

The Influence of Climate on the Stock and Recruitment of Pink and Sockeye Salmon from the Fraser River, British Columbia, Canada

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Abstract.—The relationships between the spawning stock and the subsequent recruitment of pink salmon *Oncorhynchus gorbuscha* and sockeye salmon *O. nerka* from the Fraser River improve significantly when the data are separated by climate and ocean regimes. Our analyses show changes in these relationships as regimes shift, indicating that the trend in marine survival of pink and sockeye salmon changes on a decadal scale. In general, the climate and ocean regime from 1977 to 1988 was productive for pink and sockeye salmon. However, the regime in the 1990s was characterized by reduced productivity for both species. The occurrence of a natural shift in the trend of pink and sockeye salmon production on a decadal scale should be incorporated into the management of Pacific salmon stocks to ensure that annual catches, escapements, and planned stock abundances are consistent with the productivity of a particular regime.

Ricker (1954, 1958a) proposed a dome-shaped relationship between the abundance of a spawning stock of Pacific salmon (*Oncorhynchus* spp.) and the subsequent return of adults. Similarly, Beverton and Holt (1957) used an asymptotic curve to represent this relationship for various marine species. Either approach, however, leaves open the possibility that the environment might alter the productivity of a spawning stock. Ricker (1958b) recognized the need to investigate the influence of climate when he examined more carefully the population dynamics of Pacific salmon in the Fraser River. In his computations, he assumed that the kinds of weather which affect Pacific salmon reproduction had not been shown to have recognizable trends (Ricker 1958b). This assumption meant that climate had a random annual influence on Pacific salmon. We now know that this assumption is not valid, given solid evidence of trends in climate that persist on decadal-scales and shift quickly to new states (Trenberth 1990; Mantua et al. 1997; Zhang et al. 1997; Thompson and Wallace 1998; Beamish et al. 2000; Minobe 2000; Benson and Trites 2002; Yasunaka and Hanawa 2002).

Climatologists now accept the reality of rapid climate change, as revealed by the 1993 analysis of the Greenland ice cores (Weart 2003). Recent studies have also shown that decadal-scale variability, and rapid shifts in climate have been a feature of the Pacific North American climate for

at least the past 400 years (Gedalof and Smith 2001). This reality makes it important to assess the relationship between stock and recruitment via the mode of climate variability that best captures the effect of climate and ocean conditions on the production of the species. Clark and Hare (2002) carried out such an analysis for Pacific halibut *Hippoglossus stenolepis* with rather astonishing results. Their data are among the best available in the history of fisheries management because the International Pacific Halibut Commission has assessed the Pacific halibut population continuously since its establishment in the 1920s. The authors showed that environmental variability was responsible for most variation in recruitment. They hypothesized that spawning biomass limits recruitment at some “sufficiently low level” but found the current approach to management ensured that this low level never occurred. Fishing effects were not found to affect recruitment. Instead, recruitment related directly to the productivity associated with trends in climate (Clark and Hare 2002).

States in climate that persist on a decadal scale have been termed regimes, and the abrupt transition to a new regime is called a regime shift (Latif and Barnett 1994; Hare and Francis 1995; Zhang et al. 1997; Beamish et al. 1999; Minobe 2000; Benson and Trites 2002; Yasunaka and Hanawa 2002). Accumulating evidence demonstrates that regimes are real (Hurrell 1995; Mantua et al. 1997; Thompson and Wallace 1998; Overland et al. 1999) and that these climate-ocean states are as-

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sociated with reorganizations in the structure of ocean communities (Beamish and Bouillon 1993; Mantua et al. 1997; Hare and Mantua 2000; McFarlane et al. 2000; Gregg 2002). The existence of trends in the physical environment of fish has fundamental implications for the assumptions used to assess the dynamics of Pacific salmon populations and probably other fish species as well.

In this study, we evaluate the relationships among stock, recruitment, and climate for the same population of pink salmon *O. gorbuscha* from the Fraser River investigated by Ricker (1958b). We also assess the effect of regime shifts in climate on the stock and recruitment relationships for the population of sockeye salmon *O. nerka* investigated in our earlier paper (Beamish et al. 1997). The regime in the 1990s changed in 1998 (Hare and Mantua 2000; McFarlane et al. 2000; Beamish et al. 2001; Minobe 2002; Bond et al. 2003; Chavez et al. 2003; Peterson and Schwing 2003), providing an opportunity to assess recent changes in sockeye salmon productivity trends since the publication by Beamish et al. (1997).

Methods

Pink Salmon Biology

Pink salmon have a 2-year life cycle in which they spawn in freshwater in the fall and the fry emerge from the spawning gravel in the following spring (Heard 1991). The fry migrate almost immediately into the ocean. Juveniles rear in the Strait of Georgia for several months before migrating into the Gulf of Alaska where they live for approximately 1 year. In the second summer or fall, they return to spawn in their natal streams. In the Fraser River, virtually all pink salmon spawn in odd-numbered years and enter the marine environment in even-numbered years (Neave 1952). Thus, pink salmon adults returning to spawn all originate from a single brood year or year-class, unlike other Pacific salmon. The return of adults to spawn only in odd-numbered years results in references to the Fraser River pink salmon population as an "odd-year run." The population of pink salmon in the Fraser River is the largest south of Alaska. There are approximately 100 rivers and streams within the Fraser River watershed that support spawning populations of pink salmon. Reliable estimates of escapements (fish that escaped the fishery and enter the river where they can spawn) from 1959 to 2000 ranged from approximately 1–13 million fish. The largest escapement in recorded history occurred in 2001, when over

20 million fish escaped to spawn and probably increased the number of spawning areas.

Sockeye Salmon Biology

The Fraser River is one of the major areas of sockeye salmon production on Canada's Pacific coast and throughout the range of sockeye salmon in the subarctic Pacific. About 100 stocks of sockeye salmon spawn in the river. These are grouped for management purposes into run-groups: early, summer, and late. Most sockeye salmon spawn in the fall; the fry emerge from the gravel in the following spring and enter a lake close to the spawning area. Most juvenile sockeye salmon remain in lakes for 1 year and migrate into the Strait of Georgia in their second year of life. Most of them remain in the ocean for approximately 2 years before returning at age 4 to spawn. Smaller numbers may remain in the ocean 1 more year, and some fry remain in freshwater for 2 years. Some stocks have a persistent 3-year pattern of cyclic predominance in which year 1 results in large returns, and years 2 and 3 demonstrate reduced abundance. Although a number of mechanisms have been proposed to explain the cyclic dominance pattern, there is no consensus (Larkin 1971; Collie and Walters 1987; Eggert and Rogers 1987; Walters and Staley 1987; Collie et al. 1990; Welch and Noakes 1990, 1991; Cass and Wood 1994; Ricker 1997; Meyers et al. 1998).

When juvenile sockeye salmon enter the Strait of Georgia, most move quickly out of the strait and into the coastal areas where they eventually migrate north, finding their way into the Gulf of Alaska in the next spring. They remain in this area through to the next spring or summer when they return to the Fraser River to spawn. The early Stuart group of stocks enters the river first, arriving between late June and late July. These stocks are followed in sequence by a series of stock groupings, with the last group entering the river from late September to the end of October. The numbers of sockeye salmon in the spawning populations were estimated via mark-recapture methods that have been shown to be reliable (Schubert 2000).

