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PROTECTION, PRESERVATION AND EXTENSION OF
THE SOCKEYE AND PINK SALMON FISHERIES
IN THE FRASER RIVER SYSTEM**

BULLETIN XXVI

**PRESPAWNING MORTALITIES OF
SOCKEYE SALMON
IN THE FRASER RIVER SYSTEM
AND POSSIBLE CAUSAL FACTORS**

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ABSTRACT

Annual prespawning mortality rate (complement of success of spawning) in individual Fraser River sockeye stocks has been assessed on most spawning grounds since the 1940s using three categories of egg expulsion in samples of dead females: essentially unspawned (0-25%), about half spawned (25-75%), or nearly to completely spawned (75-100%). Annual prespawning mortality rates for 14 individual stocks in the years studied have varied from approximately 0% to 90%; mean values for these stocks varied from 3.3-23.7%. Within the annual spawning of a single stock, the earliest spawners have the highest unspawned mortality rate. Correlation of annual rates between spawning grounds indicated the operation of common factors within years. Comparison of annual stock rates with environmental and biological factors indicated that, for 6 of 8 stocks analyzed in detail, temperature during migration and/or spawning ground occupation, and time of annual migration were significantly related to prespawning mortality rate. In two stocks for which data were available, river migration speed appeared directly related to migration temperature; rate of maturation may also be inhibited by lower migration temperature. Fraser River sediment load (inversely related to river temperature), although poorly correlated with prespawning mortality rates, may with other factors add to the prespawning mortality rate. The graded response of prespawning mortality rate to varying environmental and biological factors is ascribed to cumulative stress effects imposed upon the sockeye. Although disease is often the ultimate cause of death, prespawning mortalities cannot be attributed to any single cause. Fraser sockeye probably have higher prespawning mortality rates than sockeye stocks in other river systems due to higher water temperatures and more difficult migration conditions. Implications of these conclusions for fishery management, stock enhancement and for further research are considered.

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INTRODUCTION

A variable proportion of Fraser River sockeye salmon (*Oncorhynchus nerka*) die after arrival at their spawning streams (FIGURE 1) but prior to complete deposition of eggs. Annual prespawning mortality rates in the populations which compose the yearly Fraser sockeye spawning migrations have ranged from zero to about 90%. Average annual observed prespawning mortality rates vary widely between populations. However, there have been years of generally high or low prespawning mortalities observed over the period of close observation.

Spawning ground prespawning mortalities in sockeye have been attributed to several causes: high water temperatures have been implicated as a contributing cause (Cooper and Henry 1962, Colgrove and Wood 1966, Killick MS 1972, Williams 1973a, Williams et al. 1977, Cooper MS 1982, West and Mason 1987); difficult migration conditions (Cooper and Henry 1962, Godfrey et al. 1956); diseases of several types (Wood MS 1965, Colgrove and Wood 1966, Williams 1973a, Williams et al. 1977); and earliness of annual migration timing of individual stocks (Killick MS 1972, Williams 1973a, Williams et al. 1977, Cooper MS 1982). Other suspected factors are suspended sediments and dissolved atmospheric gas super-saturation (IPSFC 1983). However, because more than one of these factors is always involved in any stock spawning migration, the annual prespawning mortality of that stock cannot be ascribed to a single cause.

The action of the various factors contributing to prespawning mortality has been described in terms of stress theory (IPSFC 1983). The various physical factors adversely affecting sockeye are termed "stressors" and the complex reactions of the fish "stress response". Sockeye on their spawning migration are described as "rapidly aging", with imminent maturation, spawning and death. The effects of stressors are carried beyond the area of stressing and may be expressed as prespawning mortalities.

Prespawning mortality is determined from the female sockeye population and is treated as a rate expressed in percent. Unspawned mortality in males has been ignored not only because it is difficult to determine but also because total spawning success is governed by the extent to which females deposit their eggs. Prespawning mortality rate is then the proportion of the total number of eggs, carried by the females reaching the spawning ground, which are not expelled in the spawning process.

Prespawning mortality is important to the management of Fraser River sockeye because loss of egg deposition usually causes reduced recruitment of progeny and economic loss to the fishing industry. For this reason, the International Pacific Salmon Fisheries Commission (IPSFC) collected prespawning mortality data from all important spawning grounds beginning soon after its inception in 1937 until its dissolution in 1985. Data for 1986 and 1987 were obtained from Canada Department of Fisheries and Oceans. The IPSFC also collected data on water temperature, disease, suspended sediments in the Fraser, and super saturation of atmospheric gases, to augment data on stream flow and sediment available from various government agencies in Canada.

In this report, data on spawning ground prespawning mortalities collected over almost four decades are summarized and examined for correlations with possible causal factors. Much of the analysis is a re-evaluation of the results of Killick (MS 1972) and Cooper (MS 1982) augmented with later years' data and with information from additional spawning grounds. Some of the relationships found suggest means by which prespawning mortalities may be reduced or compensated for in the management of the fishery. The findings have consequences for projects which alter either the migration of the spawning environment in the Fraser River system, especially where they may result in increases in water temperatures. In addition, the effect of possible changes in climate, which may also increase prespawning mortalities, must be considered in the future management of Fraser River sockeye populations.

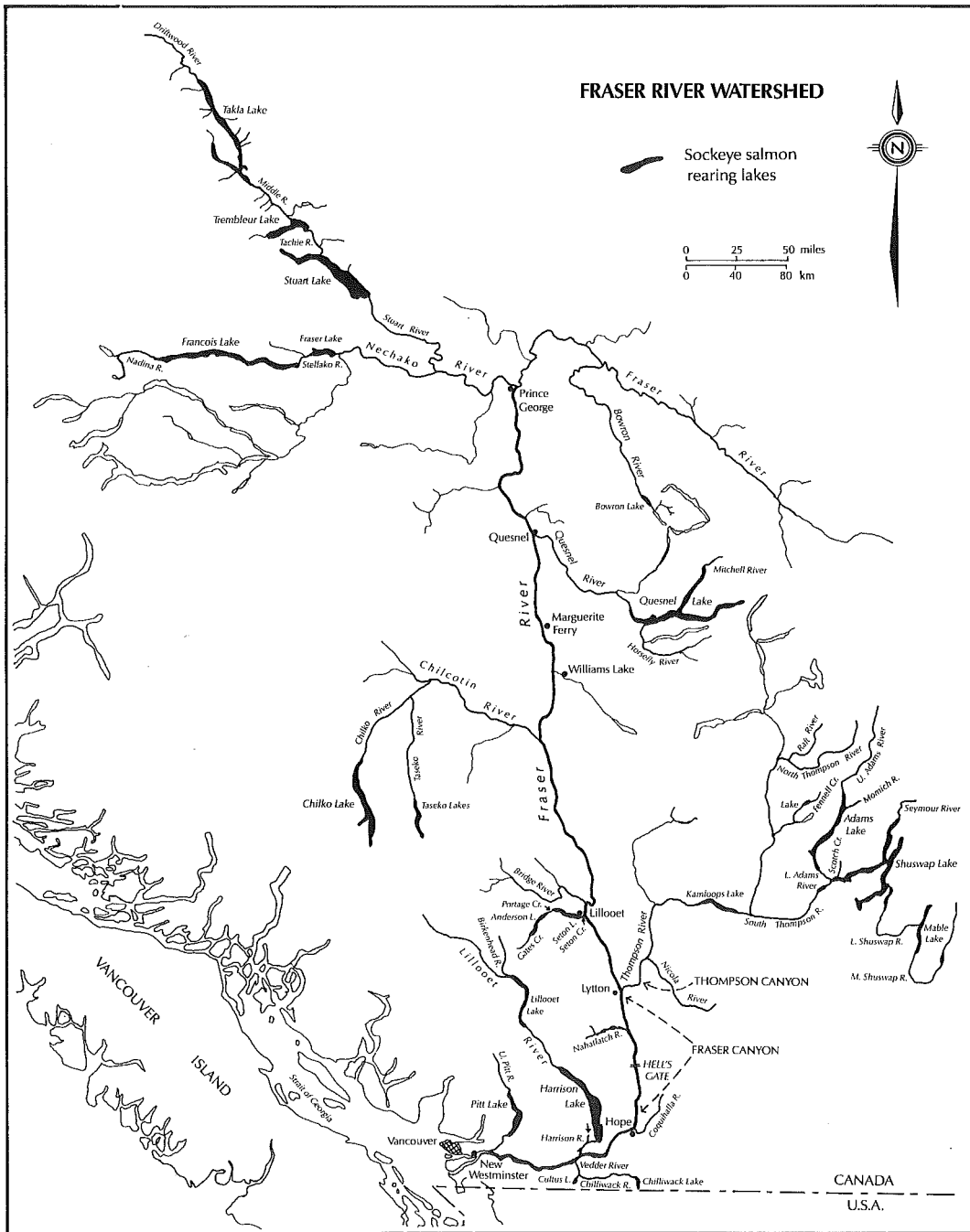


FIGURE 1. Major lakes and streams in the Fraser River watershed.

FRASER RIVER SOCKEYE SPAWNING MIGRATIONS

Migration times of component populations of maturing Fraser River sockeye salmon are unique, along both marine and fresh water migration routes. Spawning fish occupy their various home-stream spawning grounds at unique average times (TABLE 1). Component populations also exhibit distinctive patterns of annual abundance within the quadrennial cycle (Ward and Larkin 1964, Woodey 1987). These and other attributes imply genetically divergent populations, or stocks, which are treated separately in management (as far as possible) and in the analyses of prespawning mortalities.

Annual sockeye spawning runs constitute maturing fish of several stocks migrating in succession from ocean feeding areas through coastal waterways into the Fraser River and thence to specific home streams. Fraser sockeye first appear in coastal waters in mid to late June and continue to arrive until mid to late September.

River entry for most sockeye (i.e. summer-run stocks) is made without noticeable delay, while later migrating (late run) stocks delay off the river mouth for variable times (TABLE 1)

In some cases the fish delay for 30 days or more, each stock having a consistent average delay duration. Two or three stocks appear to vary in different years between delaying and nondelaying migrations (Henry 1961; IPSFC 1977, 1980).

Annual run size of individual Fraser River sockeye stocks entering coastal waters has varied from a few individuals to about 15 million fish in the years the IPSFC enumerated harvests and escapements by stock. The commercial fishery typically removed 60 to 80% of a total annual return and from a few thousand to over 400 thousand sockeye were removed by the native Indian subsistence fishery along the freshwater migration paths of the various stocks.

Daily abundance of a sockeye stock migrating riverward in salt water follows a bell-shaped or quasi-normal curve lasting for about a month (Henry 1961, Table 17). Occasionally the daily abundance curve will be bimodal and/or skewed. Stocks which delay off the river mouth may alter their abundance curve during river entry by becoming skewed and/or compacted or protracted (Gilhousen 1960). Uneven commercial harvests may also cause skewing or other irregularities. Regardless of such changes, the sockeye within the run maintain a close chronological order (Killick 1955). Annual peak occurrence at a given location is not constant, varying over a range of from 10 to more than 30 days in the various stocks. Within the annual run of a stock, the males migrate somewhat earlier than females. The female percentage is therefore low early in the migration and high toward the end of the run.

TABLE 1. Migration and spawning times of 17 major Fraser River sockeye stocks arranged by date of Fraser River entry.

| Stock | Average Peak Dates at Location or Stage | | | |
|----------------------|---|--------------------|-------------------------|------------------------------|
| | San Juan Islands | Fraser River Entry | Spawning Ground Arrival | Center, Peak Spawning Period |
| Early Stuart | July 6 | July 8 | July 31 | August 5 |
| Early Nadina | July 17 | July 19 | August 19 | August 28 |
| Gates | July 21 | July 23 | August 23 | August 30 |
| Bowron | July 22 | July 24 | August 17 | August 27 |
| Pitt | July 25 | July 27 | September 6 | September 15 |
| Seymour | August 1 | August 3 | August 25 | August 30 |
| Raft | August 1 | August 3 | August 25 | September 1 |
| Late Stuart | August 1 | August 3 | September 9 | September 17 |
| Horsefly (Quesnel) | August 2 | August 4 | August 23 | September 1 |
| Late Nadina | August 4 | August 6 | September 9 | September 17 |
| Chilko | August 4 | August 6 | September 2 | September 25 |
| Stellako | August 6 | August 8 | September 12 | September 27 |
| Birkenhead | August 7 | August 18 | September 17 | September 25 |
| Weaver | August 15 | September 18 | October 17 | October 20 |
| Adams (Late Shuswap) | August 21 | September 18 | October 13 | October 20 |
| Harrison | August 11 | October 1 | November 7 | November 15 |
| Cultus | August 19 | October 1 | October 27 | November 24 |

Most early and mid-season sockeye migrating to upper-river areas (upstream from the Fraser Canyon, FIGURE 1, Hope to Lytton) spawn within a few days of arrival at their spawning grounds (TABLE 1), having limited energy reserves and an inexorable ripening of sex products under normal conditions (Idler and Clemens 1959, Gilhousen 1980). Thus only a short delay during river migration, such as that caused by difficult flow conditions at Hells Gate (Cooper and Henry 1962), may impede or prevent arrival in their home stream. Unduly delayed sockeye may attempt to spawn in inappropriate locations but often die enroute to their homestream without spawning. Two mid-season upper-river stocks, the Chilko and Stellako River sockeye, arrive in the vicinity of their spawning grounds up to six weeks prior to spawning. These stocks can usually survive a lengthy delay and still reach their spawning grounds prior to full maturity.

Spawning normally lasts for about a month on any spawning ground, with a quasi-normal temporal distribution. Thus most of the spawning takes place during a short period called the "peak of spawning" near the center of the spawning season. In some stocks, notably the late Shuswap and Cultus Lake stocks, spawning may be protracted for several weeks after the peak spawning period.

Although the natural ratio of sexes in a sockeye stock is close to equality (Killick and Clemens 1962), spawning ground sex ratios may occasionally exhibit more than 75% females (e.g. Peterson 1954), mainly due to selectivity for males in the gillnet fisheries. Difficult migration conditions in the Fraser Canyon, which occasionally prevent portions of a stock from ascending above that location, have in some years resulted in predominantly female sockeye being found in non-natal tributary streams below the obstruction. However, this has occurred only in large, late runs primarily before the fishways were built at Hell's Gate, with no resulting authenticated large surplus of males having been noted on the home spawning grounds. Sex ratios as large as 60% males have been observed, apparently caused by greater commercial fishing depletion of the latter part of a sockeye run, in which the females predominate. Paucity of males has caused no observed reduction in resulting progeny because one male can fertilize the eggs of several females.

SOURCES OF DATA

Timing of Stock Migrations

Precise data on variable migration timing and stock size of Fraser River sockeye runs are required for scientific management of the fishery (Henry 1961). Variable harvest rates have been necessary for restoration of individual stocks, which were in various stages of recovery from a long period of depletion. Methods of stock identification by means of circuli patterns on scales were perfected in the years 1948 to 1960 (Clutter and Whitesel 1956, Henry *ibid.*). Using these methods, augmented by information on differences between stocks in fish length, age class distribution and general migration timing (Verhoeven and Davidoff 1962), daily catches of sockeye in each fishing area have been separated into stock components since 1952. The graph of daily catches for a stock in one area in a given year allows the bell-shaped or quasi-normal time abundance curve to be eye-fitted and a date of maximum or peak abundance to be estimated in the fishing area in question.

Fraser sockeye progress through the fisheries with a rather uniform speed. Consequently, fitted abundance curves can be compared and anomalous peaks in single areas can be corrected, as in Henry (1961, Figures 19-21). For major stocks, which usually form the bulk of the catch at the peak of occurrence, accuracy is more than adequate to determine peak dates used in biological analyses.

Uniform migration speed also allows peak abundance dates to be estimated at locations where no fishery exists. For example, timing at Hells Gate (FIGURE 1) for several stocks has been extrapolated from the fishery in the following analyses. Peak dates at locations farther up the river are affected by changes in migration rates due to variable river flow between years, and other factors. Peak dates have been estimated from Indian fishery catches along the river, from daily visual counts made each summer at Hells Gate, and by interpolation between beginning of the river migration and arrival on the spawning grounds. Killick (1955) gave several examples of the method of connecting escapements from relevant closures in the Fraser River gillnet fishery with observed peaks of arrival at various spawning grounds.

Spawning ground arrival is usually determined by a succession of "live counts". Live counts on the spawning grounds, made by an experienced observer walking along the river bank or counting from a drifting boat, are an acceptable index of the sockeye population size, given good observation conditions. When augmented by consistent recovery of dead sockeye, the count of live fish (usually made at intervals of 2 or 3 days to a week) plus the cumulative number of dead reaches a maximum when most of the sockeye have arrived. Median (50%) arrival date is then interpolated between counts.

Arrival is also determined in some streams by counts made at locations near the spawning grounds; these have been either index counts, made at a bridge or other convenient station for one to eight hours at the time of daily sockeye movement, or essentially complete counts made for enumeration purposes. Median or peak date of arrival is extrapolated from the counting location to the spawning grounds if the distance requires a day or more of migration. A few annual arrival curves have been determined from counts at a weir at the lower end of a spawning ground.

Estimation of Population Sizes

Escapements from the commercial gillnet fishery in the Lower Fraser River have been determined in three ways. Prior to the institution of specific programs to measure daily escapement, total escapements during each weekly closed period of the fishery were estimated from catches before and after the closure, since the fishery removes a very large

fraction of each daily sockeye migration (Gilhousen MS 1990). Beginning in the 1950s, systematic test fishing with gillnets during the closed period gave improved estimates of daily escapements (Clutter MS 1956). Starting in 1973, summed targets from a succession of echo-sounder (hydroacoustic) river transects plus stationary sounding has been used to estimate daily escapement (Woodey 1987). Test fishing is still required during each closure to provide scales and other biological data with which to determine stock composition in each day's escapement measured by the hydro-acoustic program and as a backup escapement estimate.

Spawning population size for each stock is commonly determined by two methods. Large populations (usually above 20,000) are enumerated by mark and recovery programs, in which a small proportion (i.e., about 1%) of live unspawned sockeye are tagged, with recovery of tags from much larger samples of dead sockeye (Schaefer 1951). Tagging programs can be quite accurate when properly executed (Howard 1947, Chapman 1947, Killick 1955); the most obvious error is the overlooking of tags on dead fish, corrected for by re-examination of a large proportion of previously sampled dead, which are thrown up on the river bank after the first examination.

Smaller sockeye populations, usually about 20,000 maximum, are estimated by visual counts of live and dead fish, with an expansion factor applied to the largest sum at any one time. Expansion factors have been determined from populations measured by weir counts or the tag-and-recovery method and concurrent use of the live-count method on the same stream, taking the results of tagging or weir counts as the correct population. Expansion factors are necessary due to the limited visibility in some streams and to the succession of sockeye on the spawning grounds. Expansion factors vary from year-to-year, but the average, used in practice, is consistent over most streams (Woodey 1987).

In a few cases in the early years of IPSFC investigations, sockeye spawning populations were enumerated by counting all arrivals at a weir installed across the stream just below the spawning grounds (Howard 1947, Schaefer 1951, Killick 1955). This method has always been used for the Cultus Lake sockeye run and is also used at artificial spawning grounds.

Male and female populations are calculated separately by several methods. In populations enumerated by tagging, male and female populations are calculated as separate entities from the tags applied, tags recovered and total dead examined within each sex. Where difficulties occur during dead recovery or where the population is small or not tagged, the division of the population by sex is taken from the sex ratio in the dead recovery. Where data concerning sex ratio are lacking, the ratio is taken from other runs which migrate and spawn about the same time.

Spawning Ground Prespawning Loss of Females

Prespawning mortality in a female sockeye is defined as death prior to complete extrusion of eggs. For practical purposes in a spawning population, it is the complement of the *success of spawning*, which is the percentage of the total quantity of eggs, borne by the females, that is successfully extruded. Unlike ovaries, testes of male sockeye show no clear evidence of extent of spawning. Because loss of a portion of the males is relatively unimportant, no attempts have been made to determine spawning success in males.

Considerable variation is found in the success of spawning, both daily and over the spawning season. Therefore, accurate determination of the season's proportion requires consistent sampling during the complete period of dying. In large populations, dead sockeye are examined in all areas at intervals of 1 to 3 days but in smaller populations, dead recovery may be done at longer intervals, as infrequently as only a day or two at the peak period of dying. Occasionally, heavy rains cause dead sockeye from a part of a run to be washed into areas where they are not available for sampling, resulting in possible distortion of the estimated seasonal success of spawning. Approximate correction can usually be made, especially where frequent dead recovery shows which part of the run was lost. In small runs with infrequent dead recoveries, corrections are necessarily subjective.

Sampling of dead female sockeye for percentage spawned is usually confined to a portion of the population examined in the dead recovery, although in some cases (usually small populations) all dead females encountered may be examined. In most enumerations, the proportion examined of the female dead recovered has been between 2.5 and 15%. Minimum daily sample size is 100 females unless fewer are available, and in large spawning populations several such samples may be examined each day in different areas by each of several observers.

