compelling linkage was the positive correlation between upwelling and ocean survival of Oregon hatchery coho salmon (Nickelson, 1986), which became negative and statistically insignificant after the mid-1970s when coho salmon survival declined (Pearcy, 1997). Studies of the potential change in the mid-1970s have included:

1. A comparison of survivals from 4 Washington state hatcheries before and after 1977 which indicated no change in survival (Ryding & Skalski, 1999).
2. Analysis of hatchery survivals from the Oregon Production Index area, Puget Sound, and the Strait

of Georgia over the time period 1972–1995, which indicated they were all declining (Beamish et al., 2000) and
3. A study indicating temperatures from satellite imagery were negatively correlated with survival of hatchery coho salmon in Oregon over the period 1985–1996, which was interpreted to mean that higher temperatures could explain the decline in survival (Cole, 2000).

In addition to these effects, which presumably occur at the age of entry into the ocean, higher ocean temperature conditions are known to have a negative effect on survival and growth of both coho and chinook salmon at the age of return for spawning (Johnson, 1988).

Investigations of interannual relationships between chinook salmon and the physical environment at various specific locations have included both marine and freshwater variables (e.g. Barton, 1980; van Hyning, 1973). Kope and Botsford (1990) found a negative influence of ENSO conditions on central California chinook salmon in the year in which either they returned to spawn or were caught in the fishery. Regarding decadal-scale variability, Beamish, Riddell, Neville, Thomson and Zhang (1995) noted that chinook salmon catches in the Strait of Georgia have declined since the mid-1970s.

To summarize, while the physical environment has been shown to affect CCS salmon at specific locations, and some studies suggest an inverse relation between salmon in the GOA and the CCS, there has been no strong statistical demonstration of the co-variability between the salmon abundance in the GOA and the CCS. To begin to identify mechanisms underlying changes in CCS salmon populations, an analysis of these populations over the period before and after the mid-1970s is needed. Here we examine physical and biological data over the spatial range of the CCS (i.e. Washington, Oregon and northern California) to understand more clearly how the changes in the physical state of the California Current that occurred the mid-1970s might have caused biological changes, specifically in salmon populations. To describe the physical state over this broad a scale we use SSH, sea surface temperature (SST) and Bakun's upwelling index (UWI). To describe the biological response at higher trophic levels we use salmon catch for the two predominant California Current salmon species, coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*). Neither the physical nor the biological data are completely satisfactory descriptions of the state of the populations or the ocean, however even so any co-variability between them may indicate common underlying mechanisms. Catch records can be influenced by a number of factors which would confound our interests here, primarily changes in fishery regulations, fishing effort, and hatchery production, but records of those factors are adequate to assess their effects on our analysis. Also, from above, the evidence presented for abrupt changes in Pacific salmon production comes from catch records. We also include catch records for the Dungeness crab, *Cancer magister*, in our analysis because they have been shown to co-vary with salmon (Botsford, Methot, & Wilen, 1982), their larvae are in the plankton when juvenile salmon enter the ocean and they are a significant prey of juvenile and adult salmon (Peterson, Brodeur, & Pearcy, 1982).

There have also been numerous studies of the influence of physical conditions on interannual variability in Dungeness crab abundance (see review in Botsford et al., 1989). Physical variables invoked to explain that variability include SST, wind in various directions, the UWI, and alongshore flow. Some studies have also sought to explain decadal scale change in the Dungeness crab, i.e. the collapse of the central California population in the late 1950s (Wild, 1980; Wild & Tasto, 1983).

2. Data and methods

Salmon catch data were obtained from the Pacific Fishery Management Council (Pacific Marine Fisheries Commission, 1993) for the years from the early 1950s (first data point varies with location) to 1990 (Fig.

1). We also used total salmon catch by species from the State of Alaska. Dungeness crab data were obtained from the Pacific States Marine Fisheries Commission by port grouping. To reduce computation, for each species, data from highly correlated, adjacent ports were combined as shown in Fig. 1.

Analyses of these catch data are confounded by the influences of variations in hatchery releases and fishery closures as part of management. Releases of hatchery salmon increased steadily from the early 1960s until the 1980s, and the influence of this trend may be present in the catch records used here (e.g. Pearcy, 1997, Fig. 5.2 therein). In the management of salmon stocks there was a gradual trend toward more restrictive regulations from the late 1970s through the 1980s. The exploitation rate index for coho salmon remained between 0.6 and 0.9 through 1983, when it declined to low values for three years (Pacific Fishery Management Council, 1996). A similar index for central California chinook salmon remained between 0.55 and 0.8 from 1970–1990, except for a low point in 1985. The fishing seasons have been reduced more in some locations than in others, in particular in the areas near the Klamath River in northern California, and the Columbia River.

The use of catch data in the analysis of environmental influences raises the questions of where the fish caught at each location spawned and in which ocean region were the environmental shifts effecting the fish caught at each location. Coded wire tag data, which are primarily from hatchery fish, indicate most coho salmon are caught near where they were spawned, but some travel hundreds of kilometers away from their origin (Weitkamp et al., 1995, their Fig. 19). Studies of chinook salmon indicate that fish whose natal stream is south of Cape Blanco are genetically disposed to migrate to the south, whereas fish hatched to the north of the Cape tend to migrate northwards (Nicholas & Hankin, 1988). Chinook salmon also have two types of life histories: an ocean-type life history in which only a few months are spent in freshwater as juveniles, and a stream type in which the individuals typically migrate as yearlings. Fish following the stream-type life history tend to migrate to the central north Pacific, whereas ocean-types are generally

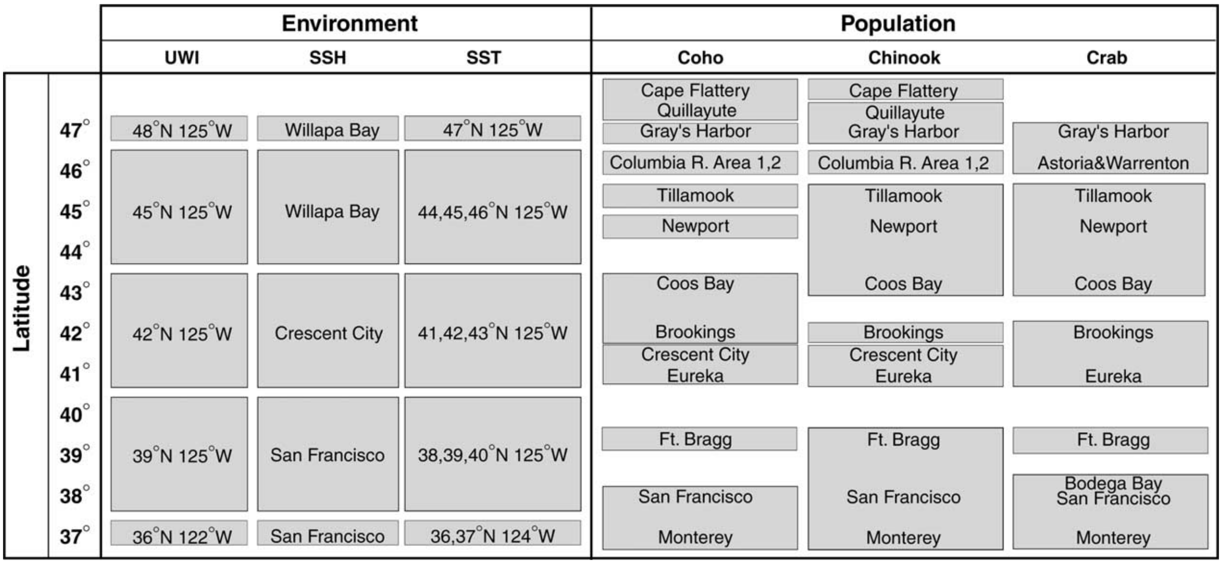


Fig. 1. Locations, displayed by latitude, from which the physical data and biological data used in this analysis were assembled. The gray boxes indicate how the data were combined zonally into five descriptors representing 37°N, 38–40°N, 41–43°N, 44–46°N and 47°N and into a species-specific number of biological descriptors (nine for coho salmon, seven for chinook salmon and five for Dungeness crab). Port acronyms used in subsequent figures and text: CF—Cape Flatttery, Q—Quillayute, GH—Gray's Harbor, AW—Astoria and Warrenton, CR1—Columbia River Area 1, CR2—Columbia River Area 2, T—Tillamook, N—Newport, CB—Coos Bay, B—Brookings, CC—Crescent City, E—Eureka, FB—Fort Bragg, BB—Bodega Bay, SR—San Francisco, M—Monterey.

found closer to the coast (Healey, 1991; Myers et al., 1998). Generalizations regarding oceanic distributions are easy to draw, but exceptions are numerous. For example, based on tagging studies, chinook salmon in central California were believed to remain near their natal origins, but in 1998 two coded wire tagged Sacramento River chinook salmon were recovered in the Bering Sea (Myers et al., 1999).

Physical data used were ocean temperatures from the COADS data set (Mendelssohn & Roy, 1996), sea levels from shore stations and Bakun's UWI (from NMFS Pacific Fisheries Environmental Laboratory (PMEL)). These three parameters from different locations along the coast were combined into a single alongshore array depicting zonal variability, as shown in Fig. 1. We also obtained monthly time series of the SOI, the extra-tropical Southern Oscillation Index (SOIx), and the extra-tropical Northern Oscillation Index (NOIx) from the NMFS PFEL. We obtained the PDO from the Joint Institute for the Study of the Atmosphere and the Oceans Climate Data Archive at the University of Washington.

The primary method used to examine co-variability between physical conditions and biological descriptors was computation of cross correlations. To account for seasonal effects in co-variability, we computed cross correlations for each of the four seasons as January through March (winter), April through June (spring), July through September (summer) and October through December (fall).

Assessing the statistical significance of computed cross correlations is complicated by two factors, intra-series correlation and multiple tests. In the former, lack of independence of adjacent values within each time series means that the number of statistical degrees of freedom is less than the number of samples in the series. There are a number of methods for accounting for this effect in any single computation (see recent assessment by Pyper & Peterman, 1998). A problem with those methods is that they depend on computations from each series (i.e. only one realization of the random process) to determine the 'general' statistical characteristics needed to correct the number of degrees of freedom. One means of improving on that approach is to determine the general statistical characteristics of each series from a number of similar series, rather than a single series (Botsford & Paulsen, 1999). We have used that approach here, calculating the effective numbers of degrees of freedom for different pairs of series, and then averaging them over categories of similar series. We do not account for the problem of multiple tests here. Rather we regard the results of this search for temporal and spatial pattern of co-variability as indications of hypotheses to be tested further, not as proven relationships.

