Juvenile sockeye rearing capacity of three lakes in the Fraser River system

Jeremy M.B. Hume, Ken S. Shortreed, and Ken F. Morton

Abstract: We used three methods to estimate sockeye salmon (*Oncorhynchus nerka*) escapements that maximize production (S_{MAX}) in Fraser River lakes: (*i*) effective female spawners and adult returns using Ricker stock-recruit analysis (SR models), (*ii*) effective female spawners and fall fry or smolts (fry models), and (*iii*) photosynthetic rates (PR model), a modification of an Alaskan sockeye production model (EV model). Adult SR models were not useful in predicting S_{MAX} because of high variability in Shuswap and Chilko lakes (r^2 < 11%) and because of linearity in Quesnel Lake. Fry models using Ricker stock-recruit analysis provided S_{MAX} escapements of 0.90, 1.38, and 1.06 million for Quesnel, Shuswap, and Chilko lakes but were still highly variable (r^2 < 51%). Fry data indicated that fry numbers did not increase above escapements of 0.85, 1.5, and 0.51 million to Quesnel, Shuswap, and Chilko lakes. PR model predictions of S_{MAX} escapements to Quesnel, Shuswap, and Chilko lakes of 1.06, 1.85, and 0.62 million were similar to escapements that first produced maximum observed fry numbers. While fry models provide a direct estimate of rearing capacity, many years of data are required to generate a relationship for any lake. The PR model appears to be a useful predictor of rearing capacity and predictions can be made after 1–2 years.

Résumé : Nous avons utilisé trois méthodes pour estimer les échappées de saumons sockeye (*Oncorhynchus nerka*) en vue de maximiser la production (S_{MAX}) dans les lacs du fleuve Fraser : (*i*) retours des géniteurs femelles efficaces et des adultes par analyse des stocks-recrues à l'aide de la technique de Ricker (modèles SR), (*ii*) les géniteurs femelles efficaces et alevins ou saumoneaux d'automne (modèles des alevins) et (*iii*) taux de photosynthèse (modèle PR), une variante d'un modèle de production de sockeye d'Alaska (modèle EV). Les modèles SR des adultes n'étaient guère utiles pour prévoir la valeur de S_{MAX}, en raison de la grande variabilité des lacs Shuswap et Chilko (r^2 < 11%) et de la linéarité dans le lac Quesnel. Les modèles d'alevins faisant appel à l'analyse des stocks-recrues à l'aide de la technique de Ricker a donné des échappées S_{MAX} de 0,90, 1,38 et 1,06 million pour les lacs Quesnel, Shuswap et Chilko, mais ces valeurs étaient encore très variables (r^2 < 51%). Les données sur les alevins indiquaient que leur nombre n'augmentait pas au-dessus des échappées de 0,85, 1,5 et 0,51 million pour les lacs Quesnel, Shuswap et Chilko. Les prévisions du modèle PR pour les échappées S_{MAX} vers les lacs Quesnel, Shuswap et Chilko, qui étaient de 1,06, 1,85 et 0,62 million, étaient semblables aux échappées qui avaient d'abord donné les nombres maximum d'alevins observés. Même si les modèles d'alevins permettent d'estimer directement la capacité d'alevinage, des données obtenues sur plusieurs années sont nécessaires pour dégager une relation pour un lac quelconque. Le modèle PR semble constituer un prédicteur utile de la capacité d'alevinage, et il est possible de faire des prévisions après 1 ou 2 ans.
[Traduit par la Rédaction]

Introduction

Sockeye salmon (*Oncorhynchus nerka*) are the most economically valuable salmon species in British Columbia, with the value of the annual catch often exceeding 100 million dollars. The Fraser River is the world's largest single river producer of sockeye salmon, with recent adult returns exceeding 15 million in some years. It is surpassed only by the combined sockeye production from several river systems flowing into Bristol Bay in Alaska (Northcote and Larkin 1989). Most Fraser River sockeye smolt after 1 year of lake residence and return to spawn in their 4th year after 2+ years at sea (age 4_2). There is often a 4-year cycle of abundance, with one dominant return, one much smaller subdominant return, and two extremely small nondominant returns (Fig. 1). The cause(s) of this is (are) unknown, but proposed explanations have ranged from biological interaction between brood years (Ricker 1950; Ward and Larkin 1964) to high fishing rates (Walters and Staley 1987). Commercial catch of Fraser River sockeye peaked in 1913, when 30 million fish were harvested, but shortly thereafter stocks precipitously declined owing to the combined influence of overfishing and blockage of the river during railway construction in the Fraser Canyon (Thompson 1945; Ricker 1947). The size of some Fraser sockeye stocks is currently increasing, but production of the whole system has not yet attained the estimated historic production of 100 million fish in dominant years (Ricker 1987). The Fraser system's exceptionally high productivity is due to the presence of many large lakes that are accessible to anadromous fish. Further, most of these lakes are sufficiently productive to sustain a zooplankton community capable of supporting juvenile sockeye

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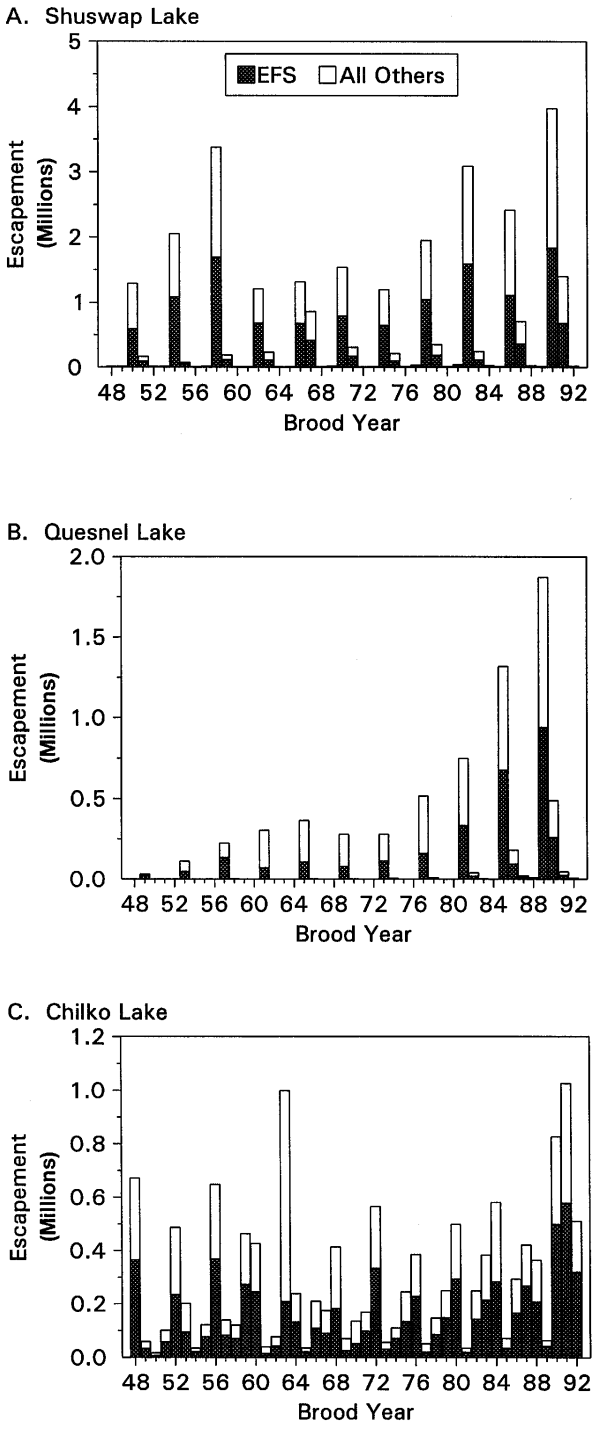
Fig. 1. Escapements to Shuswap, Quesnel, and Chilko lakes showing effective female spawners (EFS, solid bars) and all other spawners (males, jacks, and other females).



densities far higher than presently occur (Stockner and Shortreed 1983).

Because most Fraser sockeye stocks were recruitment limited for most of this century, increasing escapements within the constraints imposed by the commercial fishery have been a primary goal of Fraser River sockeye managers. Owing to uncertainties about the cause of the 4-year cycle of abundance, these rebuilding efforts have been largely restricted to the dominant and (to a lesser extent) subdominant cycle years. The rebuilding efforts have been successful on some Fraser system lakes, and particularly so on the lakes in this study. During the rebuilding period, when escapements were relatively low, rearing capacity of the lakes was not a concern. Rather, optimum escapement estimates were based on estimates of spawning ground capacity (Roos 1989). Since the 1980s in Shuswap and Quesnel lakes and 1990 in Chilko, dominant and subdominant brood year returns and escapements have been very high (Fig. 1, the 1958 return to Shuswap Lake was also high, but subsequent returns dropped considerably and have been building ever since). Determination of escapement levels that will maximize subsequent adult returns is now crucial to the efficient management of Fraser sockeye stocks. Escapements lower than the optimum will result in reduced adult returns. In any brood year, escapements higher than the optimum entail foregoing harvestable sockeye and will produce (at best) no increases in harvestable sockeye in subsequent brood years. If high escapements result in excessive fry recruitment and if the high escapements are consecutive, substantial and long-term declines in total stock size (Kyle et al. 1988) may occur, resulting in considerable economic loss.