Dead females are classified by visual examination of the body cavity as either *unspawned* (retaining 75% or more of their eggs), *50% spawned* (retaining 25 - 75% of their eggs), or *spent* (retaining less than 25% of their eggs). Typically, half-spawned females make up less than 10% of all females examined. Some investigators have counted the numbers of eggs retained in each female examined (Foerster 1968, Manzer and Miki 1985, West and Mason 1987). Such precision was not attempted by IPSFC not only because the number of unspawned eggs was normally unimportant in relation to the total, but also due to the much larger sampling effort required.

The prespawning mortality of each spawning population is calculated by determining weighted average of all the daily measures of spawning success. Daily percentage spawning success is calculated by adding half the number that were 50% spawned to the number that were fully spawned and dividing the sum by the total number sampled and multiplying by 100. The season's success of spawning is the average of the daily percentages spawned, each weighted by the respective daily total of dead females recovered.

Dead samples are usually divided into the categories *fresh* (dead for only a few hours) or *tainted-and-rank* (dead for a day or more), as ascertained from appearance. There is very little difference in the calculated success of spawning for the fresh samples of females as compared with combined fresh and tainted-and-rank samples. Consequently, success of spawning in large populations is determined from fresh samples only, whereas in small populations, it is usually necessary to combine the fresh and tainted-and-rank categories.

Environmental Variables

In most cases, water temperature was measured by fluid-mechanical thermographs of Taylor, Bristol and Foxboro manufacture with $\pm 1^\circ\text{F}$ stated accuracy. These instruments were recalibrated to achieve this or better accuracy. Thermographs used seven-day charts and calibration checks were made at this interval using hand thermometers held to $\pm 0.5^\circ\text{F}$ accuracy. Maximum - minimum thermometers (read to the nearest degree Fahr.) have been used in a few locations when thermographs were not available. Both types of instruments have been employed on migration routes and on spawning grounds.

Water temperatures recorded were daily maximum, minimum, and mean, midnight to midnight. Mean daily temperature was the average of chart readings at 6-hour intervals when diurnal variation was more than 3°F ; for lesser variation, and with maximum - minimum thermometers, the mean of the maximum and minimum was used.

Some temperature data were obtained from spot temperatures taken at recorded times with mercury hand thermometers. Mean daily temperatures were estimated from daily weather information and thermograph records of other years to show the hourly pattern of temperature variation under variable conditions of cloudiness and air temperature.

Water temperatures at Hells Gate have been recorded year round from 1950 to 1985. Thermographs were used in most years until 1969, when a daily (early morning) spot temperature was substituted. These spot temperatures have been used as the daily average values since diurnal river temperature variation in the Fraser Canyon is almost nil.

All temperature data examined were originally collected as Fahrenheit values because available thermographs and thermometers were calibrated in this unit. Conversion to Celsius has been carried to 0.1°C in order to avoid rounding errors.

River discharge data was obtained from published records of the Inland Waters Directorate, Water Resources Branch, Water Survey of Canada (Ottawa). River sediment load (suspended solids) data from several locations on the Fraser River was obtained from the same source.

Statistical Treatment of Data

Relationships between spawning ground prespawning mortality rates and the various factors which may affect the mortality rates have been analyzed using least squares regressions and correlations via the *Statgraphics* computer programs (Copyright Statistical Graphics Corp.). Prespawning mortality rates for individual spawning grounds often did not conform closely to normal distributions, as tested by *Statgraphics* procedures, hence logarithmic and arcsine (least applicable) transformations of the mortality rates were also compared (Snedecor 1946).

Irregular or non-normal distributions were not discarded. Often, an extreme prespawning mortality rate occurred with an extreme value of a variable factor; such occurrences were sometimes found to be indicative of a causal relationship otherwise less clearly revealed.

Multiple regression equations are presented where significant ($p \leq 0.05$) relationships are found. Only the untransformed prespawning mortality rate regression equations are given, although higher multiple correlation coefficients often resulted from logarithmically transformed rates, because confidence limits cannot be simply stated for transformed variables.

PRESPAWNING FEMALE LOSS ON SPAWNING GROUNDS

Relationship Between Spawning Ground Mortalities and Migration Mortalities

Prespawning death of sockeye of the various stocks may occur enroute to the spawning grounds as well as on the spawning grounds but high spawning ground prespawning mortality rates do not necessarily occur following high migration mortality rates. Sockeye which died during migration were not included in the prespawning mortality analyses presented here unless they occurred closely adjacent to the home stream and had been included in the dead recovery for that stream. Migration mortalities have been infrequently detected and the possible connections between migration mortality rates and subsequent spawning ground prespawning mortality rates have not been clarified. Stocks which are known to have suffered migration mortalities include the Early Stuart, Chilko, and Stellako.

Early Stuart sockeye have suffered migration mortalities to a greater extent than other stocks. This stock migrates earliest and therefore may encounter more frequent conditions of difficult migration in the Fraser River. Early Stuart fish encounter the higher water levels and velocities of the spring snowmelt freshet plus higher resulting river sediment load (Servizi and Martens 1987). In addition, exposure to elevated temperatures may occur both during and after migration in the Fraser River (IPSFC 1983).

Mortalities along the migration route have occurred when one or more of these stress factors have critically affected an annual Early Stuart migration (Cooper and Henry 1962, IPSFC 1965, 1969, 1976, 1983). Correlations and multiple regressions with stress factors (other than Hells Gate temperature and timing) were therefore calculated for all years and with the years 1954, 1955, 1964, 1968, 1975 and 1982 (years of significant migration mortality) omitted for the Early Stuart stock. Inclusion of data for the years with significant migration mortalities did not cause appreciable changes in the relationships found between prespawning mortality rates and possible causal factors.

Years with Hells Gate temperature and timing data available for Early Stuart included only two with significant migration losses, 1975 and 1982. Omission of these years had a similarly small effect on correlations involving prespawning mortality rate and would not have changed any conclusions drawn from the analyses.

In 1964, the Chilko spawning migration was impeded both by a record early August discharge and by a slide on the Chilcotin River (August 19), which blocked the run for several days. After the Chilcotin washed through the slide material and turbidity subsided, about three quarters of the escapement was able to reach the spawning grounds (IPSFC 1965). Prespawning mortality on the spawning grounds was low (2.2%), possibly because the weaker sockeye had been removed. Temperature involvement will be considered later. Inclusion of the 1964 data caused only negligible changes in correlations between prespawning mortality rates and compared variables.

The Stellako sockeye runs of 1954 and 1958 suffered some unusual prespawning mortalities during migration. In 1954, several hundred dead sockeye, mainly from the latest part of the spawning migration, were found in Fraser Lake and in the Nechako River close to the lake (FIGURE 2). This loss was attributed to biological factors and since it was proportionately small, the subsequent prespawning mortality rate for 1954 (determined on the spawning ground) was not omitted. The 1958 Stellako spawning migration apparently had a similar loss of late fish somewhere in the Fraser River below the Nechako River confluence (IPSFC 1959; Henry 1961). Because this migration mortality was the latest part of the run, it could not significantly change the very low 1958 spawning ground prespawning mortality rate, which was also included in the analyses.

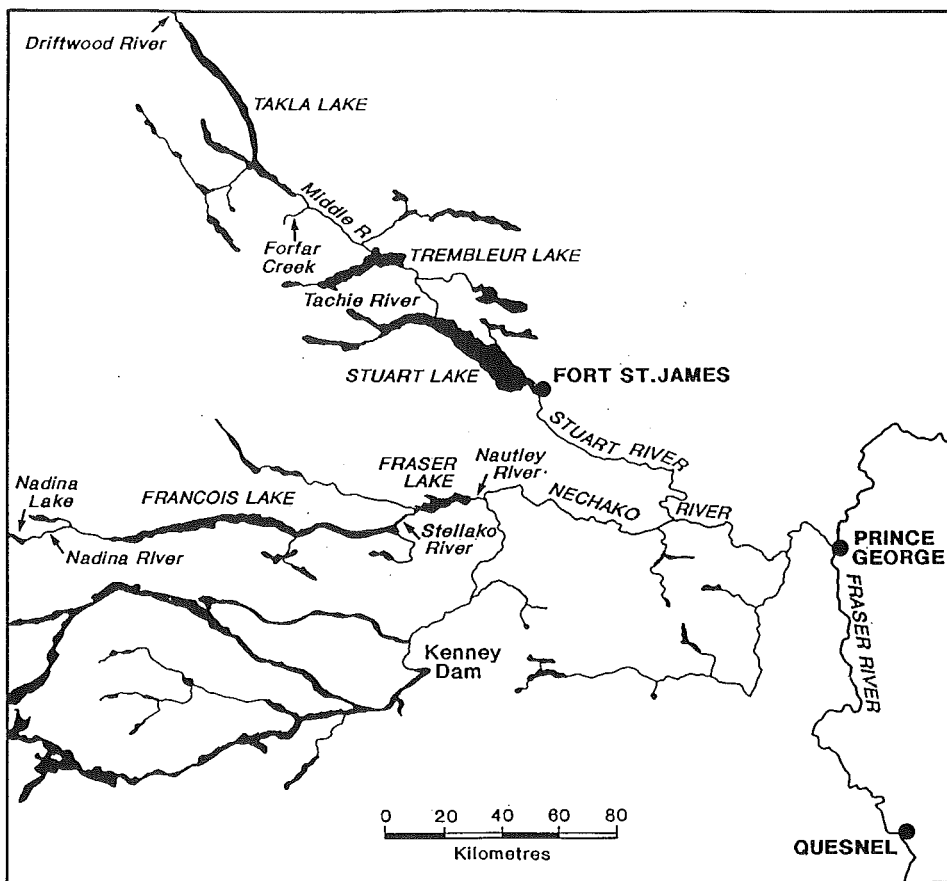


FIGURE 2. The Nechako and Stuart River systems: Early Stuart sockeye spawn in small streams tributary to Middle River and Takla Lake; Late Stuart sockeye spawn in Middle and Tachie Rivers and adjacent lake fed streams; Early Nadina sockeye spawn in Nadina River near Francois Lake; Late Nadina spawn at Nadina Lake outlet; Stellako sockeye spawn throughout the Stellako River.

Pattern of Prespawning Mortality Rates

Spawning ground prespawning mortality rates in Fraser River sockeye vary widely for individual stocks, both during a spawning period and between years, as well as between stocks. These variations yield clues as to the causes of the mortalities.

Spawning ground prespawning mortality rates have had a wide range of maximum and average values (TABLE 2). Three spawning grounds had one year with an extreme mortality rate well beyond other observed values. The mean prespawning mortality rates for Early Nadina, Gates, and Horsefly are quite high, while those for Pitt, Seymour, Weaver and Adams are relatively low on the average.

Normally, the prespawning mortality rate within a spawning period is highest among the first arrivals and thereafter decreases rapidly (FIGURE 3). The long "S" shaped descending curve results because females which spawn live longer than those which die unspawned (Williams 1973a; Williams et al. 1977). When the mortality rate is low, the only unspawned dead are the earliest arriving females which die before the onset of heavy spawning activity. Curves similar to FIGURE 3 are found for all spawning grounds.

A possible exception to the decreasing mortality rate within seasons was noted by Williams (1973a) in the 1969 Horsefly River population. The population of females was divided into three successive segments (early, peak and late) according to tags applied to the migrating

TABLE 2. Maximum and mean female prespawning mortality rates at 14 important Fraser River spawning grounds. Populations of 1000 or more females used in tabulations, except for Early Nadina in 1977 (835 females). Stocks ordered by approximate mean date of peak spawning.

| Spawning Ground | Maximum Mortality (%) | Year | Mean Mortality (%) | No. of Years |
|-----------------|-----------------------|------|--------------------|--------------|
| Early Stuart | 28 | 1978 | 11.2 | 36 |
| Early Nadina | 86* | 1961 | 19.5 | 7 |
| Gates | 57.5 | 1984 | 23.7 | 11 |
| Seymour | 31.6 | 1970 | 5.2 | 36 |
| Raft | 44 | 1950 | 13.4 | 28 |
| Horsefly | 62 | 1961 | 22.7 | 14 |
| Pitt | 9.7 | 1957 | 3.3 | 35 |
| Late Nadina | 29 | 1979 | 8.0 | 15 |
| Late Stuart | 54.5** | 1953 | 10.1 | 27 |
| Chilko | 90*** | 1963 | 11.7 | 36 |
| Birkenhead | 37 | 1969 | 12.5 | 36 |
| Stellako | 44 | 1963 | 10.1 | 36 |
| Weaver | 32.4 | 1974 | 5.2 | 36 |
| Adams | 12.8 | 1967 | 3.4 | 32 |

* next highest loss 17 % (1953)
 ** next highest loss 36% (1951)
 *** next highest loss 40% (1969)

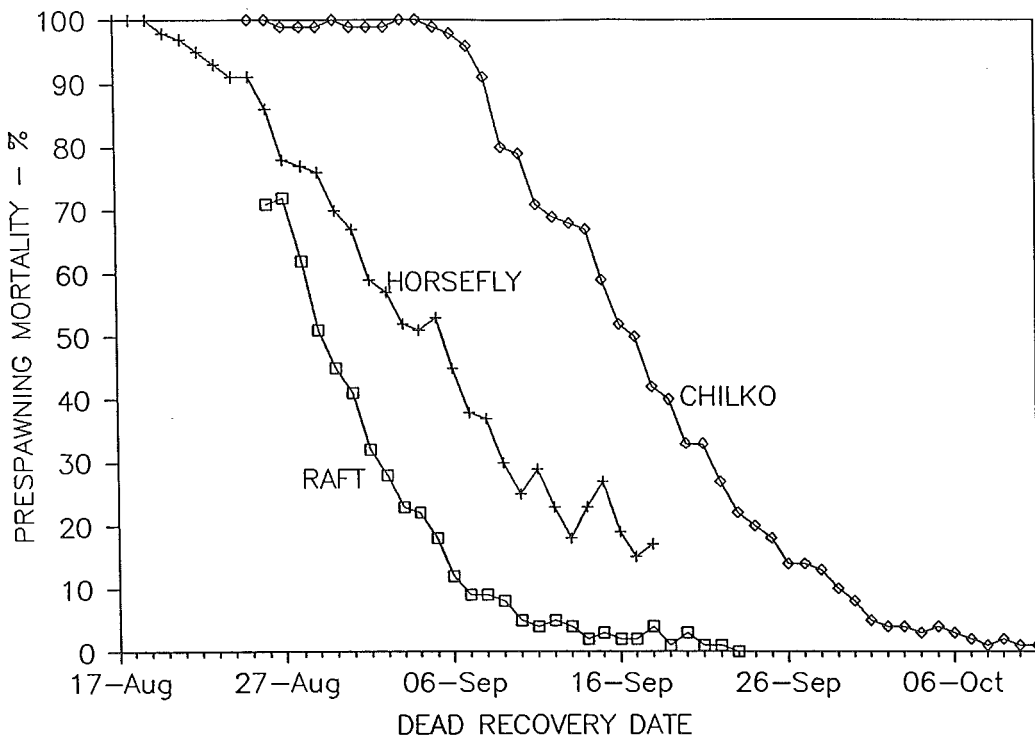


FIGURE 3. Mean female prespawning mortality in percent by calendar date of dead recovery, for three Fraser River sockeye spawning grounds; several years data averaged for each curve. Data largely from Killick MS 1972.

sockeye shortly before their arrival at the spawning grounds. No significant differences in prespawning mortality rates were found between segments but Williams et al. (1977) noted that prespawning mortality was highest among the very earliest arriving females.

Significant unspawned female mortality rate differences between stocks are shown in FIGURE 3. Horsefly females, which have average peak spawning in the first few days of September, had an average prespawning mortality rate above 50% at this time for the six large, dominant runs represented. Raft females, which have a similar peak spawning period, averaged about 20% mortality at the same date consistent with their lower average rate in TABLE 2. The peak spawning period of Chilko sockeye is at the end of September, when the rate of prespawning mortality of FIGURE 3 (about 10%) is close to the mean rate for the population in TABLE 2 (11.7%).

Sampling procedures and migration behavior affected the curves of FIGURE 3. Due to the high unspawned mortality rates and the large size of the Horsefly runs of FIGURE 3, dead sampling began very early; consequently, the first female dead were almost completely unspawned. Also, due to the heavy losses, the curve of percent unspawned for Horsefly never reached zero. In contrast, the relatively small Raft River populations were seldom sampled until there was an accumulation of dead sockeye, hence the loss curve began well below 100 percent. Because Chilko sockeye usually arrive at their spawning grounds well before normal spawning begins (TABLE 1), there was an early period of dying in this stock when almost no spawned females were found.

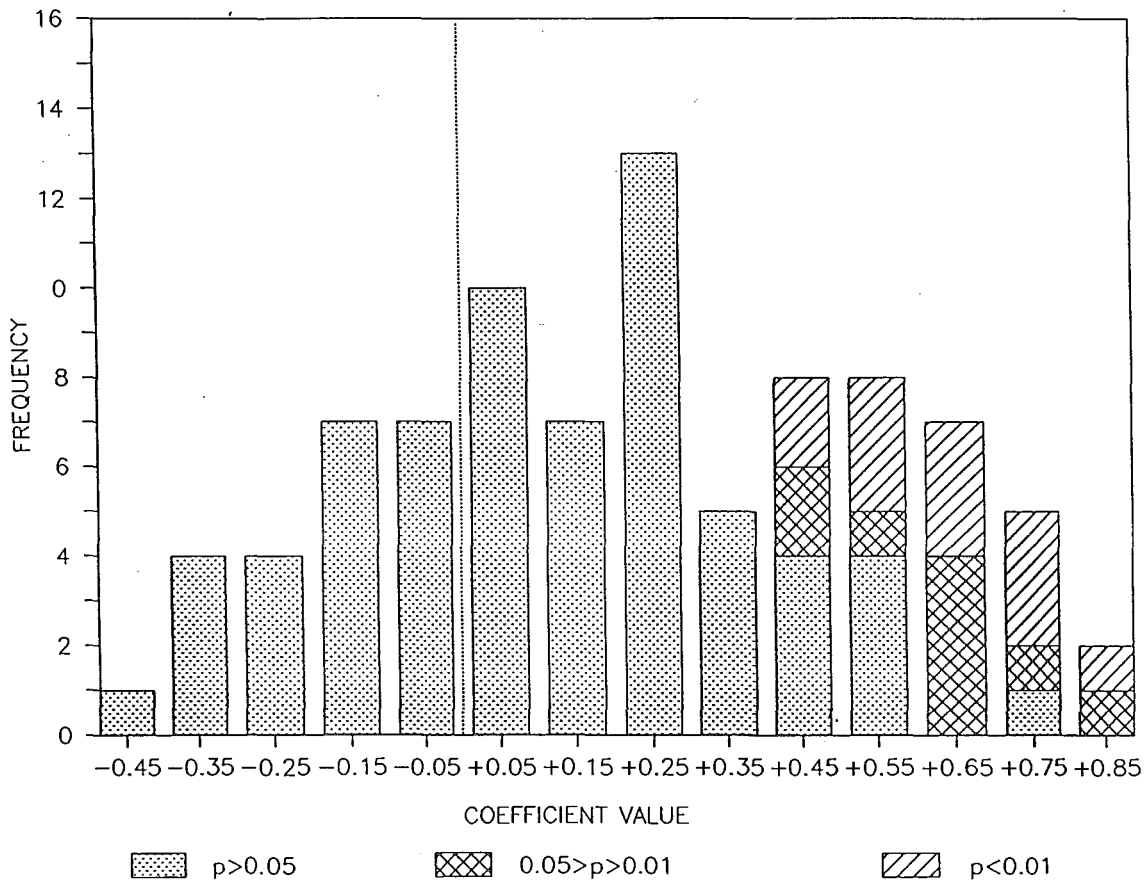


FIGURE 4. Frequency distribution of correlations of annual female prespawning mortality rates at 14 spawning grounds taken in pairs (data of TABLE 3). Frequency interval is 0.10, e.g., +0.35 interval is from +0.31 to +0.40.

Correlations between annual prespawning mortality rates for individual spawning grounds, taken in pairs, indicate that causal factors may be shared over a wide area (TABLE 3). All the early and midseason stocks spawning above Hells Gate plus the Birkenhead population had positive intercorrelations with the exception of three negative and relatively small coefficients involving the Late Nadina stock. Other negative correlations were confined to the Pitt, Weaver and Adams stocks.

The several negative intercorrelations for Pitt sockeye in TABLE 3 suggest a connection with the late migrating Weaver and Adams stocks. Pitt sockeye migrate into Pitt Lake in late July and early August, with spawning the Upper Pitt River and small tributaries in September, more closely resembling the timing of early and midseason upriver runs (TABLE 1; FIGURE 1). Because Pitt sockeye spend less time in the main Fraser River than the early and mid-season upriver runs, the reduced exposure in the main Fraser may be equivalent to the September and October exposure of the late-migrating Weaver and Adams stocks under less extreme conditions than those occurring in July and August.

The intercorrelations between prespawning mortality rates at individual spawning grounds given in TABLE 3 form a quasi-normal distribution of values (FIGURE 4). Only a quarter of the 88 correlations (21 positive and one negative) are statistically significant at the probability level of 0.05 or less. The distribution might be attributed to large random errors but the negative correlations are not random, being confined almost entirely to three of the spawning grounds. While errors in prespawning mortality rates may lower the significance of the correlations, environmental factors unique to each river system and spawning ground and the use of different sets of years in the various pairings will also be contributing causes.

