North American Journal of Fisheries Management 21:774–791, 2001

The Demise of Owikeno Lake Sockeye Salmon

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Abstract.—A persistent period of low abundance in what was once the second largest fishery for sockeye salmon *Oncorhynchus nerka* in British Columbia has kept the Rivers Inlet fishery closed since 1996. Initial speculation about the cause of the decline focused on factors such as reduced egg-to-fry survival, declining quantity and quality of spawning habitat, and reduced fry-to-smolt survival in Owikeno Lake (the only nursery lake in Rivers Inlet). We developed an index of juvenile sockeye salmon abundance by combining direct estimates of abundance from trawl surveys with indirect estimates of abundance inferred from density-dependent growth of juvenile sockeye salmon. Juvenile growth data were available as either direct samples of presmolt weight or as measurements of freshwater growth from the scales of returning adults. Collectively, these data do not indicate a long-term decline in juvenile sockeye salmon abundance since the 1950s. Throughout the 1970s and 1980s and even more recently (1991 and 1994 brood years), the juvenile abundance index exceeded the long-term mean. If freshwater abundance was either untrended or increasing, the most likely cause of the population decline would have been lower survival after the fry stage, which would have been noticeable in the 1970s and especially from 1992 to 1998. Poor marine survival is the most parsimonious explanation for the declining fry-to-adult survival in Owikeno Lake, particularly in light of coincident declines in sockeye salmon returns per spawner at Long Lake (a nearby pristine watershed) and declines in adult sockeye salmon abundance in other populations to the north of Rivers Inlet.

In the late 19th century and during much of the 20th century, the gill-net fishery in Rivers Inlet vied with that of the Skeena River to produce the second largest catch of sockeye salmon *Oncorhynchus nerka* in British Columbia (BC). The total number of cases of canned sockeye salmon packed at Rivers Inlet exceeded that of the much larger Skeena River in 24 of 49 years between 1907 and 1956 (Foskett and Jenkinson 1957), and the total number of sockeye salmon caught over that period was greater in Rivers Inlet (Godfrey 1958). Although the number of cases packed in Rivers Inlet varied annually, it was generally trendless through most of the early history of the fishery. This era of relative stability ended in 1968 with a doubling of the previous maximum catch, a run failure in 1970, and the second largest catch in 1973. These spectacular catches of 1968 and 1973, following above-average spawning escapements, led fishery managers and biologists to question whether the escapement objective for Owikeno Lake sockeye salmon was too low.

In an attempt to clarify some of the uncertainty about the productive capacity of Owikeno Lake, the Rivers Inlet sockeye salmon fishery became the object of one of the first adaptively managed fisheries in Canada (Walters et al. 1993). Spawning escapements to Owikeno Lake, the only nursery lake in Rivers Inlet, were thought to have declined (Wood 1970), and there was considerable uncertainty about what average escapement should be achieved to provide for optimum production. The fishery was dramatically curtailed (<3 d fishing/year) from 1979 to 1984 in the hope that larger escapements would provide greater returns and better fishing opportunities thereafter. They never materialized. Three alternative causes were offered to explain the apparent failure (Walters et al. 1993): (1) the anticipated returns occurred but were not detected, (2) the anticipated returns did not occur because of a coincidental sequence of years of poor survival, or (3) the spawner abundance at the outset was much lower than assumed. At the end of the experiment, it was not possible to determine whether the historical management policy of allowing 400,000 sockeye salmon to spawn should be continued or whether escapement targets should be increased or decreased. Walters et al. (1993) concluded that there was still a good chance that optimal production would be achieved at 1,000,000 spawners. After the experiment, a management regime was established that set a min-

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Received July 28, 1999; accepted February 23, 2001

imum escapement of 200,000 spawners, below which no commercial harvests would occur; between 200,000 and 400,000, a fixed 10% harvest rate was allowed; and beyond 400,000, harvest rates would increase asymptotically toward an upper limit of about 60% (Walters et al. 1993).

A popular hypothesis for the declining catch was that logging activities within the watershed had reduced the productive capacity of the spawning or rearing habitat to such an extent that Owikeno Lake was no longer capable of producing or rearing sockeye salmon juveniles at historical levels. Interest in this explanation and in projects to restore damaged habitat have intensified recently due to an unprecedented sequence of years of very low abundance during latter part of the 1990s. Assessments conducted by Fisheries and Oceans Canada suggested that the Rivers Inlet stock declined for reasons unrelated to freshwater habitat or lake productivity (Rutherford et al. 1995; 1998; Rutherford and Wood 2000).

Owikeno Lake is a coastal lake in Rivers Inlet on the mainland side of Queen Charlotte Sound that is characterized by low primary productivity (per unit area) because glacial silt limits light penetration (in the largest basins) and because poor thermal stratification and vertical mixing beneath the compensation depth restrict photosynthesis (Ruggles 1965; Narver 1969; Stockner and Shortreed 1979). In this rather unproductive rearing habitat, the mean weight of sockeye salmon smolts is typically less than 2 g (Foskett 1958), which is among the smallest of the species. Despite their small size, virtually all juvenile sockeye salmon migrate to sea after only one winter in the lake. The size and primary productivity of a nursery lake influence the total biomass of juvenile sockeye salmon that can be produced (Shortreed et al. 1999). Fry recruitment and local conditions determine whether the total biomass is distributed among fewer large individuals or an abundance of small ones (Bohlin et al. 1994).

Artificially increasing the sockeye salmon carrying capacity was the conceptual basis for applying inorganic phosphorus and nitrogen to oligotrophic nursery lakes (Parsons et al. 1970; LeBrasseur et al. 1978; Bradford et al. 2000) or enriching stream productivity with grains (Mundie et al. 1981). Simple models incorporating lake size and biological productivity have been used to predict maximum juvenile sockeye salmon biomass, maximum adult returns, and optimum spawning escapements for lakes with limited rearing habitat (Koenings and Burkett 1987; Koenings and Kyle 1997; Shortreed et al. 1999). Assessing productivity using juvenile sockeye salmon abundance data is an approach that has not been applied to Owikeno Lake sockeye salmon until recently.

In this paper we describe the data and methods used to develop new indices of sockeye salmon abundance in Owikeno Lake. Because of the number and variety of data sources, analytical treatments, and consequences of uncertainty, we introduce, describe, and evaluate each data set separately. This allows us to focus on the main objective of examining historical changes in survival and the potential causes. Finally, we explore the role of ocean and climate variability, noting that a nearby sockeye salmon population in Long Lake has undergone similar declines in adult abundance, and develop views about the basis of sockeye salmon production in Owikeno Lake, the demise of the fishery, and the near-term expectations for production.

Sockeye Salmon Abundance

Estimating Juvenile Abundance and Mean Size from Trawl Catches

An ambitious survey of juvenile sockeye salmon in Owikeno Lake began in 1960 using two-boat trawl surveys (Johnson 1956; Ruggles 1965) to determine size, survival, abundance, and distribution in spring, summer, and fall (Ruggles 1965). The detailed catch and biological data that were collected between 1960 and 1968 were published (Wood and Schutz 1970); however, from 1969 until the early 1980s only the mean presmolt weights appear to be extant. Juvenile sampling resumed in 1995 (1994 brood year) as part of Fisheries and Oceans Canada (DFO) stock assessment activities and has become a major component of the assessments (Rutherford et al. 1995, 1998).

Owikeno Lake contains four basins of unequal size, numbered consecutively from the largest and most seaward basin. Because of its size, basin 1 has two sampling stations; the other basins have one station each. Stations 1 through 5 are numbered consecutively beginning with the station nearest the outlet. Three 20-min tows at each station were conducted after civil twilight by towing a net near the surface between two boats. Trawling at night was preferred because most juvenile sockeye salmon are concentrated within the top 5 m of the Owikeno Lake at night (Chernoff 1971; Hyatt et al. 1989). Annual estimates of fry abundance were developed from the catches in all samples collected in basins 1 and 2 in July and August each

TABLE 1.—Consistency of the abundance of juvenile sockeye salmon obtained from three consecutive 20-min trawls in Owikeno Lake at each station on each sampling day, as quantified by correlation coefficients of $\log_e$(number + 1) between the 1960–1968 tows.

Month (stage)	N	Correlation coefficients[a]		
		Tows 1, 2	Tows 2, 3	Tows 1, 3
Apr (fry)	128	0.48	0.69	0.42
Apr (presmolts)	128	0.69	0.78	0.60
Jul (fry)	133	0.75	0.74	0.60
Oct (fry)	125	0.54	0.55	0.43

[a] Adjacent tows (1 and 2 and 2 and 3) were more correlated than tows separated by 20 min (1 and 3).

year (September 3–5 for the 1996 brood year). An average of 63 tows/year were conducted during this period during the 1960s, but this was decreased to approximately 18 tows/year in the 1990s.