We computed the effective number of degrees of freedom using the variance in the estimate of the cross-correlation from the following expression (Kope & Botsford, 1990)

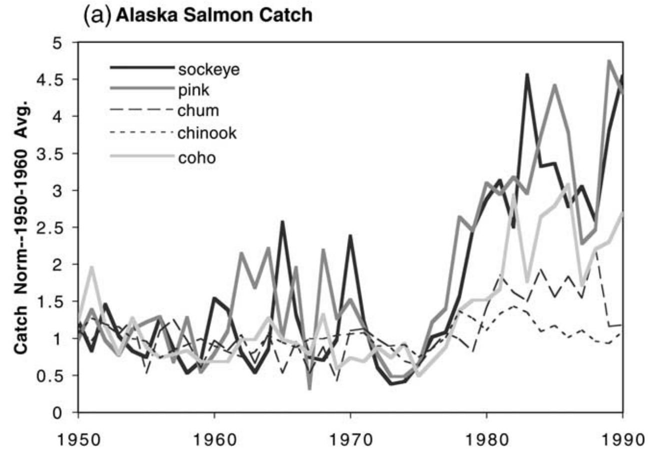
$$\mathrm{var}[R_{xy}(k)] = \frac{1}{N-|k|}\sum_{v=1-N+|k|}^{N-|k|-1}\left[1-\frac{|v|}{N-|k|}\right][\rho_{xx}(v)\rho_{yy}(v)]. \tag{1}$$

where N is the length of the series, k is the time lag, and ρ_{xx} and ρ_{yy} are autocorrelations in each variable. This expression for the variance of the cross-correlation is appropriate for testing the null hypothesis that the cross-correlation differs from zero. It is obtained by setting the cross-correlation to zero in the expression for the variance (see Botsford and Brittnacher, 1998). The variance was computed for correlations between each physical variable and each biological variable, at each location for each season. It was used to compute the degrees of freedom by comparing it to $1/(N-|k|)$, the number of degrees of freedom for independent points. The resulting number of degrees of freedom for each data type were averaged, and used to generate the levels at which correlations were deemed significant at the 0.01, the 0.05 and the 0.10 level, assuming a Gaussian distribution of computed correlation values. These values are noted on each figure presenting correlation results.

3. Results

A reasonable first step toward a better understanding of potential inverse changes in salmon populations in the GOA and the CCS in the mid-1970s is to compare the specific population behavior of the two predominant CCS species of salmon to the behavior of populations of those two species in the GOA (Fig. 2). Plotting the catch record for each species relative to catches in the 10 years before the mid-1970s indicates that in the GOA the strong increases in salmon in the mid-1970s were in pink, sockeye and coho salmon with a weaker increase in chum salmon. Of the two species common in the CCS, coho salmon increased, but any increase in chinook catches was small or negligible. In the CCS, coho salmon catches increased through the 1960s but then declined in the mid-1970s, while chinook salmon again remained relatively constant.

Catches of the CCS species plotted by port groupings from Fig. 1, and normalized by dividing by mean



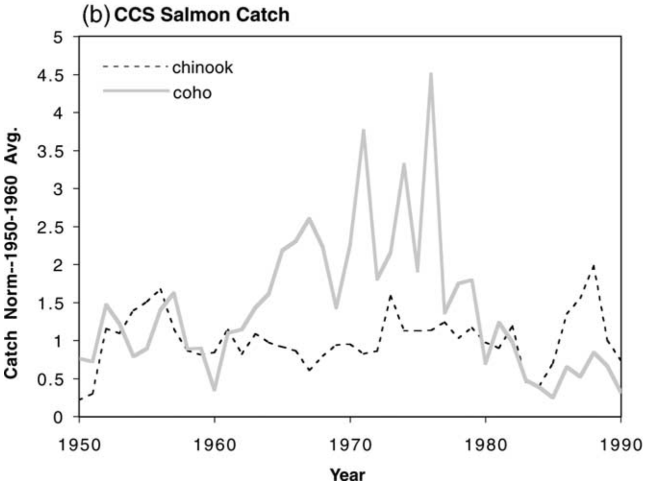


Fig. 2. Comparison of (A) catch records for various salmon species in Alaska with (B) catch records from the two salmon species dominant in the CCS (i.e. ports in Washington, Oregon and California). To place all species data on the same scale, each series was divided by its mean between 1950 and 1960

catch at each location indicate the salient features of variability over time and space (Fig. 3). The qualitative features of the coho salmon record are a gradual coastwide increase from the early 1960s through the mid-1970s, followed by a dramatic decline. The increases may in part have resulted from the increase in the numbers of hatchery releases, but the decline was neither the result of a drop in hatchery output nor to changes in fishing regulations. Variability in the catches appears to be relatively synchronous along the coast, and, at least in the 1970s, to have occurred over a relatively short time scale. Chinook salmon records, on the other hand, exhibited neither a concomitant coastwide increase, nor a decline in the mid-1970s, nor did they respond on time scales as short as those the coho salmon respond to. As noted above, these records have been affected by regulations introduced at some locations in the late 1980s.

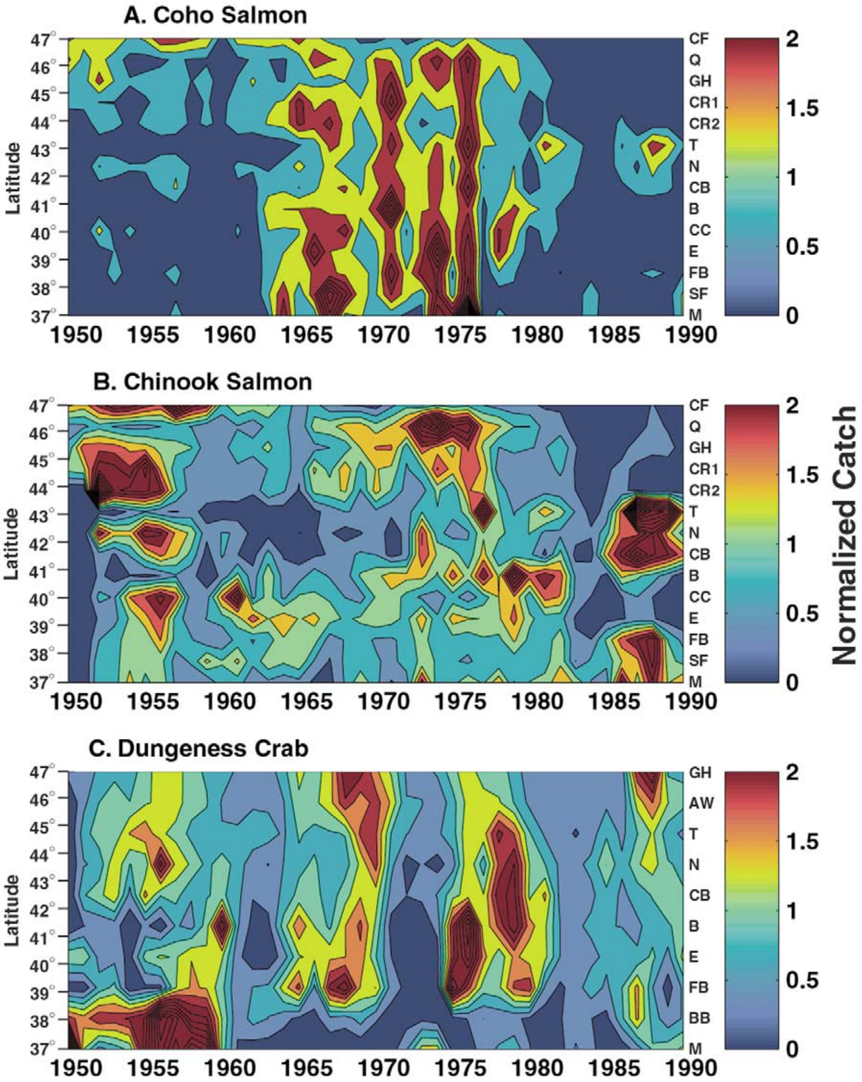


Fig. 3. The spatial distribution of catch over time for chinook salmon, coho salmon and Dungeness crab in the California Current. To emphasize spatial variability at each location, each series was divided by its mean. The catch ports from which the data were assembled are shown on the right; these location acronyms are defined in Fig. 1.

Dungeness crab catch records north of central California exhibit a synchronous variability on ten year time scales that has attracted much research attention (reviewed in Botsford et al., 1989). Dungeness crab populations (catches) in central California declined in the late 1960s (Wild & Tasto, 1983).

The apparent synchrony in each of these catch records can be quantified in terms of empirical orthogonal functions (EOFs, known in the biological literature as principal components) (Fig. 4). For coho salmon, the leading EOF reflects the synchrony apparent in Fig. 3, and describes 69% of the variance. For chinook salmon the leading EOF reflects the spatial pattern seen in Fig. 3, and describes 34% of the variance. Returns for ports in the Columbia River north co-varied with Eureka and Crescent City in northern California, while ports in central California (Fort Bragg, San Francisco and Monterey) co-varied with Oregon, south of the

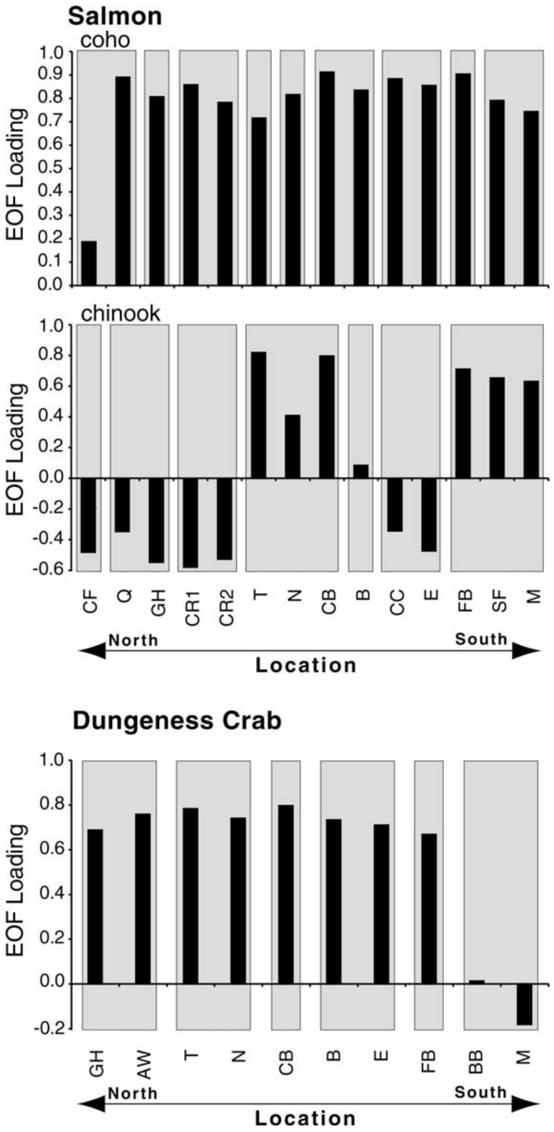


Fig. 4. Loadings of the first empirical orthogonal function over space (catch ports) for each of the three species analyzed. This EOF is referred to in the text as SEOF. The gray boxes encompass the port groupings as shown in Fig. 1.

Columbia River. Brookings in southern Oregon remained independent of these. The leading EOF for Dungeness crab reflects the almost synchronous behavior of the more northern ports seen in Fig. 3 (i.e. Fort Bragg and all ports to the north) and explains 44% of the variance. Subsequently, we refer to the leading EOFs for each species as the spatial EOFs (SEOFs).