Since the mid 1980s we have been conducting studies on these three lakes. Our studies are the first that have included detailed investigations of every major lake trophic level (from the microbial community to planktivorous fish) as well as measurement of salient physical and chemical variables. This ecosystem approach has enabled us to produce the first estimates of optimum spawning escapements based on a lake's productivity and on its ability to rear juvenile sockeye. The objectives of this study were twofold. First, we calculated and compared the size of the optimum escapements to each of the three lakes as predicted by adult sockeye stock-recruitment data and as predicted by juvenile sockeye freshwater size and abundance data. Second, utilizing pertinent limnological data, we modified a rearing capacity model developed by Koenings and Burkett (1987). This modified model enabled us to predict escapements that will maximize smolt output from a lake. We compared these predictions with observed maximum juvenile sockeye production from our study lakes. Calculated maximum smolt production and escapements that produce these maxima vary considerably among the three lakes, and we present salient limnological data to explain these differences.

Description of study lakes

Chilko, Quesnel, and Shuswap lakes are located in the south-central portion of the interior plateau of British Columbia and are three of the larger lakes in the Fraser River drainage basin (Fig. 2). The climate consists of cold winters and warm, dry summers but winters are much less severe at Shuswap than at Chilko Lake.

Quesnel Lake (52°30′N, 120°00′W) has a surface area of 270 km^2 and its maximum depth of 530 m (mean depth = 158 m) makes it the ninth deepest lake in the world. It lies at an elevation of 725 m in the Cassiar-Columbia Mountain physiographic region and the Interior Western Hemlock biogeoclimatic zone of central British Columbia (Farley 1979). Annual precipitation ranges from <75 cm at the western end of the lake to about 150 cm at the eastern end (Farley 1979). The lake has a large (5930 km^2) drainage basin and a water

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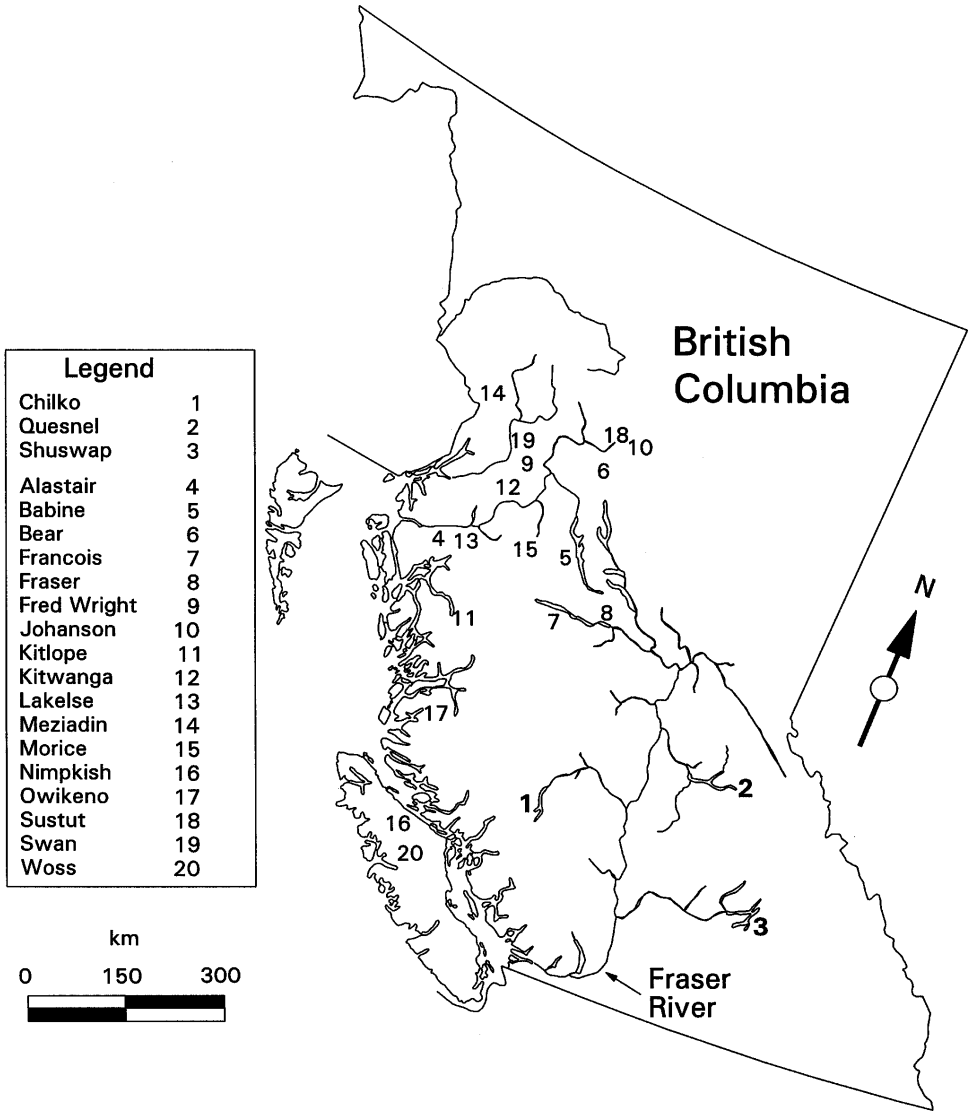
Fig. 2. Map of British Columbia showing the location of the three study lakes and other British Columbia lakes mentioned in the text.



residence time of 10.8 years (Stockner and Shortreed 1983). Quesnel Lake is dimictic, with winter ice cover occurring each year. The most important spawning areas for adult sockeye are the lake's two major tributaries, the Horsefly and Mitchell rivers, while smaller numbers of sockeye spawn in several small streams (Morton and Williams 1990). Further, unknown (but assumed to be small) numbers spawn along the shores of the lake. Two shallow bays have very low densities of sockeye fry and have been excluded from our analysis of sockeye densities (adults and juveniles), resulting in a surface area of 261 km^2.

Chilko Lake (51°20′N, 124°05′W) is situated at an elevation of 1172 m at the boundary of the coast mountain range and the interior plateau. The 185-km^2 lake is located in the Cariboo aspen – lodgepole pine and subalpine Engelmann spruce – subalpine fir biogeoclimatic zones (Farley 1979). Annual precipitation averages <100 cm. The steep-sided nature of the surrounding terrain and of the lake itself results in an extremely limited littoral area. The mean depth of the lake is 123 m, the maximum depth is approximately 330 m, and the area of the drainage basin is 2734 km^2. In most winters complete ice cover does not occur on Chilko Lake, but winter water temperatures are <4°C, with substantial vertical mixing occurring all winter, and it therefore cannot be classified as warm monomictic (Hutchinson 1957). Stockner and Shortreed (1991) classified Chilko Lake as cool monomictic (one period of circulation each year at temperatures <4°C). During our study (1984–1993) water residence times averaged 21 years. During summer, the southern portion of Chilko Lake receives several glacially turbid inflows, with the result that water clarity tends to decrease both spatially from north to south and seasonally from May to August. The orientation of Chilko Lake at the edge of the coast mountains results in frequent strong southerly catabatic winds. These winds exert a strong influence on the circulation patterns and thermal structure of the lake. Over one half of the total sockeye escapement to Chilko Lake spawns in the Chilko River, which is the lake outlet. Spawning occurs primarily in 2 km of river immediately

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below the lake outlet. A variable number (ranging from 10 to 50% of the total escapement) spawn in the lake, utilizing beaches with suitable gravel at locations scattered throughout the lake.

Shuswap Lake, with an area of 330 km^2 (including Little Shuswap and Mara lakes), is the largest in the Fraser River system. It is the most southerly (50°00′N, 119°05′W) of our study lakes and also is situated at a substantially lower elevation (347 m). Consequently, the climate is milder, resulting in a longer growing season, more prolonged and pronounced thermal stratification, and a warmer epilimnion than in Chilko or Quesnel lakes. Annual precipitation is 50–75 cm (Farley 1979). The large drainage basin (16 221 km^2) and relatively shallow depth (mean = 62 m, maximum = 162 m) results in a water residence time of only 2.1 years. While occasional strong winds do occur, the climate at Shuswap Lake is much less windy than at either Quesnel or Chilko lakes. Sockeye spawn in a number of lake tributaries and in the lake itself, with approximately 70% of the total escapement spawning in the Adams River, which enters Shuswap Lake only 2 km from the outlet of the lake. As sockeye fry occur only in low densities in the extensive shallows found in parts of the lake, we have excluded these areas in our analysis of sockeye densities (adults and juveniles), resulting in a surface area of 315 km^2.