A total of 1,058 tows (386 station days), conducted in basins 1 and 2 from 1960 to 1968, indicated that catches in consecutive tows were positively correlated (Table 1). The mean correlation coefficient among tows was 0.7 in July; if abundance was high in the first tow, it tended to be high in the second tow and the third tow, suggesting reasonably strong uniformity in the juvenile distribution. At least for the fry, these samples are presumed to indicate abundance because the trawl was operating in the depth stratum where most of the fry were located. A study conducted in Owikeno Lake in late summer 1970 that compared sockeye salmon fry abundance in surface with midwater Isaacs–Kidd trawls led Chernoff (1971) to conclude that sockeye salmon fry were uniformly distributed in the upper 3 m at night. A similar study was not conducted on presmolts in spring.

The Owikeno sockeye index (OSI) of juvenile abundance in the ith year was determined as

$$\mathrm{OSI}_i = \sum_i \frac{\sum_k x_{ijk}}{n_{ij}} (\omega_j)$$

where i, j, and k index brood year, station, and tow, respectively; n_{ij} = number of tows; ω_j = areal weight of the jth station, $x_{ijk} = \log_e$(catch of fry in numbers + 1).

Stations 1, 2, and 3 represent 38.8, 34.8, and 26.4%, respectively, of the lake surface area in basins 1 and 2. Although fry can also be relatively abundant in basins 3 and 4 in April (Figure 1), abundance declines to low levels in the upper basins in July. Chernoff (1971) reported that fry and

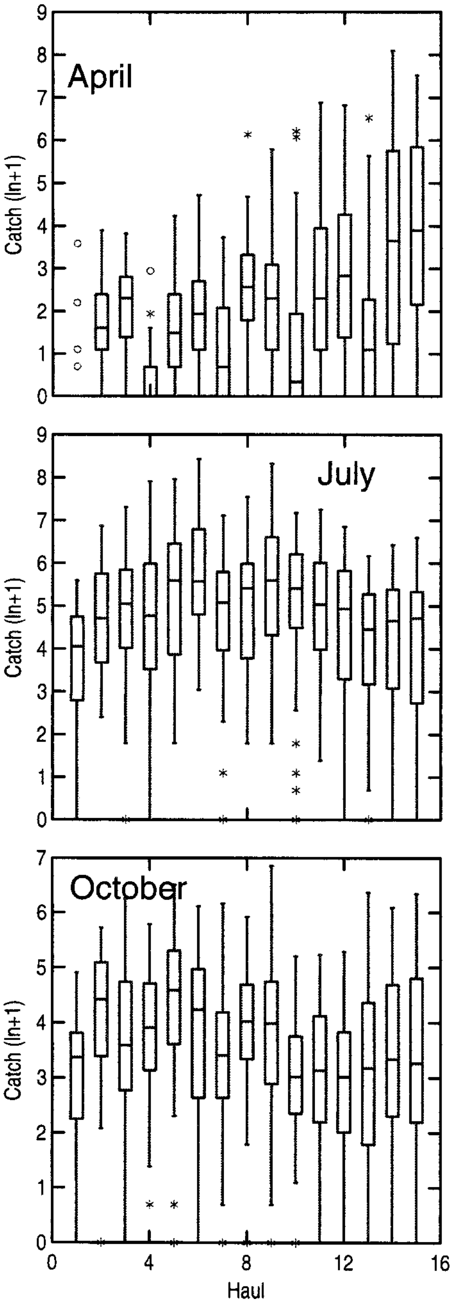


FIGURE 1.—Box-and-whisker plots of catches ($\log_e$ + 1) of age-0 sockeye salmon fry in 20-min tows in April, July, and October, 1960–1968. Hauls 1–15 are ordered from the station closest to the outlet (station 1, tow 1) to the station furthest from the outlet (station 5, tow 3). Shown are the median values (horizontal lines within the interquartile ranges [boxes]), 1.5 × the interquartile ranges (vertical lines), and individual observations outside these (asterisks and circles).

TABLE 2.—Mean weights and 95% confidence intervals of sockeye salmon presmolts sampled in basins 1 and 2 of Owikeno Lake April 16–30 for brood years 1958–1966 (Wood and Schutz 1970) and in spring 1994–1998 by the Canada Department of Fisheries and Oceans.

Brood year	Mean weight (g)	95% confidence interval	Sample size
1958	1.30	1.26–1.34	1,037
1959	1.05	1.02–1.08	847
1960	1.34	1.30–1.37	415
1961	1.46	1.43–1.50	446
1962	1.59	1.54–1.64	354
1963	0.90	0.87–0.93	409
1964	1.16	1.12–1.20	435
1965	1.89	1.84–1.95	304
1966	1.08	1.04–1.11	416
1994	1.41	1.35–1.47	424
1995	1.67	1.59–1.75	115
1996	2.74	2.62–2.87	97
1997	1.21	1.16–1.26	218
1998	2.83	2.67–3.03	57

TABLE 3.—Mean weights (preserved) and sample dates for sockeye salmon presmolts in basins 1–3 of Owikeno Lake for brood years 1967–1975, 1988, 1989, and 1991. Variance and sample sizes were generally not available; sampling procedures were similar to those described in the Table 1 caption (Canada Department of Fisheries and Oceans, unpublished data).

Brood year	Mean weight (g)	Sample dates
1967	1.61	Mar 28–May 4
1968	0.87	Mar 29–Apr 19
1969	1.05	Apr 1–23
1970	1.06	Apr 1–28
1971	1.43	Apr 1–23
1972	1.18	Mar 19–Apr 10
1973	0.93	Apr 1–23
1974	1.03	Apr 4–25
1975	1.29	Apr 4–18
1988	1.57	Mar
1989	2.25	Mar
1991	1.30	Mar

threespine stickleback *Gasterosteus aculeatus* may migrate from the upper basins into the lower basins during the summer. Because (1) basins 3 and 4 constitute only 8% and 13% of the total lake surface area, respectively, (2) they were not sampled every year, (3) their water properties differ from those of the lower basins (much lower glacial silt and lower wind mixing), and (4) the behavior of the fry was different (significantly deeper diel migration) in these basins, basins 3 and 4 were excluded from the abundance index. The best estimate of the pooled variance for the *i*th year was calculated as the mean square error from analysis of variance (ANOVA) of x_{ijk} among stations within years (Zar 1974). A random subsample of the catch was taken at each station and preserved in 10% formalin for subsequent analyses. Fork length was measured to the nearest 2 mm on all individuals in the subsample, and the total weight of all fish in each length stratum was measured to the nearest 0.1 g.

Estimating Fry Abundance from Growth

Mean annual presmolt body weight (SW) for the *i*th brood year from 1958 to 1966 was computed from all presmolts sampled in basins 1 and 2 between April 16 and April 30 (Table 2). Although age-0 fry and presmolts may coexist in the lake at this time, their length-frequency distributions do not overlap, so the fry ($<$35 mm) were easily excluded. Large sample sizes generated very precise estimates of SW_i (Table 2). For brood years 1967–1975, 1988, 1989, and 1991, the data used to estimate SW were obtained from trawl samples taken from the same basins on similar sampling dates (Table 3), but unfortunately, only the mean weights are extant from these years. Because similar sampling procedures continued during this period, the precision should not have decreased.

Mean presmolt weight was negatively correlated with cohort abundance as fry (Figure 2) and this correlation was maintained throughout the period of residence in the lake. The strength of the correlation was greatest in July. Whether sampling was conducted in the 1960s or the 1990s the relationship between SW and abundance was similar, although perhaps power was insufficient to detect small changes that may have occurred in the relationship over time. The pattern of smaller average body size with increasing abundance indicates that food supply limits juvenile sockeye salmon growth in Owikeno Lake. The strength of the size-abundance relationship (Figure 2) and its apparent persistence over a number of decades suggests that it is possible, for those years when only presmolt weight data are available, to estimate abundance in the lake from that data. The fitted linear model for the relationship between summer fry abundance and mean presmolt weight is $\mathrm{OSI}_i = 7.94 - 2.36 \cdot \mathrm{SW}_i$, for which $R^2 = 83\%$, $P < 0.0001$, $N = 14$.