Regimes

Our analyses use data from standard indices of climate and ocean trends, computed as anomalies from a standard base period. We focus on three particular indices (Figure 1): the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), the Arctic Oscillation (AO; Thompson and Wallace 1998), and the Aleutian low pressure index (ALPI; Beam-

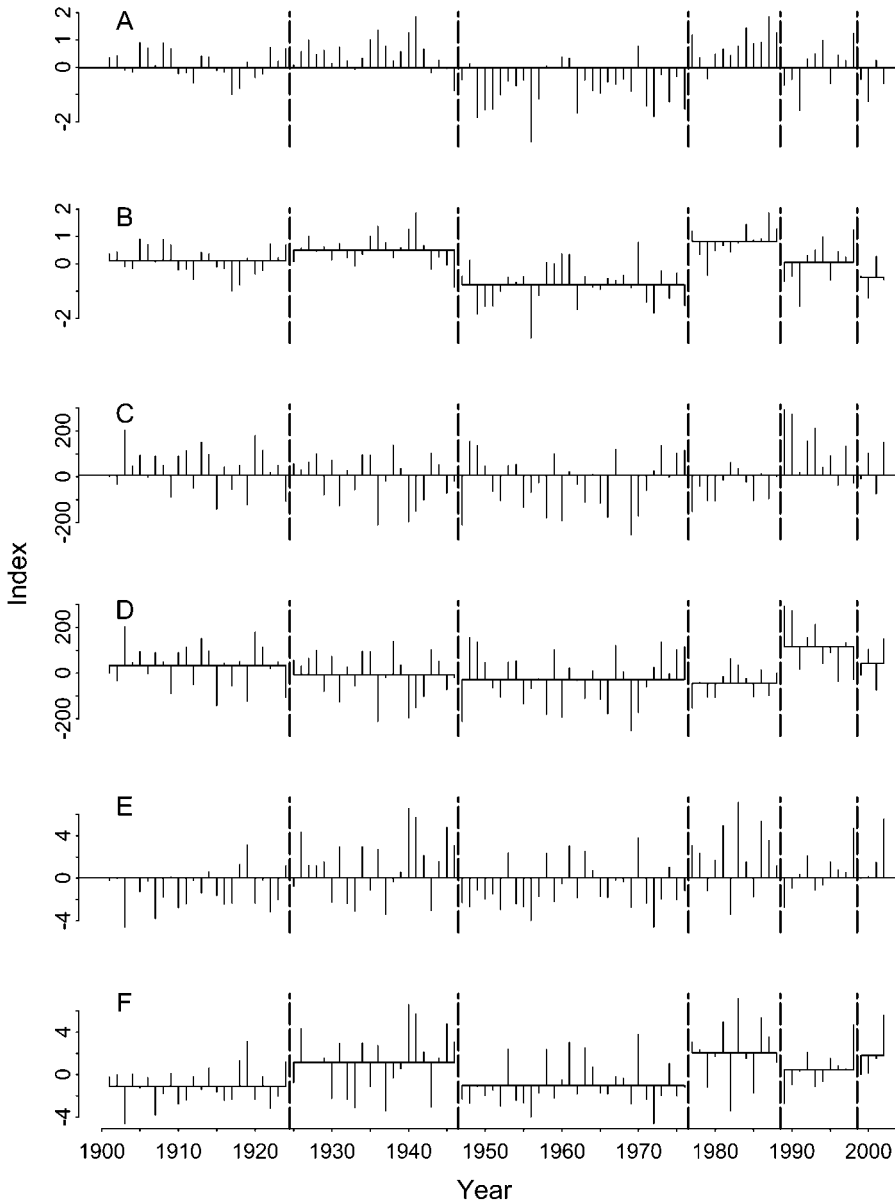


FIGURE 1.—Environmental data series pertaining to the Fraser River, showing the residuals (solid vertical lines) in relation to the hypotheses M0 (single mean for the entire series) and M1 (mean for each regime), which are described in Table 2, where panel (A) examines the MO hypothesis and Pacific Decadal Oscillation (PDO), panel (B) examines the M1 hypothesis and PDO, panel (C) examines the MO hypothesis and Arctic Oscillation (AO), panel (D) examines the M2 hypothesis and AO, panel (E) examines the MO hypothesis and the Aleutian low pressure index (ALPI), and panel (F) examines the M1 hypothesis and ALPI. Vertical dashed lines indicate breaks between six climate regimes: 1901–1924, 1925–1946, 1947–1976, 1977–1988, 1989–1998, 1999–2002. Regime shift years are 1925, 1947, 1977, 1989, and 1998.

ish et al. 1997). Consistent with the interpretations from other studies, such as Minobe (1997), Mantua et al. (1997) and Hare and Mantua (2000), we examine regime shifts in 1925, 1947, 1977, 1989,

and 1998 (Table 1). Minobe (2000) and Yasunaka and Hanawa (2002) considered some regimes shifts to be minor and some major, but we use the years common to most studies. Only the regime

TABLE 1.—Regime periods examined and associated brood (spawning) years, years to sea, and return years for pink and sockeye salmon from the Fraser River.

| Regime | Regime periods | Pink salmon | | | Sockeye salmon | | |
|--------|------------------------|-------------|-------------|-------------|----------------|-------------|-------------|
| | | Brood year | Year to sea | Return year | Brood year | Year to sea | Return year |
| I | 1947–1976 | 1959–1975 | 1960–1976 | 1961–1977 | 1957–1974 | 1959–1976 | 1961–1978 |
| II | 1977–1988 | 1977–1987 | 1978–1988 | 1979–1989 | 1975–1986 | 1977–1988 | 1979–1990 |
| III | 1989–1998 ^a | 1989–1997 | 1990–1998 | 1991–1999 | 1987–1996 | 1989–1998 | 1991–2000 |

^a As explained in the text, both the terminal year of regime III and a regime shift year.

shift years 1976–77, 1988–89, and 1998–99 are considered in our study because reliable stock and recruitment data are not available for pink and sockeye salmon until the 1950s. These define four regimes: (I) the period up to 1976, (II) 1977–1988, (III) 1989–1998, and (IV) the period after 1998 (Table 1).

Stock–Recruitment Regime Models

Classical analysis of variance (ANOVA) offers a convenient statistical framework for investigating the effect of trends in climate on the relationship between stock and recruitment. Let y_t denote an index available for a sequence of years t divided into n alleged regime periods, where break points between regimes occur in years t_i ($i = 0, \dots, n$). Regime i corresponds to the period

$$T_i = \{t | t_{i-1} < t \leq t_i\} \tag{1}$$

that starts in year $t_{i-1} + 1$ and ends in year t_i . The total time series, y_t , spans the years from $t_0 + 1$ to t_n . Suppose that y_t varies randomly around a mean level μ_i during each regime i :

$$y_{it} = \mu_i + \varepsilon_{it}, \tag{2}$$

where independent normal residuals have mean 0 and variance σ^2 : $\varepsilon_{it} \sim N(0, \sigma^2)$. The logic of ANOVA suggests testing the null hypothesis

$$H_0: \mu_1 = \mu_2 = \dots = \mu_n \tag{3}$$

against the alternative

$$H_1: \mu_1 \neq \mu_2 \neq \dots \neq \mu_n. \tag{4}$$

In practical terms, we ask whether or not the data justify using n parameters μ_i in the model (2) rather than a single common mean. Do the observations y_t really distinguish the regimes from one another?

A variant of this idea allows us to test changes in the relationship between y_t and some other measured variable x_t . For example, the linear relationship $y_t = a + bx_t$ might have parameters (a, b) that change among regimes, as in the model

$$y_{it} = a_i + b_i x_{it} + \varepsilon_{it}, \tag{5}$$

again with independent normal residuals $\varepsilon_{it} \sim N(0, \sigma^2)$. By analogy with (3) and (4), we can investigate the null hypothesis

$$H_0: a_1 = a_2 = \dots = a_n, b_1 = b_2 = \dots = b_n, \tag{6}$$

against various alternatives, such as

$$H_1: a_1 \neq a_2 \neq \dots \neq a_n, b_1 = b_2 = \dots = b_n \tag{7}$$

or

$$H_1': a_1 \neq a_2 \neq \dots \neq a_n, b_1 \neq b_2 \neq \dots \neq b_n. \tag{8}$$

In (7), only the intercept a_i varies among regimes, but the slope b remains the same. In (8), the linear relationship between y_t and x_t changes completely from regime to regime. Another analysis might compare models (2) and (5), which are the same when $b_i = 0$ and $a_i = \mu_i$. Do the data support the assumption that y_t actually depends on x_t ? Answering this question might involve testing the null hypothesis

$$H_0': a_1 \neq a_2 \neq \dots \neq a_n, b_1 = b_2 = \dots = b_n = 0 \tag{9}$$

against the alternative H_1 or H_1' .