Methods

Adult sockeye

Total adult escapements, numbers of effective female spawners (EFS), and total returns have been estimated from 1948 to 1994 for the three study lakes (Cass 1989; Roos 1989; Pacific Salmon Commission 1993; W. Saito and T. Whitehouse, Department of Fisheries and Oceans, New Westminster, B.C., personal communication). We used data from the 1948 to 1991 brood years for EFS data and from the 1948 to 1988 brood years (1992 return year) for return data. Only age-4$_2$ adult returns are used in this analysis. Age-4$_2$ sockeye account for 93, 98, and 92% of total returns to Shuswap, Quesnel, and Chilko lakes, respectively. Numbers of EFS are widely used in stock-recruitment analyses and are used here as estimators of fry recruitment. EFS are female sockeye that have successfully spawned, as determined by examination of carcasses on the spawning grounds. We make the assumption that the number of EFS is directly related to fry entering the lake from the spawning grounds (we have no data on variation in egg to fry survival). EFS averaged 95% of total females (range 87–100%) in Shuswap, 81% (range 15–100%) in Quesnel, and 90% (range 38–100%) in Chilko lakes. High prespawning mortality caused the low proportions of EFS in Quesnel and Chilko lakes in some years, and was attributed to returning adults being exposed to high water temperatures both during migration and on the grounds (Gilhousen 1990). In Shuswap Lake, EFS averaged 53% of total escapements of age-4$_2$ adults, but ranged widely from 45 to 68%. EFS in Quesnel and in Chilko lakes averaged 46 and 54% of adult escapement, respectively, with an even greater range (23–65% in both lakes).

A number of authors have analyzed stock-recruitment relationships in Fraser River sockeye populations to examine either optimum harvesting strategies or the 4-year cycle phenomenon seen in some of these stocks (Ward and Larkin 1964; Larkin 1971; Collie and Walters 1987; Cass 1989; Collie et al. 1990; Welch and Noakes 1991). Much of this analysis has been done by applying the Ricker (1975) stock-recruit model to various sockeye stocks. The form of the model commonly used for Pacific salmon is

$$R = Se^{a(1-S/b)} + \varepsilon$$

where R is total returns (catch and escapement), S is the EFS, e^a is the initial slope of the curve, b is the value of S where $R = S$, and ε is the error term. a is a measure of the stock growth rate or productivity and b is a measure of the capacity of the stock. Both a and b affect the typical parameters of interest in a stock-recruit analysis: the escapement (S_{MSY}) that maximizes the return to the fishery, and the escapement (S_{MAX}) that maximizes total return. For the purpose of estimating rearing capacity, S_{MAX} is the more appropriate parameter.

A common way of fitting a set of data to the Ricker model is by transforming the equation into the following form:

$$\ln\left(\frac{R}{S}\right) = a - \frac{a}{b}S + \varepsilon$$

and treating it as a linear regression. Calculation of variance and tests of significance are straightforward in the transformation and provide a good indicator of the reliability of the model's fit to the data (Hilborn and Walters 1992).

Juvenile sockeye

Juvenile sockeye numbers and size have been determined with hydroacoustic and trawl surveys from Quesnel and Shuswap lakes since the mid 1970s (Williams et al. 1989; Hume et al. 1994). All of our sampling was done during the hours of darkness, when the fish were dispersed and within the working range of the midwater trawl and hydroacoustic system (McDonald and Hume 1984; Burczynski and Johnson 1986; Levy 1990). Data were collected from Shuswap Lake in the year following spawning for 6 of the 12 brood years from 1974 to 1985 and for every brood year from 1986 to 1991. Quesnel Lake data were collected for 4 dominant brood years since 1977 and for all brood years from 1985 to 1991. Hydroacoustic and trawl data were collected in the summer (late July and August) or in the fall (October and early November). Smolt size data are available in Quesnel and Shuswap lakes for some dominant years since 1961. An appropriate time series of hydroacoustically derived juvenile sockeye population estimates is unavailable for Chilko Lake. However, smolt numbers and size have been determined at Chilko Lake for the brood years from 1949 to 1992 (1951–1994 smolt years), except for the 1989 brood year when only size data were collected (Roos 1989; T. Whitehouse, personal communication). Consequently, we used smolt rather than fall fry data in our Chilko Lake analyses.

Prior to hydroacoustic surveys, lakes were divided into a number of sections on the basis of lake morphometry. Within each section, two to three evenly spaced hydroacoustic transects were established. There were a total of 16 transects on Quesnel Lake and 33 on Shuswap Lake. The same transects were used on all surveys since 1975. Results from each transect were used to provide a mean estimate of density (number per hectare) for each lake section. The mean density was then multiplied by the surface area of the section to provide a population estimate for the section and then summed to provide a total population estimate for the lake. Mean lake density was calculated by dividing the lake population estimate by the total surface area. Variances were calculated for the density of each section and were then weighted by the square of the section area. The sum of the weighted variances was divided by the square of the lake area to provide a variance for the lake population estimate. In this paper we report 2 times the standard error.

From 1974 to 1984, acoustic data were collected using a Simrad EY-M echosounder with a 70-kHz transducer producing an 11° beam (at –3dB) and recorded for later processing. Data were analyzed in two stages with the duration in beam technique (Thorne 1988). First, recorded voltages were integrated with a Biosonics 121 integrator to give the relative uncalibrated density of fish in each transect. Second, targets were counted on an oscilloscope from selected transects in each lake. These counts were then regressed against the integrated data from the same transect. The regression line was then used to calibrate all of the integrated transects to provide a density estimate for each transect.

From 1985 until 1994, data were generated with a Biosonics model

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105 dual beam echosounding system with a 420-kHz dual beam (6°/15°) transducer and were digitally recorded for later processing. Data were processed as described by Burczynski and Johnson (1986). First, target strengths and mean backscattering cross sections were determined for each transect with a Biosonics model 121 dual-beam processor. Second, recorded data were echo integrated to give the relative density of targets. Target strength and equipment scaling factors were then used to scale the echo integration to provide an estimate of fish density in each transect. In 1986 on Quesnel Lake we carried out concurrent surveys with the Simrad and Biosonics equipment to test comparability of data. There was only a 4% difference in juvenile sockeye population estimates generated by the two types of equipment and methods.

Fish samples were collected from each lake section with a 7 × 3 m midwater beam trawl (maximum mesh size 10.2 cm, fished at 1.0 m/s) as described by Enzenhofer and Hume (1989). Trawls of 5–45 min were made at locations and depths suggested by fish targets on the echosounder. Trawl duration was chosen to give an adequate sample size for later analysis (100–200 fish). All fish were anaesthetized and killed upon capture with an overdose of 2-phenoxyalcohol and then preserved in 10% formalin. Fish were kept in formalin for at least 1 month before lengths and weights were recorded. Trawl data were used to determine the species and age composition of the limnetic fish community. Smolt samples were preserved and analyzed in a similar manner.

Resident populations of kokanee (landlocked *O. nerka*) complicate the interpretation of size and abundance data in both Shuswap and Quesnel lakes. Precise abundance estimates are unavailable as no spawning ground counts are done and the age-0 class is visually indistinguishable from similarly sized sockeye. Parkinson et al. (1994) compared catches of kokanee by three otter trawls (maximum mesh size 3.2 cm, two fished at 1.5 m/s, one fished at 1.0 m/s) and by a beam trawl similar to ours (maximum mesh size 10.2 cm, fished at 1.0 m/s). They found little difference between the four trawls in length-frequency histograms of the catch of age-0 and -1 kokanee up to 155 mm in length, but the two slower trawls caught fewer larger fish (age-2 and -3 kokanee) than the two fast otter trawls. The mean size of each age-class in the beam trawl catch was always midway between that of the two fast otter trawls, indicating little relative bias in estimating mean age at length using the beam trawl. In our lakes, juvenile sockeye are predominantly age 0 and do not exceed 100 mm. The relatively small numbers of age-1 sockeye do not exceed 150 mm. We conclude that bias in our trawl data is restricted to underestimates of proportions of older kokanee (age-2 and -3). Estimates of mean size of each age-class appear to be unbiased. On the basis of known electrophoretic differences between adult kokanee and sockeye in Shuswap Lake, age-0 kokanee constituted 5% of the 1987 subdominant population and 73% of the 1989 nondominant population (C.C. Wood, J.M.B. Hume, and C.J. Foote, unpublished data). In Quesnel Lake, estimates of fall fry during nondominant years have ranged from 4 to 471/ha. A large but unknown proportion of these fish would be age-0 kokanee. In dominant years where fall fry estimates range from 1886 to 2561/ha, the proportion of age-0 and older kokanee would be small. Kokanee are rare in Chilko Lake and we have not caught any *O. nerka* older than age-1 in our trawls.

