# Evidence for Cycle-line Interaction as a Mechanism for Cyclic Dominance in Fraser River Sockeye Salmon (*Oncorhynchus nerka*)

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**Abstract:** We examined interactions among cycle lines of Fraser River sockeye salmon stocks combined by freshwater rearing lake and observed negative cycle-line interaction effects on adult recruitment rates and on juvenile abundance and growth. Prior year(s) juvenile populations, as indexed by parent effective female spawners, exerted significant negative effects on juvenile growth and/or abundance in three major Fraser watersheds: Shuswap, Quesnel and Chilko. Cycle-line interaction effects were highly significant in the growth of juveniles rearing in Shuswap and Quesnel lakes where sockeye display strong cyclic dominance, but were absent in Chilko stocks that do not show classic dominance. Dominant line juvenile sockeye foraging appears responsible for following line juvenile growth limitations in Quesnel Lake. Measurable effects of prior-year juvenile abundance (i.e., effective female spawners) on juvenile growth and abundance in lakes point to negative cycle-line interaction as the driving force in cyclic dominance of Fraser River sockeye. We hypothesize that size-mediated, depensatory predation rates within some freshwater lakes in the upper Fraser River watershed utilized by juvenile sockeye is the mechanism that maintains cyclic dominance.

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# Introduction

Several Fraser River, British Columbia, sockeye salmon (*Oncorhynchus nerka*) stocks exhibit the variable pattern of recruitment on a four-year cycle termed "cyclic dominance" wherein one very abundant escapement and recruitment cycle line (the "dominant" line) is usually followed by a less abundant, yet substantial, "subdominant" line and, thence, by two much less abundant "offcycle" lines. These stocks are restricted in distribution to the interior of British Columbia in river-lake systems tributary to the upper Fraser River (Fig. 1) where the continental geoclimatic zone provides for relatively stable stream discharges (low probability of severe flooding) during fall-winter egg incubation. Stream stability may allow natural selection to act on stocks in such a way that maturity and reproduction occurs largely (> 90%) at one age (age 4) without severe risk of catastrophic mortality. The single primary age at maturity in upper Fraser sockeye stocks is one underlying requirement for cyclical dominance (Ricker 1997).

Synchrony of cyclic dominance in sockeye stocks within lake systems but asynchrony between lakes suggests that cyclic dominance is a naturally occurring, inherently efficient biological processes within sockeye lake systems in the upper Fraser watershed. Predation theories have been the cornerstone of explanations for cyclic dominance (Ward and Larkin 1964; Larkin 1971), but data collected to date do not support hypotheses developed to explain the mechanism(s) responsible for establishing and maintaining cyclic dominance (Williams et al. 1989).

Previous studies have documented negative cycle-line interaction in the adult recruitment rate data collected from cyclical stocks (Walters and Staley 1987; Collie and Walters 1987; Cass et al. 2000). Lagged effects of dominant line adult or juvenile abundance on the following non-dominant lines has spawned theories that food resources from dominant line sockeye eggs and juveniles may induce predator populations to cycle out of phase with the sockeye population, thus, generating depensatory mortality on the less abundant offcycle lines (Larkin 1971).

In the present study, interannual variation in the amount of freshwater growth measured on scales of sockeye that resided as juveniles in Shuswap, Quesnel and Chilko Lakes was examined to determine if cycle-line interaction affects juvenile growth. We
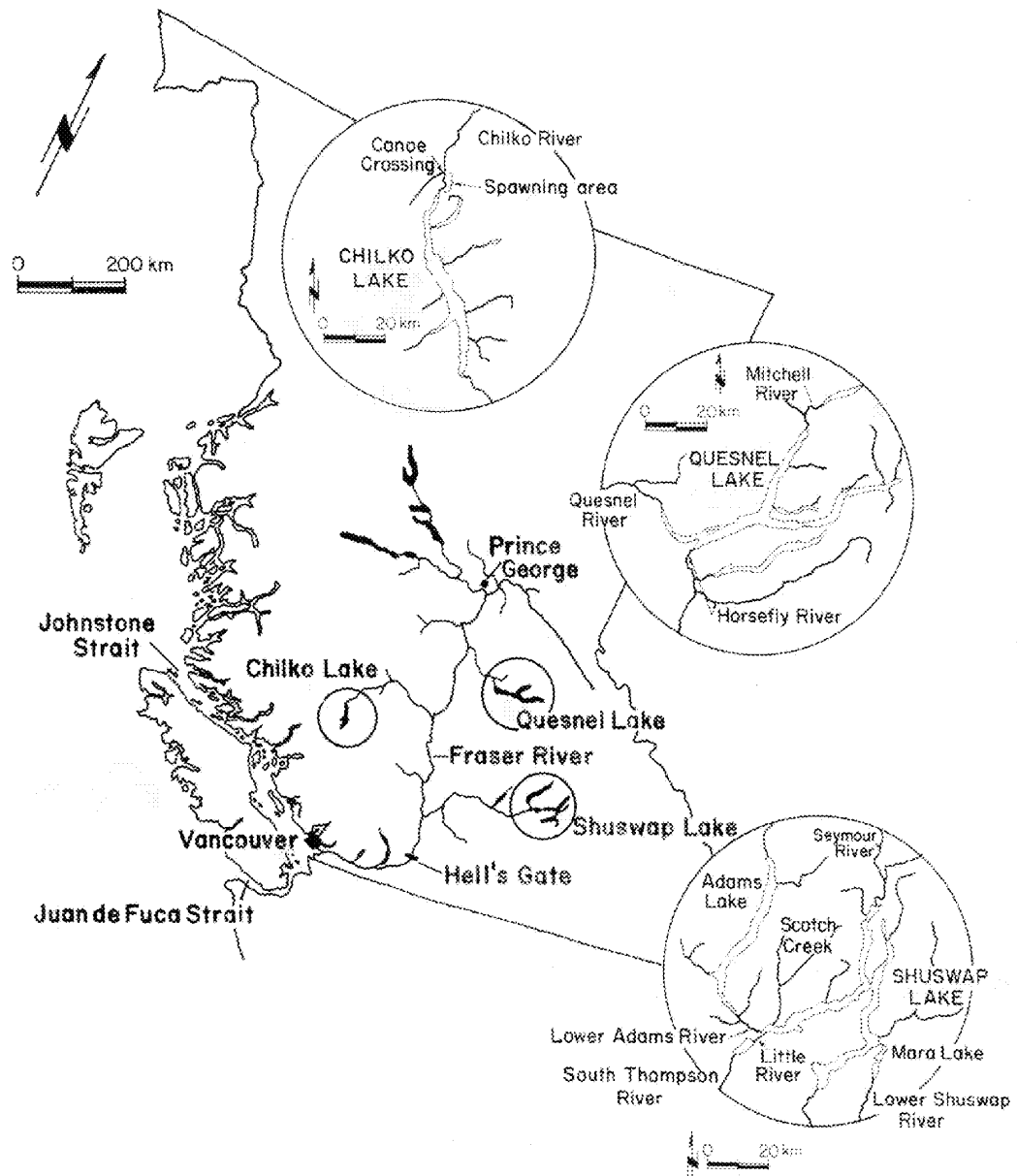
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Figure 1. Fraser River watershed map with enlargements of Shuswap, Quesnel and Chilko watersheds.

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also explored the mechanism for the control of recruitment by examining juvenile sockeye size and abundance data collected in situ from these three lake systems. Negative cycle-line interaction on juvenile growth may play a vital role in the maintenance of cyclic dominance in certain Fraser River sockeye stocks.

## Background

   The 4-year cycle of Fraser sockeye abundance was clearly recognized historically at the time of European contact in the early-mid 1800s. The "big" years were regular and anticipated. Ward and Larkin (1964) showed from Hudson Bay Company (HBC) logs and diaries that the cyclical pattern was prevalent in sockeye catches in the region of upper Fraser River and tributary HBC forts. All stocks cycled in synchrony with dominant lines on the 1901-05-09-13 (i.e., 2001) cycle. Gilbert (1914) reported that the fish maturing on the dominant line in 1913 were nearly all (> 99%) age 4 fish, confirming that the predominance of the one age group was central to the cyclical pattern of recruitment.

   After severe depletion from over-exploitation and the blockage to migration in 1913 at Hells Gate (Thompson 1945), several upper Fraser sockeye stocks rebuilt in a cyclical pattern although some shifted from the original dominant cycle. These stocks have been cyclical for up to twenty generations. The two most abundant sockeye stock complexes in the Fraser watershed, Shuswap Lake and Quesnel Lake sockeye, display strong cyclic dominance, while the third most abundant stock complex, Chilko Lake sockeye, displayed a modified cyclical recruitment pattern in the 1920s to 1980s but now does not. In total, cyclical stocks (not including Chilko) produce over 60% of the annualized Fraser sockeye recruitment (1980-1999 brood years).

   The population dynamics of Fraser River sockeye salmon stocks that display cyclic dominance has been the subject of inquiry and debate for over 50 years (see reviews of Ricker 1950; Ward and Larkin 1964; Levy and Wood 1992; Ricker 1997). The core issue is whether or not cyclic dominance is maintained by natural (intrinsic) ecological or biological mechanisms or by external (extrinsic) forces, such as exerted on the populations via exploitation (Walters and Staley 1987; Cass and Wood 1994). In the most

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recent assessment of cyclic dominance, Ricker (1997) re-analyzed Shuswap Lake stocks, focusing on Adams River sockeye. After examination of competing hypotheses, he concluded that the hypothesis of ecological/biological interaction between the four lines of cyclical stocks is the only plausible explanation for the development and persistence of cyclical production patterns and for the synchrony of cyclic dominance in several independent stocks within individual lake systems. He and Dr. R.E. Foerster had developed this hypothesis in early papers (Foerster and Ricker 1942; Ricker 1950). They reasoned that that stability of cyclic dominance in Fraser sockeye stocks must involve suppression of recruitment on nondominant lines associated with processes driven by the large abundance of spawners and/or juveniles on the dominant line (i.e., cycle-line interaction). In essence, eggs, juveniles, or smolts of smaller, nondominant line spawning populations must necessarily suffer rates of mortality sufficiently high to neutralize the survival advantages resulting from compensatory effects associated with lower densities during incubation, lake residence and early marine life. Otherwise, compensatory forces in the recruitment (higher egg to fry survival, lower foraging competition, higher post-lake survival due to larger smolt size, etc.) would allow the nondominant lines to grow relative to the dominant line. The collective term used to characterize the non-compensatory mortality presumed in cyclical stocks is "depensatory mortality" (Neave 1953).

   After reviewing alternate hypotheses, Ricker (1997) favored depensatory predation as the most likely mechanism controlling cyclic dominance. Studies on rainbow trout (*Oncorhynchus mykiss*) predation on Lower Adams River (Shuswap Lake) juvenile sockeye revealed measurable effects on the condition factor of trout associated with sockeye abundance and suggested that the populations could be cycling out of phase (Ward and Larkin 1964). Subsequently, Larkin (1971) modeled this hypothesized effect of predators in an attempt to capture the depensatory mortality theory mathematically. However, only high levels of "depensation coefficients" produced results that maintained the stability of the cyclical pattern. Moreover, Williams et al. (1989) found that trout were only one of several predator species that utilized juvenile Shuswap Lake sockeye as prey. They concluded that there was good evidence of compensatory, rather than depensatory, mortality in juvenile sockeye abundance on the dominant and subdominant

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line years they studied between1974-1982. While their findings were not in keeping with the Ricker/Foerster hypothesis, they could not extend their studies to the smaller offcycle lines owing to the difficulties inherent in measuring small populations in large lakes.

Competition between juveniles of adjacent lines has not received the degree of investigation afforded depensatory mortality. Lack of extensive temporal and spatial overlap of the dominant and following cycle line juveniles does not provided intuitive support of the hypothesis. However, lagged effects of dominant line juvenile abundance on the size/growth rate of following nondominant line juvenile sockeye may be an important component in maintaining cyclic dominance (Foerster and Ricker 1942; Ricker 1950). Their hypothesis was based on observations that higher fractions of dominant line juveniles held over in the lake for a year or more due to reduced size at age 1 associated with density-dependent growth in Cultus Lake (lower Fraser). However, comparable behaviour has not been observed in upper Fraser lake systems. Also, this hypothesis has been criticized as not being consistent with observations regarding the pattern of recruitment. In a competitive environment, dominant line juveniles would be expected to exert maximal impact on the following (subdominant) line juveniles. However, the subdominant line of Shuswap sockeye appears to have a higher average recruitment rate than the dominant, not lower. The offcycle lines appear to have lower than expected recruitment rates but the competition hypothesis appears not to offer a viable explanation of how this occurs.

Larkin's (1971) simulation modeling suggested that cycle-line interaction could be produced by introducing depensatory coefficients, but he did not attempt to measure interaction in sockeye stocks with the limited recruitment data available at that time. Walters and Staley (1987) and Collie and Walters (1987) found negative cycle-line interaction effects on Fraser sockeye recruitment but did not attribute the interaction to particular mechanisms. They simply added the three prior year spawning abundances as independent variables in the linearized fitting of the Ricker S-R model (Ricker 1954) that relates the natural logarithm of recruitment rate ($R/S$), to parental spawning stock size ($S$). This extension of the Ricker model has subsequently been termed the Larkin model because of Dr. P. Larkin's initial investigation.

In the current study, we propose that negative cycle-line interaction affecting growth and abundance of juvenile sockeye in freshwater lakes is the mechanism that drives cyclic dominance in Fraser River sockeye stocks. If true, all stocks occupying and competing within each lake system must be interdependent. Our approach, therefore, was to combine the parent and recruit population estimates for all stocks within each lake system. We tested for cycle-line interaction in adult recruitment and in the growth and abundance of juvenile sockeye by including escapements in years immediately prior to the each brood year (as surrogates for juvenile abundances) in regression relationships between parent and progeny. If our hypothesis is true, regression parameters associated with the brood year escapements should be positive with measures of abundance and biomass (i.e., juvenile mean weight X abundance) and negative (density dependent) for growth/size while regression parameters associated with prior year escapement variables should be consistently negative.

Density-dependent growth in juvenile Fraser River sockeye salmon has been measured through in-lake collections of underyearlings or smolts (Goodlad et al. 1974; Williams et al. 1989; Hume et al 1996). Most analyses have assumed direct brood year impacts. Actual juvenile and smolt collections may be used for analysis of in-lake growth, but the freshwater scale growth of adult survivors has been used as well to characterize first year growth of juvenile cohorts (Goodlad et al. 1974; Henderson and Cass 1991). In the present study we use freshwater scale circuli counts as surrogates for juvenile size measurements. More restricted data sets of in situ juvenile abundance and size were examined to support results of analyses using adult abundance and scale data and to partition effects within lakes. .

## Data sources

### Spawning stock and recruitment

We obtained spawning stock and recruitment data from the production database of Fraser River sockeye salmon maintained by the Pacific Salmon Commission (PSC). Spawning escapements of sockeye have been estimated annually for most Fraser sockeye populations in programs conducted by the International Pacific Salmon Fisheries

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Commission (IPSFC) in 1948-1985 and CDFO in 1986-2003. Total escapement, numbers of adult male, adult female and jack sockeye were estimated for each spawning population (Schubert 1998). Adult sockeye are those fish that spend two years (ages $3_1$, $4_2$, and $5_3$) or three years (ages $4_1$, $5_2$, and $6_3$) in the ocean before maturing. Jack sockeye are approximately 98% age $3_2$ and $4_3$ males that have spent only one complete year in the ocean. [We use the Gilbert-Rich age designation; e.g., a $4_2$ fish is four years old at maturity and migrated to sea in its second year.]

In addition to numbers by sex, the weighted average proportion of eggs successfully deposited by female spawners, i.e., "success of spawning", was estimated for each population based on sampling carcasses of female spawners or from comparable data collected on nearby streams. The annual percentage success of spawning was applied to the adult female population to obtain an estimate of the "effective" female spawning (*EFS*) population for each stock and year (Appendix A).

*EFS* estimates are used as the unit of spawning in cycle-line interaction studies since it accounts for a portion of the variance in relationships between parents and offspring unexplained by total escapement. Variable sex ratio and pre-spawning mortality of females affect the use of total escapement or total female escapement and add to the variance of relationships developed with these measurements of the reproducing population. While *EFS* was used in the relationships between parental abundance and offspring abundance and growth, we assume that *EFS* is a surrogate for the juvenile population abundance propagated by the *EFS* of a brood year. Due to variable sex ratio and success of spawning, the *EFS* was, on average, (dominant and sub-dominant line data only) 52.0% of total adult Lower Adams River spawners (range: 34.2 to 69.9%; S.D. = 6.4%). Similarly, Horsefly River data for years with > 3,000 *EFS*, gave a mean of 48.7% *EFS* (range: 23.1 to 65.6%; S.D. = 10.5%). *EFS* at Chilko River averaged 53.8% of adults (range: 5.7 to 67.7%; S.D. = 10.3%).

Carcasses examined on spawning grounds were also sampled for sex, length, an otolith (beginning in mid 1960s) and a scale. These data and samples were analyzed to characterize the age and size of the male, female and jack sockeye spawning populations and to provide stock identification standards using scale data. Tissue samples have been

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added to the suite of collections in recent years to provide microsatellite DNA standards (Beacham et al. 2004) for the major sockeye stocks in the Fraser watershed.

Mixed-stock First Nations and commercial fishery catches are sampled annually to obtain data for estimation of lake/stock origins of harvested fish. The IPSFC and PSC employed stock identification techniques based on freshwater scale circuli counts and measurements to allocate catch to stock of origin. Sex, length and a scale were collected from a random sample of fish caught in each fishery and analyzed to estimate catch by age and stock, or stock group, for fish originating from each brood year spawning. Scale analysis techniques (Clutter and Whitesel 1956; Henry 1961) were the primary methods used until discriminant function analysis was introduced in the mid-1980s (Gable and Cox-Rogers 1993). Microsatellite DNA techniques (Beacham et al. 2004) were developed and applied beginning in 2000-2003. Annual stock identification program results provide estimates of total recruitment (catch plus escapement) for brood years 1948 through 1999 (n = 52).

Escapement and total recruitment estimates for sockeye stocks spawning in streams tributary to or outflow of and along beaches in Shuswap, Quesnel and Chilko Lakes (Fig. 1) were selected for analyses. The *EFS* and recruitment were summed for all stocks or spawning populations estimated each year in each lake system (Appendix A). Shuswap Lake stocks included Early Summer-run stocks in Seymour, Scotch and other tributaries, and Late-run sockeye that spawn in Lower Adams and Little Rivers and a number of tributary and lake beach areas in Shuswap Lake and in the Lower Shuswap River, which although tributary to Mara Lake, produces juveniles that migrate the short distance to Shuswap Lake. Summer-run sockeye stocks in Quesnel Lake spawn in the Horsefly and Mitchell Rivers, and tributaries, and in smaller Quesnel Lake tributaries and along lakeshore beaches. Escapements of Summer-run sockeye that spawn in Chilko River and along beaches at the north and south ends of Chilko Lake were combined. *EFS* escapements in the three lake systems graphically show the different abundance patterns in the stocks (Fig. 2).