Table 2 lists four special cases of the model (5), in which observations y_{it} potentially depend on the regime i and other measurements x_{it} . We use these in subsequent analyses as null (H_0) and alternative (H_1) hypotheses in ANOVA tests based on the statistic

$$F = \frac{(S_0 - S_1)/(f_0 - f_1)}{S_1/f_1}, \tag{10}$$

where S_j and f_j denote the sum of squared residuals and degrees of freedom associated with hypothesis H_j ($j = 0, 1$). If the null hypothesis is true, this statistic follows the F -distribution with $f_0 - f_1$ and f_1 degrees of freedom.

Models (2) and (5) give regimes the same status

TABLE 2.—Hypotheses, as related to Fraser River pink and sockeye salmon production, for the linear model $y_{it} = a_i + b_i x_{it}$ for data (x_{it}, y_{it}) associated with year t in regime i , where N years of data span n regimes. The number of observations minus the number of free parameters gives the remaining degrees of freedom shown for each of the hypotheses.

| Hypothesis | Model | df | Description |
|------------|--|----------|--|
| M0 | $a_1 = a_2 = \dots = a_n = a$ $b_1 = b_2 = \dots = b_n = 0$ | $N - 1$ | Single mean for the entire data series |
| M1 | $a_1 \neq a_2 \neq \dots \neq a_n$ $b_1 = b_2 = \dots = b_n = 0$ | $N - n$ | Mean for each regime |
| L0 | $a_1 = a_2 = \dots = a_n = a$ $b_1 = b_2 = \dots = b_n = b$ | $N - 2$ | Single line for the entire data series |
| L1 | $a_1 \neq a_2 \neq \dots \neq a_n$ $b_1 \neq b_2 \neq \dots \neq b_n$ | $N - 2n$ | Distinct line for each regime |

as treatments in an experimental design. Different environmental conditions produce different means μ_i or relationships $y_t = a_i + b_i x_t$. Skeptical readers can justifiably raise at least two objections to this approach. First, unlike experimental controls, regime boundary years t_i are not certain. The subscript t in model (2), which looks like a classical treatment index, actually comes from the year t and regime definitions for model (1). Technically, the year t implies the index i , which appears redundantly in expressions like y_{it} . We could pick regime shift years that give highest support for rejecting the null hypothesis, analogous to defining experimental treatments after the data have been collected. Second, unlike an experiment with independent observations, the measurements y_t occur in serial order. They may have serial correlation or other structural properties of time series that violate the assumption of independent residuals ε_{it} in models (2) and (5).

In this paper, we can deal easily with the first objection. We identify regimes entirely from other literature, where particular years t_i are accepted regime shift years. To deal with the second objection, we would need to examine a variety of time series models that involve extra parameters and theoretical issues beyond the scope of this paper. We believe that the added complexity would actually detract from our message that regimes can alter salmon stock–recruitment relationships. Rather, we use relatively simple concepts from ANOVA as tools for exploratory data analysis with

at least some statistical grounds for assessing significant differences.

To link the statistical models above with salmon population dynamics, we use the relationship between spawning stock S and subsequent recruitment R proposed by Deriso (1980) and Schnute (1985):

$$R = \alpha S(1 - \beta \gamma S)^{1/\gamma}, \tag{11}$$

which has three parameters (α, β, γ) . Table 3 shows three special cases of historical interest that correspond to particular values of the parameter γ . Each one takes the form of model (5), given appropriate definitions for a, b, x , and y . For example, in the limit as $\gamma \rightarrow 0$, model (11) reduces to the Ricker form

$$R = \alpha S e^{-\beta S}, \tag{12}$$

which becomes a linear relationship,

$$y = a + bx, \tag{13}$$

after the substitutions

$$x = S, y = \log(R/S), a = \log \alpha, b = -\beta. \tag{14}$$

Data compilation requires careful attention to the year t . For example, suppose that a salmon stock spawns in year $t - 1$, produces fry that go to sea in year t , and finally generates adult recruitment in year $t + 1$. If we want data (x_t, y_t)

TABLE 3.—Three special cases of the stock–recruitment function (equation 11 in the text), corresponding to parameter values $\gamma = -1, 0$, and 1 . Each has a historical precedent, as indicated by the references. Furthermore, using the listed expressions for a, b, x , and y , each function takes the linear form $y = a + bx$, as in model (5).

| γ | Historical reference | Function | a | b | x | y |
|----------|--------------------------|--------------------------------|---------------|----------------|-----|-------------|
| -1 | Beverton and Holt (1957) | $R = \alpha S / (1 + \beta S)$ | $1/\alpha$ | β/α | S | S/R |
| 0 | Ricker (1954, 1958a) | $R = \alpha S e^{-\beta S}$ | $\log \alpha$ | $-\beta$ | S | $\log(R/S)$ |
| 1 | Schaeffer (1954) | $R = \alpha S(1 - \beta S)$ | α | $-\alpha\beta$ | S | R/S |

TABLE 4.—Escapement, total return, and recruits/spawner (R/S) index for Fraser River pink salmon from brood (spawning) years 1959–1997 or migration years (“years to sea”) 1960–1998. Standard deviations are in parentheses.

| Regime | Brood year | Year to sea | Escapement ($\times 10^6$) | Total return ($\times 10^6$) | R/S index |
|--------|------------|-------------|------------------------------|--------------------------------|-------------|
| I | 1959 | 1960 | 1.078 | 1.889 | 1.75 |
| | 1961 | 1962 | 1.094 | 5.477 | 5.01 |
| | 1963 | 1964 | 1.953 | 2.320 | 1.19 |
| | 1965 | 1966 | 1.191 | 12.963 | 10.89 |
| | 1967 | 1968 | 1.831 | 3.928 | 2.15 |
| | 1969 | 1970 | 1.529 | 9.767 | 6.39 |
| | 1971 | 1972 | 1.804 | 6.789 | 3.76 |
| | 1973 | 1974 | 1.754 | 4.894 | 2.79 |
| | 1975 | 1976 | 1.367 | 8.209 | 6.01 |
| | Average | | | | |
| II | 1977 | 1978 | 2.388 | 14.404 | 6.03 |
| | 1979 | 1980 | 3.561 | 18.685 | 5.25 |
| | 1981 | 1982 | 4.488 | 15.346 | 3.42 |
| | 1983 | 1984 | 4.632 | 19.104 | 4.12 |
| | 1985 | 1986 | 6.461 | 7.172 | 1.11 |
| | 1987 | 1988 | 3.224 | 16.484 | 5.11 |
| | Average | | | | |
| III | 1989 | 1990 | 7.189 | 22.173 | 3.08 |
| | 1991 | 1992 | 12.943 | 16.983 | 1.31 |
| | 1993 | 1994 | 10.768 | 12.904 | 1.2 |
| | 1995 | 1996 | 7.175 | 8.176 | 1.14 |
| | 1997 | 1998 | 2.842 | 3.586 | 1.26 |
| | Average | | | | |

relevant to ocean conditions in year t , when juveniles enter the marine environment, then a Ricker version of model (5) implies the calculation (Table 3)

$$x_t = S_{t-1}, y_t = \log(R_{t+1}/S_{t-1}),$$

where the subscripts on R and S indicate the years in which measurements were actually taken. In general, the calculated value y_t depends on the stock–recruitment model chosen in Table 3.