Environmental and Biological Factors

In the early years of the IPSFC investigations, it had been noted that large female prespawning mortalities on certain spawning grounds were associated with warm weather during spawning ground occupation. Then, at least as early as 1963, Killick (MS 1972) noted that late spawning migrations of sockeye runs (relative to the average for both a stock and an annual migration within each of the 4-year cycles) were usually subject to lower unspawned mortality rates than runs migrating earlier than average. The apparent contribution of both timing of migration and river temperature at Hells Gate to the magnitude of female prespawning mortality rate in the Horsefly River system was presented in 1973 (IPSFC 1974). Cooper (MS 1982) calculated multiple correlations for these and other possible causal factors with all valid prespawning mortality data for seven stocks up to 1981 and found several significant relationships. The statistical analyses presented below augment Cooper's analyses with more data and extended statistical treatment

Several environmental and biological factors ("compared variables") have been examined for possible causal relationships with spawning ground female prespawning mortality rates at certain spawning grounds. Those factors with demonstrated or presumptive relationships were determined as follows:

- Peak date at Hells Gate was determined by extrapolation from peak timing in the commercial or Fraser River test fisheries to Hells Gate using appropriate stock migration rates.
- First arrival dates at certain spawning grounds were determined from observations made by enumeration crews or local residents. These dates were subject to considerable error depending on the source or frequency of observations; the first fish are often difficult to detect. Early fish of a run may encounter variable migration conditions resulting in a variable relationship to peak timing. First arrival dates were sometimes available when peak arrival dates were not.
- Peak arrival dates were obtained from successive live counts on spawning grounds or from counts made of sockeye migration approaching the spawning ground. Low accuracy may result from poor counting conditions or infrequent counts, but dates are more reliable than first arrival date.
- Central date of the peak spawning period was taken from reported dates given by the

TABLE 3. Coefficients of correlation between annual prespawning mortalities in females of 14 sockeye races of the Fraser River system. Pairs with less than 5 years in common are omitted. Populations of less than 1000 females not compared (except for Early Nadina 1977). Number of years in each comparison shown in parentheses under each coefficient. Stocks ordered by approximate average date of spawning.

| | Early Stuart | Early Nadina | Raft | Gates | Seymour | Horsefly | Pitt | Late Nadina | Late Stuart | Chilko | Stellako | Birkenhead | Weaver |
|--------------|-----------------|-----------------|------------------|----------------|------------------|------------------|------------------|-----------------|------------------|------------------|------------------|----------------|----------------|
| Early Nadina | +0.204 (7) | | | | | | | | | | | | |
| Raft | +0.090 (28) | +0.391 (6) | | | | | | | | | | | |
| Gates | +0.281 (11) | --- | +0.433 (10) | | | | | | | | | | |
| Seymour | +0.048 (36) | +0.427 (7) | +0.588** (28) | +0.371 (11) | | | | | | | | | |
| Horsefly | +0.384 (14) | +0.565 (7) | +0.722* (11) | --- | +0.648* (14) | | | | | | | | |
| Pitt | -0.107 (35) | -0.232 (7) | +0.460* (27) | -0.275 (11) | +0.168 (35) | -0.056 (14) | | | | | | | |
| Late Nadina | -0.192 (11) | -0.086 (6) | +0.181 (12) | --- | +0.270 (11) | +0.284 (9) | +0.253 (15) | | | | | | |
| Late Stuart | +0.022 (27) | +0.309 (7) | +0.522* (20) | +0.781 (5) | +0.262 (27) | +0.255 (13) | +0.526** (26) | -0.084 (12) | | | | | |
| Chilko | +0.261 (36) | +0.403 (7) | +0.512** (28) | +0.526 (11) | +0.748** (36) | +0.845** (14) | +0.061 (35) | +0.658* (11) | +0.283 (27) | | | | |
| Stellako | +0.208 (36) | +0.859 (7) | +0.148 (28) | +0.504 (11) | +0.431** (36) | +0.611* (14) | -0.059 (35) | +0.422 (15) | +0.422* (27) | +0.605** (36) | | | |
| Birkenhead | +0.268 (36) | +0.547 (7) | +0.253 (28) | +0.406 (11) | +0.301 (36) | +0.756** (14) | -0.054 (35) | +0.290 (15) | +0.487** (27) | +0.638** (36) | +0.643** (36) | | |
| Weaver | +0.085 (36) | -0.369 (7) | +0.100 (28) | -0.364 (11) | -0.154 (36) | -0.283 (14) | -0.098 (35) | -0.209 (15) | -0.139 (27) | -0.055 (36) | +0.027 (36) | -0.108 (36) | |
| Adams | -0.424* (32) | +0.294 (5) | -0.143 (24) | -0.309 (11) | +0.162 (32) | -0.337 (11) | +0.167 (31) | +0.079 (12) | +0.131 (24) | -0.063 (32) | +0.080 (32) | +0.131 (32) | +0.085 (32) |

* - $p < \text{or} = 0.05$ ** - $p < \text{or} = 0.01$

enumeration crew. Peak spawning period was estimated from observation of sockeye spawning activity and, being somewhat subjective, would vary with the observer. Complications arise when spawning ground arrival was bimodal and two peaks of spawning occurred. Bimodal spawning periods were sometimes averaged where the two groups of fish were approximately equal.

— Mean Hells Gate river temperature for each annual run of a given stock was the average of mean daily temperatures during passage weighted by the numbers of sockeye passing each day. Daily numbers were extrapolated from the fishery, in the same way the peak date was extrapolated. For the Birkenhead stock, which does not enter the Fraser Canyon, average temperature of the Fraser River at New Westminster (FIGURE 1) over an 11-day period (centered on the peak date) replaced Hells Gate temperatures.

— Mean river migration temperature for the Early Stuart, Early Nadina and Stellako runs was the simple average of mean Hells Gate temperature and mean migration temperature at one station (Nechako River above Stuart River mouth) or two stations (Nechako and Stuart Rivers near their confluence) in the Nechako River system (FIGURE 2). Hells Gate temperature is an approximate measure of temperature exposure along the migration path to the mouth of the Nechako River. Although the exposure time to Fraser temperatures was longer than to those in the Nechako/Stuart system, differential weighting of the two components of the “mean river temperature” was not attempted. Advancing maturity of the sockeye may increase vulnerability to adverse temperature levels in the Nechako-Stuart system relative to the same exposure in the Fraser. Furthermore, Nechako and Stuart River temperatures were almost always higher than Hells Gate temperatures for the Early Stuart and Early Nadina migrations; because the effect of temperature appears to accelerate as the temperature level rises (Servizi and Jensen 1977), the effect of Nechako-Stuart temperatures will be greater than indicated by the shorter exposure time. Although the simple average of temperatures in the two systems is an inexact index, no better data were available.

— Average spawning ground temperatures (average of daily means) have been calculated from either first date of arrival of sockeye at the spawning ground, or date of 50% arrival, to the center of the peak spawning period. The former starting date was preferred but was not always available. Weighting of daily temperatures by sockeye abundance was not attempted since daily estimates of arrival were seldom available.

— River discharge exposure for the Early Stuart, Chilko and Stellako runs was indexed by averaging daily mean river discharge over a specific number of days bracketing the peak of each annual run at the location where river flow was measured. The length of the bracketing period was varied according to the duration of exposure in the river in question. These averages were found to be reasonably representative of exposure and avoided the weighting of daily flow values by the estimated daily abundance of sockeye (as was used for Hells Gate water temperatures); also, for small runs, daily abundance estimates are of low accuracy.

— Exposure of Early Stuart sockeye to sediment-laden water, from entry into the Fraser River until exit into the low turbidity Nechako River at Prince George, is of long duration, complicating the construction of an index of concentration of suspended solids (SS). Examination of records for several stations along this portion of the Fraser indicated a wide variation in SS between equivalent day's samples at successive stations. Averages over several days were less variable between stations. Most stations were reasonably representative of the differences between years. Suspended solids sampled daily at Marguerite Ferry (FIGURE 1) were chosen for an index since this station had the longest period of continuous and apparently consistent data. Average SS over an extended period was adopted because an individual Early Stuart sockeye spends approximately two weeks traversing this turbid section of the migration route. Daily SS measurements at Marguerite from 15 days prior to the peak date of the Early Stuart run at Hells Gate to 20 days after the peak were averaged for each annual index. Due to travel time, the index is biased somewhat toward the early part of each run, but subsequent analyses suggested that the index was reasonably representative of SS.

— Spawning ground temperatures were usually measured at convenient locations on the most important part of those spawning grounds with more than one stream or with spawning over a very long river section. For the Early Stuart stock, which spawns in many relatively small, cold creeks not arising in lakes (FIGURE 2), one convenient stream (Forfar Creek) has been used as the index stream for temperature records.

— Female population enumeration has been described. Female spawning populations and prespawning mortality rates for the various Fraser sockeye stocks are given in Appendix Tables A to I.

— Year rank, used to examine the effect of factors which changed gradually with the passage of time, was the A.D. year number (e.g. 1979); coding was unnecessary for correlation analysis.

While spawning ground female prespawning mortality data are available for a large number of years, environmental and migration timing data have not been available in some years. This is particularly true for the years before 1950 - 1953. For this reason, the number of years included in the following analyses is always fewer than the years listed for each stock in TABLE 2.

Relationships of Prespawning Mortality To Possible Causal Factors

Simple Correlations With Compared Variables

Water temperature was clearly an important factor in spawning ground female prespawning mortality rate as indicated by simple correlation analysis (TABLE 4). Mean Hells Gate temperature yielded positive correlation coefficients with all stocks except for the Late Stuart, which had a small negative coefficient. Spawning ground temperature appeared to be equal in importance to Hells Gate temperature since it yielded positive correlation coefficients at all spawning grounds where it was examined. Average migration temperature gave coefficients little different from Hells Gate mean temperature for the Early Stuart and Early Nadina sockeye but Stellako sockeye had a nonsignificant negative correlation.

Variation in time of migration is possibly equally as important as temperature in estimating prespawning mortality rate, taking the correlations of TABLE 4 at face value. Migration time at Hells Gate, first spawning ground arrival, peak arrival dates, and center of peak spawning period all produced negative coefficients. The only positive correlation (nonsignificant) was for Birkenhead sockeye migration time at New Westminster (run does not pass Hells Gate).

Size of the female population showed no consistent relationship with prespawning mortality rates (TABLE 4). The only significant correlation (negative) was for Birkenhead sockeye, whereas a positive relationship would seem more likely.

Correlation of prespawning mortality rates with time (year) produced no consistent relationships but two fairly large negative coefficients (suggesting progressive decreases in prespawning mortality rates) were found for the Early Nadina and Birkenhead runs.

Comparison of discharge of the Fraser River at Hope (Fraser Canyon) and the SS index (from Marguerite) with prespawning mortality rate for Early Stuart sockeye, produced only small negative correlations (TABLE 4).

Timing and temperatures on the spawning grounds produced correlations with prespawning mortality rates not much different overall from the same factors calculated at Hells Gate (TABLE 4). Three stocks had higher coefficients with Hells Gate (or New Westminster) temperatures and three had lower coefficients.

The above relationships between prespawning mortality rates and compared variables will be considered further in later sections involving multiple correlations and detailed examinations of individual sockeye stocks. Explanations for many of the inconsistencies in the simple correlations will be presented.

TABLE 4. Simple coefficients of correlation between annual female prespawning mortality rates at eight Fraser River sockeye spawning grounds and 11 compared variable factors.

| Variable | STOCK | | | | | | | |
|----------|----------------|---------------|------------------|------------------|--------------|------------------|-----------------|---------------------|
| | Early Stuart | Early Nadina | Horsefly | Raft | Late Stuart | Chilko | Stellako | Birkenhead |
| Year | +0.24 (32) | -0.53 (8) | -0.25 (19) | -0.12 (20) | --- | E+0.18 (21) | E+0.10 (26) | E-0.41** (36) |
| HGT | +0.61* (22) | +0.57 (8) | E+0.51 (9) | E+0.47* (20) | -0.25 (9) | E+0.33 (21) | +0.21 (26) | E+0.42*N.W. (23) |
| HGP | -0.23 (22) | E-0.45 (8) | E-0.77** (9) | E-0.31 (20) | -0.51 (9) | E-0.72** (21) | E-0.41* (26) | +0.22 N.W. (23) |
| POP | -0.37 (32) | E+0.42 (8) | E+0.33 (19) | +0.38 (20) | +0.19 (9) | -0.20 (21) | +0.19 (26) | E-0.45** (36) |
| AVT | +0.69* (16) | +0.49 (8) | --- | --- | --- | --- | -0.30 (17) | --- |
| FAD | -0.45* (32) | --- | E-0.51* (19) | --- | --- | --- | E-0.33 (18) | --- |
| PAD | --- | --- | --- | E-0.64** (20) | -- | E-0.66** (21) | --- | -0.36 (12) |
| CPS | -0.41* (32) | E-0.52 (8) | E-0.71** (19) | E-0.46 (20) | --- | E-0.58** (21) | E-0.16 (26) | E-0.40* (23) |
| SGT | E+0.20 (32) | --- | +0.38 (19) | +0.69** (20) | --- | E+0.46* (21) | +0.59** (25) | +0.22 (21) |
| SSI | -0.28 (13) | --- | --- | --- | --- | --- | --- | --- |
| AVD | -0.16 (16) | --- | --- | --- | --- | -0.30 (22) | --- | --- |

* - $p < \text{or} = 0.05$; ** - $p < \text{or} = 0.01$. Number of years correlated given in parentheses.
E - exponential relationship (prespawning mortality rate logged).

HGT and HGP: Hells Gate average temperature and peak date, respectively. POP: female spawning population. AVT: average of Hells Gate and Nechako system temperatures. FAD: first arrival date. PAD: peak or median arrival date. CPS: central date, peak spawning period. SGT: spawning ground temperature. AVD and SSI: average discharge (Hope) and suspended solids index (Marguerite), respectively, bracketing the peak of the run. N.W.: data for Birkenhead from New Westminster rather than from Hells Gate.

Relationships Within Temperature Data

Because river water temperature is determined in part by large, long-lived weather features, annual differences in river temperature are generally correlated in different parts of the Fraser watershed, often over weeks or months of a year. This relationship was evident in the data employed in the present analyses (TABLE 5, first and second rows of correlations). Hells Gate weighted mean daily temperature was highly and directly correlated with average migration temperature since the former was a constituent of the latter (data for three spawning grounds only). Spawning ground temperatures from arrival to peak spawning were also positively (but not always significantly) related to Hells Gate temperatures in all but the Birkenhead stock. Average temperature of the Fraser River at New Westminster for an 11-day period bracketing the peak of the Birkenhead run was not correlated with spawning ground temperatures averaged over an estimated mean period of spawning ground occupation (arrival dates were seldom noted). The cause of this lack of correlation is not evident.

Only weak correlations were found between Hells Gate temperatures and the peak date at Hells Gate for the eight stocks examined (TABLE 5). Correlations tended to be positive for early migrating stocks and negative for later migrating stocks, possibly resulting from the individual relationships between migration time and the maximum Fraser River temperatures (usually occurring in mid-August; FIGURE 5) in the different years represented for each stock.

Spawning ground temperatures, averaged from first date or peak date of arrival to the center of peak spawning, were inversely (but not always significantly) related to arrival or spawning time in all but the Stellako stock (TABLE 5, last three lines). At the peak of spawning, water temperature is falling from the seasonal maximum except for the Early Stuart stock, in which peak spawning occurs before the average seasonal maximum (FIGURE 5). The Early Stuart relationship will be considered further in a later section. The lack of inverse correlation between spawning ground temperature and peak spawning date for Stellako sockeye has no obvious explanation.

Annual average weighted mean daily water temperature at Hells Gate for the Early Stuart run was inversely related to average discharge of the Fraser River at Hope during the peak migration period of this stock ($r=-0.55$, $p < 0.01$, $N=22$). Higher discharges reflect cool, rainy weather or high snowmelt, either of which depresses water temperatures in the Fraser.

In parallel with discharge, the suspended sediments index for the Fraser during the migration was also inversely correlated with the weighted average Hells Gate temperature for the Early Stuart stock ($r=-0.75$, $p < 0.01$, $N=12$). This relationship clearly results from the increase in suspended sediments with higher discharges. The higher correlation between sediment and temperature than with sediment and discharge suggests that the source of suspended sediment also varies somewhat with temperature, which in turn may depend on the source of discharge, i.e. glacial or snow melt vs rainwater runoff.

The average of Hells Gate annual average weighted mean daily temperatures, for five stocks were in all cases higher than the spawning ground temperature averages for those stocks (TABLE 6). In only one stock (Stellako) in but one year (1963) was the average water temperature higher on the spawning grounds than at Hells Gate (17.8° vs. 17.6° C). New Westminster temperatures, used for the Birkenhead run, would have been very close to Hells Gate temperatures calculated for this stock, had it migrated by that route. The Birkenhead run migrates into the Fraser closer in time to the Stellako run than any other stock and the mean temperatures and temperature ranges for Stellako at Hells Gate and Birkenhead at New Westminster are almost identical.

Relationships Within Timing Data

Checkpoint dates during migration and spawning were mainly positively correlated within stocks (TABLE 7, columns 2, 3 and 4) as would be expected from the reasonably uniform within-stock migration rates and maintenance of chronological order demonstrated by Killick (1955). The exception was a near zero negative coefficient for Early Stuart sockeye (Hells

TABLE 5. Simple correlations between average annual water temperature during migration or on spawning grounds for eight Fraser sockeye stocks, and certain other compared variables.

| Variables Compared | STOCK | | | | | | | |
|--------------------|-----------------|----------------|----------------|---------------|--------------|-----------------|-----------------|---------------|
| | Early Stuart | Early Nadina | Raft | Horsefly | Late Stuart | Chilko | Stellako | Birkenhead |
| HGT vs AVT | +0.90** (16) | +0.87** (8) | --- | --- | --- | --- | +0.83** (17) | --- |
| HGT vs SGT | +0.56* (17) | --- | +0.44* (20) | +0.64 (9) | --- | +0.41 (21) | +0.27 (25) | +0.08 (22) |
| HGT vs HGP | +0.22 (22) | +0.45 (8) | +0.20 (20) | +0.07 (9) | +0.11 (9) | -0.01 (21) | -0.10 (26) | -0.11 (23) |
| HGT vs FAD | -0.60** (22) | --- | --- | +0.43 (9) | --- | --- | +0.21 (26) | --- |
| HGT vs PAD | --- | --- | -0.19 (20) | --- | --- | -0.54** (21) | --- | --- |
| HGT vs CPS | -0.48* (22) | --- | -0.09 (20) | -0.31 (9) | --- | -0.42* (22) | -0.07 (26) | -0.23 (13) |
| SGT vs FAD | -0.54* (17) | --- | --- | -0.29 (19) | --- | --- | -0.57** (25) | --- |
| SGT vs PAD | --- | --- | -0.44* (20) | --- | --- | -0.46* (21) | --- | --- |
| SGT vs CPS | -0.55* (17) | --- | -0.28 (20) | -0.23 (19) | --- | -0.53** (21) | +0.01 (25) | -0.22 (21) |

* - $p < 0.05$; ** - $p < 0.01$. Number of years correlated given in parentheses.

HGT and HGP: average water temperature and peak date at Hells Gate, respectively (Birkenhead data at New Westminster).
 AVT: average of Hells Gate and Nechako system temperatures. FAD: first arrival date.
 PAD: peak or 50% arrival date. SGT: spawning ground water temperature. CPS: central date of peak spawning period.