Plots of the data used to describe the physical environment indicate variability on time scales of several years, and there appears to be considerable co-variability between SST, SSH and UWI (Fig. 5). Because of that, and the fact that preliminary calculations of correlations between physical and biological variables indicate structure in the physical variables that would be associated with warm water (ENSO-like) conditions (i.e. negative correlations with temperature and sea level, along with positive correlations with UWI), we have computed EOFs across these three variables for each location and season (Fig. 5, Table 1).

The leading EOF of the three physical variables appears to describe a significant mode of variability

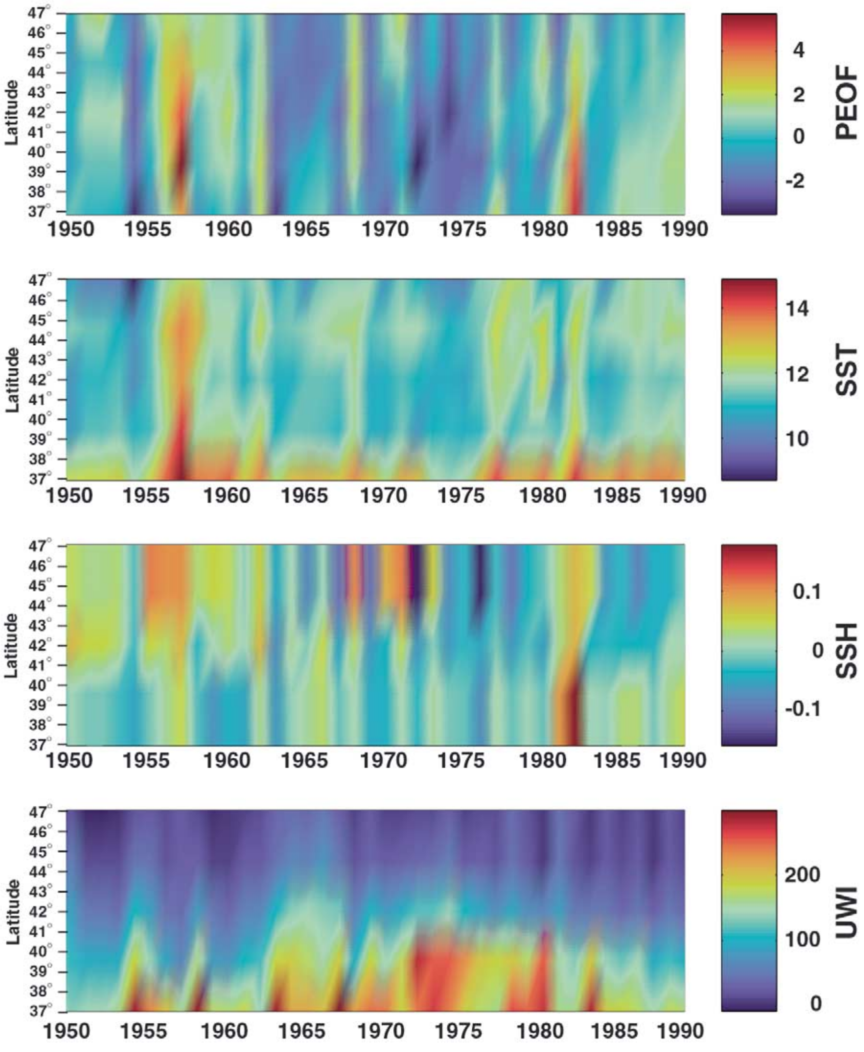


Fig. 5. Variability in the spatial distribution of SST, SSH, UWI, and the first EOF of these three (PEOF). Temperature and the UWI are given as actual values, while the SSH is divided by its mean value at each location.

Table 1
Loadings of the first empirical orthogonal function (PEOF) of sea surface temperature (SST), sea surface height (SSH), and upwelling index (UWI), by latitude and season. The fraction of the variance explained by the PEOF by latitude and season is also given

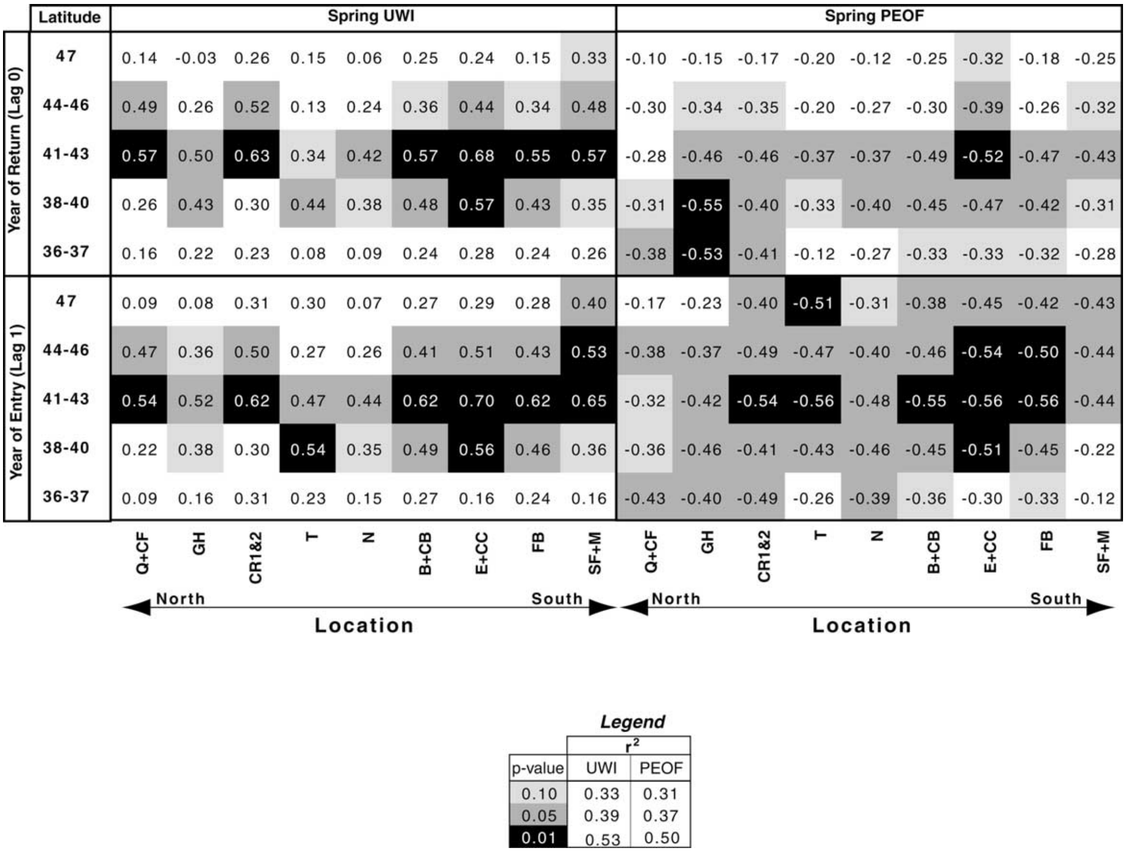
Latitude	Season	Loadings on Factors			Prop. of σ^2
		SST	SSH	UWI	
47	spring	0.160	0.725	−0.712	0.470
44–46	spring	0.726	0.635	−0.702	0.474
41–43	spring	0.736	0.649	−0.799	0.534
38–40	spring	0.887	0.635	−0.760	0.589
36–37	spring	0.762	0.785	−0.659	0.544
47	summer	0.580	0.786	−0.813	0.571
44–46	summer	0.813	0.817	−0.685	0.599
41–43	summer	0.789	0.717	−0.796	0.590
38–40	summer	0.899	0.659	−0.760	0.526
36–37	summer	0.854	0.770	−0.539	0.538
47	fall	0.799	0.597	−0.834	0.564
44–46	fall	0.759	0.744	−0.820	0.601
41–43	fall	0.764	0.889	−0.853	0.701
38–40	fall	0.918	0.622	−0.802	0.624
36–37	fall	0.763	0.794	−0.841	0.639
47	winter	0.236	0.836	−0.864	0.515
44–46	winter	0.750	0.805	−0.909	0.679
41–43	winter	0.847	0.896	−0.910	0.783
38–40	winter	0.847	0.882	−0.578	0.766
36–37	winter	0.713	0.913	−0.813	0.667

throughout the region, throughout the year (Table 1). The loadings are similar at each location; positive SST, positive SSH and negative UWI in approximately equal proportions. Hereafter, we refer to this EOF as the physical EOF (PEOF), and, in the context of this variable, we refer to high values as warm years and low values as cool years with the understanding that we are not referring solely to ocean temperature. The PEOF explains more than half the variance at almost all locations (Table 1). This variable does not show the spatial trends seen in the other variables because it is calculated from correlations at each location, i.e. it reflects local variability at each location. Note that the effects of the ENSO events in 1957–58 and 1982–83 affected all but the most northern station, and that there was a relatively cool period from 1963 to 1976 followed by a warmer period through the 1980s (Fig. 5).

3.1. Co-variability between physical environment and populations

3.1.1. Coho salmon

Correlations between coho salmon catch and the four variables representing the physical environment were dominated by the UWI and the PEOF in the spring prior to salmon returning to spawn or be caught in the fishery (lag = 0year) and entry of juveniles into the ocean (lag = 1year) (Fig. 6). Correlations with UWI were strongest at latitudes 41–43°N, where that variable affected catches at all locations. It is not surprising that physical conditions have an influence on all catches at all latitudes, because of the synchrony of the catch of coho salmon indicated by the SEOF (Fig. 3). Catches at almost all latitudes were negatively correlated with the PEOF at all latitudes, indicating cool years are favorable for coho salmon. In spring



	Latitude	Spring UWI									Spring PEOF								
		Q+CF	GH	CR1&2	T	N	B+CB	E+CC	FB	SF+M	Q+CF	GH	CR1&2	T	N	B+CB	E+CC	FB	SF+M
Year of Return (Lag 0)	47	0.14	-0.03	0.26	0.15	0.06	0.25	0.24	0.15	0.33	-0.10	-0.15	-0.17	-0.20	-0.12	-0.25	-0.32	-0.18	-0.25
	44-46	0.49	0.26	0.52	0.13	0.24	0.36	0.44	0.34	0.48	-0.30	-0.34	-0.35	-0.20	-0.27	-0.30	-0.39	-0.26	-0.32
	41-43	0.57	0.50	0.63	0.34	0.42	0.57	0.68	0.55	0.57	-0.28	-0.46	-0.46	-0.37	-0.37	-0.49	-0.52	-0.47	-0.43
	38-40	0.26	0.43	0.30	0.44	0.38	0.48	0.57	0.43	0.35	-0.31	-0.55	-0.40	-0.33	-0.40	-0.45	-0.47	-0.42	-0.31
	36-37	0.16	0.22	0.23	0.08	0.09	0.24	0.28	0.24	0.26	-0.38	-0.53	-0.41	-0.12	-0.27	-0.33	-0.33	-0.32	-0.28
Year of Entry (Lag 1)	47	0.09	0.08	0.31	0.30	0.07	0.27	0.29	0.28	0.40	-0.17	-0.23	-0.40	-0.51	-0.31	-0.38	-0.45	-0.42	-0.43
	44-46	0.47	0.36	0.50	0.27	0.26	0.41	0.51	0.43	0.53	-0.38	-0.37	-0.49	-0.47	-0.40	-0.46	-0.54	-0.50	-0.44
	41-43	0.54	0.52	0.62	0.47	0.44	0.62	0.70	0.62	0.65	-0.32	-0.42	-0.54	-0.56	-0.48	-0.55	-0.56	-0.56	-0.44
	38-40	0.22	0.38	0.30	0.54	0.35	0.49	0.56	0.46	0.36	-0.36	-0.46	-0.41	-0.43	-0.46	-0.45	-0.51	-0.45	-0.22
	36-37	0.09	0.16	0.31	0.23	0.15	0.27	0.16	0.24	0.16	-0.43	-0.40	-0.49	-0.26	-0.39	-0.36	-0.30	-0.33	-0.12