Our analyses depend primarily on the Ricker model (12–13), where $y = \log(R/S)$ measures productivity on a logarithmic scale. In this context, the four hypotheses (Table 2) about the corresponding linear relationship $y_{ti} = a_i + b_i x_{ti}$ have biological interpretations related to productivity and stock-dependent Ricker curves:

M0: no stock dependence and a common productivity for the entire data series;

M1: no stock dependence but a mean productivity that varies with regimes;

L0: a single Ricker curve for the entire data series;

L1: a distinct Ricker curve for each regime.

Linear regression gives parameter estimates (\hat{a}_i, \hat{b}_i) for each hypothesis. From equation (14), these imply corresponding estimates $\hat{\alpha}_i = e^{\hat{a}_i}$ and $\hat{\beta}_i = -\hat{b}_i$ for the Ricker parameters.

We use this analytical framework to explore four key biological questions, where the answer to each depends on a particular hypothesis test.

- (1) Does mean productivity vary with regimes? Resolve this by testing the alternative hypothesis M1 against the null hypothesis M0.
- (2) Does productivity vary with stock size; that is, do the data justify a Ricker curve? Test the alternative L0 against the null hypothesis M0.
- (3) Does the Ricker curve vary with regimes? Test the alternative L1 against the null hypothesis L0.
- (4) Given that mean productivity varies among regimes, does productivity also depend on stock size, with a distinct Ricker curve for each regime? Test the alternative L1 against the null hypothesis M1.

Treatment of Pacific Salmon Data

Our catch and escapement data for pink salmon from the Fraser River come from the Pacific Salmon Commission for the period 1959–1999 (PSC 1988, 1990, 1996, 1999, 2001; Table 4). Like Pacific halibut (Clark and Hare 2002), Fraser River sockeye salmon stocks have a particularly reliable data series maintained under a sophisticated international management system. The numbers of spawning fish and the resulting catch from each spawning were estimated initially by the Interna-

TABLE 5.—Escapement, total return, and recruits/spawner (*R/S*) index for Fraser River sockeye salmon from brood (spawning) years 1957–1996 or migration years (“years to sea”) 1959–1998. Standard deviations are in parentheses.

| Regime | Brood year | Year to sea | Escapement ($\times 10^6$) | Total returns ($\times 10^6$) | R/S index |
|--------|------------|-------------|------------------------------|---------------------------------|----------------|
| I | 1957 | 1959 | 0.686 | 3.909 | 5.698 |
| | 1958 | 1960 | 1.883 | 3.135 | 1.665 |
| | 1959 | 1961 | 0.473 | 3.453 | 7.307 |
| | 1960 | 1962 | 0.317 | 1.349 | 4.248 |
| | 1961 | 1963 | 0.412 | 2.583 | 6.275 |
| | 1962 | 1964 | 0.821 | 4.707 | 5.734 |
| | 1963 | 1965 | 0.401 | 5.674 | 14.145 |
| | 1964 | 1966 | 0.189 | 2.395 | 12.652 |
| | 1965 | 1967 | 0.301 | 3.763 | 12.483 |
| | 1966 | 1968 | 0.871 | 5.493 | 6.305 |
| | 1967 | 1969 | 0.581 | 6.716 | 11.553 |
| | 1968 | 1970 | 0.246 | 2.937 | 11.935 |
| | 1969 | 1971 | 0.330 | 5.731 | 17.385 |
| | 1970 | 1972 | 0.915 | 7.296 | 7.973 |
| | 1971 | 1973 | 0.359 | 2.853 | 7.947 |
| | 1972 | 1974 | 0.401 | 3.294 | 8.209 |
| | 1973 | 1975 | 0.467 | 4.711 | 10.091 |
| 1974 | 1976 | 0.863 | 8.790 | 10.190 | |
| | Average | | | | 8.989 (3.898) |
| II | 1975 | 1977 | 0.365 | 5.049 | 13.822 |
| | 1976 | 1978 | 0.368 | 2.372 | 6.445 |
| | 1977 | 1979 | 0.351 | 6.734 | 19.198 |
| | 1978 | 1980 | 1.263 | 11.893 | 9.417 |
| | 1979 | 1981 | 0.600 | 3.900 | 6.500 |
| | 1980 | 1982 | 0.364 | 4.373 | 12.012 |
| | 1981 | 1983 | 0.598 | 12.440 | 20.810 |
| | 1982 | 1984 | 1.874 | 13.048 | 6.963 |
| | 1983 | 1985 | 0.405 | 5.378 | 13.269 |
| | 1984 | 1986 | 0.331 | 1.812 | 5.476 |
| | 1985 | 1987 | 1.030 | 17.276 | 16.768 |
| | 1986 | 1988 | 1.656 | 20.134 | 12.157 |
| | Average | | | | 11.903 (5.158) |
| III | 1987 | 1989 | 0.789 | 10.262 | 12.999 |
| | 1988 | 1990 | 0.553 | 4.373 | 7.908 |
| | 1989 | 1991 | 1.558 | 21.145 | 13.571 |
| | 1990 | 1992 | 2.961 | 14.558 | 4.916 |
| | 1991 | 1993 | 1.645 | 2.517 | 1.530 |
| | 1992 | 1994 | 0.540 | 2.863 | 5.302 |
| | 1993 | 1995 | 3.220 | 15.103 | 4.690 |
| | 1994 | 1996 | 1.436 | 6.996 | 4.872 |
| | 1995 | 1997 | 0.798 | 2.563 | 3.212 |
| | 1996 | 1998 | 0.847 | 3.208 | 3.787 |
| | Average | | | | 6.279 (4.034) |

tional Pacific Salmon Fishery Commission (IPFSC) and by its successor, the Pacific Salmon Commission. Since 1985, the Department of Fisheries and Oceans (Canada) has estimated escapements. The escapement data used in our analysis are estimates of females that contribute to spawning (sometimes this estimate is referred to as “effective females”) and not the total number of males and females that are counted in the spawning area (Gilhousen 1990; Table 5). Reliable data are available for 11 stocks or stock complexes that account for approximately 90% of the average total escapement: Quesnel, Raft, Stellako, Early Stuart, Late Stuart, Adams, Birkenhead, Bowron, Chilko,

Seymour, and Pitt. Total returns in our analysis include ages 4 and 5.

We consider that the major effects on marine survival would be in the first ocean year, as observed in the Strait of Georgia for coho salmon *O. kisutch* (Beamish et al. 2004a). This assumption is consistent with the observations from an extensive literature review on the factors affecting the marine survival of Pacific salmon (Symons 2003). We use the year of ocean entry to allocate brood years to specific regimes (Table 1). Note that sockeye salmon juveniles enter the Strait of Georgia every year, and pink salmon juveniles enter every other year. The exact timing of the effect of a regime

shift in the climate on the marine survival of Pacific salmon is unknown, in part because there may be a lag in the productivity response in the ocean and in part because the mechanisms that regulate Pacific salmon productivity in the ocean are still being discovered (Beamish and Mahnken 2001; Beamish et al. 2004a).

As part of another study, we investigated changes in the Strait of Georgia ecosystem before and after the 1998 regime shift. We observed that in the Strait of Georgia, the basinwide change in atmospheric circulation that occurred in mid-1998 was associated with reduced sea surface temperatures in 1999 and increased Pacific salmon productivity in 2000 (Beamish et al. 2004b). There was a doubling of plankton biomass and increases in growth and survival of juvenile Pacific salmon in 2000 (Beamish et al. 2001, 2002a, b; Sweeting et al. 2003). Therefore, our use of established years of regime change probably does not precisely match the years that juvenile Pacific salmon actually experienced a change in the marine ecosystem. We evaluate a possible lag of approximately 1.5 years in the productivity changes of Pacific salmon from the year of a regime shift to the year of impact. We examine two possible scenarios for a lagged response of sockeye salmon to regime shifts. In the first scenario (lag A), juveniles entering the ocean in 1977 and 1978 are considered to be in regime I rather than regime II (Table 1). In regime II, the juveniles would enter the ocean from 1979 to 1990, and in regime III the year of entry would be from 1991 to 1998. We also consider a second scenario (lag B) in which, juvenile sockeye salmon would enter the ocean in regime II from 1979 to 1991 (i.e., we add one more year at the end of lag A). This requires that the year of entry for regime III is 1992. For pink salmon we use only lag A because the entry into the Strait of Georgia only in even-numbered years eliminates the possible relevance of lag B. For pink salmon in lag A, regime I years of entry extend to 1978, regime II years are from 1980 to 1990, and regime III years are from 1992 to 1998. We end our data series with juveniles that entered the ocean in 1998 because the most recent regime shift occurred in mid-1998 (Beamish et al. 2004b). The regime shift in 1998 occurred after juvenile Pacific salmon entered the Strait of Georgia from the Fraser River (Beamish et al. 2002a; Beamish et al. 2004b). As a result, we used the regime shift year of 1998 as part of the previous regime. This was not done in the previous regime shift years of 1989 and 1977

because we did not have evidence of when in the year the shift may have occurred.