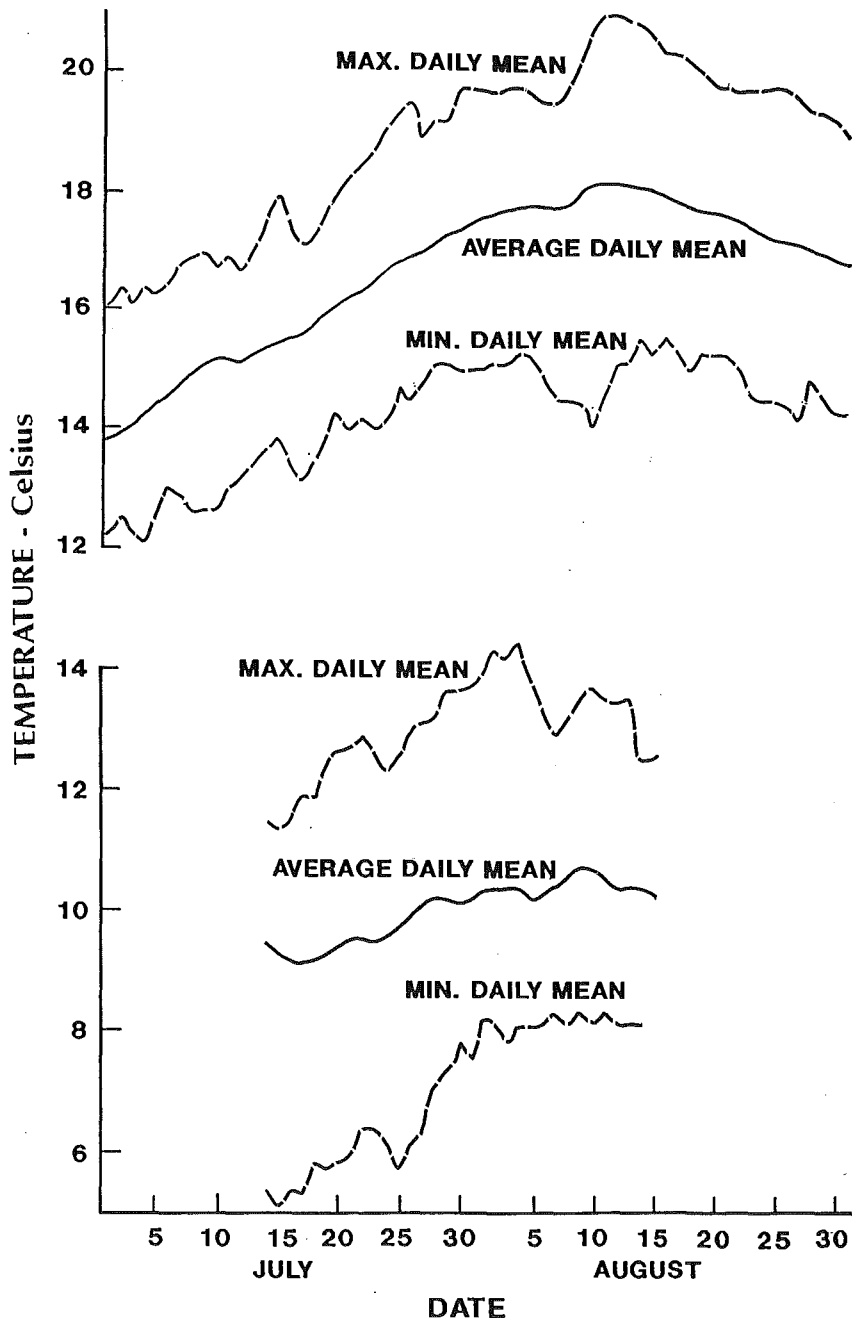


FIGURE 5. Average, maximum and minimum daily mean temperatures for Fraser River at New Westminster (upper three curves; 21 years data) and for Forfar Creek (lower three curves; representative of Early Stuart spawning streams; 17 years data).

TABLE 6. Comparison of means and ranges of annual average temperatures (Celsius) at Hells Gate and the spawning ground for each of six Fraser sockeye stocks for years in which data was available. Birkenhead temperatures are from Fraser River at New Westminster rather than Hells Gate. Stocks are listed in approximate order of spawning times.

| Stock | No. of Years | Hells Gate | | Spawning Ground | | Remarks |
|--------------|--------------|-------------------|-------------|-----------------|-------------|---|
| | | Mean* | Range | Mean** | Range | |
| Early Stuart | 17 | 15.6 | 13.6 - 17.5 | 10.5 | 8.8 - 12.6 | Ranges do not overlap |
| Raft | 20 | 17.2 | 15.0 - 19.2 | 13.4 | 11.1 - 16.5 | Hells Gate temperatures always higher |
| Horsefly | 9 | 17.5 | 16.2 - 19.0 | 15.1 | 13.0 - 18.0 | Hells Gate temperatures always higher |
| Chilko | 24 | 16.9 | 14.9 - 18.8 | 11.3 | 8.7 - 13.9 | Ranges do not overlap |
| Stellako | 21 | 17.1 | 15.1 - 18.7 | 15.2 | 13.1 - 17.8 | Hells Gate temps. higher except in 1963 |
| | | (New Westminster) | | | | |
| Birkenhead | 21 | 17.1 | 15.1 - 18.8 | 10.7 | 8.8 - 12.1 | Ranges do not overlap |

* Daily means weighted by daily abundance of migrating sockeye.
 ** Mean of daily means from first, or peak, arrival to center of peak spawning period.

Gate peak vs spawning date); the effect of other factors will be considered later. In total, these data support the hypothesis that the timing of the migration of an individual stock (whether early or late relative to its average) is consistent at Hells Gate, spawning ground arrival and peak spawning, although the relationship is clearly imprecise.

Various measures of annual stock timing were inconsistently related to female population size (TABLE 7). Although Hells Gate peak date tended to be later for larger runs of most stocks, most correlation coefficients were small. Early Nadina was exceptional, having a large negative but borderline correlation coefficient ($p=0.06$); this will be considered further in a later section. Spawning ground first arrival date and peak arrival date had three negative coefficients plus two very small positive coefficients. The significant negative correlation for Horsefly sockeye included 10 small, non-dominant runs; for the nine dominant years only, the coefficient was $+0.46$ ($p=0.20$), suggesting that the small runs had a different pattern of migration onto the spawning grounds as indicated by Williams (1973a, Table 3).

Central date of the reported period of peak spawning is also inconsistently related to population size (TABLE 7). Correlation coefficients were small except for Early Nadina (negative) and Birkenhead (positive), for which possible explanations will be proposed. The negative coefficient for Horsefly sockeye (including 10 non-dominant runs) becomes $+0.68$ ($p < .05$) for the 9 dominant years alone. Overall, the correlations do not exclude the hypothesis that larger runs tend to be later in migration than smaller runs (as suggested by Gilhousen 1960), and probably later in spawning as well, but other factors obviously affect timing variability.

Differences in Fraser River temperatures encountered by differently timed annual runs cannot explain the positive correlations between prespawning mortality rate and within-stock timing at Hells Gate, at least among the earlier migrating stocks, e.g. Early Stuart, Early Nadina, Raft and Horsefly. Later migrating runs in this group encounter, on the average, higher Hells Gate temperatures than earlier runs (cf. nearly identical temperatures at New Westminster; FIGURE 5). This is especially true for Early Stuart, which ascends the Fraser Canyon before the end of July. Furthermore, Early Stuart sockeye migrate through the Nechako and Stuart Rivers before mid-August while the average temperature trend is almost constant (FIGURE 6). Average temperatures are likewise slowly rising (but nearly constant) in Tachie and Middle Rivers when this stock migrates through them. It is concluded that within-stock time of migration has an intrinsic relationship to prespawning mortality rate, independent of temperature exposure.

TABLE 7. Comparisons between various measures of annual timing for eight Fraser sockeye stocks and certain compared variable factors.

| STOCK | Correlation Coefficient | | | | | | |
|-------------------------------|-------------------------|----------------|---------------------|---------------------|----------------|---------------|-----------------|
| | HGP vs. FAD | HGP vs. PAD | HGP vs. CPS | HGP vs. POP | FAD vs. POP | PAD vs. POP | CPS vs. POP |
| Early Stuart | --- | --- | -0.06 (21) | +0.37 (22) | -0.38* (32) | --- | -0.09 (21) |
| Early Nadina | --- | --- | +0.93** (8) | -0.69 (8) | --- | --- | -0.65 (8) |
| Raft | --- | +0.18 (20) | +0.16 (20) | +0.22 (20) | --- | -0.17 (20) | -0.23 (20) |
| Horsefly (all years) | +0.40 (9) | --- | +0.52 (9) | +0.79** (9) | -0.56* (19) | --- | -0.32 (19) |
| Horsefly (Dom. years only) | | | | | +0.46 (9) | | +0.68* (9) |
| Late Stuart | --- | --- | --- | +0.28 (9) | --- | --- | --- |
| Chilko | --- | +0.46* (21) | +0.47* (21) | +0.09 (21) | --- | +0.03 (24) | +0.10 (24) |
| Stellako | +0.29 (26) | --- | +0.17 (26) | +0.10 (26) | +0.09 (36) | --- | +0.17 (26) |
| Birkenhead | --- | --- | +0.59*(N.W) (13) | +0.24 (N.W) (23) | --- | --- | +0.85** (23) |

* - $p < \text{or} = 0.05$; ** - $p < \text{or} = 0.01$. Number of years correlated given in parentheses.

HGP: peak date at Hells Gate. POP: female spawning population. FAD: first arrival date on spawning grounds. PAD: peak or 50% arrival date on spawning grounds. CPS: central date of peak spawning period. N.W.: New Westminster peak migration dates for Birkenhead.

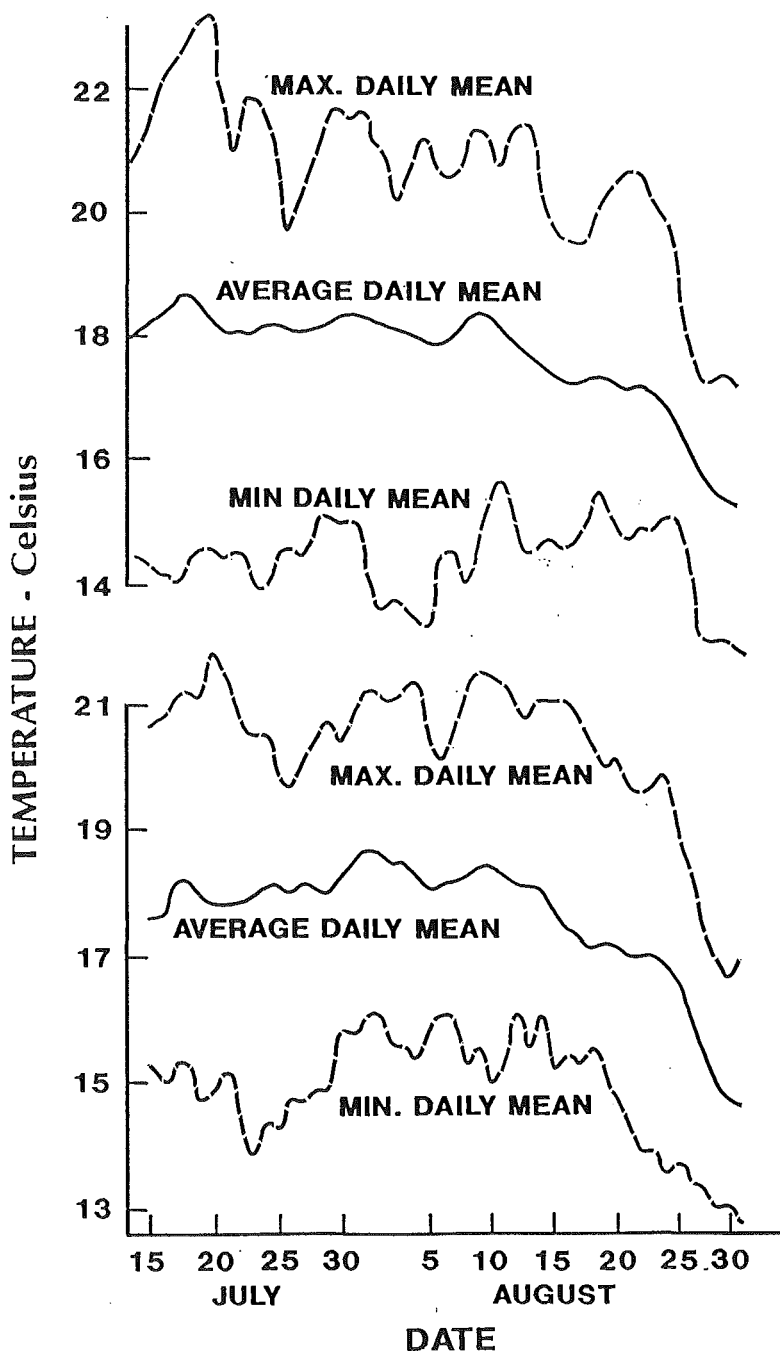


FIGURE 6. Average, maximum and minimum daily mean temperatures for Nechako River just above confluence with Stuart River (upper three curves; 22 years data), and for Stuart River at confluence (lower three curves; 18 years data).

Within-stock Multiple Relationships With Prespawning Mortality

Independent variables, taken in pairs, produced significant multiple correlations with female prespawning mortality rates for several stocks (TABLE 8). No significant multiple correlations with three independent variables were found. Among compared variables, water temperature during migration (or on the spawning grounds) and migration timing, were found to be the most important factors affecting prespawning loss of females. For several

TABLE 8. Multiple correlation coefficients for female prespawning mortality rate (dependent variable) and combinations of two compared (independent) variables. Eight stocks represented.

| STOCK | Multiple correlation coefficients | | | | | |
|--|-----------------------------------|-----------------|------------------|----------------|------------------|------------------|
| | HGP & HGT | HGP & AVT | HGP & SGT | POP & HGT | SGA & HGT | SGA & SGT |
| Early Stuart | 0.72** (22) | 0.72** (16) | 0.67** (17) | 0.82** (22) | 0.60* (18) | 0.46* (32) |
| Early Nadina | E 0.74 (8) | E 0.93** (8) | --- | 0.89* (8) | --- | --- |
| Raft | E 0.62* (20) | --- | E 0.78** (20) | 0.55* (20) | E 0.73** (20) | E 0.83** (20) |
| Horsefly | E 0.97** (9) | --- | E 0.89** (9) | E 0.76 (9) | 0.71 (9) | E 0.44 (14) |
| Late Stuart | 0.55 (9) | --- | --- | E 0.32 (9) | --- | --- |
| Chilko | E 0.74** (23) | --- | E 0.82** (15) | 0.47 (23) | E 0.67** (21) | E 0.68* (17) |
| Stellako | E 0.42 (26) | E 0.49 (17) | 0.64** (26) | 0.26 (26) | 0.53 (18) | 0.76** (17) |
| Birkenhead | E 0.46 (23) | --- | E 0.25 (22) | E 0.45 (23) | --- | E 0.45 (12) |
| * - $p \leq 0.05$; ** - $p \leq 0.01$. Number of years correlated given in parentheses. E - exponential relationship (prespawning mortality rate logged). | | | | | | |
| HGP and HGT: peak date and average temperature at Hells Gate, respectively. AVT: average of Hells Gate and Nechako system temperatures. POP: female population. SGA: spawning ground arrival date (either first or peak). SGT: spawning ground temperature. HGT and HGP for Birkenhead are average temperature and peak date at New Westminster. | | | | | | |

stocks, an exponential relationship gave somewhat higher coefficients (i.e., the logarithmic transformation of the mortality rate was compared). Arcsine transformations of prespawning mortalities produced no improvements over the logged or unlogged dependent variables. Some of the calculated multiple correlations produced high coefficients due to one or two very large annual prespawning mortalities (listed in TABLE 2) occurring with corresponding extreme values for a compared variable. These non-normal distribution effects will be considered in individual stock analyses.

Spawning ground temperatures, when paired with time of migration at Hells Gate, appeared to be about equal in importance to Hells Gate temperatures in estimating annual prespawning mortality (TABLE 8). Had complete migration path average temperatures been available for all stock migrations, this factor possibly would have given correlation coefficients higher than only Hells Gate or spawning ground temperatures. The highest multiple correlation coefficient for temperature and timing was found with Horsefly unspawned female loss rates, which were the highest among Fraser sockeye (TABLE 8). Relative accuracy in determining prespawning mortality rate is less for low mortalities, therefore weaker correlations may result from increased random relative error for stocks with low mortalities.

Although population size had no consistent relationship with prespawning mortality rate (TABLE 4), it had significant relationships in multiple correlations for the Early Stuart and Early Nadina stocks and borderline contributions in the Horsefly and Raft runs (TABLE 8). Since population size is correlated with migration time in varying degrees (TABLE 7), the basic relationship with prespawning mortality rate is thought to be for migration time rather than for female population size. Population size is therefore of questionable use in multiple regressions in which timing is a component, and this pairing was not presented in TABLE 8.

Neither average discharge nor suspended sediment data were significantly correlated with prespawning mortality rates for Early Stuart sockeye in multiple correlations in which independent factors were used (i.e. factors which were not significantly correlated among themselves).

Within-stock relationships will be considered in detail in the following section, listed in approximate order of spawning time.

Individual Stocks

Early Stuart

The linear regression of Early Stuart female prespawning mortality rate on Hells Gate (river) temperature and peak timing was calculated to be:

$$\text{PSM (\%)} = 5.35 \text{ H.G. Temp.} - 1.28 \text{ H.G. Peak Date} - 53.52$$

where temperature is in degrees Celsius and the timing is day number beginning July 1. All components of the regression equation are significant at the 95% confidence level. For each degree rise in average Hells Gate temperature, the prespawning mortality increases about 5.3% (95% confidence limits 2.7 and 8.0%), with temperature ranging from 13.6°C to 17.5°C in the years on record. For each day earlier than the latest observed date of July 18 for the peak at Hells Gate, the prespawning mortality rises approximately 1.3% (95% confidence limits 0.2 and 2.4%) over the 10-day observed range of variation. Although female population size (used in place of Hells Gate peak date) yielded a multiple correlation coefficient which was somewhat higher (TABLE 8), this relationship was rejected due to the previously mentioned correlation between population size and timing.

Because many factors are correlated with Early Stuart prespawning mortality (TABLES 4 and 8), a closer examination of the interrelationships is warranted. Prespawning mortality in this stock is significantly correlated with Hells Gate temperature (positive correlation) and spawning ground timing (inverse correlations)(TABLE 4) and these factors are also significantly correlated (TABLE 9).

TABLE 9. Simple correlations between the variable factors involved with Early Stuart prespawning mortality rates.

| VARIABLES | SGT | ELT | TRT | CPS | FAD | SSI | AHD | HGT |
|--|-----------------|------------------|------------------|------------------|-----------------|-----------------|-----------------|-----------------|
| Prespawning Mortality | +0.49* (17) | -0.21 (17) | -0.28 (17) | -0.45* (21) | -0.45** (32) | -0.34 (12) | -0.18 (22) | +0.61** (22) |
| Hells Gate Temperature | +0.56* (17) | -0.52** (21) | -0.57** (18) | -0.48* (22) | -0.60** (22) | -0.75** (12) | -0.55** (22) | |
| Average Hope Discharge | -0.39 (17) | +0.72** (17) | +0.78*** (17) | +0.63*** (21) | +0.77** (18) | +0.89** (12) | | |
| Suspended Solids Index | -0.68* (11) | +0.85*** (13) | +0.81*** (13) | +0.80** (12) | +0.79** (12) | | | |
| First Arrival Date | -0.50* (17) | +0.69** (17) | N/A | +0.74** (18) | | | | |
| Center, Peak of Spawning | -0.55* (17) | N/A | +0.71** (17) | | | | | |
| Travel Time Hells G. to FAD | -0.59** (17) | N/A | | | | | | |
| Elapsed Time Hells G. to CPS | -0.58** (17) | | | | | | | |
| * - $p < \text{or} = 0.05$ ** - $p < \text{or} = 0.01$ *** - $p < \text{or} = 0.001$ Number of years correlated given in parentheses. | | | | | | | | |
| SGT: spawning ground temperature. ELT: elapsed time, Hells Gate to CPS. TRT: travel time, Hells Gate to FAD. CPS: center, peak of spawning. FAD: first arrival date. SSI: suspended solids index. AHD: average Hope discharge. HGT: Hells Gate temperature. | | | | | | | | |

Furthermore, both average discharge at Hope and the index of suspended solids are significantly (inversely) correlated with Hells Gate temperature, directly with spawning ground timing and with each other (TABLE 9). Thus it appears that Early Stuart arrival and spawning are later with lower migration temperature, higher river levels and increased turbidity during migration. The significant correlations of spawning ground timing with migration environment may be due not only to the small (10-day) variation in peak appearance at Hells Gate but also because the Early Stuart run has the longest migration distance of any Fraser sockeye stock. Although correlation coefficients for the two measures of travel time versus migration environment are not significantly greater than for first date of arrival or center of peak spawning period alone (TABLE 9), duration of migration from Hells Gate to the spawning grounds is probably the fundamental variable.

The physical effects of high river level and high turbidity on migration speed would explain later arrival but the later spawning suggests that maturation was also prolonged. Possibly the sockeye simply held their eggs until the spawning ground was attained and the spawning site had been selected and prepared but migration temperature may also have altered maturation rate. A positive correlation between temperature and maturation rate was noted by Morrison and Smith (1986) in rainbow trout. This effect also appears to apply to sockeye, from the work of Colgrove and Wood (1966). Further, it has been suggested that suspended sediments impede the uptake of oxygen by the gills (IPSFC 1983). This may also decrease swimming performance and possibly add to the retarding effect of temperature on the rate of maturation.

Significant negative correlations of prespawning mortality rate with arrival or spawning timing would appear to be due to the effect of migration temperature (or related migration conditions) on migration speed (TABLE 9) since prespawning mortality rate is poorly related to timing at Hells Gate (TABLE 4). Moreover, the variation of time of arrival of Early Stuart sockeye on the spawning grounds and of peak spawning dates with migration conditions probably causes the negative correlations between spawning ground temperature and timing. Late arrival and spawning occur in years when overall temperatures are low, both during migration and subsequently on the spawning grounds, and early arrival and spawning in high temperature years.

Because neither the average Fraser discharge nor the SS index are significantly correlated with prespawning mortality rate in the Early Stuart stock (TABLE 9), water temperature appears to be the important environmental causal factor. This does not preclude effects on mortality from the increased energy expenditure due to high Fraser discharge and the possibly damaging effect on sockeye gills of lengthy exposure to high suspended sediment levels during mainstem Fraser migration. However, the present data are insufficient to determine the relative effects of the various factors.

Early Nadina

The Early Nadina run produced large multiple correlation coefficients when prespawning mortality was compared against migration time plus either Hells Gate or average migration temperature, the latter factor providing the stronger relationship (TABLE 8). However, only eight year's data are available and without the very large mortality in 1961 (86%; TABLE 2), no significant correlations remain. Nevertheless, because prespawning mortality rates were high on most spawning grounds in 1961, and because the same relationships were found for other stocks, the correlations for this stock are thought to be valid.