Recruitment rate (*R/EFS*) data were available by year for brood years 1948-1999. Mean recruitment rates for Shuswap, Quesnel and Chilko sockeye stocks by cycle line were calculated (Appendix B).
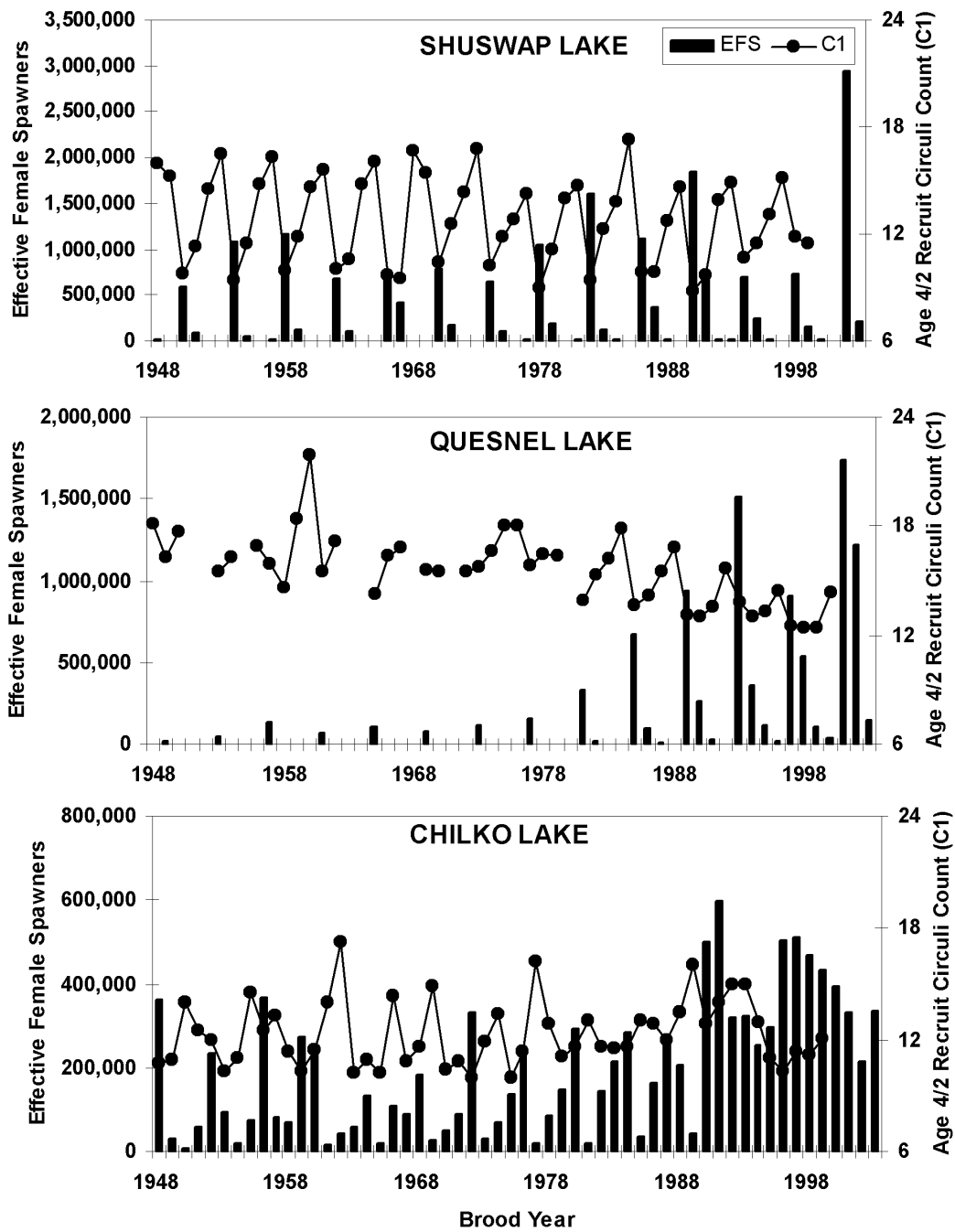
Figure 2. Effective female spawners and age $4_2$ recruit scale $C1$ for: a) Shuswap Lake sockeye, b) Quesnel Lake sockeye, and c) Chilko Lake sockeye.

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**Age and scale data**

Extensive scale age and freshwater growth data (see Appendix C for methods) for up to four stocks or spawning populations were available for Shuswap, Quesnel and Chilko watersheds. We chose to use sample data from Lower Adams River sockeye to represent Shuswap Lake stocks, Upper Horsefly River sockeye to represent Quesnel Lake stocks and Chilko River (lake outlet) spawners to represent Chilko Lake stocks (Fig. 1). In each case, the stock used as the primary source for scale data was the largest within their respective watersheds and the scale samples were the most complete.

Seymour River (early run Shuswap Lake sockeye) scale data were used in sensitivity analyses of Shuswap Lake growth relationships obtained using Adams River scales. Seymour River is located at the upper end of Seymour Arm of Shuswap Lake (Fig. 1), approximately 70 km from the Adams River and is a Summer-run stock rather than a Late-run stock such as Adams River sockeye. Annual Seymour and Adams $C1$ values were highly correlated ($P < 0.001$; $r^2 = 0.901$), however, the regression parameter value, b = 0.710, indicated incomplete mixing of the populations. At low $EFS$ values, Adams River juveniles had higher growth than Seymour while at high $EFS$, juvenile Seymour sockeye $C1$ values were higher than Adams. If most freshwater growth occurred in areas that all populations were fully mixed, we would expect a slope closer to 1.0.

Due to apparent bias and/or time series differences in the reading of pre-1990 Adams and Horsefly scales compared to 1990 and later, we reanalyzed scale circuli counts and digitized scale measurements for 1952-1989 (Appendix C). An experienced scale analyst assessed scales for circuli count and digitized scale measurement to the freshwater annulus ($C1$ and $D1$; Henderson and Cass 1991) and to the end of the freshwater growth ($C2$ and $D2$). We used the reanalyzed scale readings in the present analysis, along with the original estimates for 1990-2003, which were shown to be similar to the reanalyzed estimates (see Appendix A for data). Combined-stock regressions of reanalyzed on original annual means were applied to the original $C1$ and $C2$ estimates for Chilko River and Seymour River age $4_2$ sockeye to obtain predicted $C1$ and $C2$ estimates which would be consistent with the revised scale analysis protocols adopted in 1990.

Annual escapements of cyclical Adams River and Horsefly River sockeye were sufficient on dominant and (usually) subdominant lines to provide for adequate age $4_2$

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scale data sample sizes in the collection of post-spawned fish. However, offcycle lines, particularly at Horsefly River, supported very small spawning populations in the 1948-1984 period. All 19 offcycle year escapements were < 2,100 adult sockeye (range: 49-2,036; mean. = 342). Low abundances resulted in low carcass recovery and insufficient sample size in many of these years. Also, at times, a significant fraction of offcycle lines spawners were age 5 fish, making them unusable for the present analysis. In nine years < 10 readable age $4_2$ scales were available and in another five years there were only 11 to 15 scales. In order to avoid low precision and possible bias in scale measurements associated with small sample sizes, we excluded from our analyses years where scale measurements were available from fewer than 10 individuals.

Inclusion of all years of Quesnel data was deemed counterproductive from the standpoint that a) scale data sample sizes were inadequate in many years, and b) measurement error in visual estimation of spawning populations and imperfect stock identification of catches in the years of very low escapement would potentially obscure true relationships in analyses. Therefore, we chose to include only those brood years with at least 3,000 *EFS*. This decision resulted in the elimination of subdominant line years prior to 1978 and offcycle years prior to 1987. The result was a reduction to 26 years of data, including 13 dominant, 6 subdominant and 7 offcycle line years (Appendix A, Table 2).

Adams River offcycle spawning populations were generally larger (75-12,576 adults) and carcass collection effort was higher, resulting in a minimum sample size of 11 age $4_2$ fish. Eleven years of data had sample sizes less than 50 fish. All 52 years of Adams River (Late Shuswap) data were included in the analysis giving 13 years of data for each cycle line (Appendix A, Table 1).

Chilko River sockeye spawning abundances varied less than Adams and Horsefly sockeye and annually provided a minimum of 36 age $4_2$ sockeye scales (Appendix A, Table 3). However, Chilko Lake was the subject of a lake fertilization experiment in 1988 (fall only) and during 1990-1993 (Bradford et al. 2000). Lake fertilization altered the natural relationship between *EFS* and juvenile sockeye growth and abundance. Fertilization only occurred in the fall of 1988 and we observed no indication that juvenile growth or survival was affected for brood year 1987. However, brood year 1989-1992

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juveniles appeared to have been impacted directly by lake fertilization and brood year 1993 juveniles appeared to be affected by a carryover effect of nutrient addition in the prior four years. Therefore, we eliminated data from these latter five brood years to avoid bias in the analyses. There was no indication of carryover effects in limnological nutrient chemistry or macrozooplankton abundance (Ken Shortreed, personal communications, CDFO, Cultus Lake, B.C.) and the data from brood years 1994-1999 fit the juvenile growth relationships observed in the pre-fertilization period. Therefore, we included these data in subsequent analyses. The latter brood years were important to the analysis because several large escapements were recorded in the period.

## Juvenile sockeye size and abundance data

### Emergent fry

Chilko River sockeye fry of the 1949-1967 brood years were photographically estimated while migrating upstream into Chilko Lake. The nineteen years of fry estimates were of fish that had held for one to two or more weeks along the river banks or in a low velocity reach of the Chilko River downstream of the major spawning area (Brannon 1972). The fry migrated in narrow bands near shore in reduced velocities and were easily observed while migrating. While Chilko River fish comprised the major fraction of the Chilko system sockeye fry production, fry from sockeye spawning in Chilko Lake were not available for estimation.

### Lake resident juveniles

The abundance and size of lake-resident juvenile sockeye were obtained from Shuswap and Quesnel Lakes for brood years between 1974 and 2003 in conjunction with lake capacity studies carried out by the IPSFC and CDFO (Hume et al. 1996). Hydroacoustic sampling provided estimates of the pelagic fish population within the depth range occupied by juvenile sockeye. Mid-water beam trawls were fished at night in the depth range of fish target concentration to obtain samples for species composition and fish size in one or more locations in each lake. Fish were killed by an overdose of anesthesia and preserved in 10% formalin (Hume et al.1996). After a minimum of one month the preserved fish were rinsed and measured for fork length and blotted wet

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weight and scales were taken for age analysis. Catches of age 0 and age 1 and older juvenile *O. nerka* were used to partition the population estimates into age 0 sockeye and kokanee and older age groups. (Anadromous sockeye and non-anadromous kokanee are sympatric in both lakes.) On years when dominant and subdominant line juvenile sockeye were present, they should dominate the populations but when offcycle line sockeye were present, we expected that the juvenile *O. nerka* populations would be dominated by juvenile kokanee.

We excluded Shuswap Lake juvenile data from the five offcycle line years where escapements averaged 10,900 *EFS* (range: 7,172-15,613) and analyzed the fifteen dominant and subdominant line years that had an average of 835,000 *EFS* (range: 102,000-2,998,000 *EFS*) because kokanee were likely the dominant form in these years. We used sixteen of seventeen years of Quesnel Lake data. Only brood year 1976 with an estimate of 209 *EFS* was excluded. Seven dominant, five subdominant and four offcycle years were included having an average escapement of 588,000 *EFS* (range: 11,200-1,740,000).

Surveys were taken in summer (late July-mid September) and fall (late September-November). Fall samples were analyzed in the present study in order to minimize the effect of variable collection date on abundance and size and because much of the first year lake growth had occurred by the date of sampling. Summer samples were utilized for annual size-at-time analyses.

Survey sample unweighted mean lengths and weights of underyearling *juvenile O. nerka* collected in Shuswap and Quesnel Lakes have been used in the following analyses. Adequate sample sizes were available for Shuswap Lake each year (41 to 3,112). Sample sizes in Quesnel Lake collections were usually adequate (37 to 982), however, in 1987 and 1988 fall sampling few, if any, juveniles were obtained. These years were excluded from analyses of juvenile size but included in analysis of juvenile abundance. Mean weight was estimated by regression methods using years of complete size and abundance data and juvenile biomass estimates were calculated using predicted mean weights.

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*Smolts*

Sockeye smolts were collected in April-May annually from 1951 to 2003 at a weir installed in the Chilko River at the outlet of Chilko Lake (Fig. 1) for abundance and age and size composition of the daily outmigration (Goodlad et al. 1974). Daily estimates of total smolts were obtained by photographic methods. Beginning in 1954, approximately 300 smolts were anesthetized and measured each day of sizable seaward migration to obtain daily proportions of age 1 and age 2 smolts. Fork length to the nearest millimeter was measured and several scales were removed from individual fish that exceeded a lower length threshold. Smaller fish were assumed to be yearlings based on the aging of small size smolts collected early in the annual outmigration.

In the laboratory, the scales of the larger size smolts were examined under magnification for freshwater age. Estimates of age 1 and age 2 proportions were applied to the daily migration obtained by photographic methods to estimate the daily migration by age. Annual weighted mean lengths by age were calculated using the daily mean length estimates and proportions of the migration on the individual days where samples were collected.

In addition, samples of juvenile sockeye were killed and preserved in the field and measured after at least a month in 10% formalin solution. Three collections of 100 yearling smolts were taken annually from peak periods of migration from 1951-2003. Preserved mean length and weight and a few scales were collected from each specimen. Fork length to the nearest millimeter and blotted wet weight to the nearest hundredth gram were collected and the age determined from plastic impressions of scales. While daily estimates of sockeye smolt numbers are available from Chilko River for weighting the live lengths, sample mean lengths and weights of preserved smolts generally were similar for the three samples and have been averaged.

## Analytical methods

### Juvenile size and adult scale growth relationships

In the analysis of scale data collected from adult sockeye, we initially sought to determine whether or not scale circuli count variables were acceptable surrogates for

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juvenile growth/size. First, we questioned whether or not scale circuli counts were interchangeable with digitized scale measurements. Combined Adams River and Horsefly River mean age $4_2$ scale circuli counts were regressed on corresponding digitized scale measurements from the scale focus to the freshwater annulus ($C1$ and $D1$) and focus to the end of the freshwater growth ($C2$ and $D2$). Regression results gave highly significant correlation coefficients between scale variables (Table 1). Based on this analysis, it appeared that $C1$ and $C2$ were sufficiently similar to $D1$ and $D2$, respectively, to allow interchangeable use of these variables.

Table 1. Relationships between adult scale parameters and between scale parameters and juvenile size.

| | Y variable | X variable | n | Regression | adj. $r^2$ | P |
|---|---|---|---|---|---|---|
| Adams + Horsefly Age 4/2 | C1 | D1 | 75 | C1 = 45.886D1 - 0.694 | 0.968 | < 0.001 |
| | C2 | D2 | 75 | C2 = 44.560D2 + 0.204 | 0.966 | < 0.001 |
| Chilko Age 4/2 vs. smolt | C1 | Live Length | 48 | C1 = 0.240LL-7.544 | 0.692 | < 0.001 |
| | C2 | Live Length | 48 | C2 = 0.205LL-2.941 | 0.803 | < 0.001 |
| Chilko Age 4/2 vs. smolt | C1 | Pres. Length | 52 | C1 = 0.214PL-4.251 | 0.588 | < 0.001 |
| | C2 | Pres. Length | 52 | C2 = 0.189PL-0.671 | 0.696 | < 0.001 |
| Chilko Age 4/2 vs. smolt | C1 | Pres. Weight | 51 | C1 = 1.223PW+6.673 | 0.604 | < 0.001 |
| | C2 | Pres. Weight | 51 | C2 = 1.098PW+8.925 | 0.776 | < 0.001 |

In our second step, we examined whether $C1$ and $C2$ provided valid surrogates for juvenile size. Annual mean $C1$ and $C2$ values of Chilko age $4_2$ sockeye recruits were regressed on annual mean smolt size measurements from the same brood year. Weighted mean live length and unweighted mean preserved smolt length and weight of seaward migrants in 1951-2003 (age 1 smolts from brood years 1949-2001) were analyzed.

$C1$ and $C2$ were highly correlated with weighted mean live length (Fig. 3) and preserved length and weight (Table 1). Regressions of $C2$ on smolt measurements provided superior fit as would be expected since $C2$ is measured to the end of the

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freshwater growth, i.e., at smolt migration, rather than to the freshwater annulus formation in late winter prior to seaward migration, as in *C1*. Variable compensatory growth between annulus formation and seaward migration appeared to have introduced additional uncertainty in the relationships based on *C1*. There was no evidence of non-linearity over the range of smolt lengths and weights observed, thus it does not appear that that size-selective mortality introduced bias into relationships because that would cause small smolts to relate to larger C1 in adults.



Figure 3. Chilko River mean age $4_2$ recruit scale *C1* and *C2* regressed on mean live length of smolt cohorts.

The analyses of Chilko scale growth gave confidence that age $4_2$ recruit *C1* and *C2* represent unbiased estimates of juvenile fish size. However, there were temporal trends in the estimate of C2 associated with differences in interpretation of spring growth circuli among scale analysts. Given that *C1* was more consistently estimated, we chose to use *C1* as the primary dependent variable in analysis of adult scale data. Results of *C2* regressions are provided but discussed only in relation to *C1* results.

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## Adult recruitment

Our objective was to determine if cycle-line interaction was evident in the recruitment rate for the combined stock data of each lake system with before examining whether or not cycle-line interaction effects were present in density dependent relationships between *EFS* and juvenile growth/size and abundance. We fit the Ricker and Larkin S-R models to the updated spawning and recruitment data for Shuswap, Quesnel and Chilko stock complexes. For the Ricker model, the natural logarithm of adult sockeye recruitment rate (*R/EFS*) was regressed on the brood year (*t*) effective female spawner (*EFS*) estimates as follows:

$$\log_e(R_{rt}/EFS_{rt}) = a_r - b_r EFS_{rt} + \varepsilon_r \tag{1}$$

where $a_r$ is the intercept of the Ricker model regression and is equivalent to the logarithm of the mean rate of recruitment as *EFS* approaches 0; $b_r$ is the regression parameter associated with *EFS* (the maximum level of recruitment occurs when $EFS = 1/b_r$) and $\varepsilon_r$ was $\cong N(0, \sigma_\varepsilon)$.

For the Larkin model we added prior brood year *EFS* variables with lags of one to three years (years *t-1*, *t-2*, *t-3*) in the following formulation (Walters and Staley 1987 Collie and Walters 1987):

$$\log_e(R_{kt}/EFS_{kt}) = a_k - b_{k0}EFS_t + b_{k1}EFS_{t-1} + b_{k2}EFS_{t-2} + b_{k3}EFS_{t-3} + \varepsilon_k \tag{2}$$

where $a_k$ the intercept, was equivalent to the logarithm of the mean recruitment rate as all *EFS* values approach 0; $b_{k0...}b_{k3}$ were regression parameters associated with $EFS_t$, $EFS_{t-1}$, $EFS_{t-2}$ and $EFS_{t-3}$, respectively; and $\varepsilon_k$ was $\cong N(0, \sigma_\varepsilon)$.