The management of sockeye salmon is related to the general timing of the return of aggregates of stocks, as mentioned previously. Our primary analysis examines the effect of regimes and regime shifts on the total returns for the entire aggregate of 11 stocks cited earlier. We also consider the smaller summer aggregate of the Quesnel, Stelako, Chilko, and Late Stuart stocks, which are managed as one summer run.

Results

The average return of sockeye salmon adults from the regime I was 4.4 million and ranged from 1.3 million to 8.8 million sockeye salmon (Table 5). The average return for regime II was 8.7 million (range, 1.8–20.1 million). In regime III, the average return was 8.4 million (range 2.5–21.1 million; Table 5). The total returns of pink salmon to the Fraser River (Table 4), in regime I (Table 1) for the 9 years of catches averaged 6.2 million (range, 1.9–13.0 million). Average total returns increased in regime II to 15.2 million (range, 7.2–19.1 million). In regime III, the average return was 12.8 million (range, 3.6–22.0 million).

The results of our statistical analyses (Figures 1–5) are summarized in Table 6. The models in Figures 2, 3, and 4 produce the residuals shown in Figure 5. Paired comparisons for each environmental index (Figure 1A–F) show how the regime means (Figure 1B, D, F) compare with the data series means (Figure 1A, C, E). For each index, a model with a distinct mean for each of six environmental regimes significantly (Table 6) improves the fit over a model with only one mean for the entire data series. Similarly, over a shorter period with only three regimes, the PDO index still has significantly distinct regime means (Figure 2A, B). Additional paired comparisons pertain to variation in the productivity index, defined as $\log(R/S)$, for sockeye (Figure 2C, D) and pink salmon (Figure 2E, F) within these three regime periods. For both species, the mean productivity shows a significant regime effect; that is, the null hypothesis of a single mean for the entire time series is rejected (Table 6).

According to Ricker's (1954, 1958a) theory, the productivity index depends on the spawning stock S . We test this hypothesis for sockeye (Figure 5A, B) and pink (Figure 5D, E) salmon and find that a single Ricker curve (Figure 5B, E) significantly improves the fit from a single mean for the entire productivity data series (Figure 5A, D; Table 6),

TABLE 6.—Variance analyses obtained from three climate indices and two salmon stock productivities. Each case comes from a particular data set with a specified range of years. The null (H_0) and alternative (H_1) hypotheses correspond to hypotheses M0, M1, L0, and L1, which are described in Table 2. The panels in Figures 1, 2, and 5 show the residuals associated with each pair of hypotheses. The table lists sums of squares (S_j) and degrees of freedom (f_j) for each hypothesis H_j ($j = 0, 1$), along with the F -statistic for equation (10) in the text and the probability level for this statistic if the null hypothesis is true. The table lists scaled values S_0 and S_1 for three climate indices: the Pacific Decadal Oscillation (PDO), Arctic Oscillation (AO), and Aleutian low pressure index (ALPI). The years given for sockeye and pink salmon are the years they entered the ocean.

| Data | Years | H_0 | H_1 | Figures | S_0 | S_1 |
|------------------------|-----------|-------|-------|---------|--------|--------|
| PDO | 1901–2002 | M0 | M1 | 1A, 1B | 75.574 | 42.711 |
| PDO | 1959–1998 | M0 | M1 | 2A, 2B | 34.852 | 19.492 |
| AO ($\times 10^5$) | 1901–2002 | M0 | M1 | 1C, 1D | 12.412 | 10.309 |
| ALPI ($\times 10^6$) | 1901–2002 | M0 | M1 | 1E, 1F | 69.782 | 54.411 |
| Sockeye salmon | 1959–1998 | M0 | M1 | 2C, 2D | 13.934 | 11.020 |
| | 1959–1998 | M0 | L0 | 5A, 5B | 13.934 | 11.579 |
| | 1959–1998 | L0 | L1 | 5B, 5C | 11.579 | 8.159 |
| | 1959–1998 | L1 | L1 | | 11.020 | 8.159 |
| | 1960–1998 | M0 | M1 | 2E, 2F | 9.674 | 6.632 |
| Pink salmon | 1960–1998 | M0 | L0 | 5D, 5E | 9.674 | 6.865 |
| | 1960–1998 | L0 | L1 | 5E, 5F | 6.865 | 3.952 |
| | 1960–1998 | M1 | L1 | | 6.631 | 3.952 |
| | 1960–1998 | M1 | L1 | | 6.631 | 3.952 |

confirming a stock and recruitment relationship. However, for sockeye salmon, the stock–recruitment relationship shows significant ($P \leq 0.05$) improvement, as evident in a distinct Ricker curve for each regime (Figures 3 and 5B, C; Table 6). We also use hypotheses M1 and L1 (Table 2) to test for stock dependence within each regime and find that a regime-dependent Ricker curve significantly improves the fit relative to the regime mean. We repeated the analysis of a single Ricker curve relative to a distinct Ricker curve for each regime by using the sockeye salmon data with the lag A and lag B years. In both cases the significance of regime-dependent relationships improved (Table 6).

When we restricted the sockeye data to summer stocks only, we could still significantly ($P \leq 0.05$) reject a single Ricker curve for the entire data series relative to a distinct curve for each regime. However, a test of a single Ricker curve (Table 2; hypothesis L0) relative to a single mean (hypothesis M0) did not prove significant ($P = 0.123$).

When we conducted analyses of pink salmon similar to those for sockeye salmon, we could not always reject the null hypothesis at the 0.05 level (Figures 2E, F and 4 and 5E, F; Table 6). We found two tests significant at the $P \leq 0.10$ level (Table 6): a distinct Ricker curve in each regime (Table 2, hypothesis L1) relative to a single Ricker curve for the entire series (hypothesis L0), and a Ricker curve in each regime (hypothesis L1) relative to a mean in each regime (hypothesis M1). For the test of L1 versus M1, the lag A scenario for pink salmon has even lower significance (Table 6). Because pink salmon spawn only

every other year, we have far fewer data points for this species than for sockeye salmon. This loss of degrees of freedom (Table 6) reduces our ability to reject null hypotheses.

Discussion

Following Ricker (1954, 1958a), we have identified a significant stock and recruitment relationship for sockeye salmon from the Fraser River. Furthermore, relative to a single Ricker curve for the entire data series, a distinct Ricker curve for each climate and ocean regime significantly improves this relationship. When the data were lagged such that the effects of regime shifts might better match the changed ocean ecosystem for sockeye salmon entering saltwater, the significance associated with partitioning the data by regimes improved. This suggests that a better understanding of the mechanisms that link regime shifts in the climate with shifts in trends in sockeye salmon productivity will improve the modeling of stock and recruitment relationships.

Because sockeye salmon management is partitioned into stock groupings and not the entire population of 11 stocks, we tested one grouping, the summer stocks, to see if the effect of regimes on stock and recruitment was similar to the response of the entire population. We found that regimes significantly improved productivity and stock–recruitment Ricker curves, but for the entire data series we did not find that a Ricker curve significantly improved the fit over a single mean productivity.