Early Nadina sockeye show a peculiar relationship between migration time, population size, and the succession of years (year rank) in the data series. Early Nadina has had large spawning populations only in some of the dominant cycle years. The dominant runs built up rapidly from 1945 to 1957 and then declined steeply, only 18 spawning fish being recorded in the 1985 run. Dominant cycle female population size was highly and negatively correlated with year rank ($r = -0.89$, $p < 0.01$) from 1953 to 1981. Despite the decrease in run size, which would imply increasingly earlier migration, the run also became later; Hells Gate timing and year rank were positively correlated ($r = 0.72$, $p < 0.05$), and spawning

has also become later ($r=0.53$, $p=0.05$). Although the prespawning mortality rate should reflect the changes in timing, the simple correlation of prespawning mortality rate with year rank was not significant (TABLE 4), possibly due to the dominant effect of temperature variation. The cause of the changes in timing appear to lie in the Nechako system, because the Bowron stock, which migrates at about the same time as the Early Nadina but does not enter the Nechako River, has not been similarly reduced. A possible explanation is that a heavy selection against early fish has occurred somewhere in the Nechako system in the years since 1957.

Because arrival data were not available for this stock, analysis of the effect of Fraser water temperature on migration time or maturation rate (as for Early Stuart) was not possible.

Raft

In a previous analysis for the years 1950 to 1963, a multiple correlation was indicated between the prespawning mortality rate of Raft River sockeye and spawning ground temperature and (of borderline significance) arrival time at the spawning grounds (Gilhousen MS 1964). Inclusion of data from more recent years confirmed this relationship and produced a closer multiple correlation (TABLE 8), which was somewhat larger than for Hells Gate temperature and timing. Although Hells Gate average temperature was higher than Raft River spawning ground average temperature (TABLE 6), the timing of the small Raft sockeye runs at Hells Gate was difficult to determine accurately and may explain the lower multiple correlation.

The multiple relationship between prespawning mortality rate, Hells Gate temperature and Hells Gate migration time for Raft River sockeye is significant ($p < 0.05$), and is similar to the correlations found for Early Stuart and Early Nadina (TABLE 8). Lack of temperature data precludes assessment of migration temperature exposure for Raft sockeye to explain why spawning ground temperature was the better estimator of prespawning mortality. Exposure time in the Fraser River is estimated at about 7 days, in the Thompson River system at about 20 days and on the spawning ground at from 5 to 10 days prior to spawning. Duration of migration through the Thompson system varies widely, possibly due to conditions in Kamloops Lake and in the Thompson and North Thompson Rivers; sockeye have been reported to delay several days off the mouth of the Raft River in some years.

The multiple regression of Raft prespawning mortality rate with Hells Gate average temperature and peak date, while not as statistically significant as for the Early Stuart stock, is given here for comparison:

$$\text{PSM (\%)} = 5.90 \text{ H.G. Temp.} - 0.82 \text{ H.G. Peak Date} - 61.38$$

where temperature is Celsius and peak date is day number beginning July 1. Temperature contributes significantly to the regression ($p=0.02$) but the contribution by peak date is not significant ($p=0.11$). For each degree rise in Hells Gate temperature, mortality increases almost 6% (95% confidence limits 1.2 and 10.6%), while for each day earlier in migration, the mortality increases about 0.8% (95% confidence limits -0.2 and $+1.9\%$). Confidence limits are necessarily wide, due to the low overall probability level of the regression.

Neither arrival time at the spawning grounds nor peak spawning time was correlated with the annual average Hells Gate temperature for Raft sockeye, as was found for Early Stuart runs. The shorter migration time of Raft fish in the Fraser may explain the difference.

Horsefly

Data for Horsefly sockeye produced a very large multiple correlation coefficient between prespawning mortality rate, average temperature and peak date at Hells Gate ($R=0.97$, exponential relationship, $p < 0.01$; TABLE 8), with but 9 years data available. However, this value is reasonable since the correlation was not determined by a single extreme year and spawning ground data for the large Horsefly runs could be determined with good accuracy.

The regression equation for Horsefly prespawning mortality rate on the two primary (Hells Gate) variables was:

$$\text{PSM (\%)} = 10.89 \text{ H.G. Temp.} - 2.50 \text{ H.G. Peak Date} - 128.51$$

where temperature is in Celsius and time is day number beginning August 1. All components

of the regression equation are significant at more than the 95% confidence level. Prespawning mortality increases by almost 11% for each degree rise in temperature at Hells Gate (95% confidence limits 3.5 and 18.3%), and by about 2.5% for each day earlier at Hells Gate from the latest observed date of August 19 (95% confidence limits 3.7 and 1.3%). Both factors have a greater effect than for Early Stuart or Raft sockeye, perhaps indicating that Horsefly sockeye are more susceptible to disease or to other adverse factors.

A strong correlation was found between migration time at Hells Gate and size of the Horsefly female spawning population ($r=0.79$, $p=0.01$; TABLE 7), but population size contributed less in a multiple correlation than Hells Gate migration date in estimating Horsefly prespawning mortality rate (TABLE 8). The dominant cycle female population has been growing over the period of record (correlation of population vs. year rank: $r=0.81$, $p < 0.01$), and the peak date at Hells Gate has also tended to become later (Hells Gate peak date vs. year rank: $r=0.58$, $p=0.10$). Considering the results for other stocks, it is concluded that time of migration in the Fraser River is the important factor, and that population size affects prespawning mortality rate through its effect on migration timing.

Spawning ground temperature was not significantly related to prespawning mortality rate for Horsefly sockeye but the positive correlation ($r=0.41$, $p=0.08$, $N=19$; TABLE 4) suggests that it contributes to the mortality. Spawning ground temperature (with Hells Gate peak date) produced a borderline multiple correlation for prespawning mortality when substituted for Hells Gate temperature (TABLE 8). Average Horsefly spawning ground temperature from first arrival date to center of peak spawning period was always lower than Hells Gate weighted average temperature (TABLE 6) but the earliest arrivals at the spawning grounds in some years may have encountered higher temperature for a few days than they experienced in the Fraser Canyon.

Because Horsefly sockeye runs migrate through the Fraser Canyon around the time of maximum seasonal water temperature (FIGURE 5), neither early nor late runs encounter significantly different temperature (peak date vs. average temperature at Hells Gate: $r=0.07$; TABLE 5). Again, migration time appears to have its own effect and does not act by altering the temperature exposure in different years.

Comparison of Horsefly runs of 1961 and 1981, which had the highest Hells Gate and spawning ground temperatures, further illustrates the effect of difference in migration timing. The earlier year run had a Hells Gate average temperature 0.4°C above 1981 and a spawning ground temperature 0.3°C below 1981. The 1961 run arrived on the spawning grounds less than a week earlier than 1981, while peak of spawning was the same for the two populations. However, the 1961 run was 11 days earlier at Hells Gate. Prespawning mortality rate was 62% in 1961 and 18% in 1981, suggesting that an increased resistance to the factors causing prespawning mortality was related to the late migration timing in 1981.

Horsefly sockeye, like the Raft stock, showed no significant correlations between first arrival date or center of peak spawning period and Hells Gate temperature. If a relationship like that found for Early Stuart exists, it may be hidden by other factors occurring along the migration path after the runs leave the Fraser River.

Late Stuart

Peak date at Hells Gate was inversely related to Late Stuart prespawning mortality rate in a nonsignificant correlation (TABLE 4; $r=-0.51$, $p=0.15$); this may be the fundamental relationship even though it is only weakly supported statistically, since it is a valid relationship for several other stocks.

Late Stuart prespawning mortality rate was not correlated with Hells Gate temperature whereas the Early Stuart had a highly significant correlation (TABLE 4). Mean annual mortality rate is similar for the two stocks (TABLE 2), while temperature at Hells Gate is higher for the later run in every year with comparable data. Late Stuart sockeye appear to be less susceptible to prespawning mortalities but because environmental exposure during migration in the rivers and lakes or the Stuart River system could not be accurately determined, no firm conclusion can be drawn.

Late Nadina

Analysis of prespawning mortality rates for the Late Nadina sockeye population was complicated by construction of a spawning channel, which became operational in 1973. Sockeye numbers and prespawning mortalities differed between the river and the artificial channel (Appendix TABLE F). Channel sockeye were diverted from the river by a weir. River spawners may have been more heavily weighted with sockeye from the later segments of the runs, because priority was given to filling the channel with fish. River temperature was affected by channel water removal from Nadina Lake and by channel discharge into the Nadina River. Interpretation of the effect of these artificialities was not attempted.

Only data from the natural stream for 11 years prior to operation of the channel were examined. Late Nadina sockeye prespawning mortality rate showed no significant correlations with any factor or combination of factors, therefore this population was omitted from TABLES 4,5,7 and 8.

Chilko

Two unusual migrations occurred during years when female prespawning mortality data were collected for Chilko sockeye. In 1963, the early segment of a large and early Chilko run passed through the fishing areas before commercial fishing began (the combined result of a preset closed period and a fisherman's strike; IPSFC 1964) whereas the latter portion of the run was heavily fished, creating an unusually early Hells Gate peak date. The artificial earliness and a record escapement (over 1/2 million females) combined with the finding of high virulence *columnaris* bacteria on the fish in the escapement have been offered as the explanation for the approximately 90% mortality (IPSFC 1964). Although this extremely early run has been eliminated from analyses, it does conform to the general relationship between early migration time and high prespawning mortality. An extremely late Chilko migration occurred in 1958 (10 days later than the next latest run) but since all Fraser River sockeye runs were very late in that year it has been considered in the following comparisons.

Chilko sockeye showed only a borderline multiple regression (exponential) with the primary variable factors, mean temperature and peak date at Hells Gate, (TABLE 8, 23 years data). While the multiple correlation coefficient was highly significant ($p < 0.01$) and while Hells Gate peak date was also a significant contributor to the multiple relationship ($p < 0.01$) the contribution by mean Hells Gate temperature had low significance ($p=0.10$). The relative effect of these independent variables is similar to the simple correlations for timing and temperature at Hells Gate in TABLE 4. Although the irregular distribution of peak Hells Gate migration dates due to the very late 1958 Chilko run violates statistical requirements, omission of 1958 decreased the multiple correlation coefficient only moderately ($R=0.64$ vs. 0.74 ; exponential relationships, both $p < 0.01$), adding credibility to the relationship.

The linear multiple correlation of Chilko prespawning mortality rate with Hells Gate temperature and timing ($R=0.59$, $p < 0.05$), although weaker than the exponential relationship ($R=0.74$, TABLE 8), shows the relative effect of the factors involved. The linear regression equation for prespawning mortality rate was calculated as:

$$\text{PSM (\%)} = 3.61 \text{ H.G. Temp.} - 0.84 \text{ H.G. Peak Date} - 41.17$$

where temperature is in Celsius and peak date is day number beginning August 1. Only the Hells Gate date made a significant contribution ($p=0.03$); Hells Gate temperature had lower ($p=0.08$) significance. In general terms, an increase in temperature of 1°C at Hells Gate raises the prespawning mortality by 3.6% (95% confidence limits -0.5 and 7.7%), while for each day of peak occurrence earlier than August 29 (1958 peak date), the mortality rises by almost 1.0% (95% confidence limits 0.1 and 1.6%).

Given the correlation of prespawning mortality with Hells Gate temperature found for other stocks, it was concluded that a multiple relationship for Chilko including Hells Gate temperature as well as timing was a valid estimator of prespawning mortality rate for Chilko sockeye. Water temperatures in the Chilcotin River system, governed largely by Chilko River flow from Chilko Lake (altitude 1160 m; FIGURE 1), are relatively cool; these lower

temperatures may mitigate the effect of Hells Gate temperatures and lower the multiple correlation.

Low temperatures are also a plausible explanation for the low Chilko prespawning mortality rate in 1964, following the exposure to high water in the Fraser River and the high sediment load from the Chilcotin slide. Temperatures in both the Fraser and the Chilko River at the spawning ground were the lowest of any year in the Chilko data set and undoubtedly temperatures were also low along the Chilcotin - Chilko migration route (FIGURE 1). Minimum temperature stress presumably allowed the 1964 Chilko spawning migration to cope with the effects of high river flow and high turbidity.

Chilko, like Early Stuart, had a significant negative relationship between spawning ground timing and water temperature at Hells Gate (TABLE 10). As with the Early Stuart, travel time from Hells Gate to the spawning grounds was more closely correlated with Fraser discharge ($r=0.81$, $p < 0.001$) than with Hells Gate temperature ($r=-0.47$, $p < 0.05$); travel time from Hells Gate to peak arrival at the spawning grounds was about as closely correlated to Hells Gate temperature ($r=-0.47$, $p < 0.05$) as was the peak arrival date by itself ($r=-0.54$, $p=0.01$). The effect of Hells Gate (i.e., Fraser River) migration temperature appears to explain the good correlation between the rate of prespawning mortality and peak arrival date. The poorer correlation between prespawning mortality rate and peak spawning date likely resulted from the long average duration of spawning ground residence, which could be influenced by local conditions, as suggested by the good correlation between spawning ground temperature and peak spawning date ($r=-0.53$, $p=0.01$).

Correlations between environmental factors affecting sockeye, including an index of the discharge in the Chilcotin River system (FIGURE 1), showed several interesting relationships (TABLE 10). Chilko River discharge (Chilko River near the junction with the Chilcotin; flow averaged for a 16-day period bracketing the peak of each run) was not correlated with average Fraser discharge at Hope. Chilko discharge was, however, positively related to Hells Gate temperature, probably because the mid-summer discharge is higher in warm weather due to glacier melt into Chilko Lake. Peak arrival date at the spawning grounds was negatively related to Chilko discharge whereas it had a positive (borderline) relationship with Fraser (Hope) discharge ($p=0.06$). Since it is unlikely that sockeye have easier migration in the Chilcotin system at higher water levels, the relationship may be the effect of temperature on migration speed along the Chilko-Chilcotin migration path. Hells Gate and spawning ground temperatures are positively but not significantly related; Chilcotin system migration temperatures (data lacking) would be nearer in time to Hells Gate temperatures and a higher correlation would therefore be expected between them.

Stellako

The combination of temperature and timing was significantly correlated with prespawning mortality rate for Stellako sockeye, as in most other stocks examined (TABLE 8). Significant multiple correlations were found for Stellako sockeye but Hells Gate average water temperature was not a significant contributor in estimating prespawning mortality rate. However, the highest annual prespawning mortality (44%) for Stellako occurred in the year (1963) when Hells Gate temperature was above average (17.6°) and spawning ground temperature (17.8°) was the highest in the study period.

Hells Gate peak date plus spawning ground temperature from first arrival to center of peak period of spawning yielded a significant multiple correlation with prespawning mortality rate (TABLE 8), as did first arrival date plus spawning ground temperature. While the latter correlation is larger, the difference may not be meaningful.

Travel time for Stellako sockeye could not be examined due to inadequate data on arrival timing. Variable time periods spent between the Nautley River and the spawning grounds (FIGURE 2) appeared to obscure any relationship between river temperature or discharge during migration and time from Hells Gate to peak arrival on the spawning grounds.

TABLE 10. Simple correlations between factors involved with Chilko prespawning mortality rates.

| VARIABLES | SGT | ELT | TRT | CPS | PAD | CRD | AHD | HGT |
|--|-----------------|------------------|------------------|-----------------|-----------------|----------------|-----------------|---------------|
| Prespawning Mortality | +0.34 (24) | +0.20 (24) | -0.16 (23) | -0.39 (24) | -0.57** (24) | +0.13 (22) | -0.30 (22) | +0.33 (21) |
| Hells Gate Temperature | +0.41 (21) | -0.19 (21) | -0.47* (20) | -0.42* (22) | -0.54** (21) | +0.51* (19) | -0.66** (19) | |
| Average Hope Discharge | -0.41 (22) | +0.72*** (22) | +0.81*** (22) | +0.31 (22) | +0.41 (22) | +0.04 (22) | | |
| Chilko River Discharge | +0.40 (22) | +0.24 (22) | 0.00 (22) | -0.41 (22) | -0.45* (22) | | | |
| Peak Arrival Date | -0.44* (24) | +0.04 (23) | N/A | +0.61** (24) | | | | |
| Center, Peak Spawning Period | -0.53** (24) | N/A | +0.15 (23) | | | | | |
| Travel Time H.G. to PAD | -0.29 (23) | N/A | | | | | | |
| Elapsed Time H.G. to CPS | -0.20 (23) | | | | | | | |
| <p>* - $p < \text{or} = 0.05$ ** - $p < \text{or} = 0.01$ *** - $p < \text{or} = 0.001$ Number of years correlated given in parentheses.</p> | | | | | | | | |
| <p>SGT: spawning ground temperature. ELT: elapsed time, Hells Gate to center of peak spawning. TRT: travel time, Hells Gate to peak arrival date. CPS: center of peak spawning period. PAD: peak arrival date. CRD: Chilko River discharge index. AHD: average Hope discharge. HGT: Hells Gate average temperature.</p> | | | | | | | | |

Birkenhead

No significant multiple correlations were found for Birkenhead prespawning mortality rate versus factors incorporating water temperature and timing (TABLE 8) in spite of three significant simple correlations involving New Westminster average temperature, female spawning population size and peak spawning date (TABLE 4).

There was a highly significant simple (negative) correlation between the logarithm of Birkenhead prespawning mortality rate and year rank (TABLE 4), similar to the relatively large (but non-significant) negative correlation for Early Nadina sockeye. The cause appears to be different in the two stocks, since the Birkenhead run has been increasing in size, like the Horsefly stock, while the Early Nadina has been decreasing. The increase in size of the Birkenhead spawning population over the period of study (population vs year rank, $r=0.50$, $p < 0.01$, $N=36$) has no obvious explanation.

Concurrent with the population increase, Birkenhead spawning has become later, with a highly significant positive correlation of center of reported peak spawning period with year rank ($r=0.56$, $p < 0.01$, $N=23$), and also with population size (TABLE 7; $r=0.85$, $p < 0.001$). Since the partial correlation of peak spawning date with population, year rank held constant, was $r=0.83$ ($p < 0.001$), but the partial correlation of peak spawning date with year rank, population held constant, was $r=0.45$, ($p > 0.05$), the change in spawning time was considered to have resulted from the population increase. Furthermore, because the partial correlation of prespawning mortality rate with year, population held constant, was small ($r=-0.24$, $p > 0.05$), prespawning mortality did not appear to have changed significantly over the period of examination. The decrease in prespawning mortality rate with time ($r=-0.41$, $p < 0.01$; TABLE 4) would then be due mainly to the run becoming later over the period of study.

The larger runs have also tended to be later at New Westminster, although the positive correlation between female spawning population size and timing is not significant (TABLE 7; $r=0.24$, $p > 0.05$). This is possibly due to the errors in determining the peak date at New Westminster.

Scarcity of accurate information on the arrival time of Birkenhead sockeye at the spawning grounds and of temperature data from the Harrison - Lillooet River system precludes examination of the effect of river temperature and discharge on migration duration. There was, however, a negative but borderline correlation of estimated date of spawning ground peak arrival with the water temperature index at New Westminster ($r=-0.47$, $p=0.11$, $N=13$). This may be a real relationship, since similar correlations were found for the Early Stuart and Chilko stocks with Hells Gate temperatures.

DISCUSSION

High sockeye prespawning mortality rates can cause important economic losses to the fishing industry. Beyond the limits of the management option of allowing increased escapement for all stocks which migrate through the fishery at the same time as the reduced stock (a source of loss in itself), affected populations recover through compensatory survival rate increases and the production of 5-year-olds by the immediately preceding cycle population. However, there is an additional negative effect, since smaller numbers of 5-year-old sockeye will be produced by the reduced cycle until recovery is complete.

An extreme example occurred in 1963 when the large Chilko spawning escapement suffered an approximate 90% loss of females. As a consequence, the two subsequent runs on this cycle (1967 and 1971) were each reduced by about 40% before the run returned in 1975 to the size considered necessary for full utilization of the spawning area. Loss to the fishery is estimated at 300,000 Chilko sockeye and since other stocks suffered above-average prespawning mortalities in 1963, total loss to the fishery was considerably greater. Also, the sockeye that died unspawned could have been harvested by the fishery.

Another example is the growth of the Horsefly dominant-year runs from a few thousand fish in 1941 to over 12 million sockeye in 1989. Restoration of the historically large runs was delayed as a result of the very high prespawning mortality rates, which could only be partially compensated for due to the presence of other harvestable stocks in the fishery.

In the multiple regression equations estimating prespawning mortality rates reported here, linear relationships (flat regression surfaces) have been adopted as an expedient. However, the regressions must be curvilinear since for late timing or for low temperature, where stress effects will be low, prespawning mortality will change little and cannot be less than zero. At elevated temperature and with early timing, stress response must increase more rapidly (as it does in experimental situations) and the curve (curved surface) will rise with increasing steepness to 100% mortality. This is consistent with the logarithmic transformation of the mortality rate, which often produced the most significant correlations. Available data do not allow detailed examination of the relationships at the extremes.

In most of the multiple correlations between prespawning mortality rates and independent variables examined in this report (TABLE 8), the regression (i.e. R^2) explains only part of the variance in mortality rate. Only the regressions for Horsefly and Early Nadina determined more than 80% of the variance in the mortality rate. It is therefore concluded that the analyses presented in this report do not give a complete assessment of the causes of variations in the observed mortality rates.