## Adult scale data

In order to examine potential cycle-line interaction effects on juvenile size, we regressed adult scale circuli counts, $C1_t$ and $C2_t$, on effective female spawning populations in the brood year ($EFS_t$) and in brood years one to three years earlier ($EFS_{t-1}$, $EFS_{t-2}$, $EFS_{t-3}$). The statistical significance of prior brood year *EFS* variables were assessed by adding each earlier variable sequentially to a multiple regression of scale variable on the *EFS* variables. We continued adding lagged *EFS* terms incrementally until the slope for the added term was not significantly different from zero at the $\alpha = 0.10$ level. We terminated the analysis at this point because under our hypothesis, immediate

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prior year juveniles should have maximal impact on the growth and recruitment of the treatment year. If impacts of $EFS_{t-1}$ were not significant, we reasoned that significance of earlier year $EFS$ variables were not likely the result of a functional relationship. In the initial analyses, we constructed a multiple linear regression of the form:

$$CI_{jt} = a_j + b_{j0}EFS_t + b_{j1}EFS_{t-1} + b_{j2}EFS_{t-2} + b_{j3}EFS_{t-3} + \varepsilon_j \qquad (1a)$$

Where $CI_{jt}$ is the mean circuli count to the freshwater annulus in year $t$ estimated via the untransformed model (1a); $a_j$, the intercept, is equivalent to the mean value of $CI_{jt}$ as $EFS$ values approach 0; $b_{j0}...b_{j3}$ are the regression parameters associated with respective untransformed $EFS$ variables for years $t...t-3$; and $\varepsilon_j$ is $\cong N(0,\sigma_\varepsilon)$. Parameters for prior year spawning abundance were generally significant for only one or two years at which point, earlier year $EFS$ data were dropped from the model. This approach produced an additive model wherein each earlier brood year escapement adds to the (negative) effect of abundance on growth. Because of uncertainty in the form of the relation between $CI$ and $EFS$, we also considered a non-linear model that predicted $CI$ as a function of natural logarithm of $EFS$:

$$CI_{gt} = a_g + b_{g0}\log_e EFS_t + b_{g1}\log_e EFS_{t-1} + b_{g2}\log_e EFS_{t-2} + b_{g3}\log_e EFS_{t-3} + \varepsilon_g \qquad (1b)$$

where $CI_{gt}$ was the circuli count to the freshwater annulus in year $t$ estimated in the $\log_e$ transformed model (1b); $a_g$, $b_{g0}...b_{g3}$ were the regression parameters associated with respective log transformed $EFS$ variables for years $t...t-3$; and $\varepsilon_g$ was $\cong N(0,\sigma_\varepsilon)$. By taking the natural logarithms of $EFS$ values we fit a non-linear model that allowed growth to asymptote out at high EFS value, but treated the lagged $EFS$ variables as multiplicative rather than additive in the prediction of $CI$. The conceptual model that we used was as follows: $\exp(CI) = aEFS_t^b * EFS_{t-1}^c * EFS_{t-2}^d$.

**Juvenile sockeye abundance and size**

While the Larkin model captured estimates of line interaction in adult recruitment and adult scale variables provided a useful surrogate for juvenile size, we sought to examine juvenile abundance, mean length and weight, and biomass (abundance X mean weight) estimates measured in situ relative to $EFS$ variables. We followed the above procedures wherein the effective female spawning populations in the brood year ($EFS_t$) and in brood years one to three years earlier ($EFS_{t-1}$, $EFS_{t-2}$, $EFS_{t-3}$) were added sequentially in

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multiple regressions with juvenile dependent variables. Again, the analyses were terminated at the point when coefficient for the incremental *EFS* term was not significantly different from zero at the $\alpha = 0.10$ level. To address the uncertainty in the relationships between juvenile size and abundance and *EFS*, we constructed additive models using untransformed *EFS* variables and multiplicative models wherein *EFS* variables were log transformed.

## Results

### Adult sockeye recruitment

#### *Shuswap recruitment*

Shuswap sockeye provided significant, but weak evidence of cycle-line interaction on recruitment. The statistical fit for the Ricker model was non-significant, however, the Larkin model regression was significant ($P = 0.007$; adj. $R^2 = 0.190$); Table 2), but did not explain a substantial fraction of the uncertainty in the recruitment rate. The regression parameters associated with $EFS_t$, $EFS_{t-1}$ and $EFS_{t-2}$ were all significant (Table 2). Regression parameter values were similar, indicating that prior year escapements had measurable effects on recruitment rates.

#### *Quesnel recruitment*

The Ricker model regression for all 52 years of data was non-significant ($P > 0.10$; Table 2). Addition of prior year *EFS* data in the Larkin model generated a regression that was highly significant ($P < 0.004$; adj. $R^2 = 0.210$) but, as in the case of Shuswap Lake sockeye, explained a low fraction of the overall variation in recruitment rate. In this regression, $EFS_{t-2}$ and $EFS_{t-3}$ were significant but $EFS_t$ and $EFS_{t-1}$ were not significant, although all regression parameters had negative signs. We then analyzed the restricted 26-year data set for which there were at least 3,000 *EFS*. Again the Ricker model regression was non-significant ($P > 0.10$; Table 2). However, the Larkin model regression was highly significant ($P < 0.001$; adj. $R^2 = 0.687$; Table 2). In this formulation, the regression parameters for $EFS_t$, $EFS_{t-2}$, and $EFS_{t-3}$ were highly significant while that for $EFS_{t-1}$ was non-significant ($P = 0.156$). The regression parameters associated with the

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Table 2. Ricker and Larkin S-R model correlation coefficients, regression parameters and P values for regressions of $\log_e(R_t/EFS_t)$ vs. EFS variables (i.e., $EFS_t$, $EFS_{t-1}$, $EFS_{t-2}$, $EFS_{t-3}$).

| Lake | Stocks Included | Data Set | S-R Model | # years | adj. r²/R² | Intercept | $b_t$ | P | $b_{t-1}$ | P | $b_{t-2}$ | P | $b_{t-3}$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Shuswap | Adams, Lower Shuswap, Seymour, Scotch, plus misc. stocks | All years | Ricker | 52 | 0.026 NS | 2.213 | -3.45E-07 | NS | | | | | | |
| | | | Larkin | 52 | 0.190** | 2.857 | -8.32E-07 | 0.002 | -5.47E-07 | 0.038 | -8.33E-07 | 0.002 | -2.31E-07 | NS |
| Quesnel | Horsefly, Mitchell, plus misc. Quesnel Lake tributaries and lake beaches | All years | Ricker | 52 | 0.029 NS | 2.732 | -7E-07 | NS | | | | | | |
| | | | Larkin | 52 | 0.210** | 2.989 | -6.6E-07 | 0.107 | -3.3E-07 | NS | -1.1E-06 | 0.009 | -9.1E-07 | 0.044 |
| | | > 3000 EFS | Ricker | 26 | 0.023 NS | 2.594 | -5.20E-07 | NS | | | | | | |
| | | | Larkin | 26 | 0.687** | 3.163 | -8.6E-07 | 0.002 | -3.4E-07 | 0.156 | -1.4E-06 | < 0.001 | -9.1E-07 | 0.001 |
| Chilko | Chilko River, N. Chilko Lake, S. Chilko Lake | Brood years 1948-1988 only | Ricker | 41 | 0.089* | 2.634 | -2.02E-06 | 0.033 | | | | | | |
| | | | Larkin | 41 | 0.236** | 2.879 | -2.30E-06 | 0.019 | -2.16E-06 | 0.030 | 6.75E-08 | NS | 1.01E-06 | NS |
| | | All non-lake fert. years | Ricker | 47 | 0.368** | 2.762 | -3.39E-06 | < 0.001 | | | | | | |
| | | | Larkin | 47 | 0.529** | 2.976 | -2.60E-06 | < 0.001 | -2.49E-06 | < 0.001 | -2.99E-07 | NS | 6.66E-07 | NS |

brood year and prior three brood years $EFS$ variables were all negative and the relative regression parameters were as follows: 1:0.39:1.60:1.06. While prior year escapements clearly affected recruitment rates, we suspect that the magnitude of prior year impacts may not be accurately estimated from the 26 years of data.

## *Chilko recruitment*

Stock and recruitment data for years prior to lake fertilization (brood years 1948-1988; n = 41) were examined in the first step of the Ricker and Larkin model analyses. Significant relationships were found for both the Ricker model ($P < 0.033$; adj. $R^2$ = 0.089) and the Larkin model ($P < 0.008$; adj. $R^2 = 0.236$) regressions (Table 2). However, the proportion of the variation in recruitment rate explained by the regressions was low in both models. Regression parameters associated with $EFS_t$ and $EFS_{t-1}$ in the Larkin model were negative and significant ($P < 0.019$ and $< 0.030$, respectively). Regression parameters for $EFS_{t-2}$ and $EFS_{t-3}$ were positive and non-significant ($P > 0.10$).

Recruitment rate estimates for brood years 1994-1999, that followed four years of lake fertilization, were examined to determine if they conformed to the pre-fertilization recruitment relationship. We regressed $\log_e(R_t/EFS_t)$ on the significant independent variables in the Larkin model ($EFS_t$ and $EFS_{t-1}$) and used this formulation to predict recruitment for the post-lake fertilization period. The predictions of brood years 1994-1999 log transformed recruitment rates were close to those observed (mean predicted $\log_e$ recruitment rate = 1.03; mean residual of the prediction = 0.01; S.D. = 0.29). Based on the similarity of predicted to observed recruitment, we concluded that brood years 1994-1999 conformed to the pre-lake fertilization stock dynamics.

Brood years 1948-1988 and 1994-1999 were combined and the new data set (n = 47) was reanalyzed. The Ricker model fit improved substantially and the regression parameter was highly significant ($P < 0.001$; adj. $R^2 = 0.368$; Table 2). The addition of prior year $EFS$ variables in the Larkin model further improved the fit ($P < 0.001$; adj. $R^2$ = 0.529). Regression parameters associated with $EFS_t$ and $EFS_{t-1}$ were negative and highly significant (for both, $P < 0.001$), but were non-significant for $EFS_{t-2}$ and $EFS_{t-3}$. The relative regression coefficients for $EFS_t$ and $EFS_{t-1}$ were 1:0.96, indicating that both the brood year and the immediate prior year $EFS$ variables were important in the

prediction of recruitment rate. The improvement in the regression fits of recruitment data with the larger dataset appeared to be associated with the large escapements observed in the 1994-1999 period (254,000-509,000 *EFS*) that included the four largest *EFS* of all non-lake fertilization years. Addition of these years increased the range of *EFS* values and improved the model fit. We questioned whether the lake fertilization was the cause of the change in the model fit, but (a) the values of the multiple regression parameters associated with $EFS_t$ and $EFS_{t-1}$ were similar with and without brood years 1994-1999, and (b) the regression based on significant *EFS* variables in the brood years 1948-1988 Larkin model had accurately predicted the brood years 1994-1999 rates of recruitment. We therefore concluded that the enlarged suite of years provided an accurate estimate of the recruitment rate relationship for Chilko sockeye.

**Adult recruit freshwater scale growth**

Time series of annual *EFS* estimates and mean age $4_2$ recruit *C1* for Shuswap, Quesnel and Chilko sockeye showed differing patterns of abundance and scale growth over the period of record. Shuswap sockeye escapements recovered from depletion in the 1930s-1940s and maintained a stable cyclical pattern during the period of this study, brood years 1948-1999 (Fig. 2a). Adams sockeye scale growth patterns were consistent between four-year cycles with low *C1* values associated with the large dominant line juvenile populations in Shuswap Lake, generally followed by progressive increases in first year growth (*C1*) for the following three lines on which *EFS* abundance was lower.

Quesnel Lake stocks were nearly extirpated in the 1920s to early 1940s and escapements did not increase substantially until the mid 1980's. Horsefly scale circuli counts were high but variable in the early period and declined on all cycle lines as escapements increased (Fig. 2b). In contrast to Adams scale data, recent Horsefly *C1* values have shown a pattern of three consecutive years of low scale growth associated with the dominant, subdominant and first offcycle lines, respectively, despite much lower *EFS* on subdominant and first offcycle lines compared to the dominant line.

Sockeye escapements in the Chilko Lake system also increased prior to the late 1940s and maintained a semblance of a cyclical pattern of *EFS* until the late 1980s, after which escapements increased on all cycle lines (Fig. 2c). A general pattern of density-dependent

growth occurred, but much less pronounced than observed in Shuswap sockeye. In the early 1990s, *CI* was high in years when lake fertilization effects were evident (brood years 1989-1993), but low during the subsequent post-lake fertilization period of large escapements.

### Shuswap scale growth

A scatter plot of Shuswap scale *CI* values on $\log_e$ transformed *EFS* showed density-dependent freshwater growth of these fish as juveniles, as expected, but the individual cycle lines were clearly tracking different regressions indicating that cycle-line effects were present (Fig. 4). Dominant line Shuswap *CI* values were generally lower than observed on the other lines, but regression analysis indicated they were larger at comparable *EFS* abundance. Only five of thirty-nine nondominant line Shuswap Lake *CI* values were above the linear regression line fit to the dominant line data and extended to the lowest *EFS* values.
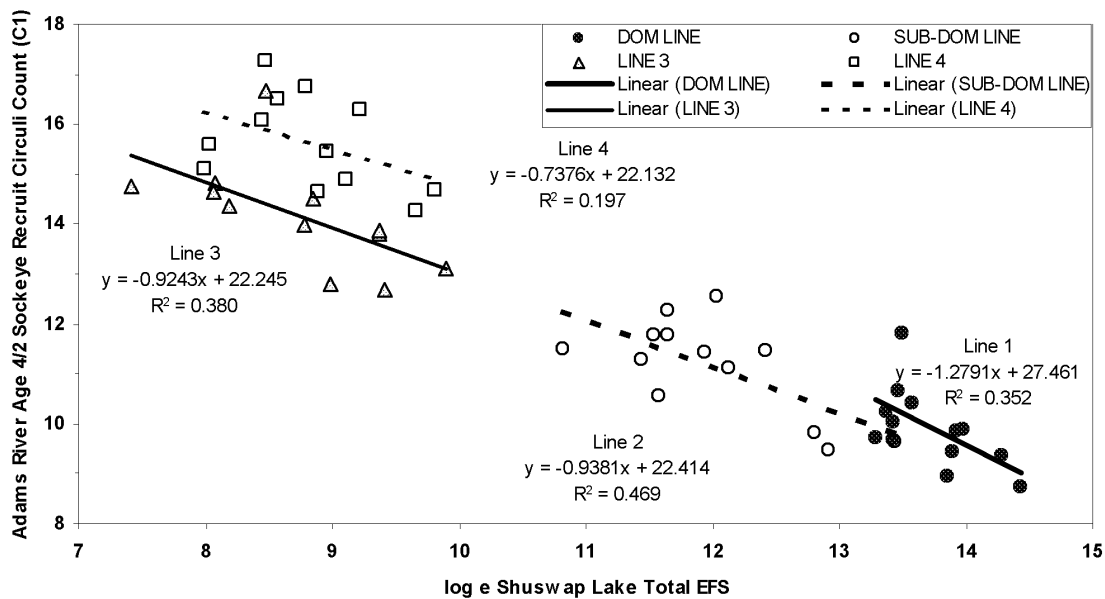


Figure 4. Relationship between Adams River age $4_2$ recruit *CI* and *EFS* for Shuswap Lake sockeye by cycle lines.

In our multiple regression analysis of cycle-line interaction, we first examined the linear relationship between $C1$ and $EFS$ variables. Regression results indicated that $EFS_{t-1}$ was significant ($P < 0.001$) in explaining variation in $C1$, in addition to the brood year population ($EFS_t$) (Table 3), but that $EFS$ variables with greater than one year lag were not significant. Regression parameters associated with $EFS_t$ and $EFS_{t-1}$ were negative indicating compensatory growth effects. The relative regression parameter values were 1:0.50, showing that the effect of $EFS_{t-1}$ on $C1$ was substantially less than $EFS_t$, but contributed a relatively large cycle-line interaction effect

Table 3. Correlation coefficients, regression parameters and P values for multiple regressions of adult scale variables on $EFS$ (i.e., $EFS_t$, $EFS_{t-1}$, $EFS_{t-2}$).

| Lake | Scale data Source | Scale Variable | Regression Model | # years | Regression adj. $r^2/R^2$ | $b_t$ | P | $b_{t-1}$ | P | $b_{t-2}$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Shuswap | L. Adams | C1 | Untransformed EFS | 52 | 0.719** | -4.50E-06 | < 0.001 | -2.23E-06 | < 0.001 | NS | |
| | | | Log$_e$ transformed EFS | 52 | 0.881** | -1.046 | < 0.001 | -0.195 | < 0.001 | NS | |
| | | D1 | Untransformed EFS | 51 | 0.734** | -8.74E-08 | < 0.001 | -4.41E-08 | < 0.001 | NS | |
| | | | Log$_e$ transformed EFS | 51 | 0.880** | -0.0237 | < 0.001 | -0.0042 | < 0.001 | -0.0043 | 0.040 |
| | | C2 | Untransformed EFS | 52 | 0.595** | -4.11E-06 | < 0.001 | -2.41E-06 | < 0.001 | NS | |
| | | | Log$_e$ transformed EFS | 52 | 0.849** | -1.044 | < 0.001 | -0.269 | < 0.001 | NS | |
| | Seymour | C1 | Untransformed EFS | 49 | 0.708** | -3.28E-06 | < 0.001 | -1.53E-06 | < 0.001 | NS | |
| | | | Log$_e$ transformed EFS | 49 | 0.865** | -0.967 | < 0.001 | -0.133 | 0.004 | -0.257 | 0.004 |
| Quesnel | U. Horsefly | C1 | Untransformed EFS | 26 | 0.668** | -2.27E-06 | < 0.001 | -1.79E-06 | < 0.001 | -1.38E-06 | 0.003 |
| | | | Log$_e$ transformed EFS | 26 | 0.819** | -0.594 | < 0.001 | -0.134 | 0.004 | -0.090 | 0.029 |
| | | C2 | Untransformed EFS | 26 | 0.762** | -3.25E-06 | < 0.001 | -2.00E-06 | < 0.001 | -1.90E-06 | < 0.001 |
| | | | Log$_e$ transformed EFS | 26 | 0.875** | -0.663 | < 0.001 | -0.146 | 0.003 | -0.181 | < 0.001 |
| Chilko | Chilko R. | C1 | Untransformed EFS | 47 | 0.110* | -4.14E-06 | 0.013 | NS | | | |
| | | | Log$_e$ transformed EFS | 47 | 0.151** | -0.619 | 0.004 | NS | | | |
| | | C2 | Untransformed EFS | 47 | 0.063* | -2.85E-06 | 0.048 | NS | | | |
| | | | Log$_e$ transformed EFS | 47 | 0.077* | -0.401 | 0.033 | NS | | | |

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Next we examined the non-linear relationship using natural logarithm the *EFS* variables in order to determine if the non linear model provided improved fits compared to the linear model. Again, the multiple regression showed that only regression parameters associated with $EFS_t$ and $EFS_{t-1}$ were significant (Table 3).