Limnological data

On Quesnel Lake, sampling for all limnological variables was carried out from 1985 to 1988 and again in 1990, except that photosynthetic rates (PR) were not determined in 1985. Data were collected once monthly (May–October) from six locations on the lake. The Shuswap Lake sampling program commenced in 1987 and concluded in 1993. At Shuswap Lake, PR was determined in every year except 1993. Each year sampling was carried out from March or April until November at locations in each of the four major lake basins. Sampling frequency was once monthly for most of the study, except for 1990 and 1991, when spring (April–June) sampling was carried out every 2 weeks. Sampling on Chilko Lake was carried out in May–October from 1984 to 1986 and from 1988 to 1993. Frequency of sampling ranged from once weekly to once monthly depending on the year and the sampling location. Numbers of locations were sampled, but for this study we used data collected from four sites spaced evenly along the lake's longitudinal axis.To calculate seasonal averages we defined the growing season in Chilko and Quesnel lakes as May 1 to October 31. This represented the period of active growth in the phytoplankton and zooplankton communities. Shuswap Lake's growing season was longer (April 1 to November 30). Time-weighted means for each sampling location were calculated by integrating seasonal data and dividing by the length of the growing season or other period of interest. Lakes were divided into zones representing major lake basins, and data from sampling locations within zones were averaged. Seasonal means for each zone were then weighted by the area of the zone and combined with data from other zones to yield a mean whole-lake value. Seasonal means of limnological data (except for zooplankton data) presented in this report are averages for the entire growing season. Zooplankton data are presented as July–November averages in Shuswap Lake and July–October averages in Chilko and Quesnel lakes to better represent the portion of the growing season when juvenile sockeye occupied the limnetic zone (Morton and Williams 1990; J.M.B. Hume, unpublished data).

We used Applied Microsystems Ltd. meters (models CTD-12 and STD-12) to measure conductivity, temperature, and depth. Photosynthetic photon flux density (PPFD: 400–700 nm) was determined with a Li-Cor model 185A light meter equipped with a model 192S underwater quantum sensor. Vertical light extinction coefficients and compensation depths were calculated. The compensation depth is the depth to which 1% of the surface light penetrates and we assumed that euphotic zone depth (EZD) was equivalent to compensation depth. We used an opaque 6-L Van Dorn water sampler to collect all water. Water from 5–9 depths from the surface to below the EZD was collected for analysis of chemical variables, phytoplankton biomass, and in situ PR. A 50 m deep water sample was also collected from each sampling location and analyzed for selected chemical variables. All chemical analyses followed methods described by Stephens and Brandstaetter (1983) and Stockner and Shortreed (1985). Water for dissolved nutrient analyses was filtered through ashed Whatman GF/F filters that were rinsed with both distilled deionized water and sample water immediately before filtration. We stored filtered water in clean glass and polyethylene bottles that were kept cold and dark before analysis. Nitrate was determined by converting to nitrite by cadmium reduction. Water for total phosphorus (TP) analysis was collected in clean, screw-capped glass test tubes, and TP was later determined with a molybdenum blue method after persulfate digestion. Samples for chlorophyll *a* (CHL) determinations were collected on Millipore AA filters (0.8-μm nominal pore size), frozen, and later analyzed fluorometrically after maceration in 90% acetone. PR was determined in situ by filling 125-mL glass bottles with water from each sampling depth, inoculating with a sodium bicarbonate solution containing ^{14}C, and incubating for 1.5–2.0 h at the original sampling depths. Incubations commenced between 09:00 and 10:00. After incubations, samples were filtered onto 0.2-μm Nuclepore filters, placed in scintillation vials containing a tissue solubilizer and scintillation cocktail, and counted in a Packard scintillation counter. Dissolved inorganic carbon concentrations were determined with the potentiometric method of the American Public Health Association, the American Water Works Association, and the Water Pollution Control Federation (1980). Hourly PR was calculated using Strickland's (1960) equation. Daily PPFD was determined with either a Li-Cor model 550 printing integrator (1984–1989) or a Li-Cor model LI-1000 data logger (1990–1993), each equipped with a model 190S quantum sensor. These data were then used to compute daily PR.

Zooplankton samples were collected with a 100-μm mesh size SCOR-UNESCO (SCOR) net (mouth area 0.25 m^2) hauled vertically

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from 50 m to the surface at Chilko Lake throughout the study, at Quesnel Lake from 1985 to 1987, and at Shuswap Lake in 1987. All other samples were collected with a 160-μm mesh size Wisconsin net (mouth area 0.05 m^2) hauled from 30 m to the surface. In our study lakes, microphytoplankton were not abundant, so clogging of the smaller mesh size SCOR net did not occur. Consequently, results obtained from comparisons between the two nets were not significantly different (*t* test, $P > 0.05$) for the macrozooplankton (>250 μm) component of the plankton community. All samples were placed in 125-mL bottles and preserved in sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton were later counted, identified to genus, and measured with a computerized video measuring system (MacLellan et al. 1993). Body length was measured as described by Koenings et al. (1987). Zooplankton biomass was calculated with species-specific length–weight regressions adapted from Bird and Prairie (1985), Culver et al. (1985), Stemberger and Gilbert (1987), and Yan and Mackie (1987).

For determination of sockeye diet, approximately 25 sockeye stomachs from each trawl sample were analyzed. Only samples collected within 3 h after the onset of darkness were analyzed to avoid bias caused by different digestion rates of prey. Stomach contents were identified and enumerated with the computerized video measuring system. Relative volume of prey types in the stomachs and an index of stomach fullness expressed as a percentage by volume were estimated using a technique modified from Hellawell and Abel (1971).

Lake fertilization

Lake fertilization is a widely used and successful sockeye enhancement technique in British Columbia (Hyatt and Stockner 1985; Stockner and Shortreed 1985). In the mid 1980s Chilko Lake was identified as an excellent candidate for fertilization (Stockner and Shortreed 1983, 1994). Consequently, nitrogen and phosphorus fertilizers were applied to the lake for 6-week periods in 1988 and for 12-week periods in 1990–1993. Details of the application methods and limnological results of the fertilization were reported in Stockner and Shortreed (1991, 1994). In this report, data collected during lake fertilization are identified and reported when pertinent to sockeye growth, zooplankton community composition and biomass, and our estimates of Chilko Lake's sockeye rearing capacity.

Results and discussion

Adult sockeye stock-recruitment relationships

The stock-recruit relationships exhibited by Shuswap Lake sockeye (all stocks combined) and by Adams River sockeye (the Adams River is the major spawning tributary on Shuswap Lake) have been extensively analyzed (Ward and Larkin 1964; Larkin 1971; Collie and Walters 1987; Cass 1989; Collie et al. 1990; Welch and Noakes 1991). On dominant cycles, Adams River sockeye averaged 95% of the total escapement until 1970. Since that time, escapements to other Shuswap Lake tributaries have increased, so that Adams River sockeye now account for about 70% of the total Shuswap Lake escapement in dominant cycles. On the subdominant cycle the Adams River escapement has varied between 75 and 98% during the same period. Adams River escapement during the two nondominant cycles is highly variable, ranging between 2 and 65% (mean 35%) of the total Shuswap Lake escapement. In this study, we use age-4 returns (catch and escapement) and escapement to all spawning grounds of each lake system.

The Pacific Salmon Commission and the Department of Fisheries and Oceans have recently revised their estimates of escapements and returns, resulting in significant changes to some data points since the previous papers were published (W. Saito and T. Whitehouse, Department of Fisheries and Oceans, New Westminster, B.C., personal communication). Using the revised EFS and return data (using brood years from 1948 to 1988) we computed a new S_{MAX} of 2.66 million EFS (83 EFS/ha, Fig. 3). As EFS averages 53% of returning adults in Shuswap Lake, the estimated optimum escapement to Shuswap Lake based on stock-recruit analysis is 5.0 million, 24% higher than the record escapement of 3.98 million in 1990 (Fig. 3). However, we found that the regression of $\log(R/S)$ on S was not significant ($P > 0.05$). We also found considerable variance (as did Collie et al. 1990) with an r^2 of only 6%. With currently available data the Ricker model cannot be differentiated from a linear model.

In Chilko Lake, Collie et al. (1990) again reported a very high variation in the *b* value (90% CI = ±63%), and a S_{MAX} of 549 000 EFS, with a confidence interval of 337 000 to 1.5 million. As with Shuswap data, we repeated their analysis with the addition of more recent data (excluding returns from fertilized brood years) and computed a S_{MAX} of 457 000 EFS (25/ha), or a total escapement of 896 000 spawners (EFS averaged 51% of total adult escapement, Fig. 3). Although the r^2 value was still low (10.9%), the regression was significant ($P < 0.05$). The first returns from fertilized brood years occurred in 1991 and 1993 and while they were among the highest ever recorded from these escapement levels, they made little difference to the stock-recruit analysis, producing an estimated S_{MAX} of 439 000 EFS when included.