Stress

The concept of *stress* in fish (Brett 1958, Wedemeyer 1970, Pickering 1989) is of fundamental importance in understanding the relationship between environmental factors and prespawning mortality. Stressors evoke a generalized neuroendocrine stress response, which engender secondary effects, e.g. changes in blood chemistry and tissue characteristics (Mazeaud et al. 1977, Wedemeyer and McLeay 1981). Removal of short-lasting stressors is followed by quick recovery of neuroendocrine hormone levels, while secondary effects may persist for several days. Long-lasting stressors cause deterioration, both in the neuroendocrine system and elsewhere in the body. In maturing Pacific salmon, with their short life expectancy and already dedicated stores of energy and building materials, such damage may not allow completion of spawning or even of the spawning migration.

Stress responses are additive in that sockeye must deal with each stressor, probably with a separate physiological response or resource allocation, and damage to the organism will reflect the sum of several stressors. Stress effects are cumulative in that a long-lasting stressor

or a succession of stressors may have an effect similar to a severe short-term stressor or several stressors acting simultaneously. Imposed stress from one environmental factor will thus decrease the ability of a salmon to withstand exposure to other adverse factors such as pathogenic infections (Pickering 1989). River migration and maturation can be interpreted as stressful processes since they make physiological demands beyond those imposed on less mature salmon not involved in upriver migration.

Plasma cortisol level in sockeye is a useful indicator of stress response (Fagerlund 1967). Cortisol measurements for early and peak segment Horsefly fish indicate that early fish react more strongly to stressors than peak fish (Williams et al. 1977). Both sockeye and pink salmon show elevated cortisol levels in river reaches requiring maximum swimming performance (Williams et al. 1986), indicating stress responses which detract from the ability to adapt to other stressors. In this study of pink salmon migration (Williams et al. *ibid.*), the fish showed an increase in prevalence of disease symptoms after negotiating the Fraser and Thompson Canyons. Clearly, sockeye will be similarly affected.

Stress response and time and place of death resulting from stressors will vary between individual fish. This variation in "vigor" is probably due largely to genetic differences, which give one individual an advantage over another in a specific situation; in another situation the advantage may be reversed. Only under the most extreme conditions will all salmon in a population be killed by a stressor or set of stressors. This graded response to stressors is especially clear in spawning ground prespawning mortalities.

Water Temperature

Water temperature has obvious and well-documented effects on salmonids (Coutant 1969, Elliott 1981). Brett (1952) determined upper and lower temperature tolerances for juvenile sockeye. Servizi and Jensen (1977) determined upper temperature resistance for Early Stuart sockeye on their spawning migration and found that adult sockeye were slightly less resistant to elevated temperature than juveniles (as determined by Brett 1952). However, the lethal effects of elevated temperature are not important in evaluating prespawning mortalities since these mortalities occur at temperatures that are far below lethal levels.

The action of elevated temperature can be described in terms of its effect on "metabolic scope" or "scope for activity" (Brett 1976), i.e. the excess of metabolic energy, after maintenance and other energy requirements are deducted, available to adapt to stressful situations. Brett (*ibid.*) has shown that, for fingerling sockeye, the scope for activity decreases as temperature increases above the optimum level and ascribed at least part of the decrease to falling availability of dissolved oxygen in air saturated river water as temperature increases.

While the maximum temperature for metabolic scope, swimming speed and several other metabolic functions for fingerling sockeye occurred at 15°C (Brett 1971), and maximum swimming speed for adult sockeye also was at 15°C (Brett and Glass 1973), river migrating adult sockeye may have a lower optimum temperature in relation to resistance to various stressors. Brett et al. (1969) showed that the optimum temperature for growth in fingerling sockeye decreased as food intake decreased. Adult sockeye on the river spawning migration are starving (i.e. surviving on stored energy) and may similarly have a depressed optimum temperature for other factors besides growth, e.g. metabolic scope.

If the regression equations for prespawning mortality rate given for Early Stuart, Raft, Horsefly and Chilko are solved for Hells Gate average temperature at zero prespawning mortality rate using earliest, peak and latest migration dates at Hells Gate, the following temperatures (Celsius) result:

Hells Gate Peak Date

| <i>Stock</i> | <i>Earliest</i> | <i>Average</i> | <i>Latest</i> |
|--------------|-----------------|----------------|---------------|
| Early Stuart | 12.2° | 13.0° | 14.3° |
| Raft | 14.2° | 14.9° | 16.9° |
| Horsefly | 12.3° | 13.8° | 16.2° |
| Chilko | 11.6° | 14.1° | 18.2° |

All zero intercept temperatures except for the latest runs of Raft, Horsefly and Chilko stocks are below 15°C. The temperatures for Raft are generally higher than for the other stocks possibly because this stock spends less time in the Fraser River; most of its migration is in the Thompson River system (FIGURE 1), where temperature exposure has not been measured.

There are three sources of error in the estimated lower temperature limits shown above. Random errors in measurements are assumed to balance one another, although with small sample sizes or low coefficients of multiple correlation, large deviations in regression slopes from "true" values may occur. More importantly, the regressions are probably curvilinear, so that the toe of the regression surface reaches zero prespawning mortality rate at lower temperatures than for the regression planes used in the above table. Error in the opposite direction results from the reduced slope of regression lines and planes derived by least squares when all variables are subject to error (Ricker 1973). The curvilinear effect would possibly override the other sources of error; if so, the estimates in the above table will be too high. In any event, minimization of prespawning mortality rates will require that temperatures be kept low enough for the earlier migration timing of various stocks rather than for the average migration timing because the earlier are more vulnerable to these mortalities. An effective optimum temperature below 15°C for maximum survival of maturing sockeye on their river migration seems probable.

In assessing temperature exposure, diurnal variation has an effect not generally recognized. Hokanson et al. (1977) found that in rainbow trout, variable daily temperature was equivalent to a constant temperature significantly above the mean of the variable regime. This relationship will undoubtedly apply to prespawning mortality rates in sockeye. In Hells Gate temperature data, the diurnal variation is seldom more than 0.5°C, hence the difference between the mean and the effective temperature is inconsequential. However, diurnal variation is large in many other areas, including spawning grounds. In the Nechako River, where the diversion of water has left low flows with large diurnal variation in temperature during hot weather (up to 4.5°C), the daily mean significantly underestimates the effective temperature exposure, possibly by as much as 1.07°C, using the relationship of Hokanson et al. (ibid.). Since this relationship has not been determined for sockeye, no corrections were applied in the present analyses.

Although great weight has been put on migration temperatures, especially Hells Gate temperature, spawning ground temperature may be equally important. In Raft, Chilko and Stellako sockeye, spawning ground rather than migration temperatures yielded the most significant correlations. Raft and Chilko spawning ground temperature averages were intermediate among the stocks studied, while those for Stellako were almost as high as the highest, that at Horsefly (TABLE 6). Because Hells Gate average temperatures were in all cases higher than spawning ground average temperatures, migration temperature (indexed by Hells Gate temperature) apparently induces a stress response, which lasts until the sockeye approach complete maturation. Spawning ground temperatures add to the mortalities by an amount which cannot be separated with the data at hand.

High migration temperatures also result in migration mortalities, as observed for the Early Stuart stock in several years, viz. 1942 (IPSFC, field reports, 1942), 1960 (Cooper and Henry 1962) and 1982 (Cooper MS 1983). Migration mortalities in several other years have been associated with lower temperatures but with high river levels and sediment loads, also suggestive of cumulative stress responses (Cooper loc. cit.). Because migration difficulty is not uniformly related to river level and because different parts of runs encounter different water levels, it has not been possible to separate the relative effect of the various factors. Nevertheless, the migration mortalities of Early Stuart sockeye in 1942 and 1960 were in part the result of difficult migration conditions and consequent imposed stress in the Fraser Canyon; 1942 was pre-fishway and 1960 was the result of unusually high river levels.

Extremely low temperatures may also produce an increase in prespawning mortality rate, although this has not been observed. Wood (1979) described some diseases in Pacific salmon which appeared at low temperatures. Bisset (1949) found that "formed antibodies" in fishes are not released at low temperatures, presumably lowering immune response to disease

under these conditions. If low temperatures cause prespawning mortalities, the total curve relating prespawning mortality rate to temperature may be "U" shaped.

Disease

Disease is a factor which has been associated with prespawning mortalities of Fraser sockeye and has received much attention (Pacha MS 1964; Robins MS 1964; Pacha MS 1965; Wood MS 1965; Colgrove and Wood 1966; Mead MS 1969; Ordal MS 1970; Williams MS 1972, 1973a; Williams et al. 1977). In the early part of sockeye runs, gill abnormalities have been more frequent than in later segments of the same runs when significant prespawning mortalities occurred (Williams 1973a and 1977; Williams et al. 1977). Gill infections have been more frequent where high prespawning mortalities occurred. Unspawned dead females have usually had more extensive disease-related gill damage than spawned females. Because disease appears to kill sockeye at temperatures below the lethal level (Servizi and Jensen 1977), it is concluded that disease, potentiated by the effects of stressors during migration, is an important final cause of prespawning death.

Disease is often closely associated with elevated temperature, especially "columnaris" disease, caused by the bacterial organism *Flexibacter* (formerly *Chondrococcus*) *columnaris*, which has highly variable virulence. Colgrove and Wood (1966) gave experimental results concerning columnaris disease appearance and reported on extensive surveys for this disease in the Fraser River watershed in 1963, 1964 and 1965. They concluded that all Fraser sockeye are exposed to the organism in the Lower Fraser River during upstream migration. It was found that "a temperature above 60°F (15.5°C) appeared necessary to initiate the pathological effects of columnaris disease among (exposed) sockeye salmon"; that prespawning mortalities due to columnaris disease seldom occurred at temperatures below 55°F (13°C); that temperature exposure during migration was probably an important factor in the development and spread of the disease.

While *columnaris* is the most commonly observed cause of disease in Fraser sockeye, other organisms appear also to be ubiquitous and to have sporadically become epizootic; the latter include bacterial gill disease and a few other bacterial diseases and certain viruses and protozoan pathogens. The apparent good correlation between the occurrence of disease, prespawning mortalities and elevated temperature led Colgrove and Wood (ibid.) to suggest that control of spawning ground temperature could reduce losses.

A pilot temperature-control structure was built at the outlet of McKinley Lake (Horsefly River tributary) to lower spawning temperatures in McKinley Creek beginning in 1969 (Cooper 1973, Williams 1973a). While temperatures were reduced to levels which controlled columnaris disease, a very high prespawning mortality occurred, possibly as the result of some other pathogen(s). It was concluded that control of spawning ground temperatures was not sufficient to eliminate prespawning mortalities and that other factors needed to be considered (Williams loc. cit.). The present analysis indicates that the 1969 Horsefly prespawning mortality resulted because the escapement was the earliest recorded (Appendix TABLE D). Extreme earliness, combined with stress response to the rigors of migration, apparently conferred a deficient resistance to disease, even though low spawning ground temperatures minimized columnaris disease.

Antibiotics have been investigated (Williams 1973b, Williams and Stelter 1977). Notwithstanding some promising results, such methods appeared impractical not only because no efficient or economical way of applying therapeutic agents could be envisaged under field conditions but also because of possible side effects.

Despite extensive studies, the action of diseases in causing prespawning mortalities remains imperfectly known, although impaired gill function has been demonstrated in columnaris infections (Colgrove and Wood 1966) and bacterial gill diseases (Mead 1969). The variable presence of different disease organisms and the poorly understood variation in virulence of some pathogens has not allowed quantitative analyses to be made. Resistance to a specific disease (IHN) was found to be heritable in sockeye (McIntyre and Amend 1978). In other salmonids, heritable resistance to several diseases has been demonstrated (Gjedrum and Aulstad 1974; Ehlinger 1977; Winter et al. 1980). Resistance to one disease

does not imply similar resistance to another pathogen (Winter et al. 1980). While it appears that prespawning mortality rates would be significantly lower if disease per se could be reduced or eliminated, the importance of other environmental factors in prespawning mortality rates in Fraser sockeye suggest that reduction of environmental stressors would be a more practical means of lowering prespawning mortality rates.

Other Environmental Factors

No other physical environmental factor was found which affected prespawning mortality rates as consistently as water temperature. Water levels or the related suspended sediment load in the mainstem Fraser River appear to be involved in the variable arrival and spawning times of Early Stuart and Chilko sockeye but these physical factors are themselves poorly correlated with prespawning mortality rate. Migration temperature, varying inversely with river flow and sediment load, is probably the more important factor. River discharge and turbidity, at the levels observed in this study, have apparently had lesser effects.

Nevertheless, both river discharge and suspended sediments will have detrimental effects as noted above. Because sockeye migration speed (for at least two stocks) varies inversely with river level, more energy stores must be consumed during the slower migrations. However, lower water temperatures at such times reduce basic physiological requirements, partially offsetting the increased energy demand. Additional hidden damage to the sockeye by the effects of high suspended sediment levels will be present (Servizi and Martens 1987). Damage to the 1964 Chilko run has been described. Extreme high water levels and resulting heavy sediment levels, above those studied here, may occur in the future; if so, significant effects on both migration and spawning ground prespawning mortalities may be expected.

Impediments to normal, rapid upstream migration will contribute to prespawning mortalities by adding to the stress load imposed on homestream-bound sockeye. Points of difficult passage occur along the migration routes of Fraser sockeye, although the most extreme have been eliminated by fishways. With very large runs, fishways with inadequate capacity will cause delays in at least part of the run encountering this problem. Crowding during delays may also allow the spread of disease organisms, especially when temperatures are elevated.

However, the elevated plasma cortisol measurements from sockeye in the Fraser Canyon and pink salmon in the Thompson Canyon, mentioned above, suggest that much of the migration path of upriver sockeye requires maximum or near maximum swimming performance; Brett's (1965) analysis of sockeye energetics reached the same conclusion. Fatigue, with blood lactic acid build-up (Black 1957) from excessive demands for swimming performance, is another facet of stress response. These considerations further suggest that migration of sockeye to the upriver areas of the Fraser system involves an irreducible level of stress imposed on the fish and thus a reduction of their metabolic scope relative to lower-Fraser sockeye having low-slope migration routes.

Supersaturation of dissolved atmospheric gases, which results from lake outflow, plunging flows at waterfalls or rapids, from photosynthetic activity or from river heating, has been monitored infrequently; no direct effects in the form of gas embolisms or gas bubble disease have been noted in sockeye (J.A. Servizi, pers. commun.). Still, this environmental factor must be an additional stressor and thus would be a contributor to prespawning mortality. The sockeye stocks migrating in the Nechako River watershed have a high probability of exposure (IPSFC 1983; Byres and Servizi 1986) and high supersaturation levels have been measured in the Fraser Canyon (Servizi et al. MS 1977, MS 1983).

With the increasing human population and economic activity along the rivers in the Fraser River system, there is an accompanying increase in river pollution, principally treated sewage and pulp mill effluent. While an attempt has been made to control each of these materials to well below mortality causing levels, they will have some effect on upstream migrating salmon. Toxic materials and particulate matter (even in the present small amounts) released into the water are stressors which will add to the cumulative stress imposed by other

environmental factors; increased prespawning mortalities must result. Accidental spills, though infrequent, will cause greater losses, both prespawning and also during migration with large or highly toxic spills.

Migration Timing

Migration timing had an effect on spawning ground prespawning mortalities similar in degree to that of water temperature but migration timing apparently did not exert its principal influence through varied water temperature exposure. While in many instances, during part of the spawning migration and spawning ground occupation, water temperature will be higher for early migrating runs of certain stocks or for the early part of certain runs, there are too many exceptions for a simple causal relationship to exist.

Among the multiple regressions calculated previously using Hells Gate temperature and peak migration date, the increase in prespawning mortality rate per day as runs became earlier varied from about 0.8% (Raft and Chilko) to 2.5% (Horsefly). As with the temperature component of the equations, the regressions are probably curvilinear due to limitations on mortality values.

Biological characteristics of different parts of an annual migration of certain stocks have been investigated in connection with prespawning mortality and disease. Colgrove (1966) found no major histological differences between early and peak fish in the 1964 Chilko run, which had a very small prespawning mortality. Plasma cortisol level, (the stress indicator mentioned previously) was higher in the early part of the 1965 Early Stuart run (Colgrove MS 1966), the 1971 Chilko run (Williams 1977) and the 1973 Horsefly run (Williams et al. 1977), suggestive of either greater exposure to stressors or a lower tolerance to stress factors. Williams (1973a) found that swimming stamina decreased from early to late segments of the 1969 Horsefly run at the spawning grounds. Relative ovary size (gonadosomatic index) increased and condition factor decreased from early to late segments in sockeye runs in general (Williams 1973a; Williams et al. 1977; Gilhousen 1980). Body fat and protein decreased and water content increased from early to late segments at a given sampling station on the migration route of a single stock (Gilhousen *ibid.*). While Williams et al. (1977) found an inconsistent relationship for these constituents in the 1973 Horsefly run, they only analyzed a small, centrally located part of the body muscle rather than the whole fish as in the other investigation.

These several changes occurring during the passage of a sockeye run (single stock) at any checkpoint suggest that fundamental changes occur during the temporal passage of a run. Data analyzed by Gilhousen (1980) indicated that sockeye of different parts of a spawning population spawn with different values of the three constituents, fat, protein and water in their body; early spawners were "less mature" in this respect (had greater energy reserves) than later spawners. Eggs taken from late spawners were found to develop more rapidly than those from earlier spawners at the same temperatures in Cultus Lake sockeye but not in other stocks (Brannon 1987).

Other less specific within-stock differences related to timing have been noted in salmonids. A northern California stock of rainbow trout has been changed, by selection of early spawners over many generations in a hatchery environment, from an April or May spawning stock to a November spawning population (Leitritz and Lewis 1976). The widely varied spawning periods of Fraser sockeye stocks (TABLE 1) and other Fraser salmon species have probably resulted from selection for optimum spawning times (which controls fry emergence timing) in the varied environments of the Fraser River system (Brannon 1987), probably during colonization of the watershed after the retreat of the glaciers of the last glacial period. Both the intra-population differences and the adaptation of colonizing stocks to a variety of spawning ground temperature regimes suggest that a genetic cline (gradient) exists in a salmonid population from the earliest to the latest individual, in migration and in spawning. Temporal differences in genetic characteristics within a sockeye population (single stock) could then account for the decrease in prespawning mortality from the beginning to the end of spawning. The earlier fish may be less resistant to disease or to other stressors in the environment due to larger allocation of physiological resources

required in some way by earliness. The persistence of these temporal differences in spawning success has no ready explanation; presumably it is balanced by some other requirement for survival that varies with time at another stage in the life cycle.

Although genetic differences may explain the change in prespawning mortality rate within a spawning period, genetic differences large enough to cause the interannual prespawning mortality rate differences within sockeye stocks related to migration time seem improbable. Successive runs in the same cycle year vary markedly in timing, though one is the offspring of the other. Annual migration time in sockeye has been attributed to conditions (mainly sea surface temperature) during their ocean residence (Killick and Clemens 1963, Blackbourn 1987); the present analyses indicated that run size also contributes to the determination of migration timing. Neither factor suggests a mechanism for altering the genetic state of stocks between years.

Timing (date) of sockeye runs within quadrennial cycles is inversely related to individual fish size and directly correlated with run size although the relationships are imprecise, as was indicated previously. Presumably this is due to food availability and competition for food in the ocean, where the final size of the fish is determined (Killick and Clemens 1963). The relationship between run size and fish size is most apparent in Fraser River pink salmon (IPSFC 1984, p.20). There may be a biological connection between the earlier than normal annual stock migrations, with their relatively larger fish, and the early and larger fish within a stock migration in relation to heightened prespawning mortality rate, but no clues as to the connection have been uncovered.

Regardless of the cause of the relationship between prespawning mortality rate and timing of migration in a sockeye population, certain possibilities may be noted. The dominant cycle Horsefly runs have been migrating later as run size has increased ($r=0.79$, $p=0.01$); this may be due in part to genetic changes. Migration through the Fraser Canyon from 1913 to 1944, when passage was difficult except for short periods of "opening" (Thompson 1945), may have selected against all but the earliest migrants and altered the genetic structure in the population. The subdominant Horsefly population has not shown the same earliness in migration (see Williams 1973a, Table 3), perhaps because of fortuitous conditions, or possibly because under difficult passage conditions in the Canyon, only small numbers of sockeye could pass. A large run would then be more heavily selected against except for the earliest (less abundant) part of the run.

With the increase in size of sockeye runs following the construction of fishways in the Fraser Canyon and change in management methods, the Fraser River sockeye populations may migrate later on the average in future. Later timing will result in decreased prespawning mortality given no increase in water temperature or change in other conditions along the migration paths.

Prespawning Mortalities in Non-Fraser Sockeye

Until recent years, spawning ground prespawning mortalities of sockeye were seldom reported from other river systems, probably because they were normally small and thus were unmentioned or ignored. Mortalities of less than 10% were noted in the Okanagan River in southern British Columbia in the autumn spawning ground occupation in 1955, 1956 and 1957 in connection with changes made to the spawning ground (Craddock 1958). Sockeye in the Columbia River have been much reduced in numbers but this is probably due to the effects of Columbia River dams. The prespawning mortality rate was low in Okanagan River sockeye in 1957 despite average daily temperatures of 15° to 20°C or possibly higher during migration (Craddock *ibid.*). Migration losses due to the high temperatures were considered to be likely, however, as some of the sockeye counted at dams farther down-river could not be accounted for.