We tested the sensitivity of the analyses that used *C1* as the dependent variable by substituting *C2* and the mean annual digitized scale measurement value to the freshwater annulus (*D1*) into the two above analyses. Regression results for *C2* were consistent with results for *C1* (Table 3). When *D1* was substituted as the dependent variable and untransformed *EFS* values were used, the regression parameters associated with $EFS_t$ and $EFS_{t-1}$ variables were highly significant and the relative regression parameter values were 1:0.50, identical to that when *C1* was the dependent variable. When log transformed *EFS* values were used the regression with *D1*, the fit improved as with *C1*, but prior year *EFS* variables lagged one and two years were both significant in addition to $EFS_t$ (Table 3). The relative regression parameter values were: 1:0.18:0.18, again indicating a sizable impact of prior year escapements.

We also sought to test whether or not potential genetic (i.e., cycle-line specific juvenile growth potential) or location of initial juvenile rearing were involved in the cycle-line interaction observed when Adams sockeye scale data were analyzed. *C1* data for sockeye spawning in the Seymour River were analyzed as above. Regression results were similar to those obtained using Adams River scale data (Table 3). The multiple linear regression and regression coefficients for $EFS_t$ and $EFS_{t-1}$ were highly significant. The relative regression parameter values for $EFS_t$ and $EFS_{t-1}$ were 1:0.47, similar to that found when Adams sockeye scale data were used. However, actual regression slope values were lower, reflecting the non 1:1 relationship of the Adams:Seymour circuli count regressions.

The non-linear model improved the fit seen in the linear model and regression parameters for $EFS_t$, $EFS_{t-1}$ and $EFS_{t-2}$ were highly significant in this model (Table 3). All were negative and the relative regression parameter values for *EFS* variables were 1:0.14:0.26.

Regression parameters for Shuswap Lake sockeye *EFS* variables were consistently negative whenever they were significant, indicating compensatory growth. $EFS_t$ and

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$EFS_{t-1}$ were both significant in explaining variation in Adams $C1$ and Seymour $C1$ whether using untransformed or log transformed $EFS$. This supported the hypothesis that the relationships found in Adams sockeye scale data were not due to genetic or locational effects but rather due to competition in Shuswap Lake and that Adams and Seymour populations mixed for much, but not all, of their lake residence period.

### Quesnel scale growth

While $EFS$ values among lines of Shuswap sockeye were only slightly overlapped, the more complete overlap of $EFS$ values among lines of Quesnel sockeye resulted in separate but approximately parallel regressions between $C1$ and brood year $EFS$ (Fig. 5). None of the thirteen nondominant line observations were above the linear regression fit to dominant line data extended to the lowest $EFS$ value in the analysis.
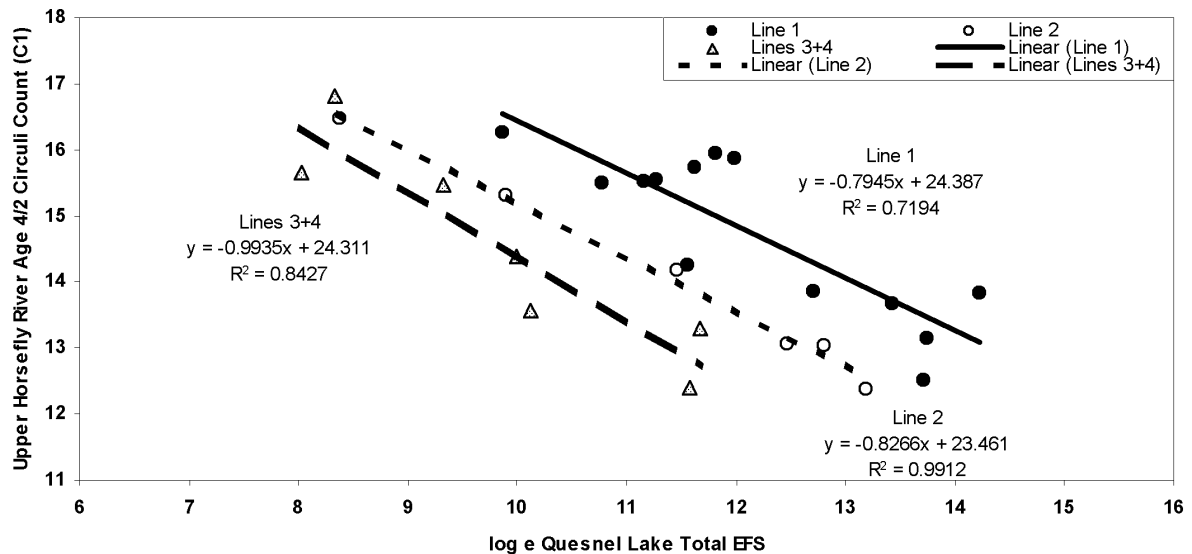


Figure 5. Relationship between Upper Horsefly River age $4_2$ recruit $C1$ and $EFS$ for Quesnel Lake sockeye by cycle line.

In analyzing for cycle-line interaction using $C1$, the multiple regression with untransformed $EFS$ variables was highly significant ($P < 0.001$; adj. $R^2 = 0.668$; $n = 26$) and yielded highly significant regression parameter values associated with the $EFS_t$, $EFS_{t-1}$ and $EFS_{t-2}$ variables (all $P < 0.001$; Table 3). All significant parameter values were negative indicating compensatory growth. Relative regression parameter values for the three significant $EFS$ variables were: 1:0.79:0.61, suggesting strong cycle-line interaction effects of escapements with lags of one and two years.

Next, we examined $C1$ with a log transformed $EFS$ model. The fit of the multiple regression improved ($P < 0.001$; adj. $R^2 = 0.819$) and again regression parameters associated with $EFS_t$, $EFS_{t-1}$ and $EFS_{t-2}$ were all significant. The relative regression parameter values associated with the three significant $EFS$ variables were: 1:0.23:0.15. Clearly, cycle-line interactions at lags of one and two years were present in this model, as with the untransformed $EFS$ model

The fit of multiple regressions using Quesnel sockeye $C2$ on untransformed and log transformed $EFS$ variables improved over regressions for $C1$ (Table 3), however, the basic result was unchanged. All significant regression parameters were negative and the relative regression parameter values were similar.

The regressions of Quesnel sockeye scale $C1$ and $C2$ on untransformed and log transformed $EFS$ variables resulted in the inclusion of the two immediate prior year escapements in all regressions. The cycle-line interaction effects were sizable and consistent between scale variables.

### Chilko scale growth

Chilko River sockeye $C1$ and $C2$ were analyzed as for Shuswap and Quesnel Lake stocks with untransformed and log transformed $EFS$ variables. In all cases, $EFS$ variables, including brood year $EFS$, explained only small proportions of the variation in $C1$ or $C2$. None of the four regressions showed significant effects of the immediate prior brood year juvenile abundance (i.e., $EFS_{t-1}$) in the regressions. While $C1$ was related to untransformed and log transformed $EFS_t$, the statistical fits were poor (Table 3).

**Juvenile sockeye abundance and size**

Shuswap and Quesnel Lakes fall juvenile sockeye and Chilko Lake fry and smolt abundance, average size and biomass estimates were examined for evidence of cycle-line interaction via multiple regression analyses. Untransformed and $\log_e$ transformed *EFS* variables were again the independent variables. Sequential addition of progressively earlier year *EFS* data continued until the incremental *EFS* value was non-significant at the $\alpha = 0.1$ level in the multiple regression. Sample sizes were marginal for Shuswap (n = 15) and Quesnel (n = 16) juvenile samples and for Chilko fry estimates (n = 18), but Chilko smolt abundance and size had a long data series (n = 48) for these analyses.

### Shuswap juvenile abundance and size

Shuswap Lake juvenile sockeye abundance was related to untransformed $EFS_t$ (P = 0.035; Table 4) but regression parameter associated with $EFS_{t-1}$ was not significant. Regression of fall mean weight on untransformed $EFS_t$ was marginally significant (P = 0.059) and biomass (abundance X mean weight) estimates were also only marginally related to untransformed $EFS_t$ (P = 0.099; Table 4). Regression parameters associated with $EFS_{t-1}$ and earlier years were not significant.

We subsequently examined these variables in relation to log transformed *EFS* variables. Significant regression parameters were found between juvenile abundance (P = 0.008), mean weight (P = 0.031) and biomass (P = 0.031) and $\log_e EFS_t$, but prior year *EFS* variables were not significant in multiple regressions. While the regression analyses using both untransformed and log transformed *EFS* variables did indicate that brood year effects were present, no significant cycle-line interaction effects were detected.

A Ricker curve fit to fall juvenile sockeye/kokanee biomass estimates vs. brood year sockeye *EFS* for the dominant and subdominant line years indicated a reasonable fit to the data (Fig. 6). The graph suggested that the reason for the improved fit with log transformed $EFS_t$ data was the curvilinearity in the data.

### Quesnel juvenile abundance and size

Unlike Shuswap sockeye, the relationship between Quesnel Lake fall juvenile abundance and untransformed *EFS* variables was highly significant (P < 0.001; Table 4).

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Table 4. Correlation coefficient, regression parameters and P values for multiple regressions of juvenile abundance, size and biomass on *EFS* (i.e., EFSt, EFSt-1, EFSt-2).

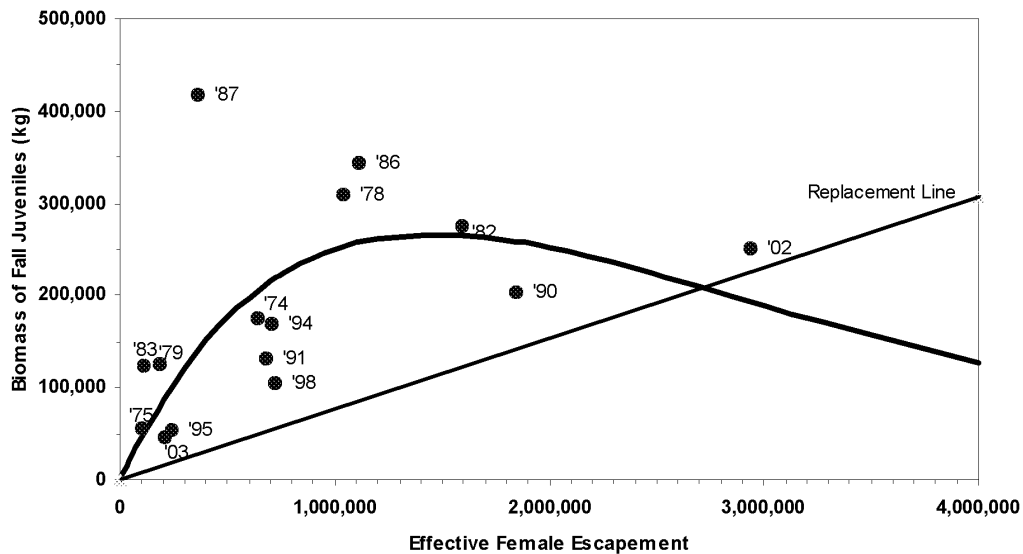| Lake | Life Stage | Y Variable | Regression Model | # years | Regression adj. $r^2/R^2$ | $b_t$ | P | $b_{t-1}$ | P | $b_{t-2}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Shuswap | Fall Juveniles | Abund. (X10⁹) | Untransformed EFS | 15 | 0.244* | 3.72E-05 | 0.035 | NS | | |
| | | | Log$_e$ transformed EFS | 15 | 0.390** | 34.524 | 0.008 | NS | | |
| | | Weight (g) | Untransformed EFS | 15 | 0.190 | -3.42E-07 | 0.059 | NS | | |
| | | | Log$_e$ transformed EFS | 15 | 0.256* | -0.293 | 0.031 | NS | | |
| | | Biomass (kg) | Untransformed EFS | 15 | 0.134 | 6.33E-02 | 0.099 | NS | | |
| | | | Log$_e$ transformed EFS | 15 | 0.257* | 6.13E+04 | 0.031 | NS | | |
| Quesnel | Fall Juveniles | Abund. (X10⁹) | Untransformed EFS | 16 | 0.635** | 2.96E-05 | <0.001 | -1.36E-05 | 0.044 | NS |
| | | | Log$_e$ transformed EFS | 16 | 0.805** | 10.018 | <0.001 | -3.676 | <0.001 | NS |
| | | Weight (g) | Untransformed EFS | 14 | 0.482* | -6.33E-07 | 0.015 | -5.50E-07 | 0.015 | NS |
| | | | Log$_e$ transformed EFS | 14 | 0.387* | -0.235 | 0.056 | -0.102 | 0.019 | NS |
| | | Biomass (kg) | Untransformed EFS | 16 | 0.496** | 7.13E-02 | 0.026 | -7.41E-02 | 0.014 | NS |
| | | | Log$_e$ transformed EFS | 16 | 0.840** | 2.50E+04 | <0.001 | -1.82E+04 | <0.001 | NS |
| Chilko | Upstr. Migr. Fry | Abund. (X10⁹) | Untransformed EFS | 18 | 0.787 | 1.69E-04 | <0.001 | NS | | |
| | | | Log$_e$ transformed EFS | 18 | 0.760 | 15.781 | <0.001 | NS | | |
| | | Fry/EFS | Untrans. EFS | 18 | 0.419** | 5.00E-04 | 0.007 | 3.37E-04 | 0.029 | NS |
| Chilko | Age 1 Smolts | Abund. (X10⁹) | Untransformed EFS | 48 | 0.510** | 6.19E-05 | <0.001 | -2.56E-05 | 0.004 | NS |
| | | | Log$_e$ transformed EFS | 48 | 0.603** | 7.626 | <0.001 | NS | | |
| | | Live Length (mm) | Untransformed EFS | 48 | 0.117* | -1.48E-05 | 0.012 | NS | | |
| | | | Log$_e$ transformed EFS | 48 | 0.144** | -2.282 | 0.006 | NS | | |
| | | Weight (g) | Untransformed EFS | 48 | 0.056 | -2.00E-07 | 0.058 | NS | | |
| | | | Log$_e$ transformed EFS | 48 | 0.076* | -0.296 | 0.032 | NS | | |
| | | Biomass (kg) | Untransformed EFS | 48 | 0.426** | 0.255 | <0.001 | -0.116 | 0.008 | NS |
| | | | Log$_e$ transformed EFS | 48 | 0.508** | 3.13E+04 | <0.001 | NS | | |

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Figure 6. Scatter plot of Shuswap Lake fall juvenile *O. nerka* biomass for dominant and subdominant line years. A Ricker model has been fit to the data using mean survival rates from fall juveniles to adults.

Regression parameters for both $EFS_t$ and $EFS_{t-1}$ were significant (P < 0.001 and (P = 0.044, respectively). While the brood year effect on abundance was positive, the regression parameter for $EFS_t$ was negative, as one would expect if cycle-line interaction affected survival as hypothesized.

Fall juvenile mean weight was also significantly related to $EFS_t$ (P = 0.015) and first $EFS_{t-1}$ (P = 0.015; Table 4). The regression parameters associated with $EFS_t$ and $EFS_{t-1}$ were both negative indicating density dependent growth. The relative regression parameter values were: 1:0.87, showing a high level of prior year impact on fall juvenile mean weight. Juvenile biomass estimates were also related to untransformed *EFS* variables (P = 0.005). Regression parameters associated with both $EFS_t$ and $EFS_{t-1}$ were significant (P = 0.026 and 0.014, respectively; Table 4).

We repeated the analyses of fall juvenile data with log transformed *EFS* variables. The relationships between juvenile abundance and biomass and *EFS* variables were highly significant (P < 0.001) and explained higher proportions of the variance in the dependent variables than did the untransformed *EFS* models (Table 4). Regression parameters associated with $\log_e EFS_t$ and $\log_e EFS_{t-1}$ were highly significant. The regression of mean

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weight on log transformed *EFS* variables was significant (P = 0.027), but at a lower level than with untransformed *EFS* variables.

Analyses of Quesnel Lake fall juvenile data revealed significant cycle-line interaction in that the regression parameters associated with $EFS_{t-1}$ along with those associated with $EFS_t$ were consistently significant. Examination of the individual cycle-line data suggested that dominant line juveniles impacted early growth and survival of subdominant line sockeye fry that entered the lake as the dominant line juveniles were smolting and migrating to sea. This impact on growth was evident in both summer and fall juvenile mean weight estimates. Dominant line juvenile mean weights in summer surveys between brood years 1985-2003 (avg. = 2.12 g; Table 5) were significantly larger (t-test P = 0.014) than subdominant line juveniles (avg. = 1.63 g) at comparable EFS (Fig. 7). Fall juvenile mean weights were 3.36 g and 3.13 g, respectively (Table 5). A t-test indicated that the difference was not significant (P > 0.05). However, when fall biomass/*EFS* estimates was plotted against brood year *EFS* abundance, we noted substantial differences in productivity associated with cycle line (Fig. 8). The dominant line produced approximately twice the juvenile biomass per effective female spawner compared to the subdominant line in the years of record.

### *Chilko juvenile abundance and size*

Estimates of upstream migrating Chilko River sockeye fry were available for nineteen brood years, 1949-1967, however, we excluded 1963 due to uncertainty in the *EFS* estimate associated with extremely high pre-spawning mortality (IPSFC 1964). A logarithmic relationship fit to the scatter plot of fry abundance on brood year *EFS* captured the trajectory of the data (Fig. 9). Compensation at high *EFS* levels (> 200,000 *EFS*) yielded very similar total fry numbers over a two-fold range of *EFS*, possibly associated with spawning ground limitations. Restricted areas of high quality gravel and intergravel water flow, and redd disturbance by later arriving fish at high escapement levels, may operate to lower survival at higher spawner densities.

Also evident in the plot of fry abundance data were several years of low fry numbers associated with low *EFS* that suggested depensatory effects could also be involved in Chilko River fry production. An examination of individual cycle-line regressions of fry

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production per *EFS* vs. brood year *EFS* indicated regressions for offcycle and intermediate lines were parallel to the dominant line regressions but had lower intercepts (Fig. 10).