Because large sample sizes were used to calculate SW_i (Table 2), we did not consider the imprecision in estimates of SW_i to be a significant contributor to the uncertainty in predicted OSI_i. Likewise, the large numbers of trawl samples, particularly in the early years of sampling, generated relatively precise estimates of fry abundance. This

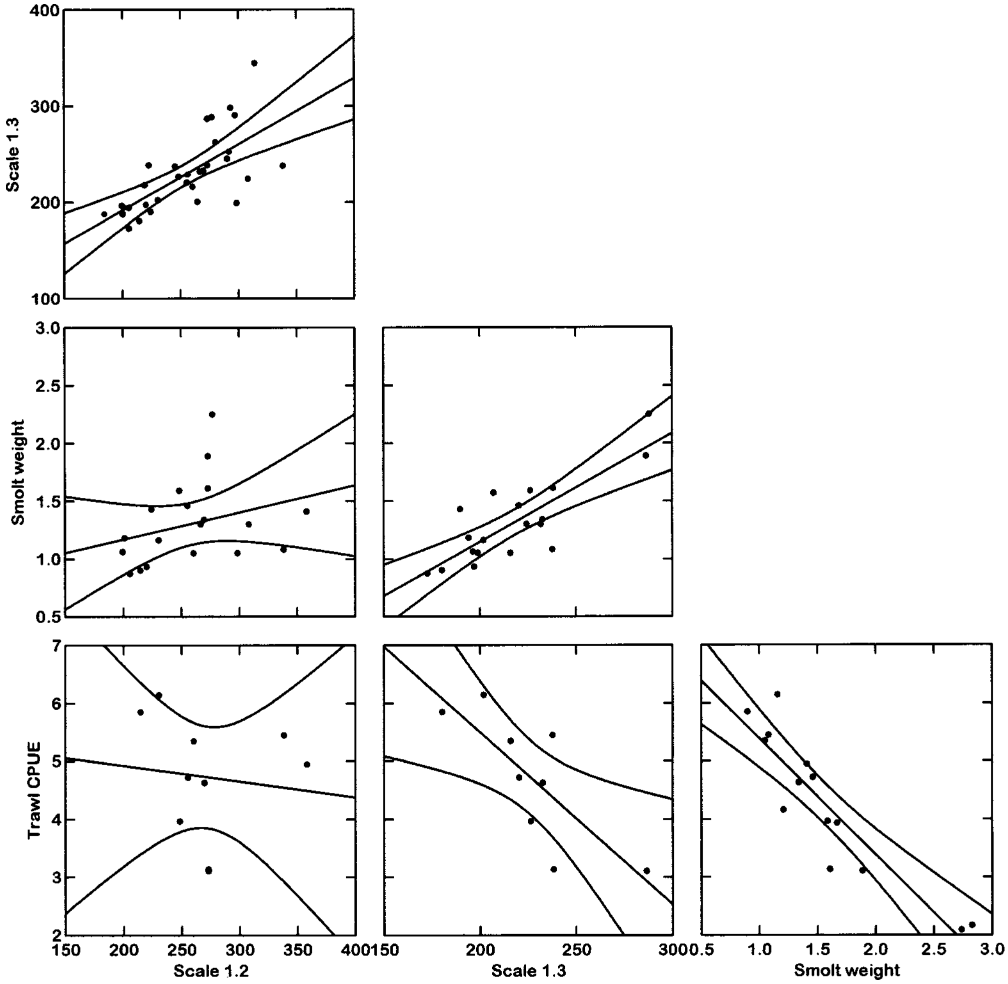


FIGURE 2.—Bivariate plots (with regression lines and 90% confidence intervals) of the relationships among measures of average juvenile sockeye salmon growth (presmolt body weight [g] and width of the freshwater zone on age-1.2 and age-1.3 scales [μm] achieved in Owikeno Lake by brood year) and the relationships between these growth measures and average summer fry abundance ($\log_e$) determined from trawl surveys (i.e., the Owikeno sockeye index [OSI]).

suggests that most of the uncertainly in predicting OSI from SW is due to the form of their interrelationship. We assumed it to be linear, recognizing that 14 years of data are probably insufficient to determine whether the true form is slightly nonlinear. Bootstrap 95% confidence intervals (CIs) on the slope (-3.02 to -1.65) and intercept (8.6 to 6.65) were calculated from 1,000 resampled linear regressions to understand the magnitude of uncertainty in predicting OSI that is created from the uncertainty in the parameter estimates of the size-abundance model.

Estimating Fry Abundance from Freshwater Scale Growth

Growth in the freshwater zone of scales collected from returning adults was used as a proxy for presmolt weight for those brood years when neither trawl surveys nor presmolt sampling were conducted. Sockeye salmon scales increase in diameter as an individual grows. When a smolt migrates to sea in spring, the amount of growth in freshwater is recorded on their scales and is relatively easy to identify and measure in scales of returning adults because circulus spacing becomes much greater in salt water (Bilton and Messinger 1975). Also, wider annulus spacing in the freshwater growth zone implies faster growth in the lake, reduced competition for food, and thus, low fry recruitment in sockeye salmon (Goodlad et al. 1974; Bugaev 1989). Scales collected from returning adults describe only the survivors, which is a potential disadvantage because size-dependent mortality has been observed in sockeye salmon in the ocean (Henderson and Cass 1991) and in other salmonids (Bilton et al. 1982; Ward et al. 1989; Bohlin et al. 1994; Unwin 1997; McKinnell and Lundqvist 2000). Although size-dependent mortality can be statistically significant in different salmon species, it may be a relatively minor component of total ocean mortality (McKinnell and Lundqvist 2000).

The annual mean width of the freshwater annulus on adult scales was determined from age-1.2 and age-1.3 sockeye salmon taken in the commercial fishery within a 1-week period at the peak of the run in mid-July. Age is designated by the number of freshwater annuli preceding the decimal and the number of marine annuli following the decimal. A mature age-1.2 sockeye salmon is four years old because the first winter of growth after hatching leaves no annulus. Scales were examined at 100× magnification using a compound microscope attached via a digital camera to the Optimas image processing system. A transect from the focus of the scale to the margin, at an angle of 20° from the long axis of the scale, was identified, and the distance from the focus to the outer edge of the last circulus in the freshwater annulus was measured. Because the commercial fishery has been closed since 1995, the recent samples were collected from spawners within rivers. Although the quality of scales collected from the spawning grounds is poor, because of resorption at the margins, the location of the freshwater check could generally be identified and total age determined from otoliths. The average numbers of scales digitized annually since 1955 were 56 age-1.3 scales and 40 age-1.2 scales. Age-1.3 sockeye salmon tend to be more abundant in Rivers Inlet, although this proportion is known to vary considerably among years in many northern BC sockeye salmon populations (Godfrey 1958; McKinnell 1995; Rutherford et al. 1998). The data were stratified by age-class because the average freshwater growth of age-1.3 sockeye salmon is less than that of age-1.2 fish.

Two linear regression models were considered for estimating juvenile abundance from freshwater scale growth. The first model predicted OSI directly from the mean size of the freshwater annulus, using either or both of the age-classes (Figure 2). Unfortunately, there were too few years when both OSI and scale data were collected, so the nature of their relationship is less certain than that defined earlier for OSI and SW. The second method involved an intermediate step of predicting presmolt weight from freshwater scale growth, then applying these estimates in the predictive model developed above for presmolt weight. Although indirect, this method was more attractive because twice the number of years of paired growth data were available, so the form of the relationship between SW and scale growth was more precisely determined than between scale growth and OSI directly. Presmolt weight predicted from freshwater scale growth is identified as SW′ hereafter.