Godfrey et al. (1956) noted high (58 to 70%) prespawning mortality rates in the Babine River sockeye run of 1952 resulting from delay at a rock slide on the migration route; the undelayed run of 1953 had only an estimated 5% unspawned mortality rate. High temperatures were not mentioned and were apparently not a factor. As in Fraser River

sockeye, the high prespawning mortality rates suggest that difficult migration conditions can be an important stressor, causing latent injury to delayed fish.

Foerster (1968) summarized the findings of several observers concerning sockeye egg retention (approximately equivalent to prespawning mortality rate) in Canada, Alaska and Kamchatka. The investigations included the very small number of eggs retained by many females that would be classified as completely spawned by IPSFC definition. Reported retention was 5% or less except under crowded experimental conditions. Retention was slightly greater for larger populations and spawner density was concluded to increase both the number of eggs retained in partially-spawned females and the proportion of females dying unspawned.

Egg retention in several stocks of sockeye of the British Columbia coast was examined by Manzer and Miki (1985). Estimated egg retention (including small numbers of eggs in essentially spent females) in five stream systems in one to three years sampling averaged from 0.6 to 9.4%. Very few females examined retained more than half their eggs. A possible direct relationship between spawner density and egg retention rate was suggested from differences found between stream and beach spawning areas, in agreement with the conclusion of Foerster (1968).

West and Mason (1987) analyzed data from certain Babine Lake sockeye populations and found "that egg retention and spawning abstention (i.e. our death unspawned) were positively and significantly correlated both with each other and with density of females". However, "the relative increases in partially spawned and unspawned females as density increased were quite low considering the wide range of spawning densities — both increases averaged less than 3% over all years". Spawning abstention was also positively related to spawning river temperature at the time when major entry into the river commenced. All above-average abstentions took place at temperatures above 16°C and reached 20% at 17°C. No correlation was found between temperature and egg retention of partially spawned females. These results suggest that, for conditions of low prespawning mortalities, a relationship between spawning density and the small numbers of eggs retained would also be found for Fraser River sockeye.

Migration conditions may explain why Fraser River sockeye often suffer higher prespawning mortality rates than sockeye from other river systems. The Fraser River is near the southern end of the range of anadromous sockeye and thus may have higher temperatures than other systems to the north. River migration distances are greater for the Fraser stocks most affected. The Fraser Canyon, even with the fishways now in place, plus the longer spawning migrations, may constitute a stress factor of greater severity than any normally encountered by sockeye runs in other systems.

Implications for Management

It has been recognized that the irregular application of commercial fishing periods by time during the sockeye season can alter the effective timing of the escapement of a stock, i.e., either the early or late portion of an escapement can be removed. Prespawning mortality in a large run may thus be reduced by harvesting early migrating sockeye, leaving late migrants to become late spawners. While this method has limited application due to the overlap of stocks moving through the fishery, it can be used when one or a few large and closely timed stocks greatly outnumber other stocks; it has been applied to the dominant Horsefly run within limitations imposed by the nature of the fishery and catch allocation requirements (IPSFC 1964, 1986).

Because average timing of runs of sockeye stocks is genetically controlled, fishery management must consider the effect of asymmetrically-timed fishing periods applied over many years to the same stock. Consistently preferential escapement of early or late sections of a stock may possibly alter not only the migration and spawning time, but also other genetically controlled characteristics of a stock. Restorative selection will occur at other stages in that stock's life history but deviation of equilibrium from the optimum condition will lower productivity.

Poor correlation in general between population size and spawning ground prespawning mortality rate, except in unusual circumstances, indicates that overlarge escapements are not an important cause of high mortality rates in Fraser River sockeye. Although the very large escapement to the Chilko River in 1963 had a very high prespawning mortality rate, the extremely early timing and warm water temperatures largely accounted for this. Restrictions need not be placed on spawning population size insofar as prespawning mortality is concerned. Indeed, large escapements appear to have beneficial effects such as late average migration time and lake enrichment from carcasses (Stockner 1987), which outweigh losses (if any) from prespawning mortality.

Increased escapements for stocks which are vulnerable to high prespawning mortality rates could be allowed in years when conditions such as high temperatures or high water levels are forecast. However, long range forecasts of weather are not yet sufficiently accurate for pre-season planning of such measures, but the effect of snow pack on river flow allows somewhat better predictions of the range of river levels to be expected.

The intermittent nature of the final commercial fishery (the Fraser River gillnet fishery) on Fraser sockeye often results in very large escapements in a very short period of time. The resultant crowding and delay to migration in the Fraser Canyon can result in stress responses with reduced resistance to disease and increased prespawning mortality rates. However, there is at present no obvious method of operating this fishery in a continuous, low efficiency mode.

Implications for Enhancement

Stock enhancement in sockeye and other species of Pacific salmon by artificial means is an attractive method of achieving greater yields from a fishery on a group of stocks, although problems with uneven stock returns have been encountered. Enhancement for sockeye has been accomplished by lake fertilization, the provision or improvement of passage past obstacles, the construction of artificial spawning grounds or the use of gravel incubation boxes; hatcheries are not used extensively for sockeye enhancement due mainly to disease problems, which can cause large production losses. Increased egg-to-fry survival in enhanced stocks could be used to offset high prespawning mortality rates in stocks which suffer this depletion.

Aside from fishways, enhancement for Fraser River sockeye (and pink) salmon has been almost entirely by means of artificial spawning grounds (channels) built to augment natural-stream spawning. Records from the Nadina River (Late Nadina stock) show that prespawning mortalities have occurred in the spawning channel and on the natural spawning ground at about the same rate (Appendix Table F). In apportioning fish to the channel, prespawning mortality could be minimized by selecting the later portion of the escapement for the channel and leaving the early fish to spawn in the natural stream. This requires knowledge of the size of the escapement before it reaches the spawning area, which is difficult to obtain. Usually, the channel is filled with the earliest arrivals and the later fish allowed to spawn in the natural stream. Without knowledge of the heritability of differences between early and late sockeye, the possible changes in the population cannot be predicted.

Need for Future Research

More records of migration path and spawning ground temperatures were collected by the I.P.S.F.C. than by any other organization studying salmon. Nevertheless, these were still insufficient to determine temperature exposure during river migration for more than 3 or 4 years for some stocks.

An expanded network of sampling stations is urgently needed to evaluate stress factors such as pollution, supersaturation, etc., as well as temperature. Stations need not be closely spaced since changes are gradual between stations, except where major tributaries join the main river. Stress factors need to be determined for important sockeye migration routes in the mainstem of the Fraser River between Hope and Prince George, the Thompson River system, the Chilko system, the Quesnel system, and especially the Nechako system, where water is being diverted with resulting elevation of water temperatures. Solid state electronic

instrumentation is now available to collect extensive records with little expenditure of labor.

Temperature exposure in lakes is an unknown factor in prespawning mortality. Means are now available to discover the course, depth and temperature exposure of sockeye fitted with special ultrasonic tags (Coutant and Carroll 1980, Quinn and terHart 1987).

Physiological studies of Fraser River sockeye are far from complete. A detailed sampling of sockeye at several points along the river migration route, for the different temporal parts of a run to evaluate the physiological effects of stressors, advancing maturity and disease organisms would be useful. In addition, the relationship between diurnal temperature variation and the equivalent constant temperature, as was assessed by Hokanson et al. (1977) for immature rainbow trout, could be evaluated.

Since Fraser River sockeye show much higher prespawning mortality rates than those in other river systems and since upper-Fraser stocks have much higher prespawning mortality rates than lower-river stocks, difficult passage conditions appear to be an important factor in the cause of the mortalities, in addition to temperatures above the level of maximum performance. Because maximum use of sockeye spawning grounds cannot be obtained with high prespawning mortality rates and also because prespawning mortalities are a loss to the fishery, management must take reasonable steps to minimize stresses imposed on migrating Fraser River sockeye. With the increasing run sizes of recent years, studies of passage conditions in the Fraser and Thompson Canyons are needed to determine where and when delay may occur as well as the effect of crowding and delay on stress response and prespawning mortality. New fishways may be required and present fishways may need augmentation.

Of particular importance for careful study are the earliest migrating sockeye stocks, the Early Stuart and Nadina. These stocks have both large size potential (large lake rearing capacity) and have the highest oil content, which makes them the most desirable for the commercial fishery and for winter food use by the native subsistence fishery along the Fraser, Nechako and Stuart Rivers. Although stress factors may not be the only impediments to the achievement of maximum size in these runs, minimization of prespawning mortality rates is needed in addition to enhancement facilities and careful management to speed optimization of these valuable early populations.

Finally, the relationship between sockeye spawning time and survival of eggs, alevins and emerged fry requires more study. River and lake temperatures will probably increase given the heightened greenhouse effects now predicted to result from man-made atmospheric changes. While later spawning will be necessary to reduce prespawning mortalities, over-winter survival of eggs and alevins may be affected. Moreover, earlier spring fry emergence may be necessary to take advantage of earlier plankton blooms. Natural selection will result in an optimum equilibrium but artificial selection might be applied to hasten adaptation.

SUMMARY AND CONCLUSIONS

1. Annual prespawning mortalities on the spawning grounds of Fraser River sockeye are quite variable between stocks and have in some years been large. Because reduction of potential egg deposition has significant effects on sockeye production, the mortalities, which have been evaluated for over 40 years, were examined to determine causes.
2. Individual Fraser River sockeye stocks enter the Fraser River in peak numbers from July to October; peak spawning occurs from early August to late November. Most sockeye arrive at their spawning grounds within a few days of spawning, but in a few stocks arrival may be up to 6 weeks prior to spawning.
3. Annual prespawning mortality rates were determined exclusively by examination of samples of dead female sockeye during spawning ground dead recovery for population enumeration and collection of other biological information. Spawning success (egg expulsion) in females was classified as either unspawned (0-25% expulsion), about half spawned (25-75% expulsion), or spent (75-100% expulsion). Annual prespawning mortality rate (%) is the complement of the daily average success of spawning weighted by daily dead recovery.
4. Annual prespawning mortality rates for 14 stocks varied between approximately 0% and an extreme value of about 90%. Mean annual rates varied from 3.3-23.7%, with highest rates for upper-river (long migration) stocks migrating upriver during July and August. Stocks migrating in September and October had low mortality rates.
5. Daily prespawning mortality rate decreased from arrival of a run at a spawning ground until spawning ended.
6. Annual prespawning mortality rates were mostly positively correlated between paired spawning grounds but only 19 in 88 coefficients were significant. Negative correlations were confined largely to 3 stocks. Variation of environmental and biological factors between areas appeared to reduce the effect of common factors affecting mortality rates.
7. Correlations between annual spawning ground prespawning mortality rates for 9 major Fraser River sockeye stocks and several environmental and biological variables were examined. Factors compared included migration and spawning timing, population size, water temperature during migration and spawning ground occupation, rate of Fraser River discharge (for two stocks) and suspended solids in the Fraser (for one stock).
8. Elevated water temperatures and early timing of migration in the Fraser River were most closely correlated (singly) with increased annual prespawning mortality rates within stocks. Both migration and spawning ground temperatures up to peak of spawning yielded significant correlations. Population size was not significantly related to prespawning mortality rate, nor was discharge or suspended solids in the Fraser River.
9. In general, variation in migration time for individual stocks did not cause correlated variation in temperature exposure. Hells Gate temperature was negatively correlated with both Fraser discharge and suspended sediment load.
10. A weak but apparently real relationship between migration timing and population size was found.
11. Significant multiple (2 independent variable) correlations between prespawning mortality rate and timing (peak date) plus average river temperature at Hells Gate were found for 4 of 8 stocks examined. In 5 of the 8 stocks, Hells Gate timing and spawning ground temperatures produced significant multiple correlations. Time of spawning ground arrival yielded weaker multiple correlations.
12. Early Stuart sockeye river-migration time was prolonged by low water temperature and the correlated higher Fraser discharge. Both Early Stuart and Chilko stocks had significant negative relationships between Hells Gate temperature and time of peak

- spawning, suggesting slowing of maturation by low temperature.
13. While the Early Nadina stock had a significant multiple correlation between prespawning mortality rate, migration temperature and timing, sockeye numbers in the dominant cycle have declined precipitously since 1957; migration and spawning have also become later. These changes remain unexplained.
 14. Prespawning mortality rate for Raft sockeye was better estimated by temperature and timing at the spawning grounds than at Hells Gate.
 15. The Horsefly stock had the highest multiple correlation between prespawning mortality rate and Hells Gate temperature and timing. High spawning ground temperatures probably increased prespawning mortalities, although this correlation had borderline significance.
 16. No significant relationships were found for the Late Stuart and Late Nadina stocks, although time of migration at Hells Gate may be a significant factor for the Late Stuart prespawning mortality rate.
 17. Chilko sockeye had a relatively weak multiple relationship between prespawning mortality rate and the temperature and migration time at Hells Gate. As with Raft sockeye, spawning ground temperature produced a closer multiple relationship than Hells Gate temperature.
 18. Like the Raft stock, Stellako sockeye had a higher multiple correlation with timing and temperature on the spawning grounds than at Hells Gate.
 19. Although no significant multiple correlations were found for Birkenhead sockeye prespawning mortality rate, the rate was significantly related to temperature at New Westminster and to peak spawning date. Prespawning mortality rate has decreased significantly with time since the 1950's, probably because the population has also increased significantly, with resulting later migration and spawning. No obvious cause has been found for the population growth.
 20. Response of annual prespawning mortality rates to environmental factors (stressors) is consistent with the concept of stress in fish, in which stressors evoke a general neuroendocrine reaction followed by secondary, often irreversible, effects on blood and tissues. Response is graded, indicating additive and cumulative stress effects. Stress effects, combined with advancing maturation, result in death of females at the spawning ground prior to spawning or before spawning can be completed.
 21. Prespawning mortality occurs at well below lethal temperatures. Metabolic scope (scope for activity; energy available to adapt to stressors) decreases above an optimum temperature, generally found to be 15°C but in maturing sockeye on a strenuous upstream migration without food intake, the optimum may be lower, as indicated by multiple regressions for prespawning mortality rate solved for zero mortality.
 22. The relationship between annual prespawning mortality rates and environmental variables is concluded to be curvilinear, accelerating as adverse conditions increase. Very low temperatures may also increase the mortality rate possibly resulting in a "U" shaped curve.
 23. Disease symptoms occur more frequently at elevated temperatures, in the earlier part of a sockeye spawning population, and in female sockeye which die unspawned. No practical method of reducing disease is known; the minimization of stress factors during migration is the better option.
 24. Other factors, including river discharge, pollution, suspended sediments, and supersaturation by atmospheric gases, while unexamined or not significantly correlated with prespawning mortality rates, are additional stressors and therefore must increase the prespawning mortality rates. Migration to upper-river spawning grounds is itself a significant stressor.
 25. Physical and physiological differences between earlier vs later parts of annual runs of individual sockeye stocks suggest that the differences may be genetically based and that the decreasing trend of prespawning mortality rate during the spawning period results therefrom. The cause of higher prespawning mortality rates in earlier annual

migrations within individual stocks is unknown.

26. Sockeye in other river systems outside the Fraser have had generally low prespawning mortality rates, presumably due mainly to lower water temperatures and less rigorous migration conditions.
27. Management of the fishery for Fraser sockeye may reduce prespawning mortality rates in an annual run by allowing heaviest escapement from the later part of affected stocks, but potential long term adverse genetic changes should be considered. Forecasts of conditions which increase the prespawning mortality rate could allow release of extra escapement to compensate. The intermittent nature of escapements from the commercial fishery may cause problems of crowding in fishways and at points of difficult passage, increasing stress responses in upstream migrants.
28. Enhancement of sockeye stocks by spawning channels or other methods of increasing egg-to-fry survival could be used to counteract high prespawning mortality rates.
29. Further research is needed regarding temperature exposure of Fraser sockeye during migration, extent of stressors such as pollution and supersaturation, and physiological changes resulting from advancing maturity and from stressors encountered during migration. Because lower river sockeye have much lower prespawning mortality rates than upper Fraser fish, the adequacy of fish passage conditions and of fish passage facilities in the Fraser and Thompson River Canyons requires careful investigation.
30. The valuable and potentially very large Early Stuart and Nadina runs are of particular importance for research and enhancement.

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APPENDIX

TABLE A. Prespawning mortality rates for female sockeye on the Early Stuart spawning grounds for 38 years, and seven factors with which they were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Ave. Temperature at Hells Gate (Deg. Cels.) | Female Population (1000'S) | Ave. Migration Temperature** (Deg. Cels.) | First Arrival Date* | Center, Peak Spawning Period* | Sp. Ground Temperature (Deg. Cels.) |
|------|---------------------------|-----------------------|---|----------------------------|---|---------------------|-------------------------------|-------------------------------------|
| 1949 | 39.0 | | | 276 | | 7/20 | 8/6 | 9.1 |
| 1950 | 10.2 | 7/10 | 15.1 | 88 | 16.4 | 8/1 | 8/10 | 8.8 |
| 1951 | 12.6 | | | 34 | | 7/17 | 8/6 | 10.2 |
| 1952 | 7.1 | | | 17 | | 7/25 | 8/4 | 11.8 |
| 1953 | 10.9 | | | 88 | | 7/16 | 8/2 | 9.4 |
| 1954 | 1.8 | | | 18 | | 7/29 | 8/5 | 9.6 |
| 1955 | 5.0 | | | 1 | | 8/5 | 8/12 | 8.7 |
| 1956 | 1.3 | | | 17 | | 7/20 | 8/2 | 12.6 |
| 1957 | 1.1 | 7/14 | 15.3 | 121 | 15.4 | 7/20 | 8/5 | 8.9 |
| 1958 | 3.9 | | | 23 | | 7/25 | 8/8 | 11.9 |
| 1959 | 3.1 | | | 1 | | 7/29 | 8/8 | 9.6 |
| 1960 | 14.2 | | | 9 | | 7/29 | 8/7 | 11.4 |
| 1961 | 19.3 | 7/16 | 17.5 | 109 | 18.7 | 7/19 | 8/1 | 11.9 |
| 1962 | 5.1 | | | 15 | | 7/22 | 8/8 | 11.2 |
| 1963 | 10.8 | | | 3 | | 7/23 | 8/6 | 10.1 |
| 1964 | 3.0 | | | 1 | | 8/5 | 8/15 | 9.1 |
| 1965 | 19.5 | 7/10 | 15.7 | 14 | 16.4 | 7/21 | 8/4 | 10.9 |
| 1966 | 6.8 | | | 6 | | 7/26 | 8/10 | 10.7 |
| 1967 | 5.2 | | | 12 | | 7/27 | 8/7 | 9.9 |
| 1968 | 12.2 | | | 1 | | 7/31 | 8/11 | |
| 1969 | 18.3 | 7/10 | 16.3 | 60 | 16.7 | | | |
| 1970 | 13.4 | 7/18 | 16.7 | 18 | 16.8 | | | |
| 1971 | 10.9 | 7/17 | 15.1 | 51 | 15.2 | 7/23 | 8/5 | 12.6 |
| 1973 | 1.3 | 7/15 | 16.4 | 156 | 16.7 | 7/25 | 8/3 | 9.9 |
| 1974 | 3.8 | 7/12 | 13.6 | 22 | 14.4 | 7/28 | 8/3 | 9.2 |
| 1975 | 20.8 | 7/13 | 16.2 | 33 | 17.7 | 7/24 | 8/4 | 9.3 |
| 1976 | 2.8 | 7/9 | 14.2 | 7 | 14.9 | 8/1 | 8/12 | 9.0 |
| 1977 | 26.3 | 7/11 | 15.8 | 72 | 15.8 | 7/21 | 8/5 | 10.8 |
| 1978 | 28.4 | 7/9 | 17.4 | 28 | 18.6 | 7/17 | | 12.2 |
| 1979 | 25.2 | 7/14 | 16.4 | 48 | 18.2 | 7/20 | 7/31 | 10.8 |
| 1980 | 25.3 | 7/10 | 16.2 | 10 | 16.8 | 7/20 | 7/29 | 10.7 |
| 1981 | 10.7 | 7/15 | 16.2 | 75 | 17.5 | 7/18 | 8/1 | 12.1 |
| 1982 | 17.7 | 7/13 | 15.5 | 3 | | 8/1 | 8/8 | 10.8 |
| 1983 | 14.4 | 7/12 | 15.2 | 15 | | 7/19 | 8/7 | 9.7 |
| 1984 | 11.1 | 7/11 | 13.8 | 25 | | 7/24 | 8/3 | |
| 1985 | 9.0 | 7/13 | 16.1 | 128 | | 7/25 | 8/4 | 10.6 |
| 1986 | 3.9 | 7/12 | 13.7 | 16 | | | 8/3 | |
| 1987 | 8.1 | 7/16 | 14.9 | 83 | | | | |

* Month/Day.