Table 5. Mean weight of Quesnel Lake juveniles on each cycle line in summer and fall surveys and mean C1 for age 4/2 recruits.

| | Dominant | | Subdominant | | First offcycle | | Second offcycle | |
|---|---|---|---|---|---|---|---|---|
| Cycle Lines | EFS | Mean Weight (g) | EFS | Mean Weight (g) | EFS | Mean Weight (g) | EFS | Mean Weight (g) |
| **Summer surveys** | | | | | | | | |
| 1985 - 88 | 676,842 | 2.30 | 94,841 | 1.82 | 11,238 | 1.39 | | |
| 1989 - 92 | 940,551 | 2.43 | 259,218 | 1.69 | 24,861 | 2.10 | | |
| 1993 - 96 | 1,507,349 | 2.19 | 365,251 | 1.89 | | | | |
| 1997 - 00 | | | | | | | | |
| 2001 - 03 | 1,740,455 | 1.54 | 1,215,952 | 1.13 | 148,296 | 1.86 | | |
| Mean | 1,216,299 | 2.12 | 483,816 | 1.63 | 61,465 | 1.78 | | |
| **Fall surveys** | | | | | | | | |
| 1985 - 88 | 676,842 | 3.42 | | | | | | |
| 1989 - 92 | 940,551 | 3.28 | 259,218 | 3.49 | 24,861 | 3.45 | | |
| 1993 - 96 | 1,507,349 | 4.00 | 365,251 | 3.58 | | | | |
| 1997 - 00 | 904,914 | 3.56 | 534,532 | 3.50 | 106,908 | 3.49 | 37,163 | 2.60 |
| 2001 - 03 | 1,740,455 | 2.56 | 1,215,952 | 1.93 | 148,296 | 3.35 | | |
| Mean | 1,154,022 | 3.36 | 593,738 | 3.13 | 93,355 | 3.43 | | |

| | Dominant | | Subdominant | | First offcycle | | Second offcycle | |
|---|---|---|---|---|---|---|---|---|
| Cycle Lines | EFS | Mean age 4/2 C1 | EFS | Mean age 4/2 C1 | EFS | Mean age 4/2 C1 | EFS | Mean age 4/2 C1 |
| **Age 4/2 recruit C1** | | | | | | | | |
| 1985 - 88 | 676,842 | 13.68 | 94,841 | 14.16 | 11,238 | 15.46 | 4,185 | 16.82 |
| 1989 - 92 | 940,551 | 13.13 | 259,218 | 13.05 | 24,861 | 13.57 | 3,046 | 15.65 |
| 1993 - 96 | 1,507,349 | 13.82 | 365,251 | 13.04 | 116,867 | 13.30 | 21,719 | 14.39 |
| 1997 - 00 | 904,914 | 12.51 | 534,532 | 12.38 | 106,908 | 12.39 | 37,163 | 14.32 |
| 2001 - 03 | 1,740,455 | | 1,215,952 | | 148,296 | | | |
| Mean | 1,007,414 | 13.29 | 313,461 | 13.16 | 64,969 | 13.68 | 16,528 | 15.30 |

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**SUMMARY SURVEYS**

Dominant
y = -0.3923Ln(x) + 7.5154
$r^2$ = 0.506

Subdominant
y = -0.2639Ln(x) + 4.9807
$r^2$ = 0.648

**FALL SURVEYS**

Dominant
y = -0.4902Ln(x) + 10.189
$r^2$ = 0.500

Subdominant
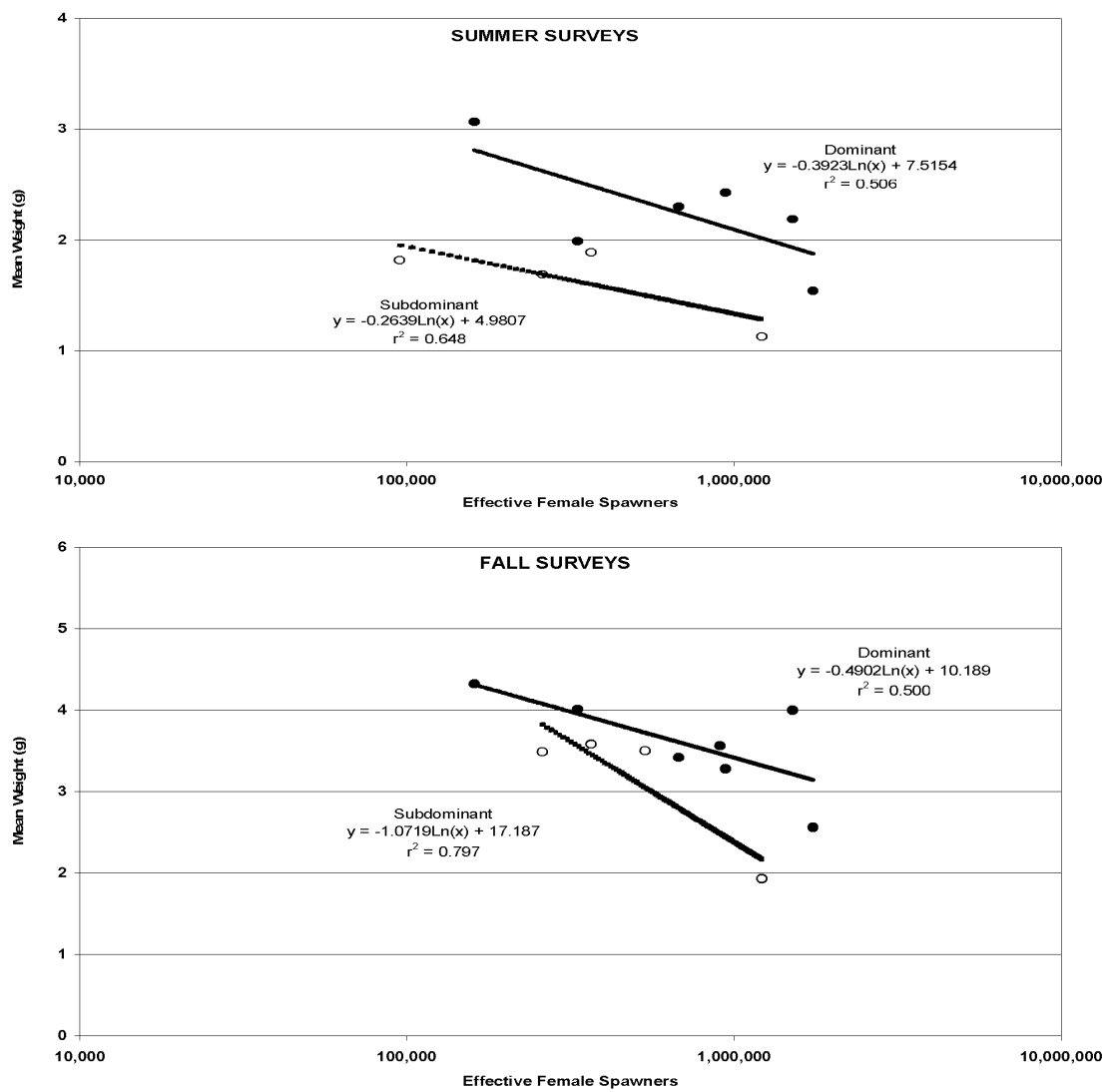y = -1.0719Ln(x) + 17.187
$r^2$ = 0.797

Figure 7. Mean weight of Quesnel Lake juvenile *O. nerka* captured in summer and fall surveys on dominant and subdominant line years.
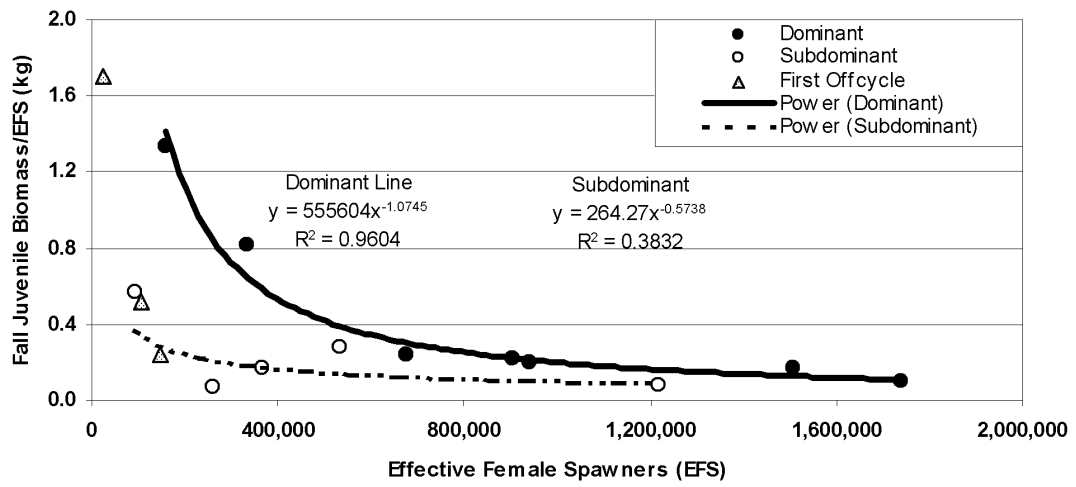
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Figure 8. Juvenile *O. nerka* biomass estimates in fall surveys of Quesnel Lake on dominant and subdominant line years.
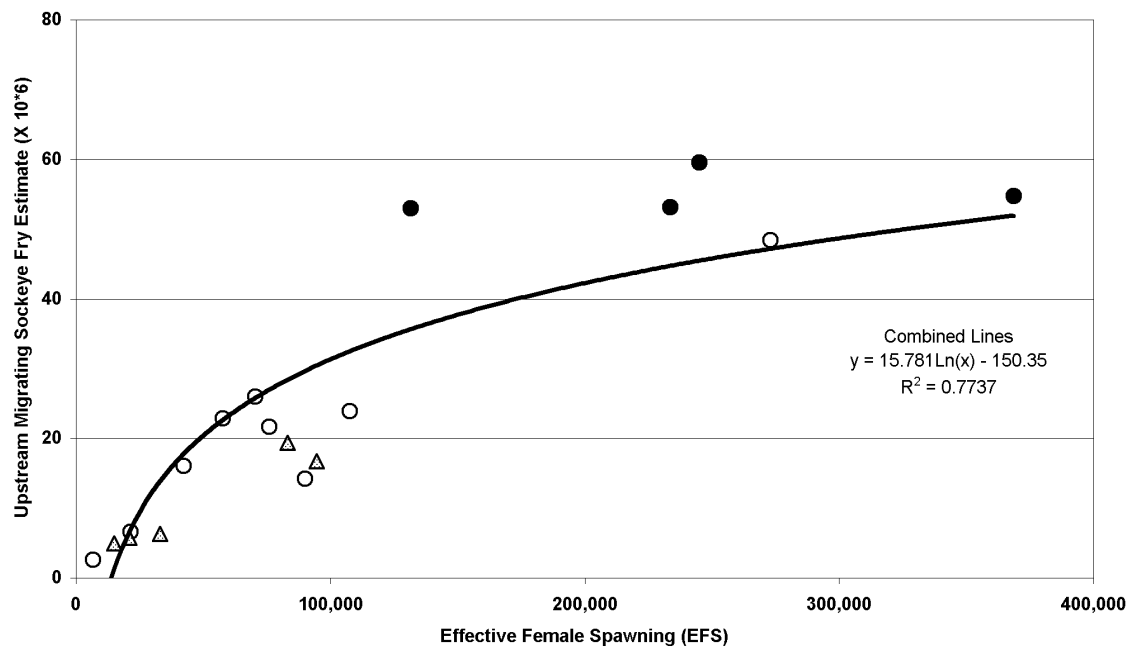


Figure 9. Scatter plot of Chilko River upstream migrant sockeye fry abundance vs. *EFS*. A logarithmic regression has been fit to the data.
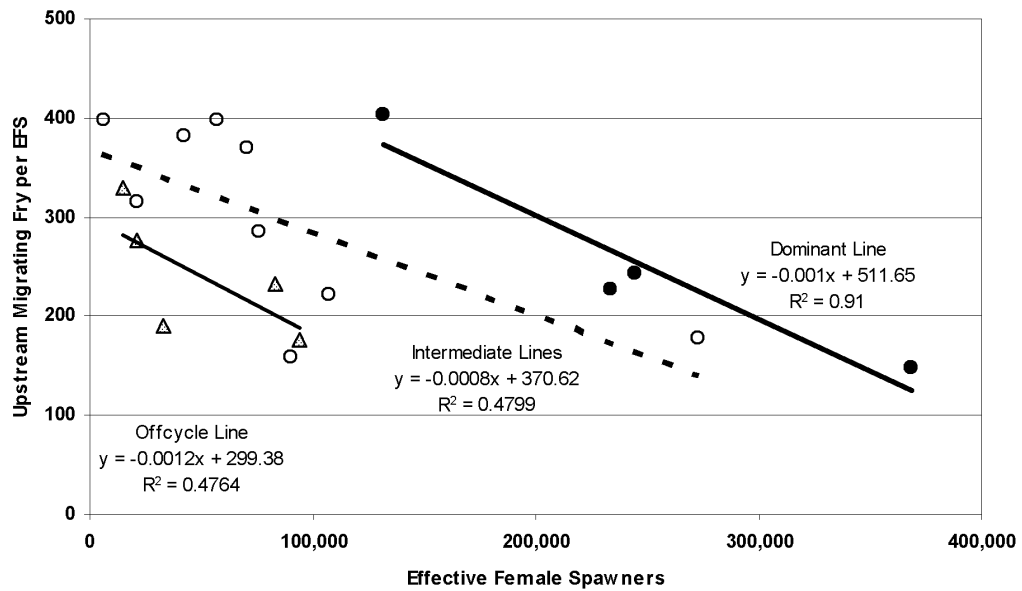
Figure 10. Scatter plot of Chilko River upstream migrating fry per *EFS* vs. effective female spawner abundance by cycle line (dominant, offcycle and intermediate lines).
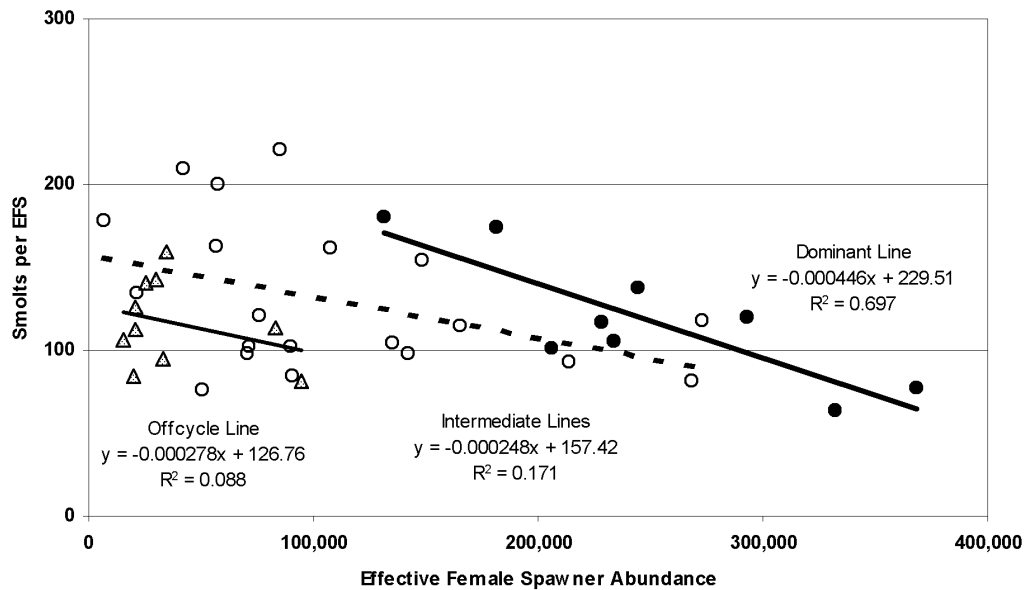


Figure 11. Scatter plot of Chilko Lake sockeye smolts per *EFS* vs. effective female spawner abundance by cycle line.

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Cycle-line interaction analyses of fry abundance on $EFS_t$ and prior brood year $EFS$ variables showed a significant positive effect of untransformed and log transformed $EFS_t$ and negative, but non-significant effects of $EFS_{t-1}$ and $EFS_{t-2}$ variables (Table 4). However, when we examined fry/$EFS$ vs. $EFS_t$ and $EFS_{t-1}$ in a multiple regression, the regression parameters for both $EFS$ values were significant (P = 0.007 and 0.029, respectively; Table 4).

Chilko smolt abundance, weighted mean live length, mean preserved weight and biomass in brood years 1949-1988 and 1994-1999 were examined in relation to untransformed and $\log_e$ transformed $EFS$ variables. Regressions of smolt abundance and biomass on untransformed $EFS$ variables resulted in significant regression parameters associated with $EFS_t$ and $EFS_{t-1}$ (both P < 0.001; Table 4), however, regressions of smolt mean live length and preserved smolt mean weight were related only to $EFS_t$, and at lower levels of significance (P = 0.012 and P = 0.058, respectively; Table 4). Abundance and biomass are closely related and the concurrent relation of these two variables to $EFS$ variables is not unexpected. Similarly, live length and preserved weight of smolts were closely related.

The above analysis was repeated with log transformed $EFS$ values to determine if the impact of the $EFS$ variables was non-linear and multiplicative rather than additive. Unlike the results with untransformed variables, all four dependent variables were related to $EFS_t$, but none to the prior year $EFS_{t-1}$. Abundance and biomass regressions were highly significant (both P < 0.001; Table 4), while mean live length and mean preserved weight were much less strongly related to $EFS_t$ (P = 0.006 and P = 0.032, respectively). Statistical fits generally improved using log transformed dependent variables but no cycle-line interaction effects on smolt size were detected.

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# Discussion

## Cycle-line interaction by lake system

### *Shuswap Lake sockeye*

Significant negative cycle-line interaction effects at lags of one and two years were observed when fitting the Larkin S-R model to Shuswap Lake sockeye recruitment rates, although the proportion of the uncertainty explained by the model was low (adj. $R^2$ = 0.190). When prior year *EFS* variables were significant, their regression parameters were negative indicating coherence to cycle-line interaction theory. However, we failed to detect significant cycle-line interaction effects in the abundance of juvenile sockeye estimated in fall surveys of Shuswap Lake. Similarly, while we found highly significant negative cycle-line interaction effects in the relationships of adult sockeye *C1*, *C2* and *D1* to *EFS* variables at lags of one and, at times, two years, the smaller data sets of juvenile mean weight did not yield comparable results. Fall juvenile mean weight was related to $EFS_t$ but not to prior year *EFS* variables.

The fifteen years of data used in the juvenile analyses were restricted to dominant and subdominant line brood years between 1974-2003 because age-0 kokanee dominated in the juvenile populations on offcycle years (Hume et al. 1996). We estimated the intercept of the regression of age 0 juvenile *O. nerka* abundance on *EFS* at approximately 10 million fish at zero sockeye *EFS*. This number of age 0 kokanee would have introduced substantial uncertainty into the juvenile abundance analyses if offcycle years were to be included in the analyses. Restriction of the range of *EFS* (102,000-2,944,000 *EFS*) may have limited the power of the juvenile abundance analysis relative to the adult recruitment analyses. The longer data series and greater range of *EFS* present in the adult analyses (1,700-1,848,000 *EFS*) would have provided greater opportunity to detect significant cycle-line interaction effects, if present.

Potentially variable numbers of age 0 kokanee mixed with juvenile sockeye may have introduced sufficiently large random variation in fall juvenile size estimates that mean weight regression analyses that only statistically significant fits were detected with $EFS_t$. Adult scale data were available for all lines, thus, the significant regression parameters

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associated with $EFS_{t-1}$ and $EFS_{t-2}$ strongly suggest that the Shuswap Lake juvenile size data were inadequate to provide definitive information on cycle-line interaction.

The similarity in the results for Adams and Seymour $C1$ and $C2$ analyses supported the notion that juvenile sockeye growth in Shuswap Lake as a whole was density-dependent and affected by total watershed juvenile abundance in the brood year and the prior year(s) as measured by $EFS$, rather than being generated by intra-population genetic or spawning location effects. We consider that the number of years available (n = 49 to 52) was sufficient to support our conclusion that the estimates of cycle-line interaction impacts obtained in the analyses were correct.