Mean annual freshwater scale growth and smolt weight share most of their variation in common because they are estimates of the same thing, the mean body size of the population at emigration. However, despite sharing a common source of variation, the correlation coefficient between freshwater scale growth of age-1.3 sockeye salmon and SW is only 0.82 ($N = 18$, $P < 0.00002$). This relatively low correlation arises because the scale growth measurements were obtained from returning adults, so they include additional sources of variation (e.g., size-dependent marine mortality, scale selection, scale measurement errors, pooled age-classes) that are absent when presmolt weight is measured directly. Note that the correlation for age-1.2 individuals was much lower ($r = 0.30$, $P < 0.22$, $N = 19$), but this is largely the result of two outliers (brood years 1966 and 1994). Only four scales were measured for the 1994 brood year, and the cause of the 1966 outlier has yet to be determined, but it was not evident in the more abundant age-1.3 data for the same brood year. Initially, we used principal component analysis to extract the component of common variation among presmolt weight and age-1.2 and age-1.3 freshwater scale growth. However, when it became apparent that age-1.3 scale growth was highly correlated with the predominant component ($r = 0.97$), we used only the age-1.3 measurements rather than the principal component scores to predict presmolt weight, that is, $SW' = -0.08 + 0.0096 \cdot S_i$, where S_i = mean freshwater scale growth (μm) for the ith brood year ($R^2 = 72.2\%$, $P < 0.00001$, $N = 18$). The 95% bootstrap confidence intervals for the intercept (0.26, −1.32)

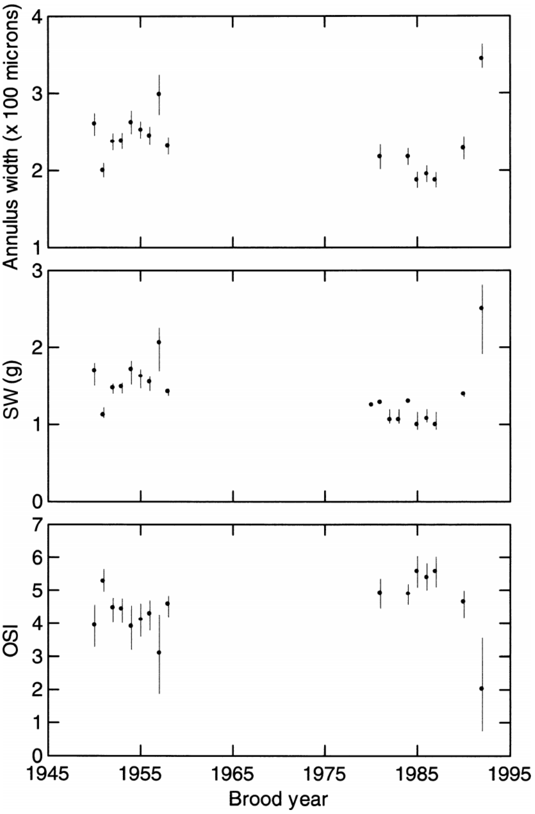


FIGURE 3.—Means and 95% confidence intervals of freshwater annulus width measured on scales collected from returning (adult) age-1.3 sockeye salmon (top panel); uncertainty in predicted presmolt weight (SW) due to uncertainty in the model parameter estimates (middle panel); and uncertainty in predicting the Owikeno sockeye index (OSI) from scale growth because of the combined effects uncertainty in SW and variability in annulus width (lower panel).

and slope (0.0048, 0.0120) were determined from 1,000 resamplings.

Although most sample sizes were adequate to generate precise estimates of the mean, there was variable precision among years (Figure 3) , and the form of the relationship between scale growth and presmolt weight is somewhat uncertain. We considered how this imprecision might affect the predictions of OSI. If the imprecision was too high, it might not be possible to distinguish a year of abundance from a year of scarcity. We examined how OSI varied when we used the upper and lower 95% confidence intervals of mean annual freshwater scale growth (from Figure 3) and the upper and lower 95% confidence intervals of the estimated parameters of the linear model used to predict SW′. This uncertainty created a range of possible values for SW′ for each year, which in turn generated a range of values of OSI predicted from scale growth (Figure 3). Overall, estimating OSI directly from trawl surveys was the most precise, whereas estimating OSI from freshwater scale growth was the least precise. Nevertheless, the uncertainty in the latter was not so great that it overwhelmed the interannual variation in juvenile abundance.

When the estimates of OSI are combined into a single time series, it appears that fry abundance was generally below average during the 1950s, perhaps reflecting concerns about recruitment overfishing during this period (Wood 1970). Thereafter, fry abundance was variable during the 1960s, above average during the 1970s and 1980s, and average to very low after 1988 (Figure 4). There is no evidence of a long-term declining trend in fry abundance, although low abundance was observed in the 1957, 1965, 1967, 1989, 1992, 1996, and 1998 brood years.

Adult Catch

Commercial sockeye salmon catch data are generally considered to be among the more reliable measures of adult sockeye salmon abundance in BC. The number of salmon caught in a fishery is determined from the total weight of the species in the catch and estimated mean weight per individual (Wong 1983). In Rivers Inlet, a linear trend in catch from 1910 to 1969 was not evident (P = 0.48; Figure 5). It has been suggested that the catches in Rivers Inlet were augmented with passing Fraser River sockeye salmon in some years, but their scale patterns were not evident in scale samples collected from Rivers Inlet catches from 1957 to 1970 (DFO, unpublished data). The Rivers Inlet fishery collapsed in 1970, and shortly thereafter an era of generally reduced catches began, including the 1979–1984 adaptive management experiment. Beginning in 1996, the fishery was closed entirely because of low abundance and has remained closed through 2000. Apart from two extreme positive anomalies in 1968 and 1973, the estimated total returns were apparently lower but stable from the 1970s until 1994, when they dropped considerably (Figure 5). Total returns before, during, and after the adaptive management experiment did not vary substantially, regardless of which estimate of escapement was used.

Spawner Escapement

Some of the rivers in the Owikeno Lake watershed are fed by melting ice from glaciers and there-

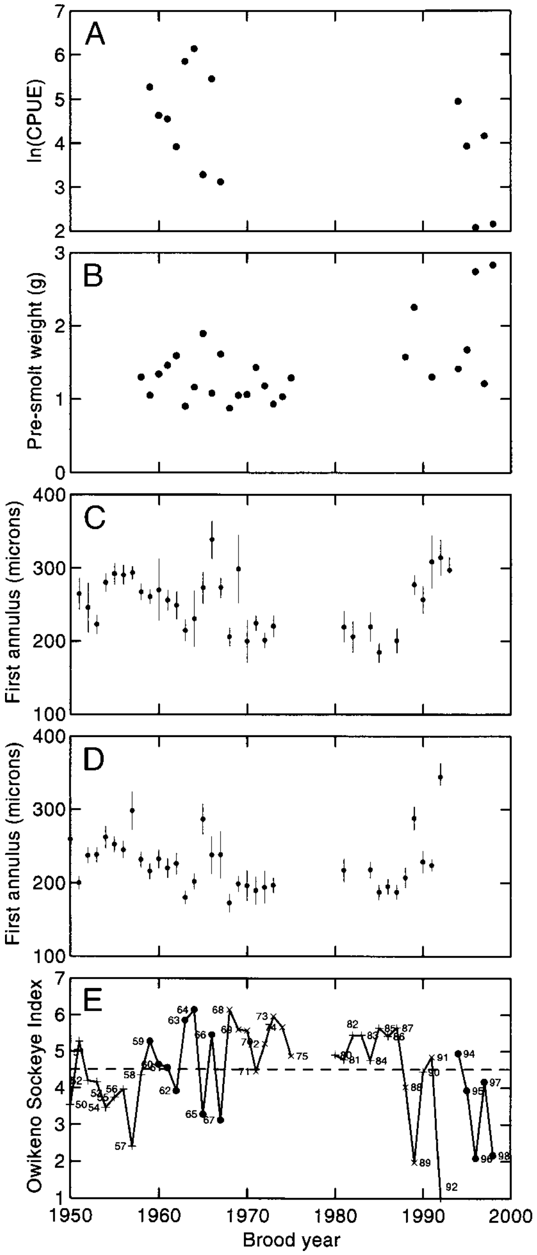


FIGURE 4.—Mean size and abundance of sockeye salmon in Owikeno Lake by brood year (1950–1998): **(A)** area-weighted mean abundance ($\log_e$) of fry in summer in basins 1 and 2; **(B)** mean weight of presmolts in spring in basins 1 and 2; **(C)** mean and 95% confidence interval of width of first scale annulus of returning age-1.2 adults; **(D)** mean and 95% confidence interval of first scale annulus of returning age-1.3 adults; and **(E)** Owikeno sockeye index of fry abundance ($\log_e$ scale), as determined from either abundance from trawl surveys (solid circles), presmolt body weight (crosses), or freshwater scale growth of age-1.3 adults (plus signs), compared with the long-term mean (dashed horizontal line).