TABLE 6.—Extended.

| $f_0 - f_1$ | f_1 | F | Probability (P) | | | |
|-------------|-------|--------|---------------------|-------|-------|-----------------------|
| | | | No lag | Lag A | Lag B | Summer sockeye salmon |
| 5 | 96 | 14.773 | 0.000 | | | |
| 2 | 37 | 14.580 | 0.000 | | | |
| 5 | 96 | 3.917 | 0.003 | | | |
| 5 | 96 | 5.424 | 0.000 | | | |
| 2 | 37 | 4.893 | 0.013 | 0.002 | 0.000 | 0.019 |
| 1 | 38 | 7.729 | 0.008 | 0.008 | 0.008 | 0.123 |
| 4 | 34 | 3.563 | 0.016 | 0.002 | 0.000 | 0.047 |
| 4 | 34 | 2.980 | 0.030 | | | |
| 2 | 17 | 3.900 | 0.040 | 0.015 | | |
| 1 | 18 | 7.366 | 0.014 | 0.014 | | |
| 4 | 14 | 2.579 | 0.083 | 0.274 | | |
| 4 | 14 | 2.372 | 0.100 | | | |

For pink salmon, we found dependencies on climate similar to those for sockeye salmon. However, due to fewer data points for a species that spawns only in alternate years, our hypothesis tests had reduced significance. Nevertheless, we found significant ($P \leq 0.05$) productivity differences among regimes. The use of lagged data for pink salmon did not significantly alter the analysis.

Our selection of regime shift years was from published studies, including our own. In an earlier study, we used an intervention analysis (Hipel and McLeod 1994) applied to the PDO and ALPI indices to detect significant ($P < 0.05$) shifts in 1925, 1947, 1977, and 1989 (Beamish et al. 2000). In another study, Beamish et al. (1999) developed a composite index of pressure-related indices from 1950 to 1996 for the North Pacific, the North Atlantic, northeast Europe, and the tropical Pacific. An intervention analysis of the standardized anomalies from this composite index identified significant ($P < 0.05$) shifts in 1977 and 1989. Thus, there is evidence that the regime shift years used in this study represent years when there were significant shifts in the trends of large scale climate and ocean indices.

We have inadequate stock and recruitment data for the current regime (regime IV). However, we know that pink salmon entering the Strait of Georgia in 2000 and 2002 have returned at historically high abundances, even though the 1999 spawning biomass of 3,422,000 was one of the lowest in the data series (Table 4). Total returns in 2001 were estimated to be approximately 20,000,000 and in

2003 preliminary estimates exceed 20,000,000. These historically high recruitments indicate that the present regime appears to be very productive for pink salmon compared with regime III. Other studies report that there was a recent regime shift. Bond et al. (2003) and Peterson and Schwing (2003) identify a regime shift late in 1998 or 1999. Bond et al. (2003) reported that in all 4 years from 1999 to 2003 the North Pacific sea surface temperatures and sea level pressures were different than those observed in the regimes before and after the 1977 regime shift. Peterson and Schwing (2003) show that the changes in the atmosphere and the marine ecosystem were associated with a doubling of zooplankton biomass in the northern California Current and improved productivity of coho salmon and chinook salmon *O. tshawytscha*.

Shifts in productivity have obvious importance to management and industry. The shift in 1977 was to a more productive state, but the shift in 1989 was to a significantly less productive regime. The shift in 1998 appears to be to a productivity that may be larger than in the 1980s. Decadal changes in marine survival trends imply corresponding natural changes in abundance that should be important considerations in the management of pink and sockeye salmon.

Our analysis spans a period in which regimes altered productivity significantly. Ricker did not have the advantage of such a long data series. Because reliable data for most Fraser River stocks did not become available until the 1950s, previous investigators in the 1980s would have data from

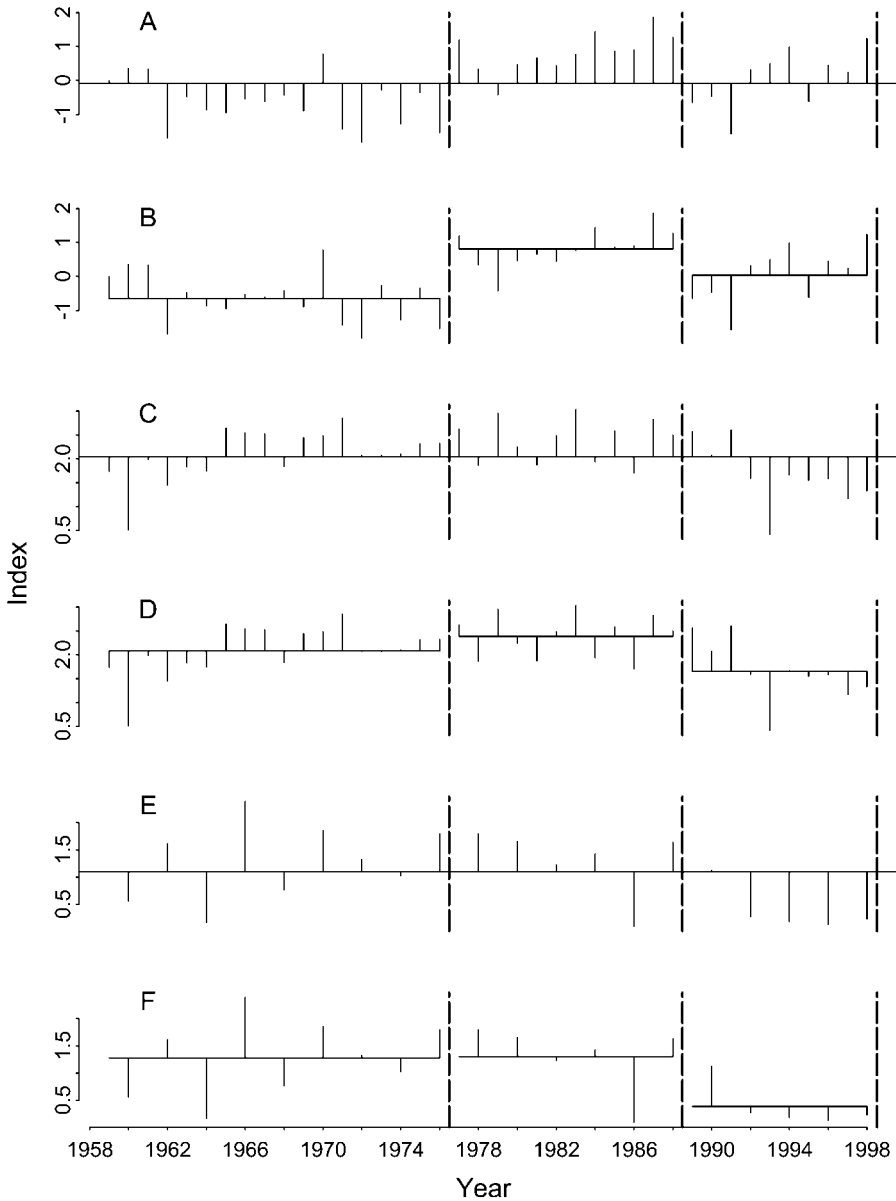


FIGURE 2.—Data series pertaining to the Fraser River showing residuals (solid vertical lines) in relation to the hypotheses M0 (single mean for the entire data series) and M1 (mean for each regime), which are described in Table 2, where panel (A) examines the M0 hypothesis and Pacific Decadal Oscillation (PDO), panel (B) examines the M1 hypothesis and PDO, panel (C) examines the M0 hypothesis and sockeye salmon productivity ($\log[R_t/S_t]$, where R_t is recruitment at time t and S_t is spawning stock at time t), panel (D) examines the M1 hypothesis and sockeye salmon productivity, panel (E) examines the M0 hypothesis and pink salmon productivity, and panel (F) examines the M1 hypothesis and pink salmon productivity. Vertical dashed lines indicate breaks between three regime periods: 1959–1976, 1977–1988, and 1989–1998. Pink salmon data are available for even years only.