Legend

	r²	
p-value	UWI	PEOF
0.10	0.33	0.31
0.05	0.39	0.37
0.01	0.53	0.50

Fig. 6. Correlations between the coho salmon catches by port grouping (see Fig. 1) and the spring PEOF and spring UWI by latitude, for lags corresponding to the age of return (lag = 0yr) and the age of ocean entry (lag = 1yr) of the salmon. Calculated significance levels account for intra-series correlation in each data type (Eq. (1)). Shading indicates the magnitude but not the sign of the significance level of the correlation.

there were also several significant correlations involving the PEOF and the UWI at longer time lags, probably as a result of intraseries correlation, since they are not associated with any obvious biological mechanism. A pattern of weaker correlations with temperature (not shown), distributed more southward was probably the reason for the distribution of correlations with the PEOF having a broader spatial distribution than the correlations with UWI. Correlations in the summer (not shown) had a similar pattern, but were weaker, being significant only where the spring correlations were strongest. There were a few random correlations in the winter, and fewer yet in the fall. None of these patterns changed after a linear trend was removed from each series, primarily because the trends were small.

Because we were interested in potential changes in the mid-1970s, we have assessed the temporal changes in the co-variability of coho salmon with the environment at that time. Examination of the pattern of residuals in the regressions of both age of entry and age of return of coho salmon on both UWI and the PEOF at latitudes 42–43°N showed that they typically declined to negative values beginning in the late 1970s, suggesting there was a change in the relationships in the later years. Separate regressions, of catches before and after 1975, on both UWI and the PEOF yielded few significant relationships, except for the UWI for the period after 1975. These were significant primarily because of a declining trend in both the

UWI and catch. Interpretation of this relationship is confounded by the fact that in the years 1984–86 there was a decline in effort that influenced the catches.

3.1.2. Chinook salmon

Correlations between chinook salmon catches and the physical environment did not lend themselves to as clear an interpretation as those for coho salmon. In general they reflected conditions associated with the PEOF, but differed from the correlations for coho salmon in two respects: (1) rather than a coastwide synchronous response, they followed the pattern in the SEOF (Fig. 4), and (2) rather than physical conditions at all latitudes having the same effect, physical conditions in the northern CCS had a different effect from conditions in the southern part of the study area. Significant correlations were spread more evenly across SST, SSH and UWI in spring and summer, and correlations with the PEOF were significant as frequently as any one of the others. Correlations were marginally strongest in summer (Fig. 7). The pattern of correlations is strongest at lag zero (year of return), with the number of correlations at non-zero lags being ~10% of the total, the number expected on the basis of chance alone. Because the ages of entry for chinook salmon vary from two to four years prior to the age of return, one would not expect correlations at single non-zero lags to be as strong as for coho salmon where virtually all non-precocious spawners from a single brood year return at the same time. Focusing on lag zero, which corresponds to environmental conditions at the time of return for spawning, correlations with the PEOF in the south (e.g. 36–37°N) are all negative, indicating a positive effect of cool conditions, as observed above for coho salmon. The response to PEOF conditions at locations further to the north (e.g. 47°N) reflect the spatial variability indicated in the SEOF for chinook salmon (Fig. 4), with significant negative correlations remaining on catches along the Oregon coast (T + N + CB) and in central California (FB + SF + M), but positive significant correlations (warm conditions favorable) along the Washington coast (CF and CR1&2).

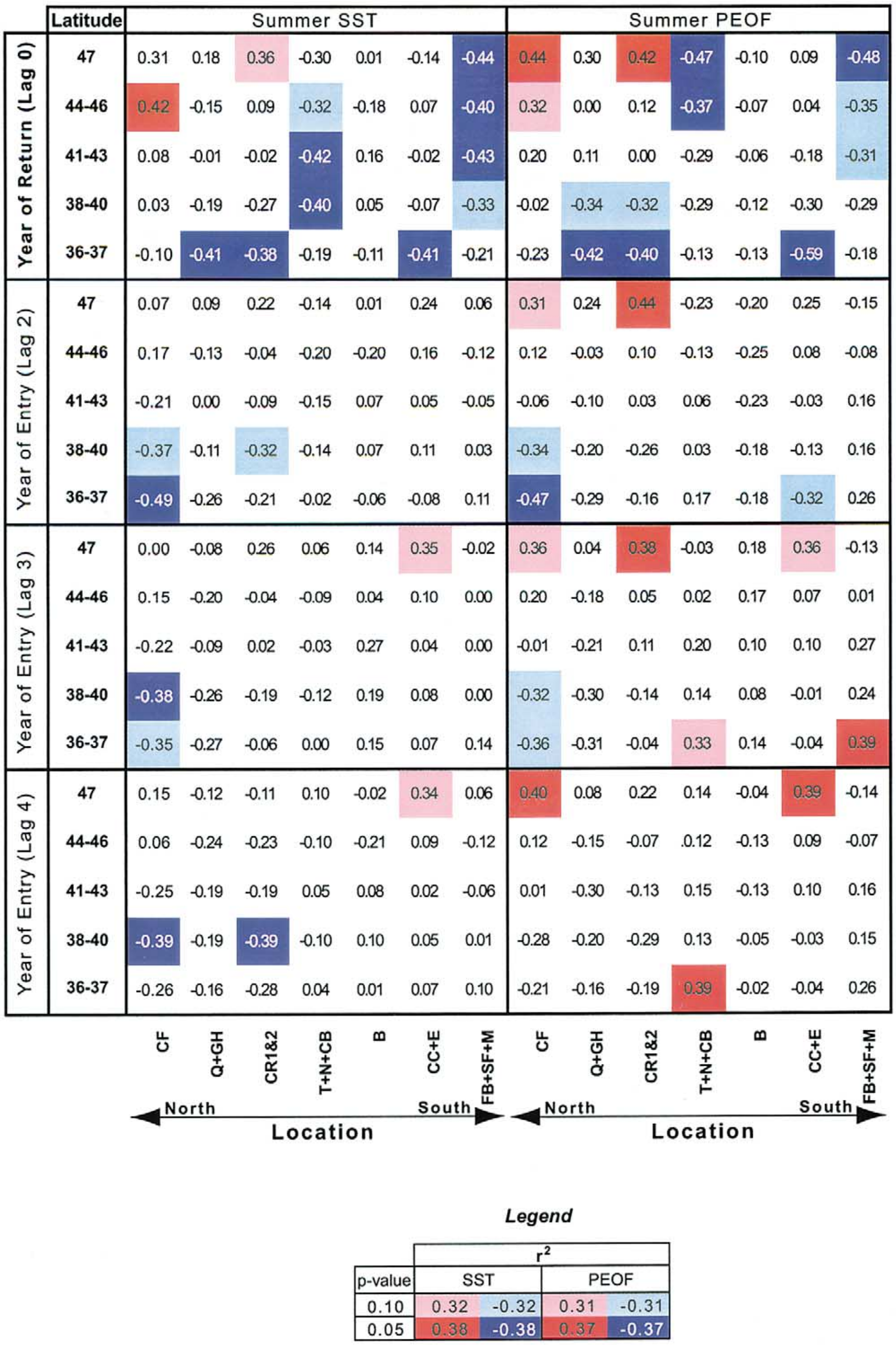
3.1.3. Dungeness crab

Correlations between Dungeness crab catch and environmental variables were strongest during winter and spring at lags of 3 and 4, and indicated cool conditions were favorable. Since most Dungeness crabs enter the fishery at ages 4 and 5 (Botsford, 1984), catch here is indexed by the year in which the season began, and the larval phase spans January through June, this indicates cool conditions have a favorable effect on the larval stage. In the winter at lag 3, negative correlations indicate an effect of temperature to the south on catch at each port (Fig. 8). Correlations with the PEOF are similar, but do not indicate as strong a directionality. In the spring at lag 3, the PEOF indicates an effect of local conditions during the larval phase on later catch, but temperature has a coastwide effect on northern catches. Correlations at lag 4 are similar. Correlations with the most southern port grouping (BB + SF + M) should be interpreted with care because the catches declined in the late 1950s, hence will tend to be correlated with any environmental series that contains a trend.

3.2. Basin-wide Indices

To determine how the relationships identified here might be influenced by basin-scale forcing, we examined co-variability between the physical variables found here to be important to these populations and several indices of basin-wide conditions: the SOI, the SOIx, the PDO, and the NOIx. We examined co-variability between these and UWI, SST, and the PEOF in spring, and just the latter two in summer and winter. To test for lagged effects and possible predictive ability, we used basin-scale indices lagged 1, 2 and 3 seasons into the past, with the seasons defined as above.

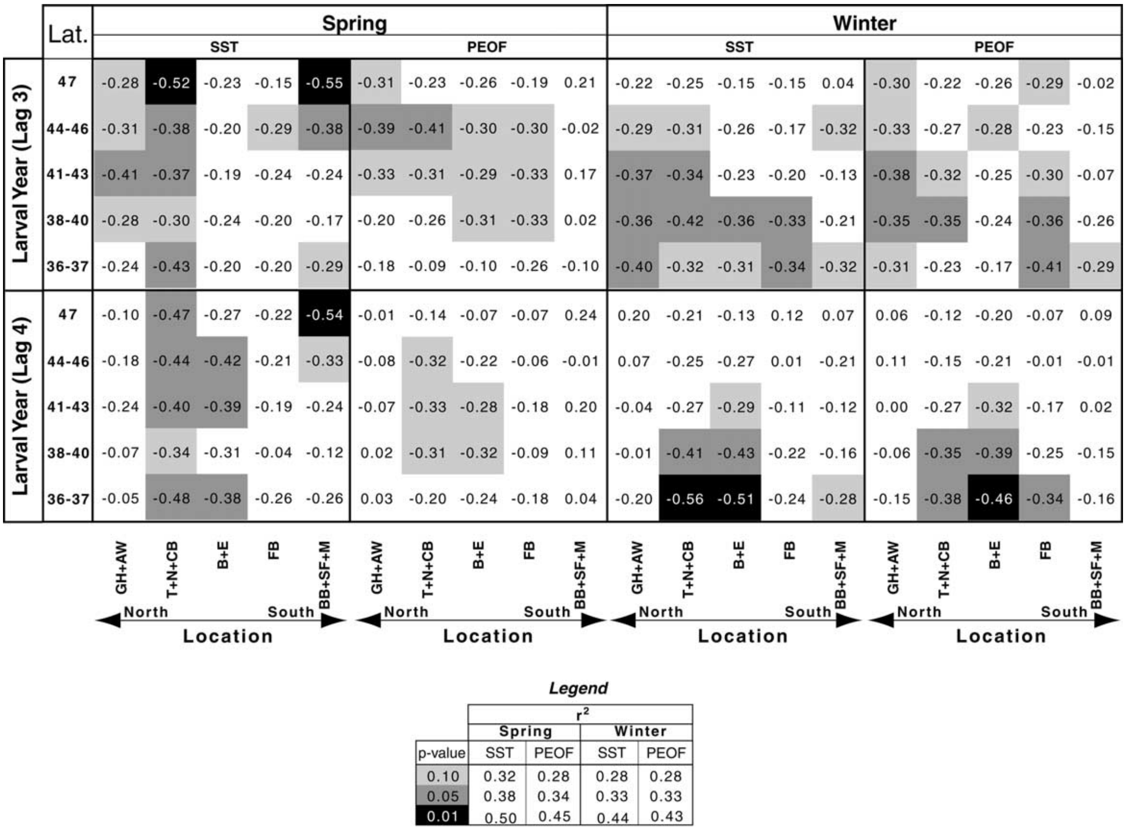
The correlations indicate an influence of all of the basin scale variables on temperature and PEOF in the same season (Fig. 9), but a weak influence on upwelling (not shown, only 17 of 80 were significant). These relationships are strongest in winter, when all indices influence local conditions, and indices in some