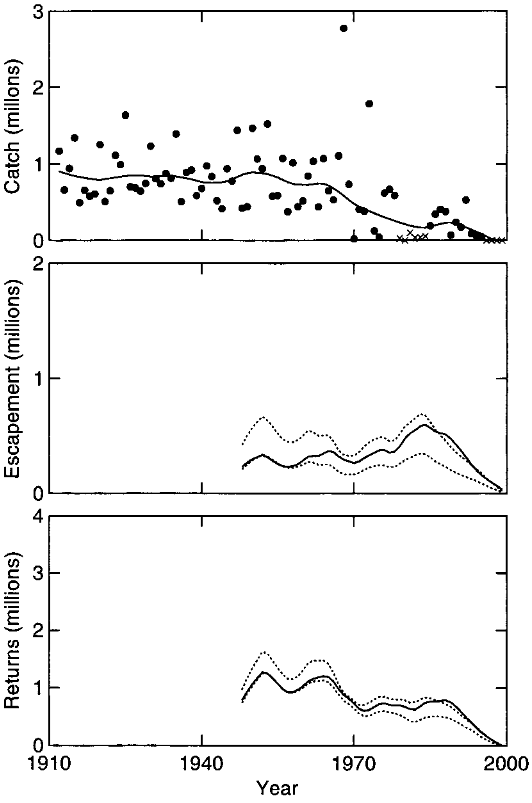


FIGURE 5.—Sockeye salmon catch (top panel), escapement (middle panel), and total return (bottom panel) in Rivers Inlet (statistical area 9) for 1912–2000, as represented by LOESS trend lines. Years with no or limited fishing are indicated by (crosses); catches from 1912 to 1951 were converted from cases of canned sockeye salmon packed at Rivers Inlet canneries. The escapements (*E*) include nominal escapement estimates (solid line) and those derived from the clear-stream index (CSI), assuming that E = CSI/0.33 (upper dotted line) or E = CSI/0.67 (lower dotted line). Total returns were calculated with the escapement ranges in the middle panel.

fore are highly turbid. The turbidity limits the reliability of estimates of total escapement (*E*) to Owikeno Lake (Walters et al. 1993). Nevertheless, the nominal escapements from glacial rivers have been included in the regional Salmon Escapement Data System (SEDS; Serbic 1991), and they have been used to assess the productivity of Owikeno Lake sockeye salmon (Walters et al. 1993). We used only escapements recorded in the clear streams around Owikeno Lake because we believed it might represent the temporal trends in total escapement more consistently than data from glacial rivers, where salmon cannot be readily seen or reliably enumerated. Although Owikeno Lake

TABLE 4.—Principal components analysis (with varimax rotation) of the correlation matrix of annual clear-stream escapements ($\log_e$-transformed).

Stream	Principal component 1	Principal component 2
Ashlum	0.90	−0.05
Dallery	0.27	0.75
Genessee	−0.03	0.89
Inziana	0.82	0.15
Washwash	0.78	0.27
Percent explained	43.1	28.9

sockeye salmon spawn in many streams within the watershed, there is sufficient straying among streams for these fish to be considered a single population (C. C. Wood, DFO, Pacific Biological Station, unpublished data). A correlation analysis indicated that the magnitude of escapements to all clear streams was positively correlated among years. Unrotated principal component analysis of $\log_e$(escapement) indicated that about half of variation in the correlation among clear streams was shared commonly. There was a tendency for the Ashlum, Genesee, and Washwash rivers to be positively correlated and for the Dallery and Inziana to be positively correlated. The rotated principal component loadings (Table 4) suggested that there was some independence between these two groups of streams. We developed a clear-stream index, CSI, as the sum of the escapements to these five streams.

In the past 50 years the most striking change in the CSI was the abrupt decline to record low levels that began in 1994 and, with the exception of 1997, continued through the late 1990s, despite the cessation of fishing in 1996 (Figure 5). Although the CSI was variable before this, there was no equivalent period with a persistently low escapement. Beginning in the early 1970s, the frequency of years with a low CSI declined, as might be expected if the total exploitation had indeed been reduced after 1970. The SEDS data indicated that E increased from the 1950s to the early 1990s, a trend that was not apparent in the CSI. For unknown reasons, the fraction of E attributed to glacial rivers, $(1 - \mathrm{CSI})/E$, increased in a remarkably linear fashion from about 33% in the early 1950s to about 67% by the mid-1990s. The trend may have arisen from changes in personnel or observational techniques over the past 50 years that gradually provided greater access to previously unknown spawning areas in glacial streams, or it may be a natural shift in the distribution of spawners within the lake. It may even have resulted from a perceptual bias introduced by those responsible for counting escapement. Whatever the source, it suggests that researchers must consider the consequences of alternative realities in the escapement data. Our approach was to consider a broad range of percentages (33–67%) of the total escapement to glacial streams and evaluate the consequences of this level of uncertainty. Because of the generally positive correlation in spawner abundance among streams, the simplest model was to consider E' as a linear function of CSI (i.e., $E' = \mathrm{CSI}/\alpha$, where $0 < \alpha \leq 1$). The relationship between CSI and E tends toward linearity as CSI becomes an increasingly larger fraction of E and is linear if $\alpha = 1$.

Although the accuracy of the escapement data are unknown, enough of a relationship between the reported number of spawners and the estimated fry abundance produced from that escapement seems to exist to enable us to detect some errors. A major outlier in spawner–fry abundance relationship was caused by an extra zero that had been inadvertently inserted into the electronic version of the 1960 escapement, probably some time during the 1980s when microcomputers became widely available in fisheries offices. This erroneously increased the 1960 escapement by 10-fold. The ability to detect this type of error in the escapement data from a biological relationship (expected spawner to fry survival) suggests that there is a reasonable amount of signal in the escapement data.

Survival Indices

Relative indices of survival are more widely available than are absolute measures because relative indices require only consistent indices of abundance. If the total exploitation rate of a sockeye salmon population is constant among years, then the annual catch is a suitable index of adult abundance. Unfortunately, the annual total exploitation of sockeye salmon in Rivers Inlet is known to have varied widely over the period of record, particularly in recent years.

An annual index of spawner-to-fry survival in freshwater was calculated as the ratio of indices of summer fry abundance to spawner abundance ($e_i^{\mathrm{OSI}}/\mathrm{CSI}_i$) by brood year. This index was largely trendless from the early 1960s to the early 1990s (Figure 6), regardless of which escapement series (E or E') was used. Using E' indicated that early freshwater survival was lower during the 1950s than at present, but the difference was not statis-

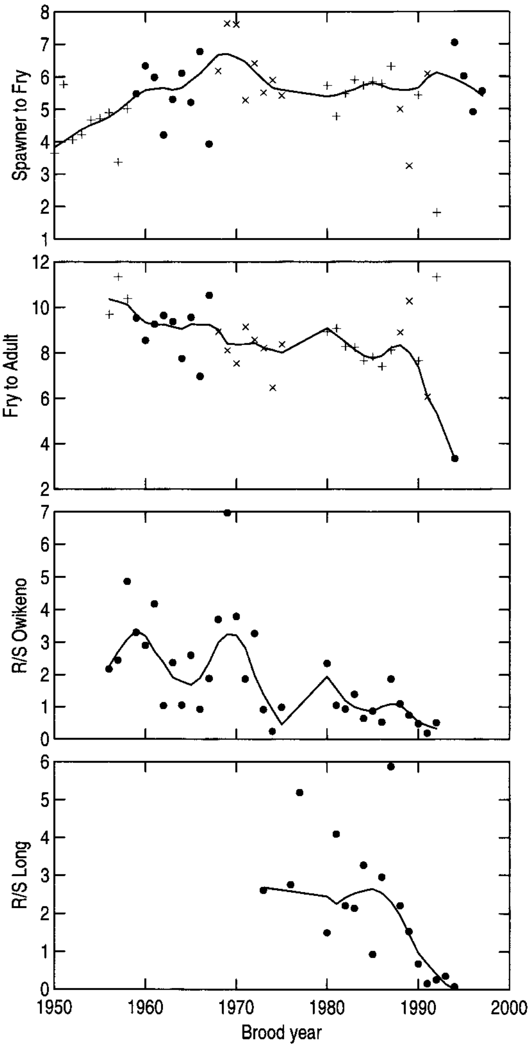


FIGURE 6.—Indices of early freshwater survival (top panel), fry-to-adult survival (upper middle panel), and recruits per spawner for Owikeno Lake sockeye salmon (lower middle panel; assumes the proportion of spawners in glacial streams is 67% of the total) and recruits per spawner for Long Lake (Smith Inlet) sockeye salmon (bottom panel). LOWESS trend lines are indicated on each panel. Plot symbols in the upper two panels indicate the origin of the juvenile abundance data as described in Figure 4.

tically significant among decades (ANOVA; P = 0.13). This trend contradicts what might be expected if habitat degradation had begun lowering spawner-to-fry survival after the pristine 1950s.