In the Adams scale $C1$ regression on untransformed $EFS$ variables, the relative regression parameter values for $b_t$:$b_{t-1}$ were: 1:0.50, indicating a strong prior line effect, whereas with log transformed $EFS$ the relative values were 1:0.19. The lower relative regression parameter value associated with the log transformed $EFS_{t-1}$ may be due to the nature of the multiplicative model that is measuring a different relationship. However, there remained a sizable fraction of the total variation in $C1$ associated with $EFS_{t-1}$, i.e., negative cycle-line interaction.

Analyses using log transformed $EFS$ values consistently provided superior fits to untransformed $EFS$ scale variables. This appears related to the logarithmic relationship between scale data and brood year $EFS$ (Fig. 4). Hume et al. (1996) presented data showing that juvenile abundance reached a maximum at an intermediate escapement level and that additional $EFS$ inputs either did not increase the juvenile abundance or may actually have resulted in a decline in abundance. However, rather than following the asymptotic trend in juvenile abundance, juvenile size in the dominant and subdominant years continue to decline with increasing $EFS$ beyond the point of maximum juvenile production (Fig. 4). Presumably, the logarithmic relationship between mean scale growth and $EFS$ reflects a continuing decline in juvenile size with $EFS$ unmodified by survival patterns, thus, providing improved data fits with the non-linear model. This observation suggests that fry numbers entering Shuswap Lake from dominant line spawnings continue to increase with larger $EFS$ escapements and that intraspecific competition limits growth and increases size-dependent mortality rates causing the biomass of

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juvenile sockeye in fall surveys to level off or decline slightly at high levels of *EFS* (Fig. 6). Fall juvenile biomass, in turn, is a good predictor of adult recruitment.

Subdominant line juveniles enter the lakes as the dominant line juveniles are about to emigrate. Cropping of zooplankton food supplies by dominant line juveniles may produce non-compensatory early growth in subdominant juveniles. In addition, the Shuswap data suggested that juvenile growth on the first offcycle line was lower than on the second offcycle line (Fig. 4) despite similar *EFS,* suggesting carryover effects of the subdominant line. Average escapements decrease sequentially from the dominant line (974,000 *EFS*) to subdominant line (213,000 *EFS*), then to first (7,900 *EFS*) and second offcycle lines (7,800 *EFS*). The first offcycle line follows the two most abundant lines and juveniles potentially encounter a more severely depleted food resource than do second offcycle line juveniles that enter the lake as the low abundance first offcycle line juveniles are about to emigrate.

The significant regression parameters associated with prior year *EFS* variables in explaining freshwater growth and abundance suggests that the large dominant line escapements and offspring numbers exert negative impacts on following lines. However, the failure to detect statistically significant effects at lags of greater than one year other than in the Larkin Model and in Adams adult scale *D1* and Seymour scale *C1* when we used log transformed *EFS* variables was troubling in postulating a mechanism for the suppression of recruitment on offcycle lines. As noted above, scales of recruits on the first offcycle line tended to have lower FW scale growth (Fig. 4) compared to the second offcycle line despite similar average *EFS.* Whether this was simply a result of subdominant line juvenile impacts at a lag of one year or a synergistic effect of dominant and subdominant lines was not clear. However, freshwater juvenile growth on most nondominant line years was less than predicted from the dominant line regression suggesting that suppression of growth carries into the second offcycle line.

*Quesnel Lake sockeye*

Analyses of Quesnel Lake adult recruitment and fall juvenile abundance estimates provided evidence of cycle-line interaction impacts at lags of one, two and, possibly, three years. In the Larkin model, adult recruitment rates were significantly related to

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$EFS_t$, $EFS_{t-2}$ and $EFS_{t-3}$ variables (Table 2), but juvenile abundance and biomass were well related only to $EFS_t$ and $EFS_{t-1}$ in both untransformed and log transformed $EFS$ models (Table 4). As in the case of Shuswap sockeye, log transformed $EFS$ variables provided improved regression fits relative to the statistical fits of untransformed $EFS$. Hume et al. (1996) documented non-linear recruitment of fall juveniles relative to $EFS$ that is likely the source of the improved fit using the log transformed $EFS$ variables. Regression parameter values for lagged $EFS$ variables were large relative to brood year $EFS$ regression parameters for both adult and juvenile data. Cycle-line interaction effects at lags of two and three years in adult recruitment were unexpectedly high and may be the result of time series biases associated with early years when all nondominant lines were small. However, the evidence for cycle-line interaction appears relatively strong in Quesnel sockeye recruitment.

In analyses of Quesnel Lake growth using adult Horsefly River sockeye scale $C1$, we observed strong negative cycle-line interactions at lags of one and two years (Table 3). Undoubtedly, the dominant line juvenile abundance influenced subdominant line juvenile growth as in Shuswap Lake, but in Quesnel Lake, there appeared to be a carry-over effect for two years. Adult mean $C1$ values for subdominant and first offcycle line sockeye were similar to dominant line fish in recent years despite much smaller $EFS$ populations (Table 5). Analyses of fall juvenile sockeye size confirmed the observation of cycle-line interaction although only with $EFS_{t-1}$.

The negative cycle-line interaction effect on juvenile growth on nondominant line years may be responsible for the cycle-line interaction effect on abundance. Subdominant line juvenile sockeye collected on summer surveys were smaller than dominant line juveniles sampled at comparable dates (Fig. 7). We suspect that the slow growth rates experienced by subdominant line juveniles during early lake residence leaves the fry more vulnerable to high predatory losses for longer periods of the growing season. While the growth rates of subdominant line juveniles may be compensatory between the summer and fall surveys, they do not fully recover from the slow growth they experience during the spring. Depensatory mortality associated with depensatory growth on nondominant line years appears to negate assumed compensation in fry production and

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may be responsible for the observation that recruitment rates are similar for all lines (Appendix B, Table 2).

### Chilko Lake sockeye

Density dependent cycle-line interaction in Chilko Lake sockeye juvenile data was only evident when $EFS$ variables were untransformed and only when abundance and biomass estimates were the dependent variables. Comparable results were observed in the adult recruitment rate relationships (Larkin model) wherein only untransformed $EFS$ variables are employed in the analyses. Cycle-line interaction observed in smolt production estimates appeared to be the source of the improved fit of the Larkin model in adult recruitment.

The relative regression parameter values associated with $EFS_t$ and $EFS_{t-1}$ (1:0.96) in the adult recruitment data regression was higher than observed in the smolt recruitment (1:0.41). Cycle-line interactions observed in the juvenile abundance data appeared to have been magnified by post-lake survival effects, resulting in very high estimates of $EFS_{t-1}$ effect in adult recruitment rate.

Unlike Shuswap and Quesnel, Chilko sockeye did not show significant cycle-line interaction impacts on juvenile sockeye growth as measured by adult scale $CI$ or smolt length and weight. While juvenile size relationships with $EFS_t$ were significant, they explained only low fractions of the uncertainty in smolt size.

At high $EFS_t$, Chilko sockeye fry production appeared to be strongly compensatory. A logarithmic relationship was detected in the estimates of upstream migrating fry relative to $EFS$ populations (Fig. 9). The ratio of largest to smallest $EFS_t$ in the time period was 56:1 while the ratio of fry numbers was only 23:1. The compensatory fry production observed may be responsible for the lack of strong density-dependent juvenile growth.

### Synthesis of cycle-line interaction analyses

Variable degrees of cycle-line interaction affecting the abundance and/or growth of juvenile sockeye were indicated by the analyses of Shuswap, Quesnel and Chilko stock complexes. First-year freshwater growth of Shuswap sockeye was strongly affected by cycle-line interaction, but evidence of effects on juvenile and adult abundance was

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equivocal. Analyses of Quesnel sockeye revealed cycle-line interaction impacts on juvenile growth and abundance and adult recruitment, the latter presumably stemming from the observed effects on juveniles. Abundance and biomass of Chilko sockeye smolts and adult recruitment rate appeared to be affected by cycle-line interaction but only brood year effects on juvenile growth were significant. Clearly, control of juvenile size and recruitment in these three stocks must stem from different mechanisms associated with the geophysical properties of the individual watersheds and differing life histories, biology and ecology of the stocks.

Density-dependent cycle-line interactions were evident in juvenile sockeye growth in Shuswap and Quesnel Lakes but not in Chilko possibly because of differing mechanisms in the production of fry. Indirect evidence from the continuous decline in $CI$ with $EFS$ in Shuswap and Quesnel (Figs. 4 and 5) indicated that the abundance of fry in these two systems was not limited by spawning ground capacity within the observed range of $EFS$. Conversely, Chilko fry production appeared to be strongly compensatory at high $EFS$, likely resulting in a lower range in fry numbers relative to brood year $EFS$ abundance.

Juvenile sockeye abundance in the Shuswap and Quesnel populations may have been generally limited by lake rearing capacity within the behavioral constraints of the species and by predation. Zooplankton food resources may not be severely depleted (Hume et al. 1996), but intraspecific competition in foraging while maintaining the protection that daytime schooling and diel vertical migration provides juvenile fish may act to produce density-dependent growth in most upper Fraser sockeye lakes (Goodlad et al. 1974; Levy 1990). Our analyses showed that juvenile mean weight was also negatively impacted by prior year $EFS$, or rather, by the competitive effect of juveniles from prior years as indexed by $EFS$. In Quesnel Lake the size of subdominant line juvenile sockeye/kokanee in summer samples was smaller than during the prior summer when more numerous dominant line juveniles were present.

Early growth of a juvenile cohort appears to be related to the impact that prior year juvenile populations have on the food resources. Hume et al. (1996) presented data that indicated a negative linear relationship between $EFS$ and subsequent growing season abundance of *Daphnia* spp., the preferred food of juvenile sockeye in Shuswap and Quesnel Lakes. Depletion of the preferred food resource by dominant line juveniles in

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their year of lake residence does not necessarily prove that following line juveniles face a depleted food environment. However, either dominant line juvenile foraging in the summer-fall of one year produces a carry-over effect that delays recruitment of adult zooplankters in the following spring-early summer, or the dominant line pre-smolt juvenile sockeye deplete the adult zooplankton in early spring, reducing food available to newly recruited subdominant line fry. Delay in spring zooplankton recruitment may be due to fewer overwintering adult zooplankters or fewer ephippial eggs of *Daphnia* to generate the following year brood due to heavy exploitation of adults prior to formation of ephippial eggs the prior fall.

Analogous over-cropping of zooplankton food supplies in small Alaskan lakes stocked with sockeye fry resulted in decreased growth and survival of following year juveniles (Koening and Kyle 1997). These authors also found substantial restructuring of the zooplankton populations, including reduction of large, preferred species and increase of more mobile and/or smaller species. While long-term restructuring of zooplankton communities are unlikely in Shuswap and Quesnel Lakes due to the multi-basin lake morphology and position of spawning stream entrances into the lakes, short-term responses of zooplankton abundance associated with dominant line juvenile foraging are not unexpected. That this type of zooplankton abundance response has not been clearly shown may reflect the short-term effects during the spring months, rather than longer-term seasonal effects (Hume et al. 1996). However, the smaller size of age 0 Quesenel Lake juveniles in summer surveys on subdominant line years clearly suggests that they encounter reduced food abundance and/or zooplankter size associated with dominant line juvenile cropping.

Chilko sockeye clearly did not follow the pattern of juvenile growth response observed in Shuswap and Quesnel sockeye. Absence of strong density-dependent growth response in Chilko sockeye was unique within the three lakes. Chilko sockeye also do not show strong cyclic dominance. Smolt size and adult scale *C1* were significantly related to $EFS_t$ but the regressions explained little of the variation in smolt size. Also, size was not strongly related to brood year fry or smolt abundance. While variable lake environmental conditions may be responsible, the data sets were sufficiently long to provide a larger signal of density-dependent growth, if present.

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The negative cycle-line interaction in Chilko smolt and adult recruitment but not in juvenile growth posed a question as to its origin. During the greater portion of the data series, the offcycle line followed the dominant line and, in turn, was followed by the two intermediate lines. Thus, one explanation for the cycle-line interaction was that the dominant line suppressed recruitment on non-dominant lines that followed with most severe effects at a lag of one year. Analyses of fry abundance data did not reveal significant cycle-line interaction, but we did detect cycle-line interaction in the fry/*EFS* vs. *EFS* relationship (Table 4). The plot of upstream migrating fry and smolt recruitment rates (Figs. 10 and 11) strongly suggested that juvenile production on the offcycle line is adversely impacted in some way by its position in the four-year cycle. This may be the source of the significant cycle-line interaction results in analyses of juvenile abundance and adult recruitment rate. The consistently higher fry and smolt recruitment rate on the dominant line for a given level of *EFS* indicated processes driven by the high escapements on this line and meets the criteria for cycle-line interaction.

While attractive, this explanation did not correspond to results obtained in analysis of Shuswap and Quesnel Lake sockeye. In these latter lakes, juvenile growth competition appeared responsible for the cycle-line interaction. However, Chilko Lake sockeye growth data did not support this hypothesis. Also, this explanation did not explain why the intermediate lines that followed the offcycle line were restricted in fry recruitment rate since the first intermediate line should have been least impacted by cycle-line interaction mechanisms. We therefore examined an alternate hypothesis for Chilko Lake based on the fry data.

Fry from lower *EFS* spawning years may simply have suffered depensatory mortality related to smaller numbers of emerging fry. As such, the sequential order of the lines: dominant-offcycle-intermediate-intermediate, may have induced multiple regression analyses to indicate significant cycle-line interaction when no actual biological/ecological interaction existed. Supporting this interpretation, the intermediate abundance years gave intermediate regression fits to the fry/*EFS* data on those lines. The cycle-line interaction that we found in smolt and adult recruitment appears to have originated in the early depensatory mortality indicated by the fry data (smolt vs. fry abundance: $P < 0.001$; adj. $r^2 = 0.828$; adult vs. fry abundance: $P < 0.001$; adj. $r^2 = 0.483$).

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Of interest, as well, was the cause of the observed depensatory mortality at low *EFS* density. Since inter-gravel egg survival should be compensatory, we speculate that predation between emergence and arrival of upstream migrating fry at the outlet of the lake may be severe and may act in a depensatory fashion to reduce the fry populations on the offcycle year by approximately 50% compared to the expected based on the dominant line regression. While the exact cause of the depensatory nature of this mortality is not clear, avian predators are abundant in the area, as well as predatory species of fish.

Upstream migration appears to be costly for Chilko River sockeye fry given that approximately one to two days would be required for fry to traverse the 4 km distance, if swimming at a constant rate of one body length per second, while vulnerable to numerous fish and avian predators.

We conclude that Chilko sockeye recruitment is limited by compensatory fry production at high *EFS* due to spawning area limitations and by depensatory mortality at low *EFS*. Thus, Chilko sockeye do not display cyclic dominance as in Shuswap and Quesnel Lakes.

**Cycle-line interaction as a mechanism in cyclic dominance**

Negative cycle-line interaction in the abundance of juvenile and adult Shuswap and Quesnel Lake sockeye is likely the result of size-mediated predation rates. We postulate that the non-compensatory growth of the less abundant juvenile sockeye on non-dominant lines leads to depensatory predation mortality in cyclical stocks. Two conditions must be present in these systems: non-spawning-ground-limited fry production and abundant piscavores. These conditions are met in Shuswap and Quesnel lakes (Williams, et al. 1989; R. Dolighan, B.C. MWLAP, personal communication).

Size-mediated, depensatory predation rates in early lake residence may be higher for subdominant line juvenile Quesnel Lake sockeye associated with slower initial growth rate. Thus, whereas emerging fry numbers probably show compensatory mortality, fall juvenile biomass on subdominant and first offcycle line years was consistently lower than observed on dominant lines at comparable EFS (Fig. 8).

In four paired dominant:subdominant line data sets (1985-2003), juvenile mean weights in summer samples were larger on dominant line years (2.12 g) than on

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subdominant line years (1.63 g) even though dominant line *EFS* was approximately 2.5 times the subdominant line average (Table 5). While kokanee stocks would be expected to comprise a higher fraction of the age 0 juveniles on subdominant line years and, thus, depress juvenile mean weights, the higher growth observed for dominant line juveniles in summer surveys was also found in fall samples and in adult scale *C1* (Table 5). Evidence of compensatory growth was evident subsequent to the summer surveys, narrowing the gap between dominant and subdominant line juvenile size but not achieving equity, as evidenced by the adult scale *C1*. A portion of the compensatory growth may be also associated with size-selective predation on the juvenile sockeye/kokanee population. This pattern carried into the first offcycle line where juvenile growth measured by adult *C1* was lower than the dominant line in two of four years despite an order of magnitude or greater lower *EFS*.

Whereas juvenile data for Quesnel sockeye may have been somewhat unique, the consistent negative cycle-line interaction in regressions relating juvenile size and abundance to brood year and prior year *EFS* for both Shuswap and Quesnel sockeye points to suppression of following lines of juvenile sockeye by dominant and, in all probability, by subdominant line juveniles. Suppression of juvenile growth and, as a result, increase of predation mortality on subdominant line juveniles associated with dominant line juvenile abundance and by the combined dominant and subdominant line juvenile effects on the offcycle lines suppress juvenile recruitment on the two offcycle lines. However, the lower abundances on the two offcycle lines may allow zooplankton populations to recover and, thus, do not induce negative impacts on the following dominant line juvenile growth and survival. This leaves the dominant line to be virtually self regulating while the nondominant lines suffer depensatory mortality stimulated by dominant (and subdominant) line juveniles.

The above hypothesis does not require cycling of the predator populations, as proposed by Ward and Larkin (1964) and Larkin (1971), but requires the assumption that predation rate is dependent on the size and abundance of the prey.

A possible scenario in the control of reproduction in cyclic dominant sockeye stocks based on this study, and incorporating previous work and theory, follows:

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(1) dominant line: sockeye fry enter the lakes after one or two years of low *EFS*
abundance and, thus, low juvenile foraging effect on populations of large, preferred
zooplankton (e.g., *Daphnia*). Production of fry from spawning areas is compensatory.
However, at the escapements observed, fry production continues to increase (Figs. 4
and 5). At high *EFS*, such large numbers of fry enter the lakes that density-dependent
growth rates are low and size (*C1*) is best fit by a logarithmic relationship with *EFS*
(i.e., linear with fry abundance). The restricted growth rate of juveniles, in turn,
extends the period of high vulnerability to predation. At very high *EFS*, predation
losses cause the fall juvenile abundance to asymptote or decline slightly. The
leveling off of abundance, combined with continued decline of juvenile size,
produces lower fall juvenile biomass than observed at intermediate escapements. The
effect is that the dominant line year recruitment fits the classical Ricker Curve,
reaching a maximum at an intermediate *EFS* level and declining beyond that point.

(2) subdominant line: fry emergence is compensatory (higher fry/*EFS*) but fry encounter
a depleted food supply either due to the prior year foraging by dominant line juveniles
or by their effect on zooplankton in the spring prior to seaward migration. Growth
rates may be higher than dominant line juveniles but lower than predicted based on
dominant line regressions of growth on *EFS*. Cycle-line interaction is observed as a
result of non-compensatory growth and subsequent depensatory mortality associated
with the lower juvenile density. Fall biomass estimates may be substantially lower
than at a comparable dominant line *EFS* level.