The Ricker *b* value for Quesnel Lake data is negative, meaning that the curve is nearly linear and S_{MSY} and S_{MAX} cannot be computed (Fig. 3). Since 1977, escapements in dominant brood years have increased from 160 000 to over 900 000 EFS and returns per EFS have declined, indicating some limitation to the productivity of the stock, but there are insufficient data at higher escapement levels to properly estimate the parameters of the Ricker model. Because of this we examined a number of other possible curves. Examination of the residuals showed that a quadratic model fitted the data slightly better than a linear fit (decreasing both the standard error of the residuals and the mean average error by 34 and 30%, respectively). The quadratic curve peaked (equivalent to S_{MAX}) at about 930 000 EFS (36/ha), or a total escapement of 2.0 million (EFS average 46% of total adult escapement, Fig. 3).

Juvenile sockeye populations

In both Quesnel and Shuswap lakes the summer (late July or August) fry densities were linearly correlated with EFS up to densities of about 35 EFS/ha (in both cases $r^2 > 0.87$, $P < 0.05$, Fig. 4). Quesnel and Shuswap lakes exhibited similar EFS to summer fry relationships, indicating that from egg deposition to the following summer, sockeye fry in both lakes had similar survival rates up to EFS numbers of 35/ha (analysis of covariance, neither the slopes nor the intercepts were significantly different from each other, $P < 0.05$). At the two highest observed EFS numbers in Shuswap Lake (50 and 58/ha), summer fry numbers decreased. The lower survival at these densities may be a result of spawning ground or lake rearing limitation.

Fall fry (October to early November) abundance in Shuswap and Quesnel lakes exhibited a strong curvilinear or asymptotic relationship to EFS (Fig. 4). Ricker stock-recruit curves fitted to the data resulted in a S_{MAX} in Shuswap Lake

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Fig. 3. Total adult (4_2) returns to Shuswap, Quesnel, and Chilko lakes produced by effective female spawners. Selected brood years are labelled and the optimum escapements estimated by the photosynthetic rate (PR) model are shown by the two-headed arrows. Ricker stock-recruit curves (solid lines) have been fitted to the data. A quadratic curve was fitted to the Quesnel Lake data.

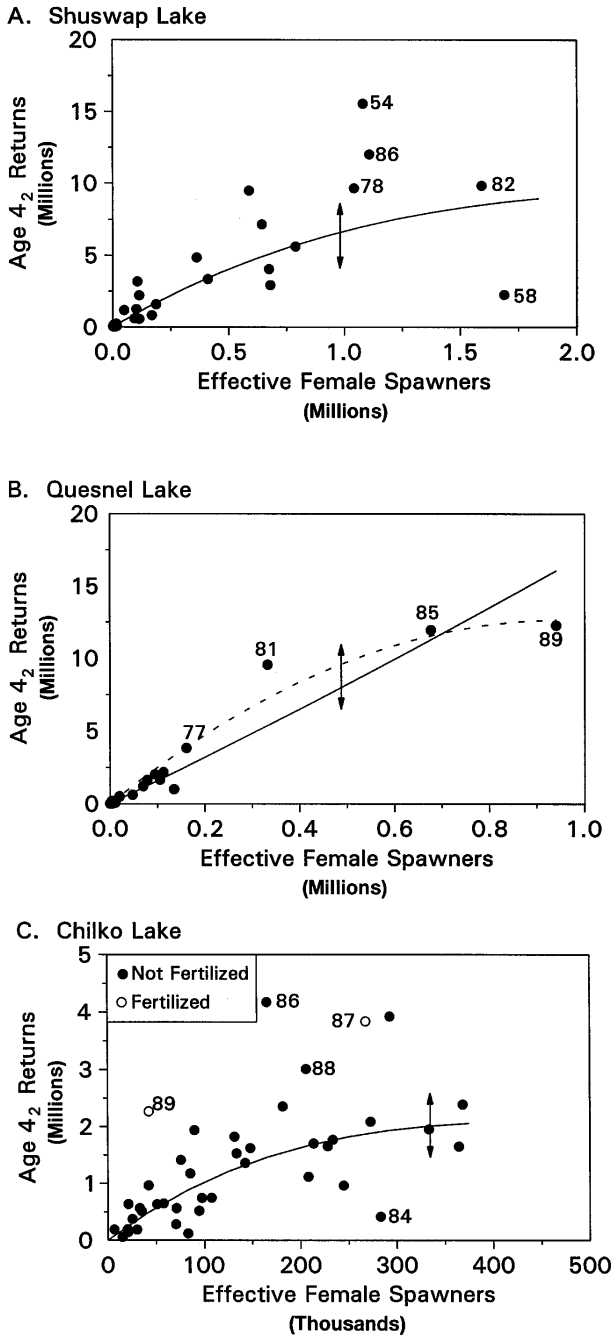
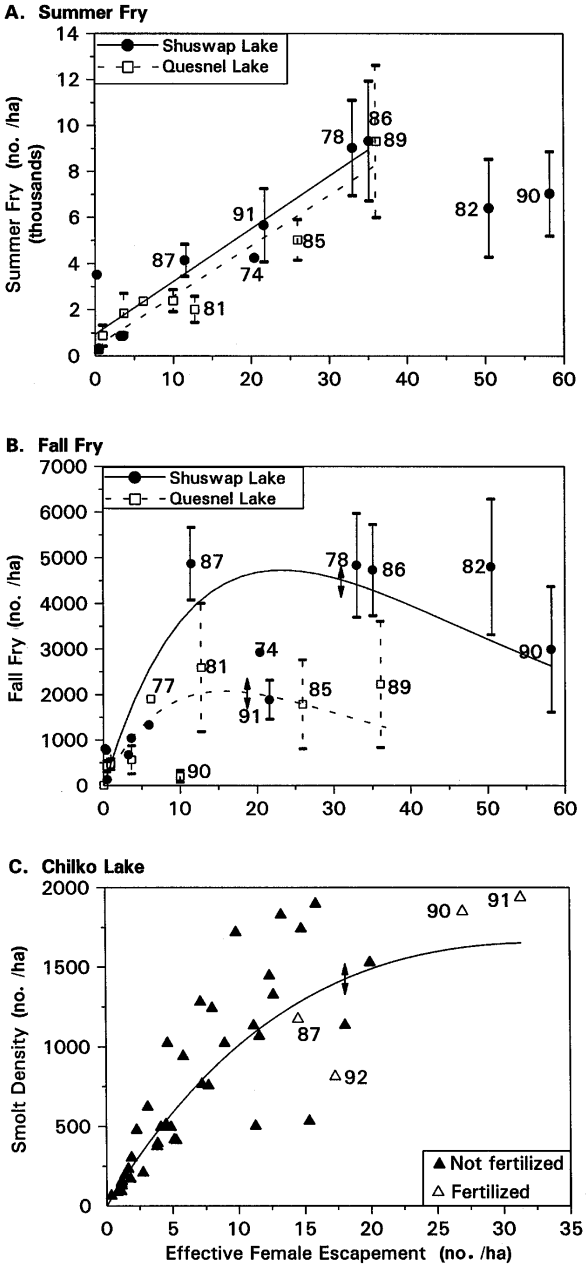


Fig. 4. Summer and autumn fry densities in Shuswap and Quesnel lakes and smolt densities in Chilko Lake produced by effective female spawners. Smolts affected by fertilization in Chilko Lake are indicated by the open triangles. Where possible 95% confidence intervals are shown by a vertical line and horizontal bars. Selected brood years are labelled and the optimum escapements estimated by the photosynthetic rate (PR) model are shown by the two-headed arrows. Ricker stock-recruit curves (solid lines) have been fitted to the data in B and C.



of 23.2 EFS/ha (732 000 EFS, 1.38 million total escapement, $r^2 = 0.51$, $P < 0.05$) and a S_{MAX} in Quesnel Lake of 15.9 EFS/ha (415 000 EFS, 0.90 million total escapement, $r^2 = 0.41$, $P > 0.05$). Although the Ricker model describes these data better than it does the adult stock recruit data, 50% or more of the variation in the relationships was still unexplained.