	Latitude	Summer SST							Summer PEOF						
		CF	Q+GH	CR1&2	T+N+CB	B	CC+E	FB+SF+M	CF	Q+GH	CR1&2	T+N+CB	B	CC+E	FB+SF+M
Year of Return (Lag 0)	47	0.31	0.18	0.36	-0.30	0.01	-0.14	-0.44	0.44	0.30	0.42	-0.47	-0.10	0.09	-0.48
	44-46	0.42	-0.15	0.09	-0.32	-0.18	0.07	-0.40	0.32	0.00	0.12	-0.37	-0.07	0.04	-0.35
	41-43	0.08	-0.01	-0.02	-0.42	0.16	-0.02	-0.43	0.20	0.11	0.00	-0.29	-0.06	-0.18	-0.31
	38-40	0.03	-0.19	-0.27	-0.40	0.05	-0.07	-0.33	-0.02	-0.34	-0.32	-0.29	-0.12	-0.30	-0.29
	36-37	-0.10	-0.41	-0.38	-0.19	-0.11	-0.41	-0.21	-0.23	-0.42	-0.40	-0.13	-0.13	-0.59	-0.18
Year of Entry (Lag 2)	47	0.07	0.09	0.22	-0.14	0.01	0.24	0.06	0.31	0.24	0.44	-0.23	-0.20	0.25	-0.15
	44-46	0.17	-0.13	-0.04	-0.20	-0.20	0.16	-0.12	0.12	-0.03	0.10	-0.13	-0.25	0.08	-0.08
	41-43	-0.21	0.00	-0.09	-0.15	0.07	0.05	-0.05	-0.06	-0.10	0.03	0.06	-0.23	-0.03	0.16
	38-40	-0.37	-0.11	-0.32	-0.14	0.07	0.11	0.03	-0.34	-0.20	-0.26	0.03	-0.18	-0.13	0.16
	36-37	-0.49	-0.26	-0.21	-0.02	-0.06	-0.08	0.11	-0.47	-0.29	-0.16	0.17	-0.18	-0.32	0.26
Year of Entry (Lag 3)	47	0.00	-0.08	0.26	0.06	0.14	0.35	-0.02	0.36	0.04	0.38	-0.03	0.18	0.36	-0.13
	44-46	0.15	-0.20	-0.04	-0.09	0.04	0.10	0.00	0.20	-0.18	0.05	0.02	0.17	0.07	0.01
	41-43	-0.22	-0.09	0.02	-0.03	0.27	0.04	0.00	-0.01	-0.21	0.11	0.20	0.10	0.10	0.27
	38-40	-0.38	-0.26	-0.19	-0.12	0.19	0.08	0.00	-0.32	-0.30	-0.14	0.14	0.08	-0.01	0.24
	36-37	-0.35	-0.27	-0.06	0.00	0.15	0.07	0.14	-0.36	-0.31	-0.04	0.33	0.14	-0.04	0.39
Year of Entry (Lag 4)	47	0.15	-0.12	-0.11	0.10	-0.02	0.34	0.06	0.40	0.08	0.22	0.14	-0.04	0.39	-0.14
	44-46	0.06	-0.24	-0.23	-0.10	-0.21	0.09	-0.12	0.12	-0.15	-0.07	0.12	-0.13	0.09	-0.07
	41-43	-0.25	-0.19	-0.19	0.05	0.08	0.02	-0.06	0.01	-0.30	-0.13	0.15	-0.13	0.10	0.16
	38-40	-0.39	-0.19	-0.39	-0.10	0.10	0.05	0.01	-0.28	-0.20	-0.29	0.13	-0.05	-0.03	0.15
	36-37	-0.26	-0.16	-0.28	0.04	0.01	0.07	0.10	-0.21	-0.16	-0.19	0.39	-0.02	-0.04	0.26

	r^2			
p-value	SST		PEOF	
0.10	0.32	-0.32	0.31	-0.31
0.05	0.38	-0.38	0.37	-0.37

Fig. 7. Correlations between the chinook salmon catches by port grouping (see Fig. 1) and summer PEOF and SST by latitude, at lags corresponding to age of return (lag = 0yr) and various ages of entry (lags = 2, 3 and 4 yr) of the salmon. Calculated significance levels account for intra-series correlation in each data type (Eq. (1)). Positive correlations are shown in red and pink; negative correlations are shown in blue.



	Lat.	Spring										Winter									
		SST					PEOF					SST					PEOF				
		GH+AW	T+N+CB	B+E	FB	BB+SF+M	GH+AW	T+N+CB	B+E	FB	BB+SF+M	GH+AW	T+N+CB	B+E	FB	BB+SF+M	GH+AW	T+N+CB	B+E	FB	BB+SF+M
Larval Year (Lag 3)	47	-0.28	-0.52	-0.23	-0.15	-0.55	-0.31	-0.23	-0.26	-0.19	0.21	-0.22	-0.25	-0.15	-0.15	0.04	-0.30	-0.22	-0.26	-0.29	-0.02
	44-46	-0.31	-0.38	-0.20	-0.29	-0.38	-0.39	-0.41	-0.30	-0.30	-0.02	-0.29	-0.31	-0.26	-0.17	-0.32	-0.33	-0.27	-0.28	-0.23	-0.15
	41-43	-0.41	-0.37	-0.19	-0.24	-0.24	-0.33	-0.31	-0.29	-0.33	0.17	-0.37	-0.34	-0.23	-0.20	-0.13	-0.38	-0.32	-0.25	-0.30	-0.07
	38-40	-0.28	-0.30	-0.24	-0.20	-0.17	-0.20	-0.26	-0.31	-0.33	0.02	-0.36	-0.42	-0.36	-0.33	-0.21	-0.35	-0.35	-0.24	-0.36	-0.26
	36-37	-0.24	-0.43	-0.20	-0.20	-0.29	-0.18	-0.09	-0.10	-0.26	-0.10	-0.40	-0.32	-0.31	-0.34	-0.32	-0.31	-0.23	-0.17	-0.41	-0.29
Larval Year (Lag 4)	47	-0.10	-0.47	-0.27	-0.22	-0.54	-0.01	-0.14	-0.07	-0.07	0.24	0.20	-0.21	-0.13	0.12	0.07	0.06	-0.12	-0.20	-0.07	0.09
	44-46	-0.18	-0.44	-0.42	-0.21	-0.33	-0.08	-0.32	-0.22	-0.06	-0.01	0.07	-0.25	-0.27	0.01	-0.21	0.11	-0.15	-0.21	-0.01	-0.01
	41-43	-0.24	-0.40	-0.39	-0.19	-0.24	-0.07	-0.33	-0.28	-0.18	0.20	-0.04	-0.27	-0.29	-0.11	-0.12	0.00	-0.27	-0.32	-0.17	0.02
	38-40	-0.07	-0.34	-0.31	-0.04	-0.12	0.02	-0.31	-0.32	-0.09	0.11	-0.01	-0.41	-0.43	-0.22	-0.16	-0.06	-0.35	-0.39	-0.25	-0.15
	36-37	-0.05	-0.48	-0.38	-0.26	-0.26	0.03	-0.20	-0.24	-0.18	0.04	-0.20	-0.56	-0.51	-0.24	-0.28	-0.15	-0.38	-0.46	-0.34	-0.16

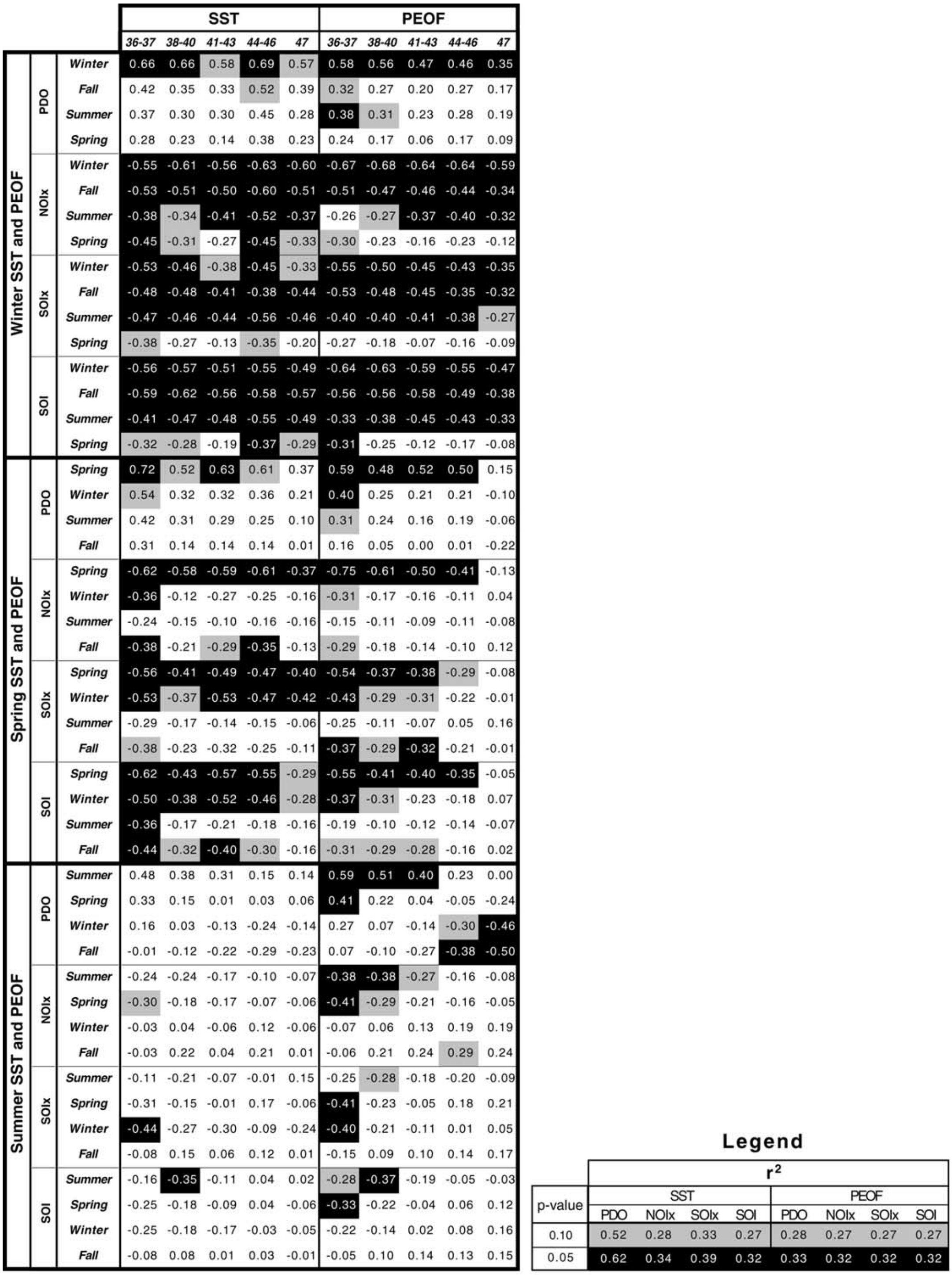
Legend

	r^2			
	Spring		Winter	
p-value	SST	PEOF	SST	PEOF
0.10	0.32	0.28	0.28	0.28
0.05	0.38	0.34	0.33	0.33
0.01	0.50	0.45	0.44	0.43