(3) first offcycle line: reduced abundance of fry enter lakes that may remain depleted of
large, preferred *Daphnia* but with large piscivore populations. Non-compensatory
growth and high predation rates result in depensatory mortality.

(4) second offcycle line: low spawner abundance results in low fry production and high
predation mortality despite improved growth rates as the lake zooplankton
populations recover following the first offcycle juvenile sockeye foraging.

**Effects of cycle-line interaction on stock-recruitment model selection**

Understanding the mechanisms leading to and maintaining cyclic dominance is
essential to the management of the stocks. Fisheries and Oceans, Canada's current Fraser

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River Sockeye Spawning Initiative (FRSSI; Cass et al. 2003) seeks to rationalize the management of Fraser River sockeye stocks through the inclusion of biological, economic and social values in the development of escapement management objectives. The focus of the Initiative is on optimizing exploitation rates on the four major sockeye run-timing groups (PSC 1989) through a simulation study involving (1) stock-recruitment (S-R) models for each stock, and (2) an "objective function" that incorporates user group and stakeholder preferences. Cass et al. (2000) reported that all the large Fraser sockeye stocks display significant negative cycle-line interaction in adult recruitment and stressed the need to account for the interaction in decision analyses. However, the Larkin model they used presents computational difficulties in estimation of the escapement producing maximum recruitment ($P_{max}$), escapement at maximum sustained yield (MSY) and optimum exploitation rate. Thus, the tendency in the FRSSI process has been to use the Ricker model as a default S-R model because it appears to capture essential stock dynamics for many stocks and is computationally easier to implement in the simulation model. Because of the uncertainty surrounding the causes of cyclical patterns in Fraser sockeye, the FRSSI currently considers both cyclic and non-cyclical patterns of recruitment for cyclical stocks in Ricker models used in simulations.

However, the cycle-line interaction effects found in juvenile Shuswap and Quesnel sockeye growth, as well as, abundance requires that appropriate S-R models be used to emulate the population dynamics of these stocks. Stock-recruitment models that assume independence of individual brood year spawning and juvenile populations, such as the Ricker model, will likely not represent these dynamics correctly. The use of the Ricker model to estimate the annual escapement level providing $R_{max}$ and MSY may be highly biased for both dominant and off-cycle lines. The bias in estimating optimal escapement on the dominant line stems from the non-compensatory recruitment on non-dominant lines. Fitting of the Ricker model to all years of data results in lower Ricker regression parameter values (a and b) than obtained from fitting only dominant line data, resulting in over-estimation of $P_{max}$ and $P_{msy}$ and under-estimation of optimum exploitation rate.

The bias in the estimation of optimum P for non-dominant lines results from the fact that the fitting of cyclical stock data the model must, by definition, use those data collected while the stock is in a cyclical pattern wherein cycle-line effects are manifest in

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the recruitment. Hence, the application of the Ricker model to cyclic dominant Fraser sockeye stocks must necessarily be restricted to cyclical patterns of abundance. When simulated in a non-cyclical pattern, the cycle-line interaction effects would not be represented correctly, over-estimating the annual escapement level required for $R_{max}$ and MSY and underestimating the optimum exploitation rate.

In addition, as data for cyclical stocks have been collected under the constraints of juvenile survival rates associated with the cyclical pattern of abundance and the effect of highly variable juvenile sockeye abundance on the ecology of the lake environment, models that suggest that equal annual escapement would provide the optimum recruitment (Collie and Walters 1987; Welch and Noakes 1990; Welch and Noakes 1991) fail to anticipate changes to lake dynamics following equalization of annual juvenile sockeye populations under a constant annual escapement policy. Zooplankton population structure would likely change due to annual cropping by juvenile sockeye and predator populations would likely increase as their juvenile sockeye forage base becomes less variable.

## Conclusions

Shuswap and Quesnel Lake stocks display cyclic dominance associated with cycle-line interaction in the growth of juveniles. In Quesnel Lake, we saw how the mechanism may work: dominant line juveniles deplete the food resources available to juveniles of following broods, resulting in non-compensatory growth and probable non-compensatory abundance in the subdominant and offcycle line juvenile populations. This mechanism was not evident in Shuswap juvenile sockeye that were available, but was indicated from the longer term of growth data from adult scales.

Recruitment of Chilko sockeye does not follow the classical cyclic dominance pattern observed in Shuswap and Quesnel sockeye. Chilko sockeye recruitment appeared to be related to strong compensation in egg-to-fry survival at high *EFS* and to depensatory mortality at low *EFS*. The cycle-line interaction observed in Chilko sockeye appears related to fry production, however the available data did not allow us to discern a

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mechanism for the effect. No cycle-line interaction was apparent in the lake survival and adult recruitment other than that initiated in the production of fry.

The weight of evidence suggests that cyclic dominance in Fraser River sockeye salmon stocks is biological in nature rather than being maintained by extrinsic forces, such as via exploitation patterns. Cass and Wood (1994) arrived at the conclusion that the fishery effect could only be argued in the case of the Adams River Late-run sockeye population. Non-compensatory recruitment (Appendix B) resulting from size-mediated depensatory predation appears to be the mechanism that maintains cyclic dominance.

## Sources of error

Data quality varied between stocks associated with the stock size and location in the watershed. Large, accessible stocks may provide more accurate *EFS* and recruitment estimates due to lower relative error in estimation procedures. In contrast, stocks inhabiting remote locations may be subject to larger random error of estimates associated with conducting escapement estimation programs when access is poor. Also, effective female spawner and recruitment estimates used in this study may be subject to errors since they were collected by differing field methods depending on abundance and other factors. Use of information collected with inconsistent methods may introduce uncertainty and bias into the analyses. While random errors may simply affect the fit of the data, bias, if present, could invalidate some analyses.

The summing of *EFS* and recruitment estimates for all stocks within each lake system ignores the dynamics of individual stocks and local variation, such as environmentally induced survival, particularly in the unique stream environments. While individual stock data were summed to analyze juvenile growth and abundance in the lakes where we could not assign individual juvenile fish to stock of origin, there could be negative effects associated with interannual variation in the contributions of individual stocks to the combined total. Compensatory fry production on some stocks and not on others may obscure issues of juvenile growth and survival.

As well, growth estimates from both adult scales and juvenile collections may contain random errors or biases. In the latter case, we sought to minimize time series effects

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caused by the change in scale analysis protocols by utilizing reanalyzed scale age and circuli count data. However, we relied largely on the consistency of the regression parameter signs and data fits between adult and juvenile data sets to conclude that we were observing functional relationships.

We identified four issues associated with use of Shuswap and Quesnel Lake juvenile sockeye data: (1) short time series of data (15-16 years), (2) data primarily from dominant and subdominant lines, (3) measurement error/imprecision in estimates of juvenile abundance in lake surveys, and (4) potential bias introduced by age 0 kokanee. We assumed that the abundance of age 0 kokanee in each lake were similar from year to year and were not cycling out of phase with age-0 sockeye. If this assumption was incorrect, biased estimates of the intercept relating abundance to sockeye *EFS* would be expected but should not invalidate tests of hypothesis regarding cycle-line interaction on abundance. Tests of hypotheses regarding estimates of juvenile size are more sensitive to the inclusions of juvenile kokanee as they are normally smaller than juvenile sockeye at a common age (Hume et al. 1996). However, we attempted to minimize this effect by limiting our analysis of juvenile size to years of high sockeye abundance. The analysis of paired dominant:subdominant Quesnel summer juvenile mean weight data from brood years 1985-2002 showed a consistent difference between lines regardless of escapement level, indicating that kokanee did not overly influence the outcome of the analysis.

At times, high regression fits between abundance or growth and *EFS* became a concern. Cyclic dominant sockeye stocks provide natural, large ranges (up to three orders of magnitude) in the independent variables. Density dependence in abundance and growth were expected and observed in brood year relationships. The finding that prior brood year *EFS* variables had significant impacts may simply be an artifact of biases associated with time series events due to the regular pattern of abundance. However, we examined the residuals of the regression fits and found no significant biases associated with cycle line.

We also examined data for other Fraser River sockeye stocks in an attempt to ascertain if the effect we measured for the three lakes in this analysis was typical. In upper Fraser watershed lakes, we found that more stocks provided evidence of cycle-line interaction (Gates, Stellako, Stuart and Trembleur) than did not (Bowron and Takla).

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# Recommendations

Additional studies should be undertaken to elucidate the uncertain aspects of juvenile sockeye growth and survival in Shuswap and Quesnel Lakes. Particularly important is collection of information on smolt recruitment on all cycle lines to obtain ending point information on juvenile production dynamics. Studies of outmigrant smolts at Chilko Lake have proved invaluable in research and management of that stock complex. Similar data programs on the other large sockeye stocks in the Fraser watershed appear warranted given the results of our study. Estimation of fall juvenile abundance and size are attempts to obtain similar information in another manner. While successfully measuring population parameters in the fall they suffer from a degree of imprecision and may be affected by resident kokanee populations, especially in years of low sockeye abundance. In addition, unlike smolt data, they do not reflect all of the environmental influences of the full lacustrine life history period.

Studies on sockeye fry recruitment from low *EFS* escapement years in cyclical and non-cyclical stocks would be invaluable in ascertaining whether or not presumed cyclic dominance in some stocks stems from depensatory fry mortality, such as indicated at Chilko River, rather than from cycle-line interaction effects observed in Shuswap and Quesnel Lakes. Fry populations that have treacherous downstream or upstream migration may suffer strong depensatory mortality associated with piscivorous fish and avian predation. Clarifying these issues is essential to understanding the population dynamics of individual Fraser sockeye stocks.

Simulation modeling of stock-recruitment relationships employing information generated by this study has been conducted (Holt et al. 2005), however, dynamic modeling of the growth and mortality relationships based on insights from these studies and other research is needed to resolve questions that remain in regard to potential recruitment on offcycle lines. Particular attention should be focused on predictions of juvenile mortality rates associated with predator population changes if management policies were to change from that of supporting the natural cyclic dominance to one wherein achieving equal annual escapements through harvest management became policy.

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## Acknowledgements

## References

Beacham, T.D., Lapointe, M., Candy, J.R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Deng, L., Miller, K.M., and Withler, R.E. 2004. Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. Trans. Am. Fish. Soc. **133**:1117-1137.

Bradford, M.J., Pyper, B.J., and Shortreed, K.S. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. N. Am. J. Fish. Managemt. **20:** 661-671.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. Intern. Pac. Salmon Fish. Comm. Bull. No. 21.

Cass, A.J., and Wood, C.C. 1994. Evaluation of the depensatory fishig hypothesis as an explanation for population cycles in Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **51**: 1839-1854.

Cass, A.J., Folkes, M., and Pestal, G. 2003. Methods for assessing harvest rules for Fraser River sockeye salmon. Fish. and Oceans Canada. Pacific Scientific Advice Review Committee Working Paper S2003-14. 86 p.

Clutter, R.I, and Whitesel, L.E. 1956 Collection and interpretation of sockeye salmon scales. Int. Pac. Salmon Fish. Comm. Bull. No. 9.

Collie, J.S., and Walters, C.J. 1987. Alternative recruitment models of Adams River sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. **44**: 1551-1561.

Foerster, R.E., and Ricker, W.E. 1942. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Bd. Can. **5**: 315-336.

Gable, J., and Cox-Rogers, S. 1993. Stock identification of Fraser River sockeye salmon: methodology and management application. Pac. Salmon Comm. Tech. Rep. No. 5

Gilbert, C.H. 1914. Contributions to the life history of the sockeye salmon. No. 1. *In* Report of the Commissioner of Fisheries for British Columbia for 1913. B.C. Prov. Dept. Fish. pp. 53-78.

Goodlad, J.C., Gjernes, T.W., and Brannon, E.L. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. **31**: 871-892.

Henderson, M.A., and Cass, A.J. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48**:988-994.

Henry, K.A. 1961. Racial identification of Fraser River sockeye and pink salmon by means of scales and its application to salmon management. Int. Pac. Salmon Fish. Comm. Bull. No. 12.

Holt, C.A., Peterman, R.M., Woodey, J.C., and Lapointe, M.F. 2005. Simulation of the Juvenile Growth model for cyclical stocks of Fraser River, British Columbia, sockeye salmon (*Oncorhynchus nerka*). *Manuscript in preparation*.

Hume, J.M.B., Shortreed, K.S., and Morton, K.F. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Can. J. Fish. Aquat. Sci. **53**:719-733.

57

International Pacific Salmon Fisheries Commission. 1964. Annual Report for 1963. 46 p.

Larkin, P.A. 1971. Simulation studies of the Adams River sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. **28**:1493-1502.

Larkin, P.A. and MacDonald, J.G. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Anim. Ecol. **37**:229-258.

Levy, D.A., and Wood, C.C. 1992. Review of proposed mechanisms for sockeye salmon cycles in the Fraser River. Bull. Math. Biol. **54**: 241-261.

Levy, D.A. 1990. Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerka* Can. J. Fish. Aquat. Sci. **47**: 1796-1802.

Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J.Fish. Res. Bd. Can., **9**: 450-491.

Pacific Salmon Commission. 1989. Report of the Fraser River Panel to the Pacific Salmon Commission on the 1988 Fraser River sockeye salmon fishing season. 38 p.

Ricker, W.E. 1950. Cyclic dominance among the Fraser sockeye. Ecol. **31:** 6-26.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**:559-623.

Ricker, W.E. 1997. Cycles of abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **54**:950-968.

Schubert, N.D. 1998. The 1994 Fraser River sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Tech. Rpt. Fish. Aquat. Sci. No. 2201.

Thompson, W.F. 1945. Effect of the obstruction at Hells Gate on the sockeye salmon of the Fraser River. Int. Pac. Salmon Fish. Comm. Bull. No. 1.

Walters, C.J. and Staley, M.J. 1987. Evidence against the existence of cyclic dominance in Fraser River sockeye salmon (*Oncorhynchus nerka*). pp. 375-384. *In*: H.D. Smith, L. Margolis, and C.C. Wood (eds.). Sockeye salmon population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci., No. 96.

Ward, F.J. and Larkin, P.A. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fisheries Comm., Prog. Rep. No. 11.

Welch, D.W., and Noakes, D.J. 1990. Cyclic dominance and optimal escapement of Adams River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **47:** 838-849.

58

Welch, D.W., and Noakes, D.J. 1991. Optimal harvest rate policies for rebuilding the Adams River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **48:** 526-535.

Williams, I.V., Gilhousen, P., Saito, W., Gjernes, T., Morton, K.F., Johnson, R., and Brock, D. 1989. Studies of the lacustrine biology of the sockeye salmon (*Oncorhynchus nerka*) in the Shuswap system. Int. Pac. Salmon Fish. Comm. Bull. No. 24.

Woodey, J.C. 1987. In-season management of Fraser River sockeye (*Oncorhynchus nerka*): meeting multiple objectives. pp 367-374. *In*: H.D. Smith, L. Margolis, and C.C. Wood (eds.). Sockeye salmon population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci., No. 96.

# Appendix A

**Table 1.** Total adults and effective female spawner (*EFS*) abundance and total recruitment, and sample size and mean circuli counts (*C1 and C2*) from scales.

a) Shuswap Lake sockeye salmon.

| Brood Year | Adult Escapement | Effective Females (EFS) | Total Recruits | L. Adams River recruit scale data | | |
|---|---|---|---|---|---|---|
| | | | | n | C1 | C2 |
| 1948 | 14,255 | 9,787 | 58,039 | 50 | 15.98 | 18.66 |
| 1949 | 16,157 | 6,498 | 68,023 | 50 | 15.18 | 18.04 |
| 1950 | 1,282,474 | 587,760 | 10,120,078 | 50 | 9.72 | 11.76 |
| 1951 | 167,818 | 93,602 | 598,525 | 50 | 11.30 | 14.24 |
| 1952 | 13,292 | 7,001 | 29,216 | 50 | 14.50 | 16.76 |
| 1953 | 10,528 | 5,310 | 81,171 | 35 | 16.49 | 19.11 |
| 1954 | 2,051,483 | 1,080,073 | 16,330,861 | 50 | 9.42 | 12.02 |
| 1955 | 72,841 | 49,815 | 1,175,522 | 50 | 11.48 | 14.28 |
| 1956 | 5,819 | 3,213 | 20,737 | 50 | 14.82 | 17.70 |
| 1957 | 16,052 | 10,043 | 50,402 | 44 | 16.28 | 20.65 |
| 1958 | 3,375,559 | 1,174,746 | 2,411,618 | 50 | 9.90 | 13.92 |
| 1959 | 187,136 | 115,043 | 558,282 | 50 | 11.78 | 14.48 |
| 1960 | 4,808 | 3,184 | 11,386 | 50 | 14.64 | 18.02 |
| 1961 | 5,370 | 3,106 | 69,361 | 50 | 15.60 | 19.26 |
| 1962 | 1,202,202 | 679,405 | 3,109,210 | 50 | 10.02 | 12.48 |
| 1963 | 230,129 | 106,990 | 3,245,432 | 50 | 10.56 | 13.36 |
| 1964 | 3,349 | 1,666 | 38,124 | 50 | 14.76 | 17.94 |
| 1965 | 10,086 | 4,660 | 128,193 | 50 | 16.06 | 19.34 |
| 1966 | 1,309,752 | 674,118 | 4,211,207 | 50 | 9.68 | 13.78 |
| 1967 | 858,261 | 409,696 | 3,405,502 | 50 | 9.48 | 12.70 |
| 1968 | 7,524 | 4,777 | 44,426 | 50 | 16.66 | 19.88 |
| 1969 | 16,574 | 7,768 | 76,588 | 50 | 15.44 | 19.32 |
| 1970 | 1,536,797 | 789,114 | 5,813,456 | 50 | 10.42 | 12.86 |
| 1971 | 308,968 | 168,457 | 837,435 | 50 | 12.54 | 15.36 |
| 1972 | 6,998 | 3,575 | 102,874 | N/A | 14.36* | 18.24* |
| 1973 | 12,758 | 6,589 | 116,760 | 50 | 16.74 | 19.70 |
| 1974 | 1,193,741 | 644,094 | 7,163,948 | 50 | 10.24 | 13.96 |
| 1975 | 210,003 | 102,280 | 1,242,320 | 50 | 11.78 | 14.56 |
| 1976 | 13,120 | 7,990 | 32,890 | 50 | 12.80 | 16.86 |
| 1977 | 31,870 | 15,648 | 201,417 | 50 | 14.26 | 17.36 |
| 1978 | 1,952,755 | 1,041,382 | 9,261,075 | 50 | 8.96 | 12.54 |
| 1979 | 348,547 | 186,780 | 1,637,171 | 50 | 11.12 | 14.16 |
| 1980 | 10,914 | 6,494 | 77,687 | 49 | 13.98 | 17.08 |
| 1981 | 40,604 | 18,191 | 65,712 | 13 | 14.69 | 18.08 |
| 1982 | 3,095,326 | 1,594,308 | 9,822,874 | 50 | 9.38 | 13.56 |
| 1983 | 242,208 | 114,789 | 2,261,840 | 50 | 12.26 | 15.90 |
| 1984 | 21,916 | 11,816 | 71,816 | 49 | 13.82 | 17.82 |
| 1985 | 10,293 | 4,809 | 92,998 | 24 | 17.25 | 20.71 |
| 1986 | 2,430,505 | 1,114,128 | 11,756,987 | 219 | 9.87 | 13.76 |
| 1987 | 706,078 | 363,187 | 4,406,633 | 220 | 9.81 | 12.83 |
| 1988 | 22,924 | 12,289 | 23,411 | 13 | 12.69 | 16.15 |
| 1989 | 13,481 | 7,213 | 49,108 | 104 | 14.63 | 17.91 |
| 1990 | 4,006,439 | 1,848,126 | 8,334,597 | 272 | 8.74 | 13.46 |
| 1991 | 1,402,463 | 684,736 | 955,510 | 253 | 9.66 | 13.30 |
| 1992 | 21,520 | 11,811 | 39,379 | 46 | 13.87 | 15.91 |
| 1993 | 20,047 | 9,060 | 38,030 | 24 | 14.88 | 18.42 |
| 1994 | 1,544,343 | 705,201 | 3,066,626 | 227 | 10.64 | 13.00 |
| 1995 | 502,712 | 247,574 | 873,921 | 230 | 11.47 | 13.66 |
| 1996 | 44,372 | 19,809 | 118,453 | 11 | 13.09 | 14.91 |
| 1997 | 7,007 | 2,943 | 37,314 | 46 | 15.11 | 18.17 |
| 1998 | 1,480,395 | 722,812 | 7,617,169 | 212 | 11.81 | 14.35 |
| 1999 | 372,359 | 153,359 | 837,801 | 244 | 11.44 | 13.64 |