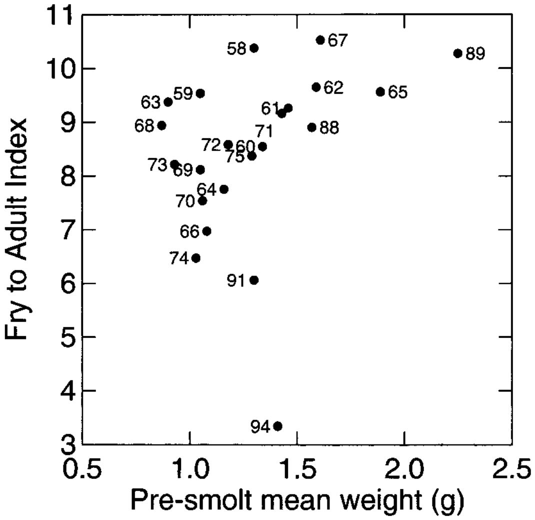


FIGURE 7.—Fry-to-–adult survival index ($\log_e$ scale) versus mean smolt weight (g) of Owikeno Lake sockeye salmon smolts for 21 brood years (numbered data points) between 1958 and1991.

A fry-to-adult survival index was calculated as the ratio of total returns to fry abundance by brood year: $R_i'/\exp(\mathrm{OSI}_i)$. This index has been highly variable, but the overall trend is downward (Figure 6). There are some substantial outliers, most of which are negative. Most (R^2 = 38%) of the interannual variation in $\log_e$(fry-to-adult survival) was associated with SW, but the relationship is not simply linear (Figure 7). In years of small presmolt size, the survival index varied widely between the overall low and high, but in years when the mean presmolt weight was large, there were relatively fewer years with poor survival. The first strongly negative fry-to-adult survival anomaly was the 1966 brood year. It was initially detected during the juvenile sockeye salmon survey in the summer of 1967 and, when combined with expectations for the age composition of the 1965 brood (largely age 1.2), Wood (1970) correctly forecast that returns in 1970 would not exceed the escapement target. Despite low returns and the forecast of low returns, the fleet continued to fish heavily. The manager(s) of the day had no prior experience with extremely low abundance in Rivers Inlet. Strongly negative fry-to-adult survival anomalies also occurred in the 1974, 1991, and 1994 brood years. Presmolt size was somewhat lower than average for these anomalous years, suggesting that smolt size may have contributed to the fry–adult survival anomaly.

Climate Variability and Spatial Scale

Numerous indices of large-scale climate variability in the North Pacific Ocean are correlated with the abundance of sockeye salmon (Beamish and Bouillon 1993, 1995; Hare and Francis 1995; Adkison et al. 1996; Hare and Mantua 2000). If large-scale factors are responsible for regulating the abundance of Rivers Inlet sockeye salmon, then coherent temporal trends in survival among adjacent populations and perhaps species might be expected; the spatial scale of coherence will be related to the spatial scale of the forcing. Nearby Smith Inlet, the adjacent inlet south of Rivers Inlet, has supported a smaller fishery on the sockeye salmon population that uses Long Lake as its freshwater nursery (Hyatt et al. 2000). Unlike Owikeno Lake, the magnitude of the escapement to Long Lake is known because all returning adults must pass through a counting fence to reach the spawning grounds. When added to the sockeye salmon catch in Smith Inlet, the data provide an accurate reflection of the total returns and total survival (Figure 6). What is apparent in Smith Inlet is that beginning with the 1990 brood year (1992 ocean entry year), the recruits per spawner has been persistently less than 1 (i.e., generations have not been replacing themselves; Figure 6). This is a significant point because Long Lake has received artificial applications of inorganic nitrogen and phosphorus to augment sockeye salmon fry growth and survival (Rutherford and Wood 1995) and the watershed is considered pristine (it is unlogged).

The climate regime shift of 1976–1977 appears to have affected one aspect of watershed hydrology. The discharge from Owikeno Lake via the Wannock River has been recorded continuously for several decades and intermittently back to 1928 (AES 1998). Peak flows occur in summer when rainfall is lowest indicating that melting snow and ice are the major sources of discharge. Mean summer discharge was significantly lower after 1976 (529.8 m3/s) than before (649.0 m3/s; ANOVA, $P < 0.0001$). Mean Secchi depths in Owikeno Lake did not differ among years (ANOVA, $P = 0.94$), but interannual differences may be difficult to detect with such a large component of the variability occurring on a seasonal basis.

In the coastal ocean, the Queen Charlotte Sound–Queen Charlotte Strait region has largely been unmonitored, except for two physical variables. Sea surface temperature (SST) and salinity (SSS) have been recorded daily at the Pine Island lighthouse from 1937 to the present. Mean SSTs at Pine Island in the spring have increased by as much as 0.9°C since 1977, and SSTs in the 1990s decade were the warmest on record (Figure 8). What is remarkable about this observation is that Pine Island is situated in an area of strong tidal mixing so this increase may also reflect what is occurring at depth. Bertram et al. (2001) suggested that a component of the spring SST anomalies was caused by the persistence of winter wind patterns into April that maintained poleward flow of warmer southern waters into Queen Charlotte Sound during most of the 1990s. Coincident changes in large-scale atmospheric circulation patterns and sea levels in the 1990s were reported at the southern end of Vancouver Island (Beamish et al. 1999). The persistent SST anomaly at Pine Island abated in 1999.

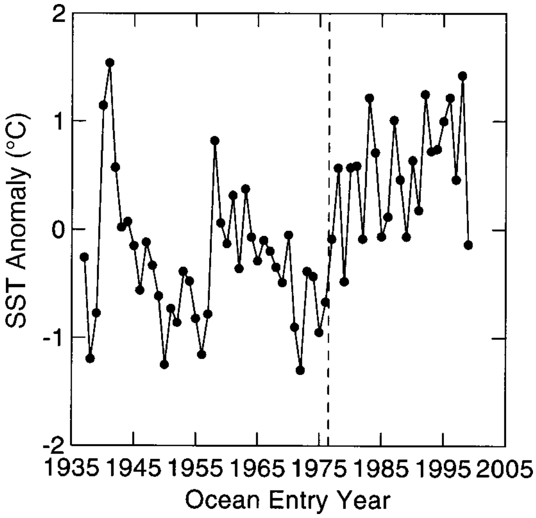
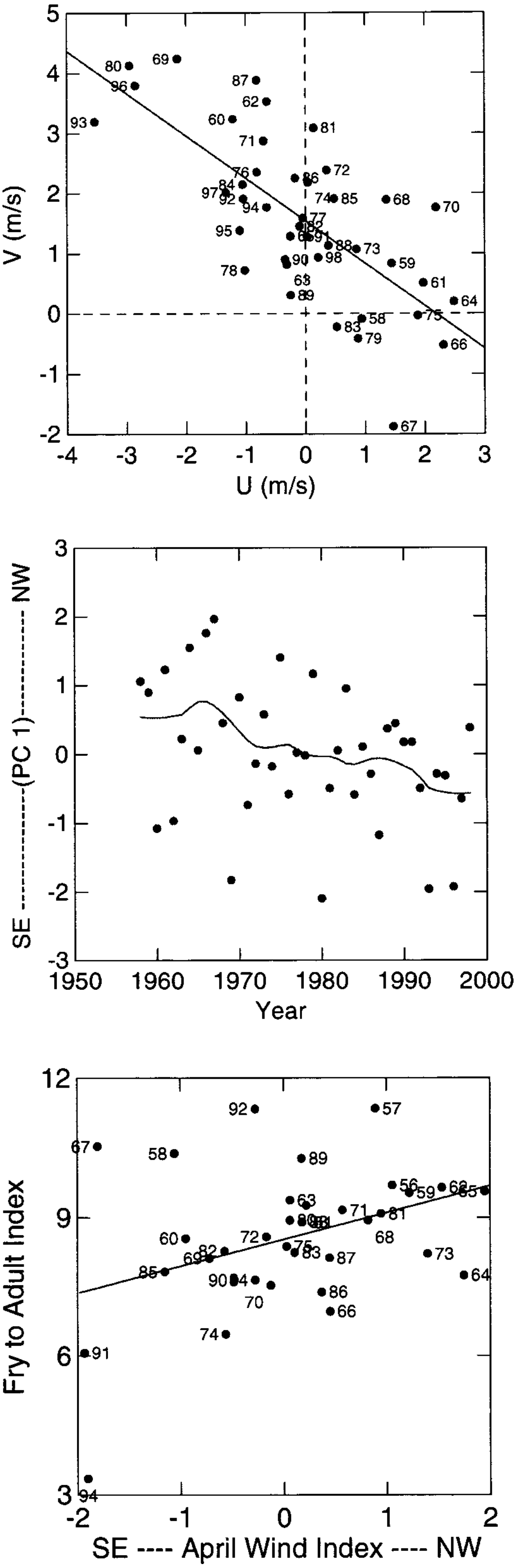


FIGURE 8.—Mean monthly sea surface temperature (SST) anomaly (°C) at Pine Island (Queen Charlotte Strait) in April. The vertical line indicates the date of the 1976–77 climate regime shift.