Fig. 8. Correlations between Dungeness crab catches by port grouping (see Fig. 1) and winter and spring values of the PEOF and SST by latitude, at lags corresponding to an influence on the larval phase. Calculated significance levels account for intra-series correlation in each data type (Eq. (1)). Shading indicates the magnitude but not the sign of the significance level of the correlation.

previous seasons also are correlated. These influences are weaker in spring with significant correlations primarily with local effects in the same season. They are weaker still in the summer. For all seasons, relationships are stronger with the more southern locations; locations south of 47°N were all correlated with the basin-scale indices, with 47°N being correlated only for the winter values of sea surface temperature (SST) and PEOF. Of the four indices, NOIx and SOI provide the strongest correlations within the season, and the SOI provided the strongest correlation in previous seasons. Note that there is only one reversal of the sign of the dependence on previous seasons, between the PDO and the PEOF in summer.

Plots of zero mean, unit variance versions of the basin-wide indices (i.e. for each index time series, the mean of the series was subtracted and the series was divided by its variance) and the values of PEOF along the coast indicate there are time periods of greater and less co-variability between local conditions (PEOF) and basin-scale indicators (Fig. 10). First, in both the basin indicators and the PEOFs at the five latitudes, year-to-year differences in the mean of each are stronger than variability within each data type. We treat each of them here as single indicators, one of basin wide conditions, the other of local physical conditions (of biological importance). The two variables appear to co-vary strongly through the 1950s, but not from 1960 through 1975. In particular, the basin indicators do not indicate the cool period (high values) from 1964 to 1969, which appears to be important to coho salmon (Figs. 2 and 3). Both sets of variables decline and the two co-vary annually following 1975, with common low values (warm years) in 1978 and 1983, and high values in 1982 and 1985 (cool years).



			SST					PEOF				
			36-37	38-40	41-43	44-46	47	36-37	38-40	41-43	44-46	47
Winter SST and PEOF	PDO	Winter	0.66	0.66	0.58	0.69	0.57	0.58	0.56	0.47	0.46	0.35
		Fall	0.42	0.35	0.33	0.52	0.39	0.32	0.27	0.20	0.27	0.17
		Summer	0.37	0.30	0.30	0.45	0.28	0.38	0.31	0.23	0.28	0.19
		Spring	0.28	0.23	0.14	0.38	0.23	0.24	0.17	0.06	0.17	0.09
	NOIx	Winter	-0.55	-0.61	-0.56	-0.63	-0.60	-0.67	-0.68	-0.64	-0.64	-0.59
		Fall	-0.53	-0.51	-0.50	-0.60	-0.51	-0.51	-0.47	-0.46	-0.44	-0.34
		Summer	-0.38	-0.34	-0.41	-0.52	-0.37	-0.26	-0.27	-0.37	-0.40	-0.32
		Spring	-0.45	-0.31	-0.27	-0.45	-0.33	-0.30	-0.23	-0.16	-0.23	-0.12
	SOIx	Winter	-0.53	-0.46	-0.38	-0.45	-0.33	-0.55	-0.50	-0.45	-0.43	-0.35
		Fall	-0.48	-0.48	-0.41	-0.38	-0.44	-0.53	-0.48	-0.45	-0.35	-0.32
		Summer	-0.47	-0.46	-0.44	-0.56	-0.46	-0.40	-0.40	-0.41	-0.38	-0.27
		Spring	-0.38	-0.27	-0.13	-0.35	-0.20	-0.27	-0.18	-0.07	-0.16	-0.09
	SOI	Winter	-0.56	-0.57	-0.51	-0.55	-0.49	-0.64	-0.63	-0.59	-0.55	-0.47
		Fall	-0.59	-0.62	-0.56	-0.58	-0.57	-0.56	-0.56	-0.58	-0.49	-0.38
		Summer	-0.41	-0.47	-0.48	-0.55	-0.49	-0.33	-0.38	-0.45	-0.43	-0.33
		Spring	-0.32	-0.28	-0.19	-0.37	-0.29	-0.31	-0.25	-0.12	-0.17	-0.08
Spring SST and PEOF	PDO	Spring	0.72	0.52	0.63	0.61	0.37	0.59	0.48	0.52	0.50	0.15
		Winter	0.54	0.32	0.32	0.36	0.21	0.40	0.25	0.21	0.21	-0.10
		Summer	0.42	0.31	0.29	0.25	0.10	0.31	0.24	0.16	0.19	-0.06
		Fall	0.31	0.14	0.14	0.14	0.01	0.16	0.05	0.00	0.01	-0.22
	NOIx	Spring	-0.62	-0.58	-0.59	-0.61	-0.37	-0.75	-0.61	-0.50	-0.41	-0.13
		Winter	-0.36	-0.12	-0.27	-0.25	-0.16	-0.31	-0.17	-0.16	-0.11	0.04
		Summer	-0.24	-0.15	-0.10	-0.16	-0.16	-0.15	-0.11	-0.09	-0.11	-0.08
		Fall	-0.38	-0.21	-0.29	-0.35	-0.13	-0.29	-0.18	-0.14	-0.10	0.12
	SOIx	Spring	-0.56	-0.41	-0.49	-0.47	-0.40	-0.54	-0.37	-0.38	-0.29	-0.08
		Winter	-0.53	-0.37	-0.53	-0.47	-0.42	-0.43	-0.29	-0.31	-0.22	-0.01
		Summer	-0.29	-0.17	-0.14	-0.15	-0.06	-0.25	-0.11	-0.07	0.05	0.16
		Fall	-0.38	-0.23	-0.32	-0.25	-0.11	-0.37	-0.29	-0.32	-0.21	-0.01
	SOI	Spring	-0.62	-0.43	-0.57	-0.55	-0.29	-0.55	-0.41	-0.40	-0.35	-0.05
		Winter	-0.50	-0.38	-0.52	-0.46	-0.28	-0.37	-0.31	-0.23	-0.18	0.07
		Summer	-0.36	-0.17	-0.21	-0.18	-0.16	-0.19	-0.10	-0.12	-0.14	-0.07
		Fall	-0.44	-0.32	-0.40	-0.30	-0.16	-0.31	-0.29	-0.28	-0.16	0.02
Summer SST and PEOF	PDO	Summer	0.48	0.38	0.31	0.15	0.14	0.59	0.51	0.40	0.23	0.00
		Spring	0.33	0.15	0.01	0.03	0.06	0.41	0.22	0.04	-0.05	-0.24
		Winter	0.16	0.03	-0.13	-0.24	-0.14	0.27	0.07	-0.14	-0.30	-0.46
		Fall	-0.01	-0.12	-0.22	-0.29	-0.23	0.07	-0.10	-0.27	-0.38	-0.50
	NOIx	Summer	-0.24	-0.24	-0.17	-0.10	-0.07	-0.38	-0.38	-0.27	-0.16	-0.08
		Spring	-0.30	-0.18	-0.17	-0.07	-0.06	-0.41	-0.29	-0.21	-0.16	-0.05
		Winter	-0.03	0.04	-0.06	0.12	-0.06	-0.07	0.06	0.13	0.19	0.19
		Fall	-0.03	0.22	0.04	0.21	0.01	-0.06	0.21	0.24	0.29	0.24
	SOIx	Summer	-0.11	-0.21	-0.07	-0.01	0.15	-0.25	-0.28	-0.18	-0.20	-0.09
		Spring	-0.31	-0.15	-0.01	0.17	-0.06	-0.41	-0.23	-0.05	0.18	0.21
		Winter	-0.44	-0.27	-0.30	-0.09	-0.24	-0.40	-0.21	-0.11	0.01	0.05
		Fall	-0.08	0.15	0.06	0.12	0.01	-0.15	0.09	0.10	0.14	0.17
	SOI	Summer	-0.16	-0.35	-0.11	0.04	0.02	-0.28	-0.37	-0.19	-0.05	-0.03
		Spring	-0.25	-0.18	-0.09	0.04	-0.06	-0.33	-0.22	-0.04	0.06	0.12
		Winter	-0.25	-0.18	-0.17	-0.03	-0.05	-0.22	-0.14	0.02	0.08	0.16
		Fall	-0.08	0.08	0.01	0.03	-0.01	-0.05	0.10	0.14	0.13	0.15

Legend

	r^2							
	SST				PEOF			
p-value	PDO	NOIx	SOIx	SOI	PDO	NOIx	SOIx	SOI
0.10	0.52	0.28	0.33	0.27	0.28	0.27	0.27	0.27
0.05	0.62	0.34	0.39	0.32	0.33	0.32	0.32	0.32

Fig. 9. Correlations by season between local physical variables (SST and PEOF) found to influence CCS salmon and Dungeness Crab, and basin-scale climate indices (PDO, NOIx, SOIx, SOI, see text for descriptions). Correlations between the local and basin-scale indictors were calculated for the current season and at lags of three seasons into the past for the basin-scale indices. Calculated significance levels account for intra-series correlation in each data type (Eq. (1)). Color indicates the magnitude but not the sign of the significance level of the correlation.