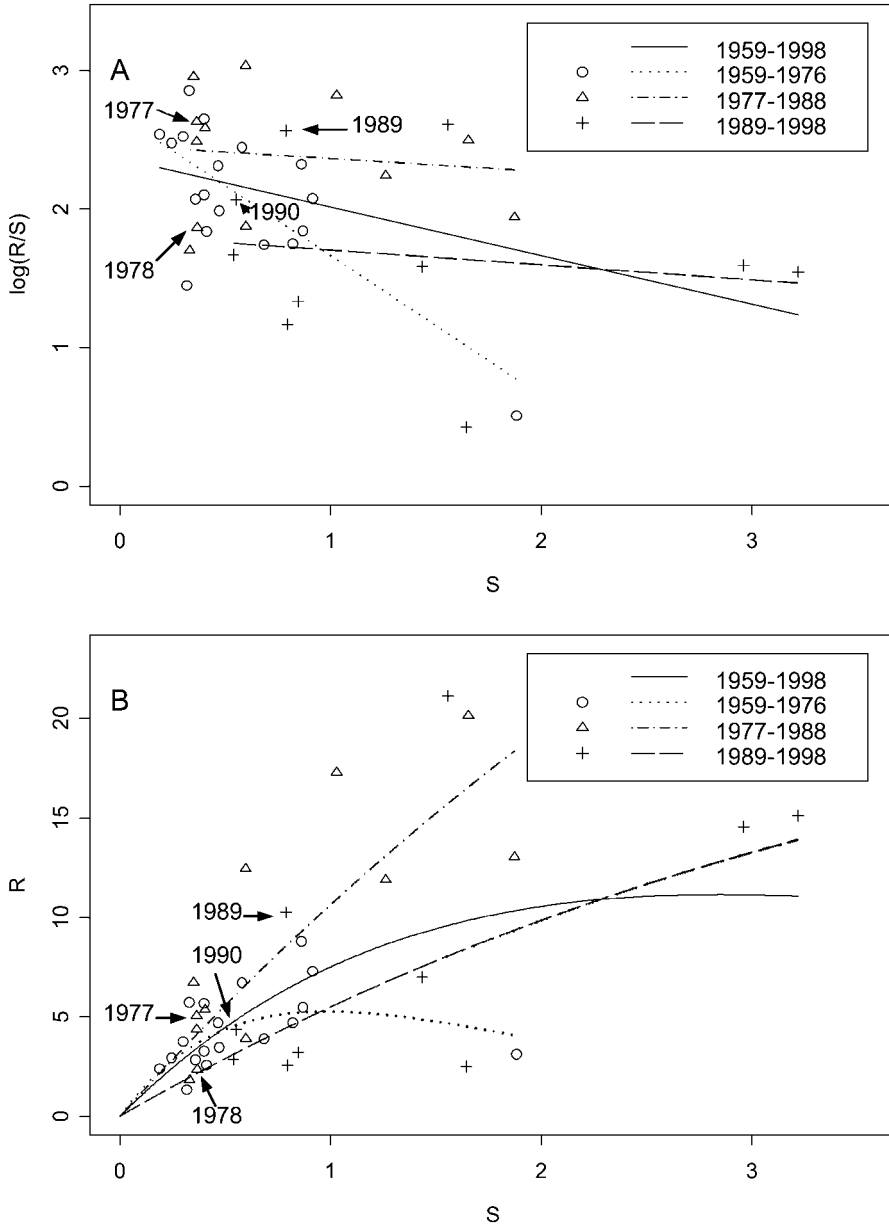


FIGURE 3.—Overall and regime-dependent relationships between spawning stock (S) and recruitment (R) for Fraser River sockeye salmon obtained from the hypotheses L0 (single line for the entire data series) and L1 (distinct line for each regime), which are described in Table 2. The Ricker model (equations 12–13 in the text) gives (A) linear relationships between $\log(R/S_t)$ and S_t ($t = \text{year}$) and (B) the corresponding curves relating R_t and S_t . Labels show the years that were also lagged. The solid line is the relationship for the entire data series. The regimes are identified with broken lines. The years 1977 and 1978 are identified to show that in the lagged analysis they are included in regime I. The years 1989 and 1990 are identified to show that in the lagged analysis they are included in regime II.

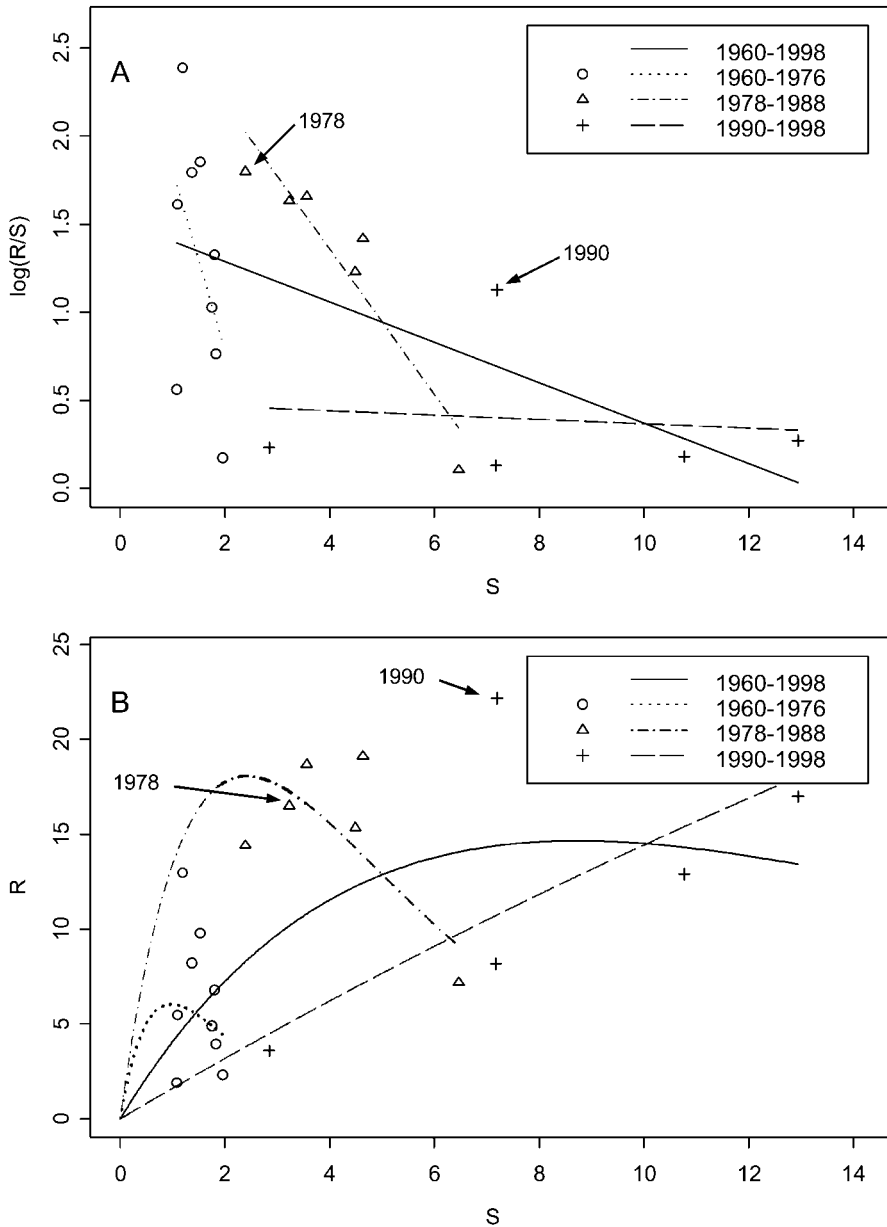


FIGURE 4.—Overall and regime-dependent relationships between spawning stock (S) and recruitment (R) for Fraser River pink salmon obtained from the hypotheses L0 (single line for the entire data series) and L1 (distinct line for each regime), which are described in Table 2. The Ricker model (equations 12–13 in the text) gives (A) linear relationships between $\log(R/S)$ and S_t ($t = \text{year}$) and (B) the corresponding curves relating R_t and S_t . Labels show the years that were also lagged. The solid line is the relationship for the entire data series. The regimes are identified with broken lines. The years 1978 and 1990 are identified to show that in the lagged analysis they are included in regimes I and II, respectively.