The 95% confidence intervals of S_{MAX} (based on the regression of $\ln(R/S)$ against S) were still too large (ranging from 9.8 to 41.3 EFS/ha in Shuswap Lake and from 0 to infinity in Quesnel Lake) to be a practical predictive tool. Escapements greater than 25 EFS/ha (total adult escapements of 1.5 million) to

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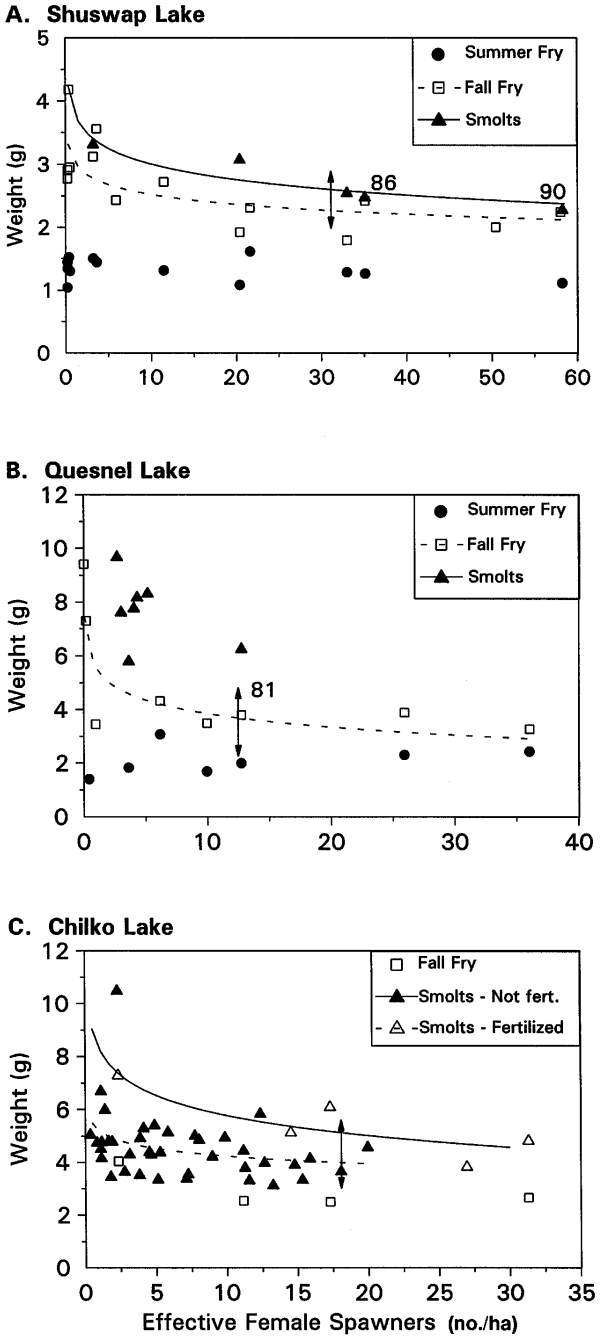
Fig. 5. Size of juvenile sockeye in the summer and fall and as spring smolts in Shuswap, Quesnel, and Chilko lakes. The optimum escapements estimated by the photosynthetic rate (PR) model are shown by the two-headed arrows. Smolts affected by fertilization in Chilko Lake are indicated by the open triangles. Logarithmic curves have been fitted to the fall fry and smolt data.



Shuswap Lake did not produce any more fall fry, peaking at 4900 fry/ha. Similarly escapements to Quesnel Lake of 15 EFS/ha (total adult escapements of 0.8 million) also did not produce any more fry, peaking at 2600 fry/ha. These observed escapements agree closely with the Ricker S_{MAX} calculated for the two lakes.

In Chilko Lake production of smolts per EFS decreased only slightly with increasing EFS escapement. While the Ricker fit was significant ($r^2 = 0.29$, $P < 0.05$), a linear fit was better ($r^2 = 0.64$, $P < 0.05$, Fig. 4). The Ricker analysis resulted in a S_{MAX} of 31.1 EFS/ha (575 000 EFS, 1.06 million adults). This is beyond the highest observed EFS escapement and had 95% confidence intervals of 27.0–68.3 EFS/ha. However, interpretation of the effects of spawning density on smolt production was complicated by lake fertilization. Juvenile sockeye from two of the highest escapements (26 and 31 EFS/ha) were from fertilization years. Since a well-documented effect of lake fertilization is increased fry to smolt survival (Hyatt and Stockner 1985; Koenings and Burkett 1987), these 2 brood years may have produced fewer smolts if the lake had not been fertilized. As a result, S_{MAX} would have been smaller. In any case, even with fertilization, no more smolts were produced at densities of 25–31 EFS/ha than at densities of 15 EFS/ha (i.e., maximum observed smolt output was reached at total adult escapements of 0.5 million).

Other lakes have exhibited EFS to fall fry relationships similar to those found in our study. Babine Lake is a large (491 km^2 in area) sockeye producer in the Skeena River system and is the only British Columbia sockeye lake for which direct estimates of fry recruitment are available (McDonald and Hume 1984; MacDonald et al. 1987). Densities of fry at the time of emergence from the gravel ranged from 1000 to 10 300 fry/ha (approximately 13 to 29 EFS/ha) and there was a linear relationship between emergent fry numbers and subsequent smolt production (i.e., no density-dependent survival). At this range of densities fry to smolt survival averaged 35%. In Leisure Lake, a much smaller (1.1 km^2) lake in Alaska, Koenings and Burkett (1987) found that smolt numbers did not increase after spring fry numbers exceeded 10 000/ha. At densities >10 000 fry/ha (approximately 19 EFS/ha) smolt numbers did not increase further, with smolt numbers declining at the highest fry densities. These results are very similar to the curvilinear relationship we found between EFS and subsequent summer and fall fry numbers in Shuswap and Quesnel lakes (Fig. 4).

Juvenile sockeye size

Summer fry size in Quesnel and Shuswap lakes did not vary with spawner density ($P > 0.05$, Fig. 5). Summer fry averaged 2.1 g (range 1.3–3.1 g) in Quesnel Lake and 1.3 g (range 1.1–1.6 g) in Shuswap Lake. Possible causes for these size differences are discussed in a later section and are most likely related to differences in thermal regimes between the two lakes.

Fall fry and smolt size in all three lakes declined rapidly as EFS density increased to about 10 EFS/ha. At escapements >10 EFS/ha fall fry size did not significantly decline in either Shuswap or Quesnel lakes (Fig. 5). Chilko Lake smolt size also showed little density-dependent effects at escapements >10 EFS/ha, but results at the highest densities in Chilko Lake were confounded by fertilization. Smolts from fertilized years tended to be larger than smolts from comparable unfertilized years, and the highest EFS densities in Chilko Lake occurred only during fertilized years (Fig. 5). In an Alaskan lake, Koenings and Burkett (1987) also found a decreasing change in growth rates at the highest stocking densities. In our study lakes, brood years when both fall fry and smolt sizes are available are limited, but available data do show that overwintering

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growth can exceed 2 g in low-density brood years (e.g., 1981 in Quesnel Lake). In high-density brood years overwintering growth can be negligible (1986 and 1990 in Shuswap Lake, Fig. 5).

Fall fry and returning adults

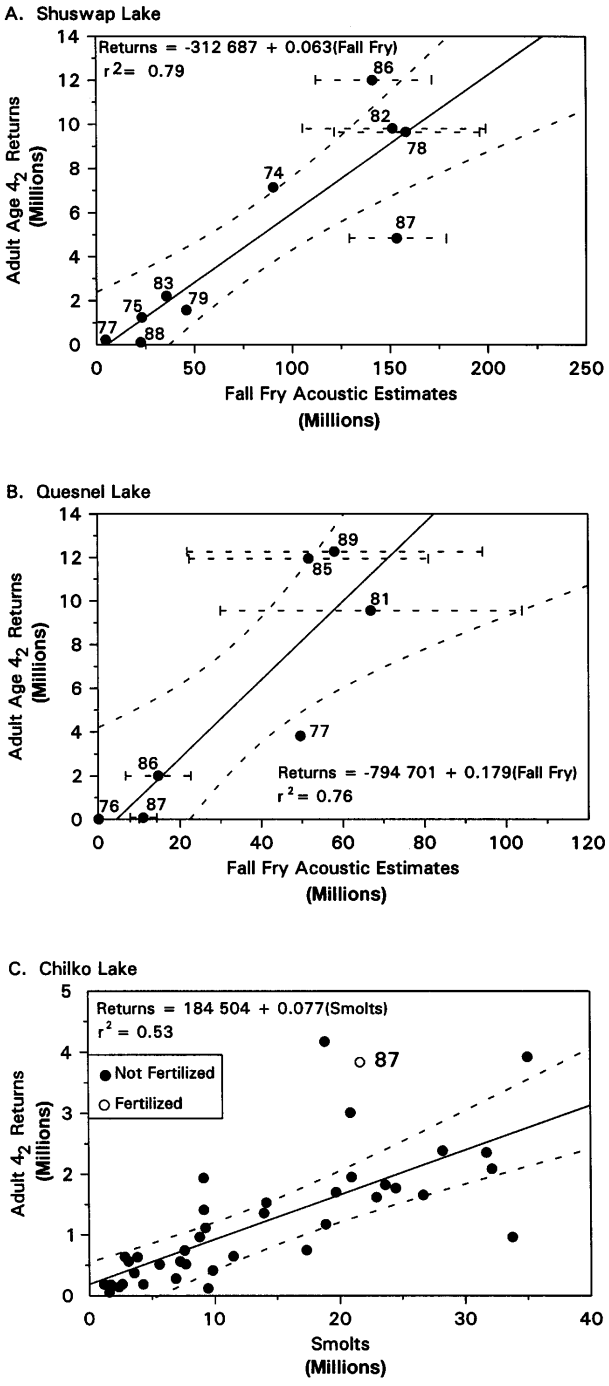
Unlike the lake resident life history, there were no obvious density-dependent effects on marine survival for any of our study lakes. In all three lakes there were highly significant linear relationships between numbers of fall fry or smolts and subsequent adult returns (Fig. 6). Fall fry to adult survival averaged 5.6% for Shuswap Lake and 14.8% for Quesnel Lake. At Chilko Lake smolt to adult survival averaged 9.1%. These survival rates were not significantly related to density but were significantly different from each other (least significant difference test on angular transformed data, $P < 0.05$, Sokal and Rohlf 1981). Fall fry in Quesnel Lake averaged about 4 g at higher densities, about twice the 2-g size of Shuswap Lake fall fry and the same size as Chilko Lake smolts. The limited smolt data available for our lakes indicate that at equivalent EFS densities Shuswap Lake produced the smallest smolts and Quesnel the largest. This may indicate size-dependent smolt to adult survival as seen in other sockeye populations (Hyatt and Stockner 1985; Koenings et al. 1993), where smolt to adult survival rates were strongly size dependent over the size ranges seen in this study. However, different winter and early spring growth rates because of different EFS densities and environmental conditions make it inappropriate to estimate smolt size from fall fry size. There are few smolt size data for any Fraser system lake except Chilko Lake, where considerable smolt data are available. Chilko smolt data do not exhibit a relationship between size and survival from smolts to adults between brood years. However, Henderson and Cass (1991) did find a relationship within brood years at Chilko Lake. They speculated that factors such as run timing, river conditions, or total system smolt abundance may play a larger role than smolt size in determining survival rates between brood years in the Fraser River system.