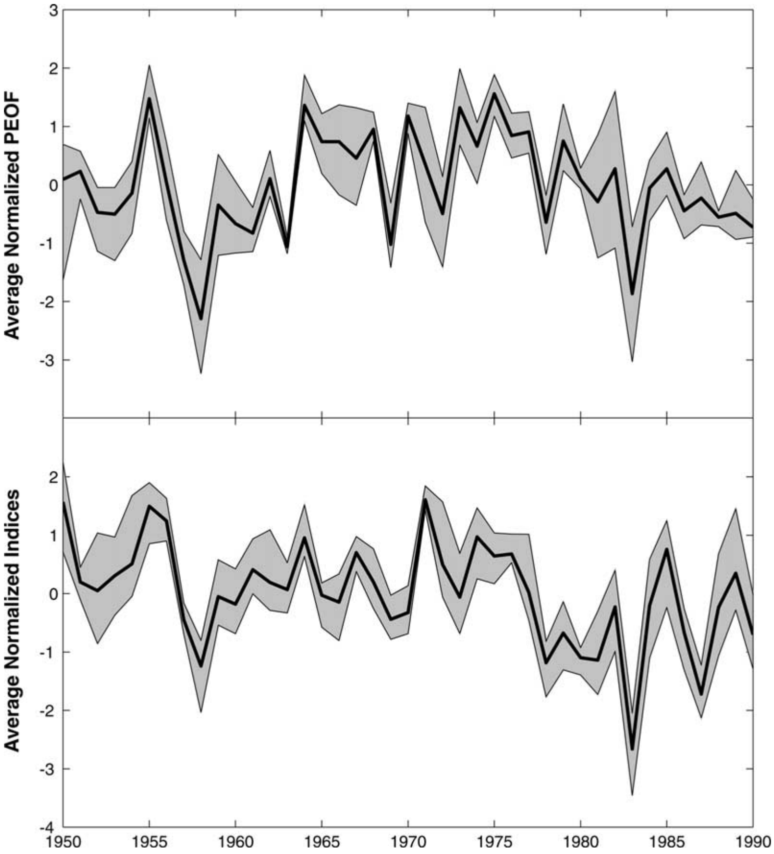


Fig. 10. Comparison of zero mean, unit variance versions of (A) the PEOF and (B) the basin-scale climate indices. In each panel, the mean (heavy line) and the envelope of maximum and minimum values are shown. The PEOF panel (A) includes the time series of PEOF at each of the latitudes used here, 36–37°N, 38–40°N, 41–43°N, 44–46°N, and 47°N. Panel (B) includes all of the climate indices shown in Fig. 9 (PDO, NOIx, SOIx, and SOI), however, the negative of the PDO was used.

4. Discussion

The patterns presented here indicate the variability in salmon populations is more complex than a simple inverse relationship between GOA and California Current stocks. While CCS coho salmon populations did collapse in the mid-1970s, apparently following a shift to warmer conditions (Figs. 2, 3 and 5), there was no uniform decline in CCS chinook salmon, nor did total chinook salmon catch increase in the GOA, as is generally believed. Furthermore, rather than varying synchronously in the CCS, as did coho salmon catches, chinook salmon populations seem to exhibit greater spatial variability, and the effects of physical conditions in the northern CCS differ from those in the south. However, our results do indicate that CCS salmon populations and one associated prey species are significantly influenced by common, coastwide environmental forcing, which is likely to act on these species through variability in biological productivity at lower trophic levels. Furthermore, conditions responsible for this common forcing, represented by the PEOF, co-vary with indices of basin-wide conditions during the 1950s and from 1975–1990.

These findings raise the question for the GLOBEC program as to why the populations of the two dominant CCS salmon species, coho and chinook, behave differently. Chinook salmon have much more varied life history, in terms of the age distribution of spawning and time spent in fresh water (i.e. ocean versus stream types). However, this variation is more likely to cause difficulties in detecting physical–biological linkages than to be responsible for completely different mechanisms. Chinook salmon spend more time at sea and migrate farther from their natal streams, thus catches of them may reflect the integration of marine conditions over longer temporal and larger spatial scales. At present there is no clear explanation for these observed differences between the two salmon species.

Many of the results obtained here are neither completely new, nor unexpected; rather, it is their demonstration on a CCS-wide scale that is potentially useful in interpreting results from field studies at specific locations within the CCS. That the physical variability can be described in terms of co-variability in the three variables used in all seasons, at all locations is useful, but unsurprising. Loosely speaking, it is now common to expect either an El Niño year with low upwelling or a La Niña year with high upwelling in the CCS. Also, Kope and Botsford (1990) formulated a similar EOF in central California and found the same dependence of local conditions in the winter on a basin-scale index, the SOI. One advantage of the PEOF description over any of the single raw indicators is that it appears to be more consistently related to biological variability than the other indicators. A second reason for using the PEOF descriptions, rather than single variables, is that it is probably impossible statistically to prove that one of the single variables is the prime cause of observed biological variability anyway, given the consistent co-variability indicated in Table 1. That it is composed of variables that are direct measurements of ocean state, as well as a variable based on the state of the atmosphere (the UWI, which is computed from pressure observations), suggests it may reflect a combination of remote forcing through the ocean and atmospheric teleconnection.

As noted in the introduction, some of the biological dependencies on the physical environment were previously identified at specific locations, but quantification of the spatial scale of these effects and their spatial variability provides further insights. For coho salmon our results are consistent with the positive influence of upwelling as indicated in earlier studies (Cole, 2000; Nickelson, 1986), but the coastwide coherence of abundance and dependence on coastwide PEOF conditions extend the geographic scope of these conclusions. For one, the PEOF is related to the basin scale indicators, whereas spring upwelling is not. The change in coho abundance in the mid-1970s appears to have been coastwide (in contrast to chinook salmon), although its cause remains uncertain. The negative residuals in regressions with upwelling and the PEOF following 1975 suggest there was a fundamental change in the relationship between the biology and the physical environment, which is consistent with Pearcy's (1997) identification of the disappearance of the significant relationship between upwelling and OPI survivals. However, the latter observation may simply indicate that the mean environment is now at such an extreme state that inter-annual variability no longer expresses, i.e. the biological response may be saturated.

For chinook salmon, the effects of the physical environment are not as clear, but the negative effects of PEOF conditions in the south at the age of return is consistent with the findings of Johnson (1988) and Kope and Botsford (1990) regarding the negative influence of ENSO events. The difference in effects of the physical conditions between the north and the south may follow from the inverse relationship between physical conditions in the CCS and conditions in the GOA, and a greater number of fish in northern CCS stocks migrating northward into the GOA. Rainfall and streamflow are also correlated with ENSO conditions, and there is a zonal trend in that dependence, with lower rainfall during ENSO conditions in the northern CCS, and less response in California (Redmond & Koch, 1991). Zonal variability in rainfall is similar on both ENSO and decadal time scales (Dettinger, Cayan, Diaz, & Meko, 1998), and the decadal scale variability accounts for 20–50% of the variance in rainfall (Cayan, Dettinger, Diaz, & Graham, 1998). Variation in rainfall could affect salmon in freshwater, through streamflow, or in the marine environment through outflow. Explanation of the spatial pattern of variability suggested by the SEOF is difficult, and attempts to do so must be prefaced by the caveat that regulations in the 1980s sought to provide special protection to stocks on the Klamath River in northern California and the Columbia River. However, the spatial pattern also appears to be present earlier. A possible contributing factor is suggested by the fact that the two areas that are counter to the expected negative effect of ENSO (central California and northern

Oregon) are areas subject to the largest river outflows (i.e. from the Sacramento River and the Columbia River). In addition to the possible effects of the large rivers themselves, most of the stream-type chinook salmon occur in these rivers. The decline of chinook salmon catches in Georgia Strait appears to have been more clearly linked to physical changes: a shift in bottom and surface temperatures in the Strait, as well as a decrease in Fraser River discharge (Beamish et al., 1995).

The dependence of the Dungeness crab larval stage on cool years (low PEOF) provides a consistent explanation for seemingly disparate explanations for recruitment variability in this species. Wild (1980) noted that warmer years have a negative influence on crab recruitment in California, and proposed a direct effect on egg mortality. This is consistent with the results of McConnaughey, Armstrong, Hickey and Gunderson (1992) and McConnaughey, Armstrong, Hickey and Gunderson (1994) who explained poor recruitment years off Washington on the basis of northward transport, out of the settlement area. Their alongshore transport was calculated from coastal SSH, with high SSH corresponding to northward transport. Recalling the co-variability between temperature and sea level, instead of warmer water leading to higher egg mortality, and northward flows leading to transport beyond the settlement area, both of these correlations may be result from the generally lowering of biological productivity in the California Current during warm years. Other proposed relationships between crab catches and the environment have depended on winds in specific directions (onshore), hence it is difficult to relate them to ENSO or PEOF variability. In addition to the results reported here, we assessed the co-variability between CCS salmon and crab populations identified earlier (Botsford et al., 1982) by computing cross correlations at various lags, but there were no compelling results. The only known strong link between CCS salmon and Dungeness crab is that crab larvae of this species are often an important prey of salmon (e.g. Peterson et al., 1982). If the effects of PEOF conditions on Dungeness crab larvae are mediated through fluctuations in food production, then they may indicate a similar effect on other zooplankton and ichthyoplankton prey of the salmon. It is interesting to note that although this time period has not been the focus of this study, the dramatic decline of the central California Dungeness crab population in the late 1950s has been attributed to a shift in ocean conditions indicated by an increase in the mean ocean temperature (Wild & Tasto, 1983), as well as a population dynamic mechanism (Botsford, 1981).

Interpretation of oceanographic influences on decline in CCS salmon is confounded by the long-term declining trend in the quality of the freshwater habitats of both chinook and coho salmon. Even if we observe that a salmon population has declined synchronously with a change in ocean conditions, we would not be able to separate the marine influence from the influence of the freshwater habitat deterioration without survival data. Even if the ultimate cause of a long-term decline were to be found in the freshwater phase, a decline would be just as likely to occur during a dramatic change in marine conditions, since both freshwater and marine survival determine lifetime survival.

The relationships obtained here raise questions concerning population dynamics that require further elucidation if we are to interpret GLOBEC results. Firstly, how can populations that appear to be subject to the same environmental forcing on 3–7 year time scales (and possibly decadal scales) respond on such different time scales (yearly for coho salmon, 3–5 years for chinook salmon, and 10 years for Dungeness crab)? This is of course possible, but it is contrary to the common assumption that causally related populations and environments vary on similar time scales. A second question arises from the fact that the physical environment appears to affect salmon at both the age of ocean entry and the age of return to freshwater to spawn. How do these effects combine in these two different species, and what will the GLOBEC field program be missing by studying only the juvenile stage (intensive sampling of the adult stage would be prohibitively expensive)? Thirdly what differences should we expect in the responses of coho salmon and chinook salmon to the environment based on their different age distributions of spawning? As noted above, there will be differences in detectability of effects on survival at younger ages from observations of adults, but it is doubtful that such differences in age structure underlie the fact that coho salmon stocks have collapsed, while those of chinook have not. There is also a trend toward chinook spawning at older ages in the north, but that is unlikely to be the source of the spatial variability in environmental effects. However, the differing age structure may partially explain the difference in temporal scale of response (annual versus several years). We are pursuing answers to each of these questions.

In addition to the need for population modeling efforts and observational approaches, our results also imply that additional retrospective analyses will be fruitful. Our exploratory analysis of catch data is merely a first step necessary because the initial suggestions of inverse variability were made using the catch data. Although other types of biological data avoid some of the problems associated with catch data, invoke other problems. We are pursuing analyses of spawner data, which are not as broadly and consistently available as catch, as well as survival data, which are available primarily for hatchery fish.