After linear detrending and removing the seasonal cycle, the mean monthly salinity time series at Pine Island contained a large persistent positive anomaly through most of the period from 1992 to 1998. Because this anomaly does not appear in the equivalent Kains Island time series on the northwest side of Vancouver Island, it is tempting to consider that it may have originated at depth and been transmitted to the surface by strong tidal mixing that is known to occur in the region (Thomson 1981). What is potentially important about this observation is that the most extreme anomalies in the salinity record coincided with the collapse of two major sockeye salmon populations in the region during the late 1990s. Although the coincidence may be spurious, its timing and extreme magnitude may lead to clues about the source of the atypical mortality. This salinity anomaly does



not, however, appear to explain the general decline in fry-to-adult survival since the 1970s.

Wooster (1961) hypothesized that fishing success is ultimately determined by variation in the large-scale wind field. Coastal wind speed and direction are now monitored rather well via meteorological buoys distributed along the BC coast. Buoy 46204 is located near the center of Queen Charlotte Sound, but it has been operating only since the early 1990s. To extend the time series beyond its relatively short operational period (less than 1 decade), Faucher et al. (1999) combined National Center for Environmental Prediction (NCEP) reanalysis winds, which have a much longer history, with the observational wind record to reconstruct 6 hourly winds from 1958 to 1998 (ftp.ocgy.ubc.ca\pub\faucher). The data are reported as *U* (west–east) and *V* (south–north) components of velocity (in m/s). Winds blowing toward the east have positive values of *U*, and winds blowing toward the north have positive values of *V*; westward and southward components have negative values of *U* and *V*, respectively. The correlations between observed and reconstructed winds during the validation period (1990–1995) varied from 0.61 to 0.98, depending on season and buoy. There is a high positive correlation between the monthly average *U* and *V* components in Queen Charlotte Sound in spring (Figure 9a), summer, and fall because of the contrasting influence of the two major climate systems in the region (the Subtropical High and the Subarctic Low). By month, we extracted the dominant principal component scores of the *U*/*V* correlations to produce annual indices of the relative influence of the two major atmospheric patterns (cloud, storms, and winds from the southeast versus clear skies and winds from the northwest) in each month. A significant trend (linear regression, $P < 0.002$) toward more southeasterly winds in Queen Charlotte Sound existed in April for 1958–1998 (Figure 9) but not for May to September. Mean monthly sea levels at Prince Rupert were correlated with the wind index in each month; greater southeasterly winds pro-

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FIGURE 9.—Mean wind speed (m/s for the two components *U* [west–east] and *V* [south–north]) in April in Queen Charlotte Sound, 1958–1998 (from Faucher et al. 1999; top panel); first principal component of the correlation in the top panel (middle panel); and Owikeno Lake fry–-to-adult survival index ($\log_e$ scale; bottom panel) versus April wind patterns; a robust regression model is indicated.

duced significantly higher sea levels related to water being pushed into Queen Charlotte Sound. Variation in April and August wind patterns accounted for 53.2% of the variation in the Rivers Inlet recruits per spawner. Comparing the wind patterns with the fry-to-adult survival index for sockeye salmon from Rivers Inlet, a robust linear regression (SYSTAT 9.0, NONLIN) identifies a similar association between greater northwest winds in April and better survival, although clearly the index appears to be independent of wind patterns in April in some years (Figure 9). A forward-stepping linear regression indicated that northwest winds in April and August also accounted for 72.9% of the variation in Long Lake recruits per spawner ($P <$ 0.002).

Discussion

For most of 20th century, the basic requirement for a persistent salmonid fishery was a sufficient number of spawners and a suitable freshwater habitat in which to spawn and rear. This view of salmonid production led to statements about the Rivers Inlet sockeye salmon fishery such as‘‘Under the present rates of exploitation, and in the absence of harmful changes in the watershed, the stock should maintain itself indefinitely at an average yield of 5 or 6 million pounds a year’’ (Larkin and Ricker (1964).

This reveals that some of the most highly respected fisheries scientists had not considered the ocean ecosystem to be sufficiently variable to have a major effect on sockeye salmon production. Our results suggest that the BC coast and the Rivers Inlet sockeye salmon fishery have recently experienced variability that was apparently unimaginable during the 1960s.

The factors responsible for regulating the abundance of Rivers Inlet sockeye salmon have been a conundrum since the adaptive management experiment of the 1980s. This uncertainty persisted because the environmental component of recruitment variation was assumed to be random and without autocorrelation. Our concept of sockeye salmon production from Owikeno Lake is that spawner abundance and spawning habitat have been sufficient to produce a generous supply of fry for most of the century. Low primary productivity in Owikeno Lake causes strong density-dependent growth, so even modest escapements tend to produce small fry and small smolts. Throughout most of this century, these small smolts have survived in sufficient numbers in the ocean to maintain an annual average catch of more than 750,000 sockeye salmon. Intermittently, high smolt abundance combined with good marine survival has provided bonanza catches for the fishery, but biologists could not predict when these years would occur. The largest commercial catch on record was produced from the smallest average smolt size on record, which is consistent with recent ideas about the greater importance of relative size rather than absolute size on survival of salmonids (McKinnell and Lundqvist 2000). There were apparently six other years when fry abundance was as great or greater than that observed in 1963, but only one of these (the 1968 brood year) produced an outstanding catch.

The period before 1970 was characterized by almost a century of relatively high average catch, punctuated occasionally by bonanza years of very high catch. Thirty years ago, Wood (1970) suggested that evidence of recruitment overfishing existed as early as the mid to late 1950s, noting a significant linear decline in sockeye salmon catch from 1907 to 1969; the rate of decline ranged from 130,000 fish/year to 300,000 fish/year, depending on whether the anomalously high catch of 1968 was included. The trend was attributed to improvements in the effectiveness of the gill-net fleet as they switched from natural to synthetic gill nets during the early 1950s. Although the annual catch records provide the longest series of sockeye salmon abundance data in Rivers Inlet, there is some risk of misinterpreting the purported trend. Certainly, the potential to overharvest sockeye salmon existed because of rapid technological improvements in salmon fishing during the 1940s and 1950s, accompanied by rather minimal changes in fishing regulations (Wood 1970). However, in our view it is more likely that the apparent long-term decline in catch arose from changes in how the catch was reported. Before the mid-1950s, catch was recorded as the annual number of cases packed by the canneries in Rivers Inlet. The number of sockeye salmon caught each year was then determined from the average number needed to fill one case, which in turn depended on the mean weight of the fish. Beginning in 1952, the catch in numbers was determined from the total round weight of the catch in Rivers Inlet and lower Fitzhugh Sound (Statistical Area 9), as reported on sales slips, divided by the average weight per fish (Wong 1983). Wood’s (1970) declining abundance coincided with this methodological change. The unadjusted number of cases packed from 1907 to 1956 does not have a significant linear trend, nor does the DFO catch statistics from 1952 to 1969 (excluding 1968, following Wood 1970). Only if these two series are combined using Wood's multiplier, does a significant decline arise. There was no significant linear trend in our combined series, which was calculated using updated estimates of average sockeye salmon weight. On the other hand, the larger mean weight of juvenile sockeye salmon in Owikeno Lake during the 1950s suggests reduced juvenile sockeye salmon abundance during this period. This could have arisen from either lower spawner abundance or lower freshwater survival. The relative contributions of overfishing and reduced freshwater survival are difficult to distinguish because of the quality of the escapement data, but because the Owikeno Lake watershed was considered pristine during the 1950s (Foskett 1958), it is not readily apparent why this would have been one of periods of lowest freshwater survival in the past 50 years. Nevertheless, the apparently low juvenile abundance is perhaps better evidence of recruitment overfishing during the 1950s than the catch data. There is no evidence in the fry growth and abundance data that recruitment overfishing continued after the 1950s.