Macrozooplankton and sockeye planktivory

The role of selective planktivory in structuring zooplankton community composition has been well documented (see Northcote 1988 for review). Intense salmonoid planktivory has been linked with a reduced abundance of large-bodied zooplankton in a number of lakes (Brooks and Dodson 1965; Brooks 1969; Stenson 1972, 1976; Kerfoot 1975; Kerfoot and Sih 1987; Goodlad et al. 1974; Kyle et al. 1988). While intense grazing pressure may have a large effect on zooplankton community composition, the effect on total macrozooplankton biomass may be much less pronounced (Kyle et al. 1988, our Table 1). Principal diet items of juvenile sockeye differed among our study lakes.To document depletion of their forage base, we needed to first determine preferred diet items by stomach content analysis. For example, macrozooplankton biomass was not substantially affected by high fish density in Shuswap Lake, where sockeye grazed almost entirely on *Daphnia* spp. (Table 1). However, *Daphnia* biomass declined significantly with increased grazing pressure (Fig. 7).

In Shuswap and Quesnel lakes, the copepods *Leptodiaptomus* and *Diacyclops* spp. constituted 45–80% of macrozooplankton biomass. Daphnids were the dominant cladocerans (30–50%)

Fig. 6. Relationship between fall fry and subsequent adult (4_2) returns. The broken line indicates the 95% confidence intervals on the regression lines and where possible 95% confidence intervals on the data points are shown by a horizontal line and vertical bars. Selected brood years are labelled.



in these lakes, except during the fall of dominant years, when they declined to 13–30%. Significant negative correlations occurred between EFS and *Daphnia* biomass in both Shuswap ($r^2 = 0.96$, $P < 0.01$) and Quesnel ($r^2 = 0.93$, $P < 0.05$) lakes (Fig. 7). In both lakes average *Daphnia* biomass decreased by approximately 60% in dominant brood years, declining from an average of 522 mg/m^2 (nondominant) to 224 mg/m^2 in

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Table 1. Seasonal means of salient limnological variables from the study lakes.

	Mean epilimnetic temp. (°C)	Epilimnetic depth (m)	EZD (m)	TP (μg/L)	Nitrate (μg/L)	CHL (μg/L)	Daily PR (mg C/m^2)	*Daphnia* biomass (mg/m$^{2)}$	Macrozooplankton biomass (mg/m^2)
Chilko									
Unfertilized	7.5	21.4	14.8	2.3	12.0	0.68	79	4.7	715
	(0.3)	(0.5)	(5.1)	(0.6)	(3.9)	(0.24)	(1.0)	(8.4)	(513)
Fertilized	9.3	17.6	20.5	4.1	12.7	0.88	103	152	1150
	(1.2)	(2.90)	(1.9)	(0.3)	(3.4)	(0.34)	(30)	(192)	(139)
Shuswap	14.9	10.0	12.3	5.1	18.4	1.81	171	400	1005
	(0.5)	(1.1)	(0.5)	(1.1)	(5.8)	(0.31)	(23)	(104)	(141)
Quesnel	12.4	12.2	15.1	2.7	69.3	1.03	102	247	894
	(0.4)	(1.5)	(1.0)	(0.4)	(8.8)	(0.07)	(11)	(99)	(278)

Note: Values in parentheses are two standard errors. Chilko Lake unfertilized averages were calculated for the years 1984–1986 ($n = 3$) and fertilized averages for 1990–1993 ($n = 4$). Quesnel Lake averages are for 1985–1989 and 1993 ($n = 6$). Shuswap Lake averages are for 1987–1993 ($n = 7$).

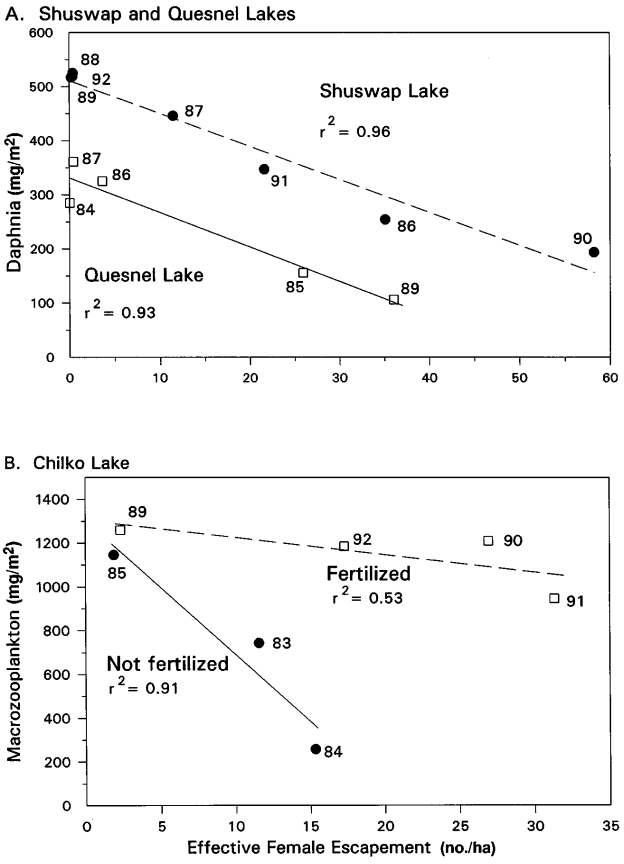

Fig. 7. Mean seasonal (summer to fall) *Daphnia* biomass in Shuswap and Quesnel lakes, and mean seasonal macrozooplankton in Chilko Lake. Brood years (1 year prior to sampling) are labelled.

Shuswap Lake and from 323 to 131 mg/m^2 in Quesnel Lake. In Shuswap Lake *Daphnia* biomass was significantly higher at equivalent fry densities than in Quesnel Lake (covariance analysis; equal slopes, $F = 0.84$, $P > 0.05$; different intercepts, $F = 55.12$, $P < 0.01$; Sokal and Rohlf 1981). *Daphnia* spp. comprised 90% of total stomach volume in Quesnel and Shuswap lakes, except in the fall of dominant brood years. At those times sockeye diet consisted of the smaller cladocerans *Eubosmina* spp., the copepods *Diacyclops* and *Leptodiaptomus* spp., and small quantities of *Daphnia* spp. Stomach fullness averaged >90% when *Daphnia* spp. were the major food item in Shuswap and Quesnel lakes and <50% when *Daphnia* spp. were depleted and sockeye were forced to switch prey.

Before fertilization in Chilko Lake, macrozooplankton community biomass was dominated by the small cladocerans *Eubosmina* spp. (10–50%) and by the copepods *Diacyclops* (20–30%) and *Leptodiaptomus* spp. (40–60%). These three genera comprised 100% of sockeye stomach contents. *Daphnia* spp. were not found in the stomachs examined and they comprised <1% of total macrozooplankton biomass (Table 1). Prior to fertilization, we found no change in species composition with increasing EFS densities, but there were large changes in biomass. Macrozooplankton biomass declined rapidly with increasing sockeye density, from 1145 mg/m^2 at 2 EFS/ha to 257 mg/m^2 at 15 EFS/ha (Fig. 7). In contrast, during fertilization, increasing EFS density had little effect on macrozooplankton biomass. Even with density at a historic maximum of 31 EFS/ha, mean seasonal macrozooplankton biomass was >900 mg/m^2 (Fig. 7). In spite of high sockeye densities during 3 of the 4 fertilized years there was a large increase in *Daphnia* biomass during fertilization. After averaging 4.7 mg/m^2 prior to fertilization, *Daphnia* biomass averaged 152 mg/m^2 during fertilized years (Table 1). As a proportion of macrozooplankton biomass, *Daphnia* spp. increased from <1 to 13% during fertilized years. This occurred even though daphnids became a major component (up to 75% of stomach volume) of sockeye diet in some fertilized years. Stomach fullness also increased from an average of <25%, containing only *Eubosmina*, *Diacyclops*, and *Leptodiaptomus* spp., in unfertilized years, to >75% full, containing primarily *Daphnia* and *Eubosmina* spp.