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* Estimated based on regression of re-analyzed means on original reading means. Original mean = 14.9 circuli.

b) Quesnel Lake sockeye salmon.

| Brood Year | Adult Escapement | Effective Females (EFS) | Total Recruits | U. Horsefly River recruit scale data | | |
|---|---|---|---|---|---|---|
| | | | | n | C1 | C2 |
| 1948 | 100 | 48 | 1,132 | 24 | 18.13 | 21.33 |
| 1949 | 30,664 | 19,210 | 485,864 | 50 | 16.26 | 18.22 * |
| 1950 | 398 | 264 | 2,048 | 34 | 17.65 | 19.62 |
| 1951 | 49 | 9 | 413 | | | |
| 1952 | 184 | 51 | 562 | | | |
| 1953 | 110,917 | 47,564 | 610,245 | 50 | 15.48 | 17.90 * |
| 1954 | 299 | 146 | 10,692 | 50 | 16.24 | 17.64 |
| 1955 | 63 | 30 | 180 | | | |
| 1956 | 81 | 39 | 2,553 | 36 | 16.86 | 19.17 |
| 1957 | 223,667 | 134,562 | 998,113 | 50 | 15.94 | 19.14 * |
| 1958 | 1,863 | 1,269 | 3,412 | 50 | 14.64 | 16.48 |
| 1959 | 65 | 29 | 165 | 20 | 18.35 | 20.20 |
| 1960 | 292 | 123 | 1,475 | 20 | 21.90 | 23.60 |
| 1961 | 302,565 | 70,003 | 1,240,890 | 50 | 15.52 | 18.12 * |
| 1962 | 1,078 | 566 | 7,287 | 50 | 17.16 | 18.94 |
| 1963 | 83 | 40 | 956 | | | |
| 1964 | 254 | 77 | 2,812 | | | |
| 1965 | 364,706 | 105,393 | 1,667,172 | 50 | 14.24 | 17.16 * |
| 1966 | 1,753 | 1,040 | 7,462 | 50 | 16.38 | 18.98 |
| 1967 | 119 | 24 | 1,761 | 12 | 16.83 | 19.92 |
| 1968 | 699 | 333 | 497 | | | |
| 1969 | 278,961 | 78,637 | 1,640,763 | 50 | 15.54 | 17.90 * |
| 1970 | 1,368 | 388 | 20,339 | 50 | 15.46 | 16.88 |
| 1971 | 171 | 16 | 747 | | | |
| 1972 | 111 | 46 | 1,392 | 16 | 15.50 | 17.13 |
| 1973 | 278,061 | 112,411 | 2,161,425 | 50 | 15.74 | 18.52 * |
| 1974 | 4,459 | 2,587 | 21,222 | 50 | 16.66 | 18.62 |
| 1975 | 193 | 105 | 1,713 | 12 | 18.00 | 20.08 |
| 1976 | 305 | 209 | 1,233 | 9 | 18.00 | 20.44 |
| 1977 | 516,199 | 160,719 | 3,878,522 | 50 | 15.86 | 17.02 * |
| 1978 | 8,614 | 4,349 | 196,724 | 50 | 16.46 | 18.14 * |
| 1979 | 511 | 238 | 6,011 | 22 | 16.36 | 18.55 |
| 1980 | 308 | 98 | 2,446 | | | |
| 1981 | 748,621 | 332,290 | 9,786,652 | 50 | 13.86 | 15.82 * |
| 1982 | 39,841 | 20,043 | 558,961 | 50 | 15.30 | 17.52 * |
| 1983 | 2,155 | 1,098 | 41,856 | 45 | 16.20 | 18.09 |
| 1984 | 914 | 551 | 6,953 | 39 | 17.87 | 19.85 |
| 1985 | 1,317,751 | 676,842 | 12,518,670 | 50 | 13.68 | 14.98 * |
| 1986 | 181,467 | 94,841 | 2,532,784 | 268 | 14.16 | 16.16 * |
| 1987 | 20,546 | 11,238 | 176,592 | 28 | 15.46 | 16.82 * |
| 1988 | 6,832 | 4,185 | 28,464 | 11 | 16.82 | 18.18 * |
| 1989 | 1,870,820 | 940,551 | 10,640,256 | 267 | 13.13 | 13.66 * |
| 1990 | 487,644 | 259,218 | 3,294,605 | 249 | 13.05 | 14.65 * |
| 1991 | 46,259 | 24,861 | 151,606 | 14 | 13.57 | 15.29 * |
| 1992 | 5,862 | 3,046 | 27,790 | 23 | 15.65 | 16.78 * |
| 1993 | 2,620,454 | 1,507,349 | 6,908,501 | 301 | 13.82 | 14.70 * |
| 1994 | 659,499 | 365,251 | 2,691,804 | 214 | 13.04 | 14.60 * |
| 1995 | 216,109 | 116,867 | 167,188 | 77 | 13.30 | 14.69 * |
| 1996 | 41,187 | 21,719 | 91,070 | 77 | 14.39 | 15.99 * |
| 1997 | 1,858,652 | 904,914 | 4,741,124 | 241 | 12.51 | 14.12 * |
| 1998 | 1,179,252 | 534,532 | 4,519,940 | 238 | 12.38 | 13.71 * |
| 1999 | 189,360 | 106,908 | 768,158 | 119 | 12.39 | 14.26 * |

* Years > 3,000 EFS selected for use in estimating parameters of Quesnel Lake models.

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c) Chilko Lake sockeye salmon.

| Brood Year | Adult Escapement | Effective Females (EFS) | Total Recruits | Chilko River recruit scale data | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | | | n | C1* | C2* |
| 1948 | 670,622 | 364,597 | 1,947,973 | 326 | 10.78 | 11.45 |
| 1949 | 58,247 | 33,029 | 623,138 | 139 | 10.93 | 12.75 |
| 1950 | 17,308 | 6,555 | 205,875 | 167 | 13.98 | 14.40 |
| 1951 | 100,116 | 57,564 | 752,327 | 151 | 12.54 | 12.93 |
| 1952 | 485,585 | 233,628 | 1,858,476 | 159 | 11.96 | 13.25 |
| 1953 | 200,691 | 94,471 | 619,456 | 129 | 10.34 | 11.46 |
| 1954 | 34,296 | 21,247 | 712,749 | 141 | 11.03 | 12.54 |
| 1955 | 121,167 | 75,834 | 1,513,275 | 352 | 14.54 | 14.97 |
| 1956 | 646,906 | 368,607 | 2,435,670 | 544 | 12.52 | 14.82 |
| 1957 | 138,464 | 83,128 | 138,228 | 149 | 13.29 | 13.90 |
| 1958 | 120,104 | 70,433 | 433,371 | 534 | 11.35 | 12.80 |
| 1959 | 463,060 | 272,891 | 2,212,583 | 480 | 10.28 | 12.46 |
| 1960 | 426,546 | 244,864 | 1,053,335 | 528 | 11.47 | 12.06 |
| 1961 | 39,101 | 15,038 | 69,453 | 176 | 14.02 | 14.61 |
| 1962 | 77,713 | 42,125 | 985,562 | 169 | 17.23 | 18.32 |
| 1963 | 998,231 | 57,207 | 1,206,303 | 197 | 10.24 | 11.71 |
| 1964 | 238,272 | 131,590 | 2,040,082 | 565 | 10.94 | 11.83 |
| 1965 | 35,335 | 20,813 | 158,944 | 232 | 10.25 | 13.62 |
| 1966 | 209,619 | 107,541 | 889,200 | 549 | 14.31 | 14.94 |
| 1967 | 174,715 | 90,006 | 2,004,710 | 368 | 10.85 | 14.24 |
| 1968 | 413,862 | 181,912 | 2,476,069 | 381 | 11.59 | 14.28 |
| 1969 | 70,902 | 25,519 | 402,359 | 294 | 14.91 | 15.84 |
| 1970 | 135,388 | 50,923 | 694,456 | 331 | 10.35 | 12.93 |
| 1971 | 157,193 | 90,643 | 852,842 | 311 | 10.82 | 13.78 |
| 1972 | 562,650 | 332,338 | 2,033,998 | 372 | 9.93 | 12.58 |
| 1973 | 55,675 | 30,231 | 220,403 | 339 | 11.86 | 14.61 |
| 1974 | 110,026 | 71,169 | 620,588 | 309 | 13.41 | 13.86 |
| 1975 | 244,631 | 135,247 | 1,640,640 | 281 | 9.98 | 12.85 |
| 1976 | 384,390 | 228,398 | 1,699,775 | 314 | 11.34 | 15.27 |
| 1977 | 51,330 | 20,787 | 199,200 | 311 | 16.21 | 17.09 |
| 1978 | 146,842 | 85,570 | 1,265,579 | 256 | 12.86 | 13.38 |
| 1979 | 249,391 | 148,320 | 1,721,513 | 123 | 11.08 | 14.59 |
| 1980 | 497,759 | 293,222 | 4,441,927 | 96 | 11.65 | 13.28 |
| 1981 | 34,540 | 20,164 | 208,706 | 36 | 13.02 | 14.33 |
| 1982 | 249,578 | 142,534 | 1,599,217 | 216 | 11.66 | 15.21 |
| 1983 | 382,833 | 213,715 | 2,119,741 | 216 | 11.56 | 12.44 |
| 1984 | 580,178 | 283,147 | 676,360 | 146 | 11.66 | 14.69 |
| 1985 | 71,975 | 34,995 | 572,968 | 191 | 13.02 | 15.36 |
| 1986 | 293,804 | 165,505 | 4,800,439 | 262 | 12.89 | 14.67 |
| 1987 | 421,015 | 268,105 | 4,420,836 | 268 | 11.99 | 14.40 |
| 1988 | 363,389 | 206,156 | 3,296,360 | 214 | 13.43 | 14.05 |
| 1989 | 63,268 | 42,813 | 3,117,371 | 145 | 15.99 | 16.26 |
| 1990 | 825,837 | 497,991 | 2,633,844 | 301 | 12.85 | 14.08 |
| 1991 | 1,037,737 | 597,537 | 1,411,982 | 217 | 14.02 | 14.98 |
| 1992 | 511,267 | 319,959 | 1,876,043 | 201 | 14.98 | 15.71 |
| 1993 | 555,226 | 322,298 | 3,904,015 | 316 | 14.97 | 15.87 |
| 1994 | 450,745 | 253,976 | 1,230,103 | 181 | 12.90 | 14.34 |
| 1995 | 544,364 | 298,074 | 1,276,189 | 155 | 11.03 | 13.45 |
| 1996 | 974,349 | 504,469 | 1,370,791 | 199 | 10.27 | 12.38 |
| 1997 | 985,827 | 509,298 | 912,432 | 183 | 11.34 | 13.01 |
| 1998 | 879,010 | 467,624 | 578,634 | 157 | 11.16 | 12.78 |
| 1999 | 891,567 | 432,565 | 1,507,005 | 253 | 12.03 | 14.23 |

* Chilko C1 and C2 for brood years 1948-1985 estimated by regression.

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# Appendix B

Table 1. Sockeye salmon recruitment by stock and cycle line.

a) Shuswap Lake sockeye (all stocks) cycle line mean escapement and recruitment data, brood years 1948-1999.

| Line | # Years | Mean EFS | Mean R | Arith. Mean R/EFS | Mean log e(R/EFS) | Geo. Mean R/EFS |
|------|---------|----------|--------|-------------------|-------------------|-----------------|
| 1 (1950-98) | 13 | 974131 | 7,685,347 | 8.43 | 1.99 | 7.29 |
| 2 (1951-99) | 13 | 212576 | 1,696,283 | 10.98 | 2.11 | 8.22 |
| 3 (1948-96) | 13 | 7946 | 50,973 | 8.74 | 1.87 | 6.50 |
| 4 (1949-97) | 13 | 7836 | 91,317 | 14.30 | 2.47 | 11.86 |

b) Quesnel Lake sockeye cycle line mean escapement and recruitment data, brood years 1948-1999.

| Line | # Years | Mean EFS | Mean R | Arith. Mean R/EFS | Mean log e(R/EFS) | Geo. Mean R/EFS |
|------|---------|----------|--------|-------------------|-------------------|-----------------|
| 1 (1950-98) | 13 | 391,573 | 4,406,015 | 16.34 | 2.65 | 14.21 |
| 2 (1951-99) | 13 | 98,807 | 1,066,714 | 22.52 | 2.69 | 14.79 |
| 3 (1948-96) | 13 | 20,113 | 101,334 | 23.99 | 2.71 | 15.02 |
| 4 (1949-97) | 13 | 2,348 | 12,952 | 18.79 | 2.52 | 12.40 |

c) Chilko Lake sockeye cycle line mean escapement and recruitment data, brood years 1948-1999.

| Line | # Years | Mean EFS | Mean R | Arith. Mean R/EFS | Mean log e(R/EFS) | Geo. Mean R/EFS |
|------|---------|----------|--------|-------------------|-------------------|-----------------|
| 1 (1950-98) | 13 | 284,068 | 2,092,835 | 8.38 | 1.95 | 7.05 |
| 2 (1951-99) | 13 | 96,353 | 857,436 | 14.26 | 2.18 | 8.88 |
| 3 (1948-96) | 13 | 152,553 | 1,280,740 | 14.73 | 2.37 | 10.65 |
| 4 (1949-97) | 13 | 210,593 | 1,741,534 | 11.86 | 2.28 | 9.79 |

# Appendix C

**Scale and age analysis methods**

Scale and otolith samples were stored dry in sample books along with sex, length and other observational information for each fish. Plastic impressions were made of the scales soon after sampling. Archival collections of scale impressions were used in the re-analyses of scale samples in this study. Otoliths were stored dry and analyzed in water. Scales of sockeye caught in marine and lower Fraser waters generally show all freshwater and most marine circuli. Thus, the number of freshwater and marine annuli and freshwater scale circuli counts are readily obtained for stock identification programs. However, scales collected from fish recovered post-spawned on the rivers and streams of the Fraser watershed generally are resorbed to the point that the last marine annulus, or more, is absent. Scale age (when available), length and circuli counts were used to apportion the escapement into age group by sex for samples collected between 1952 and mid 1960s. Beginning in early to mid 1960s, otoliths were added to the collections and analyzed to estimate the freshwater age and determine the marine age of individual fish more precisely. The freshwater growth portion of the scale is also used to estimate the freshwater age. Use of both scale and otolith ages generally provide accurate estimates of freshwater and marine ages.

Spawner age estimates for Lower Adams River and Upper Horsefly River sockeye stocks were reexamined for the current study because of concern that errors in age determination had not been addressed earlier. Corrections for misinterpretation of false annuli in the freshwater growth zone of age $4_2$ Adams sockeye (originally classified as age $5_3$) have been reported elsewhere (Ricker 1997). However, more recent evidence of misinterpretation of age $3_1$ fish (originally classified as age $4_2$ based on otolith appearance) has now been addressed by reexamination of scales and length data for samples collected at these sites. While minor in nature for most years, both types of aging error had the impact of overestimating recruitment on the second offcycle line at the expense of the dominant line. Recruitment estimates attributed to second offcycle line years were overestimated by up to 200%. Herein we use the revised age estimates to identify age $4_2$ fish for selection of scale samples and for recruitment estimates.

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Counts of circuli on the freshwater portion of the scale provide measures of the size of the fish at annulus formation in the winter-spring in the rearing lake and as a seaward migrant smolt. Original circuli count analyses were conducted each fall/winter of the collection year. In addition to circuli counts, the distances from the scale origin to the first annulus and to the end of the freshwater growth were measured using a digitizing pad beginning in 1990.

Plastic impression of Adams River and Upper Horsefly River adult sockeye scales collected between 1952 and 2003 were reexamined to ensure consistency of scale analysis. We reanalyzed annual samples of 50 (or as many as were available when n ≥ 10) Adams River and Upper Horsefly River sockeye scales collected from age $4_2$ recruits returning in 1952-1989 (brood years 1948-1985), plus four randomly chosen years between 1990-2003, to determine if revised scale analysis protocols introduced in 1990 resulted in scale reading biases between periods. An experienced scale analyst assessed scales for circuli count and digitized scale measurement to the freshwater annulus (*C1* and *D1*; Henderson and Cass 1991) and to the end of the freshwater growth (*C2* and *D2*). The reanalysis of 1952-1989 scales were found to be at variance with original readings, but more significant was a lack of consistency of original readings relative to the new readings. Regression of reanalyzed on original annual mean *C1* and *C2* showed counts were highly correlated in Adams and Upper Horsefly scales, however, the data points fell off the 1:1 line. Examination of the annual differences between readings showed a consistently higher 0.5-1.0 circuli in original mean *C1* readings. However, mean *C2* circuli counts showed time-series bias with similar original and reanalyzed readings from 1952 to the late 1960s, but original circuli counts from the late 1960's to1989 were 0.3-1.4 circuli higher than the reanalyzed counts. Reanalyzed scale samples from the 1990-2003 period showed annual mean scale circuli counts and digitized measurements close to the original readings with mean differences of < 0.1 circulus (Adams: C1 mean = 0.02; S.D. = 0.058; Horsefly: C1 mean = -0.09; S.D. = 0.076).

Due to the apparent bias and/or time series differences in the reading of pre-1990 Adams and Horsefly scales, the 2004 reanalyzed scale circuli counts and digitized scale measurements for 1952-1989 were used in the present analysis, along with the original estimates for 1990-2003, which were shown to be similar to the reanalyzed estimates (see

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Appendix A for data). Combined stock regressions of reanalyzed on original annual means were applied to the original $C1$ and $C2$ estimates for Chilko River and Seymour River age $4_2$ sockeye to obtain predicted $C1$ and $C2$ estimates which would have been consistent with the revised scale analysis protocols adopted in 1990.