In summary, this exploratory search for patterns that might be useful in interpretation of results of GLOBEC field studies has yielded some clear changes in perception of recent changes in the CCS, and other, less certain suggestions of previously unreported variability. It is clear that:

1. There was not a uniform decline in CCS chinook salmon populations in the mid-1970s (nor did total GOA chinook populations increase).
2. These three CCS species appear to be driven by common ecosystem level physical forcing manifested in warm/cool years, and
3. The conditions driving the ecosystem are related to conditions at the basin scale, at least during the 1950s and 1975–1990.

Less certain suggestions include that:

1. There appears to be a spatial pattern to the chinook salmon variability.
2. Physical forcing of chinook salmon differs from that of coho salmon, hence mechanisms may be different, and
3. The physical mechanism forcing coho salmon populations may have changed in the mid-1970s, so this species may not be merely following the same mechanism through a dramatic change in physical conditions.

The latter group of suggestions must be regarded as hypotheses for possible mechanisms that are consistent with the (imperfect) observations, but with no claim to proof. As noted above, not only are catch records not an accurate reflection of abundance, but also the three physical variables are only indices of possible changes in circulation and hydrography. Moreover, we are limited statistically in trying to interpret such slow changes with these short data series. Ongoing next steps in these investigations are:

1. To answer the population dynamic questions raised above.
2. To analyze spawner and survival data, which although are not available over as broad a geographical range, and are location specific, but are not dependent on fishing effort.

Acknowledgements

This work was supported by GLOBEC NEP grant OCE-9711448. We thank Steve Bennett and Linda Bernheim for computational assistance. We thank Hal Batchelder, Peter Moyle, Robert Kope, Bill Pearcy, Tom Wainwright and Ron Yoshiyama for comments on this manuscript.

References

Barton, A. C. K. (1980). *Factors influencing the life history of spring chinook salmon (Oncorhynchus tshawytscha) spawning in the Columbia River watershed from 1960-1977*. PhD dissertation, Oregon State University, Corvallis, 243 pp.

Beamish, R. J., & Bouillon, D. R. (1993). Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 1002–1016.

Beamish, R. J., Noakes, D. J., McFarlane, G. A., Pinnix, W., Sweeting, R., & King, J. (2000). Trends in coho marine survival in relation to the regime concept. *Fisheries Oceanography*, *9*, 114–119.

Beamish, R. J., Riddell, B. E., Neville, C. E. M., Thomson, B. L., & Zhang, Z. (1995). Declines in chinook salmon catches in the Strait of Georgia in relation to shifts in the marine environment. *Fisheries Oceanography*, *4*, 243–256.

Botsford, L. W. (1981). The effects of increased individual growth rates on depressed population size. *American Naturalist*, *117*, 38–63.

Botsford, L. W. (1984). Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*, 99–107.

Botsford, L. W., Armstrong, D. A., & Shenker, J. M. (1989). Oceanographic influences on the dynamics of commercially fished populations. In M. R. Landry, & B. M. Hickey (Eds.), *Coastal Oceanography of Washington and Oregon* (pp. 511–565). Amsterdam: Elsevier.

Botsford, L. W., & Brittnacher, J. G. (1998). Viability of Sacramento River Winter-Run Chinook Salmon. *Conservation Biology*, *12*, 65–79.

Botsford, L. W., Methot, R. D. Jr., & Wilen, J. E. (1982). Cyclic covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries. *Fishery Bulletin, U.S.*, *80*, 791–801.

Botsford, L. W., & Paulsen, C. (1999). Co-variability in abundance among substocks of Columbia River spring/summer chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 616–627.

Brodeur, R. D., Frost, B. W., Hare, S. R., Francis, R. C., & Ingraham, W. J. Jr. (1996). Interannual variations in zooplankton biomass in the Gulf of Alaska and covariation with California Current zooplankton biomass. *California Cooperative Oceanic Fisheries Investigations Reports*, *37*, 80–99.

Cayan, D. R., Dettinger, M. D., Diaz, H. F., & Graham, N. E. (1998). Decadal variability of precipitation over western North America. *Journal of Climate*, *11*, 3148–3166.

Chelton, D. B., Bernal, P. A., & McGowan, J. A. (1982). Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research*, *40*, 1095–1125.

Chelton, D. B., & Davis, R. E. (1982). Monthly mean sea level variability along the west coast of North America. *Journal of Physical Oceanography*, *12*, 757–784.

Cole, J. (2000). Coastal sea surface temperature and coho salmon production off the north-west United States. *Fisheries Oceanography*, *9*, 1–16.

Dettinger, M. D., Cayan, D. R., Diaz, H. F., & Meko, D. M. (1998). North-south precipitation patterns in western North America on interannual-to-decadal time scales. *Journal of Climate*, *11*, 3095–3111.

Francis, R. C., & Hare, S. R. (1994). Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: A case for historical science. *Fisheries Oceanography*, *3*, 279–291.

Francis, R. C., Hare, S. R., Hollowed, A. B., & Wooster, W. S. (1998). Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, *7*, 1–21.

Francis, R. C., & Sibley, T. H. (1991). Climate change and fisheries: What are the real issues? *The Northwest Environmental Journal*, *7*, 295–307.

Hare, S. R., & Francis, R. C. (1995). Climate change and salmon production in the northeast Pacific Ocean. In R. J. Beamish (Ed.), *Climate Change and Northern Fish Populations* (pp. 357–372). Canadian Special Publication of Fisheries and Aquatic Sciences, 121.

Hare, S. R., Mantua, N. J., & Francis, R. C. (1999). Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries*, *24*, 6–14.

Healey, M. C. (1991). Life history of chinook salmon (*Oncorhynchus tshawytscha*). In C. Groot, & L. Margolis (Eds.), *Pacific salmon life histories* (pp. 311–393). Vancouver: UBC Press.

van Hyning, J. M. (1973). Factors affecting the abundance of fall chinook salmon in the Columbia River. *Oregon Fishery Commision Research Report*, *4*, 87 p.

Johnson, S. L. (1988). The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. *Fisheries Research*, *6*, 105–123.

Kope, R. G., & Botsford, L. W. (1990). Determination of factors affecting recruitment of chinook salmon, *Oncorhynchus tshawytscha*, in central California. *Fishery Bulletin US*, *88*, 257–269.

Lagerloef, G. S. E. (1995). Interdecadal variations in the Alaska Gyre. *Journal of Physical Oceanography*, *25*, 2242–2258.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, *78*, 1069–1079.

McConnaughey, R. A., Armstrong, D. A., Hickey, B. M., & Gunderson, D. R. (1992). Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 2024–2028.

McConnaughey, R. A., Armstrong, D. A., Hickey, B. M., & Gunderson, D. R. (1994). Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: Larval advection and the coastal landing strip. *Fisheries Oceanography*, *3*, 22–38.

McGowan, J. A., Cayan, D. R., & Dorman, L. M. (1998). Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science*, *281*, 210–217.

McGowan, J. A., Chelton, D. B., & Conversi, A. (1996). Plankton patterns, climate and change in the California Current. *California Cooperative Oceanic Fisheries Investigations Reports*, *37*, 45–68.

Mendelssohn, R. & Roy, C. (1996). Comprehensive Ocean Data Extraction Users Guide. *NOAA Technical Memorandum NOAA-TM-NMFS-SWFC-228*, 67 pp.

Miller, A. J. (1996). Recent advances in California Current modeling: Decadal variation. *California Cooperative Oceanic Fisheries Investigations Reports*, *37*, 69–79.

Myers, J. M., Kope, R. G., Bryant, G. J., Teel, D., Lierheimer, L. J., Wainwright, T. C., Grant, W. S., Waknitz, F. W., Neely, K., Lindley, S. T., & Waples, R.S. (1998). Status review of chinook salmon from Washington, Idaho, Oregon and California. *NOAA Technical Memorandum NMFS-NWFSC-35.*

Myers, K. W., Walker, R. V., Davis, N. D, Aydin, K. Y., Hyun, S.-Y., Hilborn, R. W., & Burgner, R.L. (1999). Migrations, abundance, and origins of salmonids in offshore waters of the north Pacific, 1999. *Annual Report, High Seas Salmon Research Program*, FRI-UW-9909.

Nicholas, J. W., & Hankin, D. G. (1988). Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths. *Oregon Department of Fish and Wildlife, Information Report*, 88-1.

Nickelson, T. E. (1986). Influences of upwelling, ocean temperature and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in Oregon production area. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*, 527–535.

Pacific Fishery Management Council. (1996). *Review of 1995 Ocean Salmon Fisheries.*

Pacific Marine Fisheries Commission. (1993). *Historical Ocean Salmon Fishery Data for Washington, Oregon and California. September 1993*. 254 pp.

Pearcy, W. G. (1992). In *Ocean Ecology of North Pacific Salmonids* (p. 179). Seattle: University of Washington Press.

Pearcy, W. G. (1997). Salmon production in changing ocean domains. In D. J. Stouder, P. A. Bisson, & R. J. Naiman (Eds.), *Pacific salmon and their ecosystems: Status and future options* (pp. 331–352). San Francisco: Chapman and Hall.

Pennington, J. T., & Chavez, F. P. (2000). Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989–1996 in Monterey Bay, California. *Deep-Sea Research II*, *47*, 947–973.

Peterson, W. T., Brodeur, R. D., & Pearcy, W. G. (1982). Food habits of juvenile salmon in the Oregon coastal zone, June 1979. *Fishery Bulletin US*, *80*, 841–851.

Polovina, J. J., Mitchum, G. T., & Evans, G. T. (1995). Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960–1988. *Deep-Sea Research I*, *42*, 1701–1716.

Polovina, J. J., Mitchum, G. T., Graham, N. E., Craig, M. P., Demartini, E. E., & Flint, E. N. (1994). Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography*, *3*, 15–21.

Pyper, B. J., & Peterman, R. M. (1998). Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2127–2140.

Redmond, K. T., & Koch, R. W. (1991). Surface climate and streamflow variability in the western United States and their relationship to large-scale circulation indices. *Water Resources Research*, *27*, 2381–2399.

Roemmich, D. (1989). Mean transport of mass, heat, salt and nutrients in southern California coastal waters - implications for primary production and nutrient cycling. *Deep-Sea Research A*, *36*, 1359–1378.

Roemmich, D., & McGowan, J. A. (1995). Climate warming and the decline of zooplankton in the California Current. *Science*, *267*, 1324–1326.

Ryding, K. E., & Skalski, J. R. (1999). Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 2374–2384.

Strub, P. T., & James, C. (2000). Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. *Deep-Sea Research II*, *47*, 831–870.

Venrick, E. L., McGowan, J. A., Cayan, D. R., & Hayward, T. L. (1987). Climate and chlorophyll-a: long term trends in the central North Pacific Ocean. *Science*, *238*, 70–72.

Weitkamp, L. A., Wainwright, T. C., Bryant, G. J., Milner, G. B., Teel, D. J., Kope, R. G., & Waples, R.S. (1995). Status review of coho salmon from Washington, Oregon and California. *NOAA Technical Memorandum NMFS-NWFSC-24.*

Wild, P. W. (1980). Effects of seawater temperature on spawning, egg development, hatching success and population fluctuations of the Dungeness crab, *Cancer magister*. *California Cooperative Oceanic Fisheries Investigations Reports*, *21*, 115–120.

Wild, P. W., & Tasto, R.N. (1983). Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. *California Department of Fish and Game Fish Bulletin, 172.*