The second stanza began around 1970 with the failure of the 1966 brood year. Average total returns during this period were intermediate between the first and third stanzas, and with the exception of 1973, there have been none of the intermittent bonanza years that characterized the first 70 years. One possible explanation for the second stanza is that by decreasing the average exploitation after 1970, fishery managers shifted a greater percentage of the adults from the catch to the escapement, where counting was more difficult and underestimation is expected. However, it seems that the changes have been too great for this view to be accepted. Whether total returns are determined from the nominal escapement (E) or from expansions of clear-stream escapements (E'), the declines are qualitatively similar. Reduced catches from 1979 to 1993 were at least partly, if not entirely, due to reduced fishing effort beginning in 1979. The foregone catch does not appear to have contributed to increasing the abundance of adult sockeye salmon.

An alternative, and perhaps more plausible explanation for the decline is that marine survival also declined. The relatively constant average juvenile abundance in Owikeno Lake during a period of lower adult abundance is consistent with this interpretation. However, without a suitably reliable index of smolt abundance for Owikeno Lake, we cannot reject the hypothesis that changes in fry-to-adult mortality occurred in freshwater after the summer fry surveys but before emigration. Our inclination is not to consider this as the major period of population abundance regulation because a strong relationship between spring presmolt size and summer fry abundance has persisted across several decades and through the most recent period of very low survival. More importantly, parsimony suggests that the strong correlation in survival between Long and Owikeno lakes arose from a common effect in the shared early ocean environment rather than from equivalent effects in separate freshwater environments.

The final abundance stanza began in 1994 with the returns from the failed 1990 brood year (1992 ocean entry). This recent collapse of the population to approximately 0.1% of its former peak abundance is unprecedented and occurred despite severe restrictions on the fishery. Coincident trends in total survival were also observed in nearby Smith Inlet during this period (Rutherford and Wood 2000), despite the fact that the freshwater habitat in Long Lake is pristine (no logging) and fry growth that has been enhanced by artificially supplementing the limnetic ecosystem with inorganic nutrients. Although these dramatic declines in salmon abundance and survival are documented most reliably for Rivers and Smith Inlet sockeye salmon populations, corresponding declines in abundance have also occurred for sockeye salmon in DFO Statistical Area 8 (adjacent to the north of Rivers Inlet; Rutherford and Wood 2000); for coho salmon *O. kisutch* in the Georgia Strait and Puget Sound area (Beamish et al. 1999; Beamish et al. 2000), Fraser River (Bradford and Irvine 2000), and northwestern USA (Cole 2000); and for steelhead *O. mykiss* in southern BC (Welch et al. 2000). Rivers and Smith Inlet sockeye salmon are located near the northern boundary of this extensive spatial pattern.

The ocean ecosystems of the Gulf of Alaska have undergone significant changes during the latter part of the 20th century that were associated with changes in climate (Beamish and Bouillon 1993; Brodeur and Ware 1992; Freeland et al. 1997; Sugimoto and Tadokoro 1997; Francis et al. 1998; McKinnell et al. 1999; Hare et al. 2000, Ware and Thomson 2000; Smith and Ward 2000). Recruitment of many marine species changed abruptly in association with the most prominent of these changes: the climate regime shift of 1976–1977 (Ebbesmeyer et al. 1991; Beamish and Bouillon 1995; Hollowed and Wooster 1995; Hare and Mantua 2000). We were unable to attribute any significant amount of the variation in juvenile sockeye salmon abundance in Owikeno Lake to the freshwater environment (rainfall, air temperature, discharge timing, or volume), but associations between sockeye salmon production and the ocean–climate system seem to be a more promising area of research. Wickett and Ballantyne (1980) examined the combined effects of sockeye salmon spawner abundance, sea-level variation during August and September in the summer of seaward migration, and ocean transport at 50°N, 170°W during the second year at sea. From these factors they accounted for 78% of the interannual variation in the Rivers Inlet sockeye salmon catch from 1948 to 1972. Unfortunately, they did not comment on the relative contributions of each factor. Our results are qualitatively similar; downwelling conditions in Queen Charlotte Sound were associated with reduced marine survival, although we used winds rather than sea level to show this.

The relationship between increasing mean sea level at Prince Rupert and increasing influence of southeasterly winds in spring is causal. Surface drifter experiments conducted in 1995 indicated that water is retained within Queen Charlotte Sound during downwelling winds and released when they relax or reverse (W. Crawford, DFO, Institute of Ocean Sciences, personal communication). The persistence of downwelling winds in spring maintains convergent flow toward the mainland coast, thereby increasing sea level. This may delay or reduce biological activity because nutrient resupply from depth may be diminished under such conditions. If the mortality of Rivers Inlet sockeye salmon occurs soon after ocean entry, it may occur because the smolts encounter a relatively impoverished ocean caused by delayed biological production. Wickett and Ballantyne (1980) thought that downwelling winds might restrict the smolt distribution along the coast, thereby giving piscivorous seabird predators greater access to them. Another possibility is that a delayed transition from downwelling to upwelling winds may place the outmigrating smolts in a situation where they are carried offshore after the wind pattern changes. The timing and intensity of the transition may affect survival.

The migratory behavior of sockeye salmon smolts leaving the Wannock River is largely unknown. Reduced estuarine circulation from lower freshwater discharge may have reduced biological productivity and thereby lowered the food supply for smolts, although there is no evidence of this in first-year marine scale growth (DFO and D.W.W., unpublished data). Reduced freshwater volumes or higher salinities may have reduced the amount of transition habitat available to the sockeye salmon smolts if they are physiologically restricted to less saline waters for some time after leaving the Wannock River. Observations in 1999 that sockeye smolts were captured most frequently in areas of low salinity during seine surveys of Rivers Inlet is consistent with this speculation (D.T.R. and C.C.W., unpublished data.) In a tagging study in Norway, small smolts of Atlantic salmon *Salmo salar* did not migrate as quickly as large smolts from a coastal release site, and as a consequence they were more vulnerable to predation by Atlantic cod *Gadus morhua* (Skilbrei et al. 1994).

For its size and productivity, Owikeno Lake has the capacity to produce a remarkable abundance of adult sockeye salmon. This abundance seems to be achieved by distributing the potential juvenile sockeye salmon biomass among a greater number of individuals than in other lakes. Using their photosynthetic rate model, Shortreed et al. (1999) estimated the carrying capacity of Owikeno Lake to be 41,000 kg of sockeye salmon smolts annually. This corresponds to a spawning escapement of approximately 170,000 spawners, assuming typical sex ratio, fecundity, and egg-to-smolt survival. The equivalent value for the euphotic volume model (Koenings and Kyle 1997) was 23,000 kg (K. Shortreed, DFO, personal communication). Thus, sockeye salmon productive capacity in Owikeno Lake, as estimated from two habitat models, is consistent with the hypothesis that the optimum number of spawners certainly does not exceed 400,000. We suggest that escapement goals of 1,000,000 spawners in Owikeno Lake should be abandoned under prevailing conditions; however, bonanza years do not occur without above-average juvenile abundance in the lake, and this typically requires more spawners. At least since 1973, there has been no commercial payoff for maintaining high juvenile abundance.

The current situation of extremely low spawner abundance inspires responsible agencies to do something to rectify the problem. The most important management action needed under the recent circumstances was to stop fishing, and this was done some years ago. Improving spawning habitat that was degraded by logging is sensible environmental stewardship for the logging companies to undertake, but there is little or no evidence that declining spawning habitat was responsible for declining abundance. Adults returning to spawn presumably now have a rather extensive choice of good spawning habitat because there is so little competition for it.

Sockeye salmon returns to Rivers Inlet in 2001 and 2002 may offer a pleasant surprise for fishermen and a pleasant relief from ocean morality for the sockeye salmon. Adult spawner abundance in 1997 was one of the largest in recent years and juvenile surveys indicated an average abundance of fry in the lake. The critical point for survival was that these smolts entered ocean conditions that had not occurred since the late 1970s. Temperatures were much colder in spring 1999 and the coastal zooplankton community had reverted to pre-1992 conditions (Mackas et al. 2001). We expect that returns of the 1997 brood year in 2001 and 2002 will be the highest in recent years, provided ocean ecosystem changes were the cause of the mortality.

Acknowledgments

The data used in this paper were generated by the collective efforts of biologists, technicians and fishery officers in Fisheries and Oceans Canada over the years. In this regard, the efforts of S. Bachen deserves special acknowledgment. Al Wood and Dave Schutz are commended for publishing the detailed sockeye salmon and environmental data from the 1960s. Three anonymous referees forced us to go the extra mile, but the extra work and the passage of time only strengthened the arguments and resulted in a better paper.

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