** Incomplete. See text.

TABLE B. Prespawning mortality rates for female sockeye on the Early Nadina spawning grounds for eight dominant years, and the four factors with which they were compared.

| Year | Prespawning Mortality (%) | Peak Date at Hells Gate* | Ave. Temperature at Hells Gate (Deg. Cels.) | Ave. Migration Temperature** (Deg. Cels.) | Female Population (Hundreds) |
|------|---------------------------|--------------------------|---|---|------------------------------|
| 1953 | 17.0 | 7/20 | 15.0 | 16.9 | 134 |
| 1957 | 4.1 | 7/19 | 15.8 | 16.6 | 162 |
| 1961 | 86.0 | 7/23 | 18.6 | 18.8 | 111 |
| 1965 | 11.3 | 7/27 | 17.4 | 18.3 | 20 |
| 1969 | 6.6 | 7/21 | 16.9 | 17.0 | 47 |
| 1973 | 6.1 | 7/21 | 16.7 | 17.4 | 12 |
| 1977 | 1.2 | 8/3 | 17.1 | 18.2 | 8 |
| 1981 | 5.5 | 7/30 | 17.4 | 18.4 | 5 |

* Month/Day.

** Incomplete. See text.

TABLE C. Prespawning mortality rates for female sockeye on the Raft spawning grounds for 20 years, and the five factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Ave. Temperature at Hells Gate (Deg. Cels.) | Spawning Ground Temperature** (Deg. Cels.) | Spawning Ground Arrival Date*** | Female Population (100's) |
|------|---------------------------|-----------------------|---|--|---------------------------------|---------------------------|
| 1952 | 33.7 | 7/30 | 18.1 | 14.3 | 8/20 | 158 |
| 1953 | 20.8 | 7/29 | 16.3 | 15.8 | 8/18 | 82 |
| 1954 | 0.8 | 7/31 | 16.3 | 12.0 | 8/27 | 106 |
| 1955 | 8.3 | 7/29 | 15.3 | 13.6 | 8/24 | 54 |
| 1957 | 0.7 | 8/13 | 16.3 | 11.3 | 8/26 | 73 |
| 1958 | 1.0 | 8/16 | 18.3 | 13.2 | 9/1 | 102 |
| 1960 | 4.9 | 7/28 | 17.9 | 11.9 | 8/23 | 56 |
| 1961 | 24.9 | 7/30 | 19.2 | 14.5 | 8/26 | 73 |
| 1962 | 5.3 | 8/3 | 18.2 | 11.8 | 8/27 | 76 |
| 1963 | 43.2 | 7/31 | 17.8 | 14.6 | 8/17 | 87 |
| 1964 | 4.2 | 7/31 | 15.0 | 11.1 | 8/31 | 55 |
| 1965 | 34.7 | 7/31 | 18.3 | 14.1 | 8/25 | 66 |
| 1966 | 12.0 | 8/2 | 16.8 | 14.4 | 8/24 | 63 |
| 1969 | 12.4 | 7/30 | 16.9 | 13.2 | 8/20 | 54 |
| 1972 | 28.3 | 8/5 | 17.9 | 15.5 | 8/26 | 112 |
| 1973 | 10.6 | 8/3 | 18.8 | 13.9 | 8/24 | 27 |
| 1975 | 2.6 | 7/27 | 16.2 | 12.0 | 9/1 | 27 |
| 1976 | 0.4 | 7/27 | 15.8 | 11.6 | 8/31 | 87 |
| 1979 | 16.2 | 7/29 | 18.0 | 16.5 | 8/28 | 18 |
| 1980 | 5.5 | 8/9 | 17.3 | 12.6 | 8/23 | 54 |

* Month/Day.
 ** Average of mean daily water temperatures, peak arrival to center of peak spawning period.
 *** Estimated peak date of arrival on spawning grounds (Month/Day).

TABLE D. Prespawning mortality rates for female sockeye on the Horsefly spawning grounds for 19 years, and the six factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Average Temperature at Hells Gate (Deg. Cels.) | Female Population (1000's) | First Arrival Date* | Center, Peak Spawning Period* (Deg. Cels.) | Sp. Ground Temperature** (Deg. Cels.) |
|------|---------------------------|-----------------------|--|----------------------------|---------------------|--|---------------------------------------|
| 1953 | 25.0 | 8/3 | 16.2 | 60 | 8/4 | 8/28 | 15.4 |
| 1957 | 5.0 | 8/12 | 16.2 | 136 | 8/5 | 9/3 | 13.0 |
| 1958 | 1.6 | | | 12 | 8/15 | 9/8 | 16.7 |
| 1961 | 62.0 | 8/6 | 19.0 | 169 | 8/5 | 8/29 | 17.7 |
| 1962 | 5.1 | | | 1 | 8/23 | 9/1 | 12.2 |
| 1965 | 46.8 | 8/5 | 17.8 | 195 | 8/6 | 8/31 | 16.3 |
| 1966 | 8.5 | | | 1 | 8/15 | 9/4 | 13.8 |
| 1969 | 50.3 | 8/2 | 17.0 | 142 | 8/7 | 8/29 | 13.4 |
| 1970 | 58.2 | | | 1 | 8/24 | 9/5 | 15.6 |
| 1973 | 27.6 | 8/9 | 18.4 | 130 | 8/14 | 8/31 | 13.4 |
| 1974 | 1.0 | | | 3 | 8/20e | 9/8 | 14.1 |
| 1977 | 38.2 | 8/4 | 17.6 | 224 | 8/11 | 9/4 | 14.8 |
| 1978 | 1.6 | | | 4 | 8/20 | 9/7 | 13.2 |
| 1981 | 18.5 | 8/17 | 18.6 | 352 | 8/11 | 8/29 | 18.0 |
| 1982 | 2.5 | | | 21 | 8/20e | 9/9 | 14.4 |
| 1983 | 24.5 | | | 1 | 8/15e | 9/6 | 15.6 |
| 1984 | 4.5 | | | 1 | 8/15e | 9/6 | 13.7 |
| 1985 | 5.3 | 8/19 | 16.8 | 583 | 8/10e | 9/8 | 13.7 |
| 1986 | 6.6 | | | 73 | 8/15e | 9/7 | 15.9 |

* Month/Day.
 ** Average of mean daily temperatures from first arrival to peak spawning.
 e Partly an estimate; data less reliable than other years.

TABLE E. Prespawning mortality for female sockeye on the Late Stuart spawning grounds for the nine latest dominant years, and the three factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Ave. Temperature at Hells Gate (Deg. Cels.) | Total Female Population (1000's) |
|--------------|---------------------------|-----------------------|---|----------------------------------|
| 1953 | 54.5 | 8/2 | 16.4 | 173 |
| 1957 | 4.3 | 8/11 | 16.2 | 314 |
| 1961 | 21.7 | 8/8 | 18.6 | 248 |
| 1965 | 6.1 | 8/8 | 18.3 | 131 |
| 1969 | 5.9 | 8/4 | 16.6 | 121 |
| 1973 | 3.7 | 8/15 | 17.6 | 121 |
| 1977 | 1.8 | 8/4 | 17.8 | 77 |
| 1981 | 8.0 | 8/6 | 18.7 | 131 |
| 1985 | 3.4 | 8/11 | 17.4 | 163 |
| * Month/Day. | | | | |

TABLE F. Prespawning mortalities for female sockeye at the Late Nadina spawning grounds for 26 years, and the three factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | | Female Population (100's) | | Hells Gate Peak Date* | Ave. Temperature at Hells Gate (Deg. Cels.) |
|--|---------------------------|------------------|---------------------------|------------------|-----------------------|---|
| | River | Spawning Channel | River | Spawning Channel | | |
| 1953 | 4.0 | | 76 | | 7/30 | 16.2 |
| 1957 | 8.4 | | 140 | | 8/19 | 16.0 |
| 1961 | 5.6 | | 88 | | 8/8 | 18.9 |
| 1962 | 4.7 | | 10 | | | |
| 1963 | 18.8 | | 37 | | 8/8 | 17.7 |
| 1965 | 1.1 | | 56 | | 8/3 | 16.9 |
| 1966 | 0.5 | | 10 | | | |
| 1967 | 13.9 | | 45 | | 8/6 | 17.9 |
| 1969 | 11.3 | | 175 | | 8/1 | 16.7 |
| 1970 | 3.4 | | 22 | | | |
| 1971 | 1.0 | | 80 | | 8/10 | 18.3 |
| 1972 | 7.2 | | 14 | | | |
| 1973 | 3.0 | 5.7 | 51 | 49 | 7/29 | 17.4 |
| 1974 | 2.1 | 3.7 | 16 | 5 | | |
| 1975 | 8.9 | 12.9 | 29 | 66 | 8/13 | 16.8 |
| 1976 | | 2.8 | | 7 | | |
| 1977 | | 3.8 | | 93 | 7/29 | 18.4 |
| 1978 | | 1.0 | | 14 | | |
| 1979 | 19.3 | 44.8 | 97 | 228 | | |
| 1980 | | 8.9 | | 16 | | |
| 1981 | 3.4 | 2.8 | 7 | 106 | 8/5 | 18.3 |
| 1982 | | 1.1 | | 13 | | |
| 1983 | 2.7 | 2.9 | 19 | 140 | | |
| 1984 | | 1.8 | | 33 | | |
| 1985 | 2.4 | 1.2 | 10 | 68 | | |
| 1986 | | 1.1 | | 20 | | |
| * Peak date assumed to be the same for both population components (Month/Day). | | | | | | |

TABLE G. Prespawning mortality rates for female sockeye on the Chilko spawning grounds for 22 years, and the six factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Ave. Temperature at Hells Gate (Deg. Cels.) | Female Population (1000's) | Peak Arrival Date* | Center, Peak Spawning Period* | Sp. Ground Temperature** (Deg. Cels.) |
|------|---------------------------------|--------------------------|---|----------------------------------|--------------------------|-------------------------------------|---|
| 1948 | 7.2 | 8/8 | 16.9 | 393 | | | |
| 1952 | 10.6 | 8/4 | 18.1 | 261 | 8/28 | 9/22 | 11.4 |
| 1953 | 13.6 | 8/2 | 16.4 | 109 | | 9/17 | |
| 1954 | 2.7 | 8/7 | 16.3 | 22 | 9/6 | 9/24 | 9.3 |
| 1955 | 5.9 | 8/8 | 15.3 | 81 | 9/3 | 9/24 | 11.3 |
| 1956 | 4.6 | 8/11 | 17.9 | 386 | 9/1 | 9/24 | 11.9 |
| 1957 | 0.5 | 8/16 | 15.9 | 84 | 9/3 | 9/25 | 11.1 |
| 1958 | 0.1 | 8/29 | 17.6 | 71 | 9/12 | 9/29 | 11.1 |
| 1959 | 0.2 | 8/15 | 16.7 | 273 | 9/4 | 9/30 | 9.6 |
| 1960 | 1.0 | 8/15 | 15.7 | 247 | 9/3 | 9/28 | 10.3 |
| 1961 | 36.2 | 8/8 | 18.8 | 24 | 8/26 | 9/26 | 12.7 |
| 1962 | 14.9 | 8/7 | | 50 | 9/7 | 9/27 | 10.4 |
| 1963 | 89.5 | 8/1 | 17.3 | 543 | | 9/18 | |
| 1964 | 2.2 | 8/9 | 14.9 | 134 | 9/14 | 10/1 | 8.7 |
| 1965 | 9.7 | 8/5 | 17.3 | 23 | 8/25 | 9/26 | 10.9 |
| 1966 | 6.2 | 8/9 | | 115 | 8/28 | 9/24 | 10.9 |
| 1967 | 11.9 | 8/7 | 16.0 | 102 | 9/5 | 9/26 | 13.2 |
| 1968 | 24.4 | 8/9 | 16.7 | 241 | 9/2 | 9/25 | 11.2 |
| 1969 | 39.8 | 8/5 | 17.1 | 42 | 8/26 | 9/21 | 11.8 |
| 1970 | 29.2 | 8/14 | | 72 | 8/25 | 9/23 | 11.6 |
| 1971 | 8.9 | 8/18 | 17.8 | 99 | 8/29 | 9/26 | 10.6 |
| 1972 | 1.3 | 8/16 | 17.3 | 337 | 8/31 | 9/26 | 11.9 |
| 1973 | 2.1 | 8/7 | 17.7 | 31 | | 9/22 | 10.4 |
| 1974 | 3.0 | 8/11 | 15.2 | 73 | 9/2 | 9/26 | 13.0 |
| 1975 | 13.6 | 8/16 | 16.6 | 118 | | 9/25 | |
| 1976 | 1.7 | 8/19 | 16.3 | 215 | | 9/25 | |
| 1977 | 31.3 | 8/6 | 18.1 | 29 | | 9/21 | |
| 1978 | 0.5 | | 16.9 | 83 | 9/6 | 9/28 | 10.8 |
| 1979 | 12.6 | 8/12 | 18.3 | 154 | 8/30 | 9/18 | 13.9 |
| 1980 | 7.5 | 8/13 | 16.7 | 298 | | 9/27 | |
| 1981 | 6.3 | 8/7 | 18.7 | 21 | | 9/24 | 13.2 |

* Month/Day.
** Average of mean daily temperatures from peak arrival to center of peak spawning period.

TABLE H. Prespawning mortality rates for female sockeye on the Stellako spawning grounds for 33 years, and the seven factors with which the mortalities were compared.

| Year | Prespawning Mortality (%) | Hells Gate Peak Date* | Ave. Temperature At Hells Gate (Deg. Cels.) | Ave. Migration Temperature (i) (Deg. Cels.) | Female Population (100's) | Date of First Arrival* | Center, Peak Spawning Period* | Sp. Ground Temperature** (Deg. Cels.) |
|------|---------------------------|-----------------------|---|---|---------------------------|------------------------|-------------------------------|---------------------------------------|
| 1952 | 2.9 | 8/2 | 17.7 | | 205 | 8/20 | 9/28 | 14.3 |
| 1953 | 2.9 | 8/2 | 16.5 | 17.4 | 210 | 8/18 | 9/25 | 15.8 |
| 1954 | 3.8 | 8/6 | 16.3 | 16.9 | 751 | 8/29 | 9/26 | 14.6 |
| 1955 | 3.8 | | | | 311 | 9/1 | 9/24 | 12.9 |
| 1956 | 1.8 | | | | 227 | 8/28 | 9/25 | 16.4 |
| 1957 | 6.0 | 8/12 | 16.0 | | 192 | 8/25 | 10/1 | 14.1 |
| 1958 | 0.6 | 9/1 | 16.2 | 15.8 | 619 | 9/5 | 10/1 | 14.1 |
| 1959 | 1.3 | | | | 424 | 9/1 | 9/27 | 12.7 |
| 1960 | 2.5 | | | | 233 | 8/31 | 9/26 | 13.9 |
| 1961 | 28.8 | 8/7 | 18.7 | 18.9 | 255 | 8/20 | 9/27 | 17.5 |
| 1962 | 32.4 | | | | 659 | 9/4 | 10/1 | 18.2 |
| 1963 | 44.0 | 8/11 | 17.6 | 17.2 | 742 | 8/20 | 9/25 | 17.8 |
| 1964 | 2.1 | | | | 165 | 9/5 | 9/28 | 12.8 |
| 1965 | 2.9 | 8/17 | 17.5 | 17.3 | 211 | 8/21 | 9/28 | 16.6 |
| 1966 | 5.8 | 8/11 | 16.2 | 15.8 | 547 | 8/26 | 9/28 | 14.2 |
| 1967 | 40.0 | 8/13 | 17.8 | 17.8 | 540 | 8/25 | 9/28 | 17.4 |
| 1968 | 11.3 | 8/11 | 15.1 | 15.7 | 154 | | 9/24 | 15.9 |
| 1969 | 10.0 | 8/16 | 15.8 | 14.7 | 285 | 8/25 | 9/26 | 14.6 |
| 1970 | 8.5 | | | | 292 | | 9/30 | |
| 1971 | 2.8 | 8/22 | 17.4 | 17.2 | 207 | 8/25 | 9/26 | 15.3 |
| 1972 | 1.6 | 8/9 | 17.7 | 17.3 | 207 | | 9/27 | |
| 1973 | 3.4 | 8/14 | 17.6 | 16.5 | 160 | 9/5 | 9/25 | 14.9 |
| 1974 | 3.1 | 8/15 | 16.0 | 16.6 | 245 | 8/25 | 10/2 | 15.3 |
| 1976 | 12.4 | 8/8 | 16.1 | | 746 | | 10/1 | 14.8 |
| 1977 | 11.7 | 8/6 | 18.2 | | 123 | 9/8 | 9/26 | 13.1 |
| 1978 | 2.6 | 8/14 | 17.7 | 17.0 | 334 | 9/1 | 9/27 | 14.7 |
| 1979 | 7.0 | 8/15 | 18.7 | 18.9 | 1641 | | 9/30 | 15.3 |
| 1980 | 27.3 | 8/5 | 17.1 | 17.1 | 391 | | 9/26 | 13.9 |
| 1981 | 3.8 | 8/16 | 18.7 | | 125 | | 10/1 | 15.8 |
| 1982 | 9.3 | 8/15 | 16.1 | | 385 | | 9/27 | 14.9 |
| 1983 | 8.1 | 8/16 | 18.1 | | 668 | | 9/22 | 14.4 |
| 1984 | 2.1 | 8/15 | 17.4 | | 334 | | 9/22 | 14.4 |
| 1985 | 4.6 | 8/20 | 16.4 | | 230 | | 9/25 | 14.1 |

* Month/Day.

** Average of mean daily temperatures from first arrival date to peak spawning.

(i) Incomplete; see text.

TABLE I. Prespawning mortality rates for female sockeye on the Birkenhead spawning grounds for 34 years, and 5 variable factors with which they were compared.

| Year | Prespawning Mortality (%) | New Westminster Peak Date* | Westminster Ave. Temp. (Cels.) | Female Population (1000'S) | Center, Peak Spawning Period* | Sp. Ground Temperature** (Deg. Cels.) |
|------|---------------------------|----------------------------|--------------------------------|----------------------------|-------------------------------|---------------------------------------|
| 1952 | | | | 287 | 9/27.5 | 11.7 |
| 1953 | 30.4 | | | 234 | 9/24.5 | 11.2 |
| 1954 | 11.2 | 8/16 | 15.3 | 97 | 9/26 | 10.5 |
| 1955 | 4.9 | 8/13 | 15.1 | 86 | 9/24 | 10.8 |
| 1956 | 12.2 | 9/7 | 17.2 | 309 | | 11.8 |
| 1957 | 5.7 | 8/24 | 16.5 | 75 | 9/26.5 | 11.4 |
| 1958 | 10.2 | 9/5 | 16.6 | 61 | 9/27.5 | 10.4 |
| 1959 | 10.2 | 8/19 | 15.7 | 127 | 9/25.5 | 10.8 |
| 1960 | 10.5 | 8/11 | 18.6 | 215 | 9/25 | 10.8 |
| 1961 | 35.5 | 8/18 | 19.6 | 164 | 9/26 | 10.8 |
| 1962 | 10.8 | 9/1 | 16.4 | 160 | 9/25 | 11.3 |
| 1963 | 34 | 8/17 | 18.6 | 315 | 9/23 | 12.2 |
| 1964 | 2.3 | 8/16 | 15.4 | 286 | 9/20 | 10.4 |
| 1965 | 8.2 | 8/16 | 18.6 | 106 | 9/19.5 | 11.0 |
| 1966 | 7.5 | 8/17 | 16.4 | 145 | 9/21.5 | 11.1 |
| 1967 | 22.9 | 8/18 | 19.4 | 228 | 9/20 | 12.1 |
| 1968 | 24.2 | 8/14 | 16.9 | 410 | 9/23 | 10.7 |
| 1969 | 37.1 | 8/18 | 16.4 | 228 | 9/24.5 | 11.1 |
| 1970 | 7.5 | 8/26 | 18.0 | 208 | 9/25 | 10.1 |
| 1971 | 3.9 | 8/18 | 18.8 | 168 | 9/23.5 | 09.5 |
| 1972 | 11.2 | 8/18 | 17.9 | 295 | 9/24.5 | 17.9 |
| 1973 | 7.6 | 8/18 | 17.4 | 307 | 9/24.5 | 10.6 |
| 1974 | 3.3 | 8/27 | 17.1 | 884 | 9/28.5 | 10.2 |
| 1975 | 36.3 | 8/14 | 16.9 | 366 | 9/25.5 | 08.8 |
| 1976 | 2.6 | 8/22 | 14.9 | 513 | 9/25.5 | 11.4 |
| 1977 | 9.8 | | | 142 | 9/24.5 | 10.7 |
| 1978 | 0.5 | | | 484 | 9/27.5 | 09.7 |
| 1979 | 9.7 | | | 393 | 9/26.5 | 11.9 |
| 1980 | 24.8 | | | 436 | 9/24 | 11.3 |
| 1981 | 4.5 | | | 284 | 9/26.5 | 11.6 |
| 1982 | 1.4 | | | 734 | 9/25 | 10.9 |
| 1983 | 11.6 | | | 239 | 9/24.5 | |
| 1984 | 4.6 | | | 244 | 9/24.5 | 10.3 |
| 1985 | 5 | | | 61 | 9/20.5 | 10.1 |
| 1986 | 1.2 | | | 2002 | 10/5.5 | 10.1 |
| 1987 | 4.4 | | | 936 | | |

* Month/Day.

** Average of mean daily temperatures from Sept. 10 to 25.