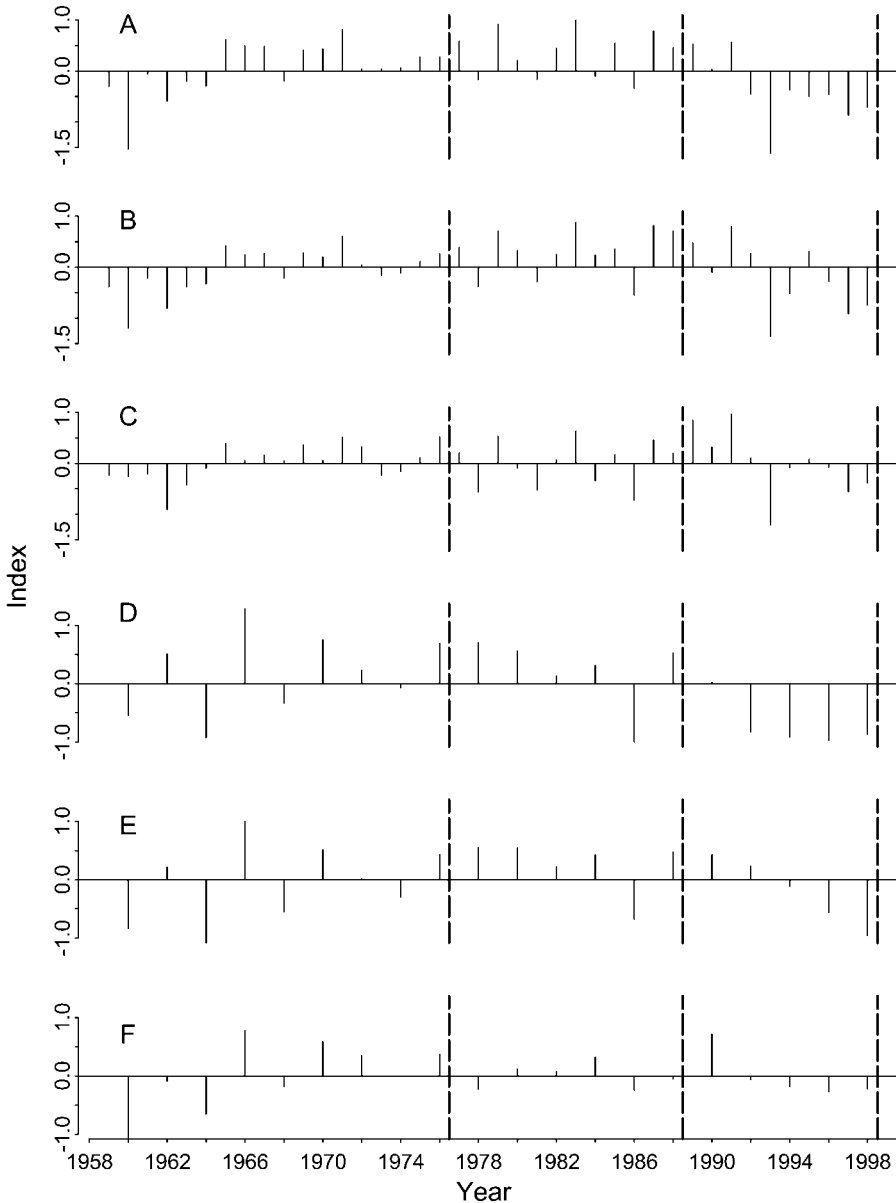


FIGURE 5.—Residuals (solid vertical lines) for regression models of salmon data under the hypotheses M0 (single mean for the entire data series), L0 (single line for the entire data series), and L1 (distinct line for each regime), which are described in Table 2, where panel (A) examines sockeye salmon productivity ($\log[R_t/S_t]$, where R_t is recruitment at time t and S_t is spawning stock at time t) and M0, panel (B) examines sockeye salmon productivity and L0, panel (C) examines sockeye salmon productivity and L1, panel (D) examines pink salmon productivity and M0, panel (E) examines pink salmon productivity and L0, and panel (F) examines pink salmon productivity and L1. Vertical dashed lines indicate breaks between three regimes: 1959–1976, 1977–1988, and 1989–1998.

only one or two regimes. Our study benefited from the contrasting low productivity in the 1990s (regime III). The major differences in productivity among regimes occurred before and after the 1989 regime shift or between regimes II and III. The

regime in the 1990s (regime III) was characterized by significantly reduced marine survival and reduced recruitment per spawner. It was the contrasting trends between regimes II and III that exposed the importance of trends in climate on re-

cruitment. Regime IV most likely will also provide a level of productivity that will stand out when regime IV ends and the results are compared with regimes I, II, and III.

Forecasting Regime Shifts

Regime shifts may be forecasted once the mechanisms that cause the shift are discovered. At present we can only speculate that if the previous three shifts occurred at about 10-year intervals (1977, 1989, and 1998), the next shift will occur about 10 years after the 1998 shift, or in 2008. If there were a lag of about 1–2 years between the physical shift and the change in the productivity, as we observed in the Strait of Georgia (Beamish et al. 2004b), then juvenile Pacific salmon entering the Strait of Georgia in 2010 would be the first to be affected. The shift could be later because the time between the regime shifts in 1925 and 1947 was notably longer than 10 years. However, it would not hurt to be looking for evidence of a regime shift in about 2008. The value in this speculation is less in forecasting the timing of a potential change and more in the message to managers and industry that changes will occur quickly and will probably result in a new level of production that may require both biological and economic adjustments.

The processes that cause the changes in trends of productivity remain to be worked out, but some clues exist. The 1998 regime shift was associated with a doubling of the euphausiid biomass in the Strait of Georgia in 2000 compared with 1998 and 1999 (Beamish et al. 2001). The increased plankton production was associated with synchronous increases in growth, stomach volumes, and abundances among juvenile Pacific salmon rearing in the Strait of Georgia (Beamish et al. 2004b). Subsequent adult returns were larger than before the regime shift, suggesting that the improved salmon production was linked to the improved early marine growth (Beamish et al. 2004b). We speculate that a shift in the trend of atmospheric circulation alters the timing and amount of prey available to the juvenile Pacific salmon in the Strait of Georgia, which in turn affects the trends in marine productivity. According to this speculation, physical factors that affect prey production would provide indices useful for determining production capacity of this marine ecosystem.

Implications for Fisheries Management

Ricker's (1958b) assumption—that the effect of climate on the population dynamics of Pacific

salmon could be assessed using a random model—influenced fisheries research for decades. It has only been in recent years that there has been a focus on understanding the effects of climate variability on fish populations. Almost at the same time, we discovered that the accumulation of greenhouse gases is changing our climate (IPCC 2001) and that our climate is changing. For example, the last decade includes 8 of the warmest years from the past 150 years. Furthermore, most scientists acknowledge that the effects of greenhouse gas-induced climate change on the biota will be unprecedented (IPCC 2001). Recognizing that we may be rapidly changing our climate, that climate plays an important role in the stock–recruitment relationships of fishes, and that we understand poorly how climate affects the mechanisms that naturally regulate the abundance of fish, we conclude that we may not be prepared to manage Pacific salmon and possibly a number of other fishes in the future. Certainly we need to be cognizant of the inevitable effects of a changing climate on pink and sockeye salmon from the Fraser River, which are at the southern limits of the distribution of these species.

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