Lake physics

Thermal regimes varied considerably between the three lakes in this study. With its milder climate and calmer conditions, Shuswap Lake is stratified from early May to November and has epilimnetic temperatures >20°C from early July until mid September. It has a very strong, stable, and shallow (10 m) seasonal thermocline (Table 1). Because of the warm epilimnion, juvenile sockeye are restricted in their use of this productive area during this period (Levy 1989; J.M.B. Hume, unpublished data). Quesnel Lake also stratifies strongly, but to

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a lesser degree than does Shuswap Lake. Although stratification is stable from June to October, epilimnetic temperatures rarely exceed 17°C, and the average depth of the epilimnion is 12.2 m. On occasion the Quesnel Lake epilimnion is not utilized by juvenile sockeye (Levy et al. 1991), but for much of the summer and fall grazing sockeye can use the whole water column. In Shuswap Lake July–September epilimnetic (<10 m) *Daphnia* biomass averaged 13 times greater than biomass below the thermocline (10–30 m), while in Quesnel Lake epilimnetic *Daphnia* biomass averaged only twice as great as deeper biomass. We suggest that because of its stronger stratification and warmer epilimnion, Shuswap Lake provides a thermal refuge for zooplankton, resulting in a larger proportion of the zooplankton community being unavailable to grazing sockeye. As a result of this refuge, Shuswap Lake maintains higher *Daphnia* numbers than Quesnel Lake but produces smaller fall fry at similar fish densities. Chilko Lake's high elevation and exposure to frequent strong winds result in a dynamic thermal structure and a cool epilimnion, with summer epilimnetic temperatures seldom exceeding 14°C. Thermal stratification does develop (July–October) on Chilko Lake, but epilimnion depths are variable, ranging from 10 to 50 m, and the entire water column is available to foraging sockeye. Our study lakes were all clear, with average EZDs ranging from 12.3 m in Shuswap Lake to 20.5 m in Chilko Lake (Table 1).

Trophic status and lake productivity

We found that the study lakes are oligotrophic, with spring TP concentrations <10 μg/L. Nevertheless, they cover a wide range of oligotrophy, with Chilko being ultraoligotrophic, Quesnel slightly more productive, and Shuswap approaching mesotrophy. Phosphorus availability is the primary factor limiting productivity in all three lakes, but there are substantial differences between lakes. Seasonal average TP was 2.3 μg/L in unfertilized Chilko Lake, 2.7 μg/L in Quesnel Lake, and 5.1 μg/L in Shuswap Lake. During summer in Shuswap Lake and at times in Chilko Lake, a complex co-limitation of nitrogen and phosphorus occurs (Stockner and Shortreed 1994; K.S. Shortreed, unpublished data). Quesnel Lake has an abundant nitrogen supply, so phosphorus is the major limiting nutrient throughout the season (Table 1). Average phytoplankton biomass (as CHL) was highest (1.81 μg/L) in Shuswap Lake and lowest (0.68 μg/L) in unfertilized Chilko Lake. Average CHL was 1.03 μg/L in Quesnel Lake and 0.88 μg/L in fertilized Chilko Lake. PR also reflected the differing productivities of the three lakes. Average seasonal PR was 102 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ in Quesnel Lake and 171 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ in Shuswap Lake. Chilko Lake PR averaged 79 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ in unfertilized years and 103 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ in fertilized years (Table 1).

Predictive models for lake rearing capacity

A predictive model that reliably characterizes a lake's rearing capacity for juvenile sockeye would be a valuable tool in determining optimum adult sockeye escapements. To date such models have not been available for British Columbia lakes. A model was developed by Alaskan limnologists (Koenings and Burkett 1987) and is being successfully used for management and enhancement of some Alaskan sockeye stocks. This euphotic volume (EV) model provides Alaskan fisheries managers with a method for setting escapement goals for lakes that incorporates actual lake productivities. At present in Alaska, the EV model together with freshwater and ocean survival data (Koenings et al. 1993) enables Alaskan managers to set escapement goals that incorporate both lake productivity and optimum smolt size for maximizing adult production. The EV model is based on the premise that a lake's carbon production (determined from PR measurements) is correlated to rearing capacity. Several studies have correlated various measures of lake productivity with fish yield (Oglesby 1977; Liang et al. 1981; Mills and Schiavone 1982; Fee et al. 1985). One disadvantage of determining PR is that it is a more difficult measurement to obtain than most limnological variables. Koenings and Burkett (1987) found that in their study lakes, PR (seasonal average values expressed as mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) was strongly and positively correlated to seasonal average EZD ($PR = 13.9(EZD) - 17.6$, $r^2 = 0.81$, df = 11). This occurred because widely varying levels of glacial turbidity resulted in their lakes having a relatively narrow range of nutrient loadings and a wide range in clarity. Because EZD is relatively easy to measure they used it as a surrogate for PR. They then multiplied EZD by lake surface area to yield the total volume of a lake's euphotic zone. One EV unit was defined as 10^6 m^3 of euphotic zone. In a series of experimental manipulations of fry numbers, Koenings and Burkett (1987) found that maximum numbers of smolts (23 000/EV) were produced at spawning escapements of 400–450 adults/EV. Further increasing escapements resulted in increased freshwater mortality, decreased growth, and decreased marine survival. This resulted in production of the same or fewer numbers of smaller smolts, lower marine survival, and lower adult returns. Adult sockeye productionwas maximal at an average spawning density of 425 adults/EV, which produced 23 000/EV of 4- to 5-g smolts (Koenings and Burkett 1987; Koenings et al. 1993).

A similar model would be a useful tool in British Columbia sockeye lakes, but in Fraser River system lakes, as with most regions in North America, PR and EZD are negatively correlated (Fig. 8). This occurs because Fraser system lakes have a narrower range of water clarity and a wider range of nutrient loading than found in the Alaskan lakes (Koenings and Burkett 1987). While EZD is a suitable surrogate for PR in the Alaskan lakes studied, this is not true for Fraser system lakes.

Since we routinely measure PR in our study lakes, we modified the Alaskan EV model to directly use PR rather than its surrogate EZD. We did this by replotting the Alaskan PR and EZD data with EZD as the dependent variable. The resulting equation was

$$EZD = 0.0583 \times PR + 3.25$$

where EZD is the seasonal average euphotic zone depth (m) and PR is the seasonal average PR (mg $C{\cdot}m^{-2}{\cdot}d^{-1}$). The original calculation of EV units was

$$\text{EV units} = \frac{\text{EZD (lake area)}}{10^6}$$

where lake area is the lake surface area (m^2). We then modified the calculation of EV units to use PR instead of EZD. Our modified equation was

$$\text{PR units} = \frac{(0.0583 \times PR + 3.25)\ \text{(lake area)}}{10^6}$$

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Table 2. Predicted optimum escapements (S_{MAX}) of adult sockeye with predicted and observed smolt output from our study lakes.

Lake	Lake area (km^2)	PR units	Predicted optimum escapement (millions)			Maximum smolt output (millions)	
			From PR model	From adult SR model	From juveniles[a]	Predicted from PR	Observed
Chilko							
Unfertilized	185	1447	0.62 (1436–1458)	0.90 (0.57–0.66)	1.06	33 (0.81–2.45)	34
Fertilized	185	1706 (1382–2033)	0.72 (0.55–0.91)			39	
Quesnel	270	2494 (2314–2674)	1.06 (0.93–1.20)	0.93[b] (0–infinity)	0.90	57	47[c]
Shuswap	330	4363 (3912–4814)	1.85 (1.56–2.17)	4.7 (0.54–2.59)	1.38	100	107[c]

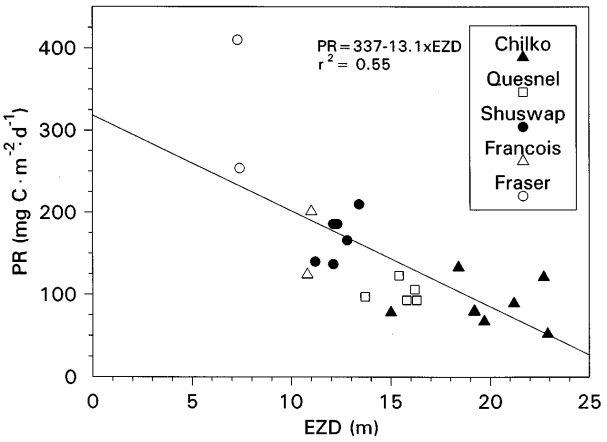
Note: Estimated range or 95% confidence limits are given in parentheses. See text for calculation methods. PR, photosynthetic rate model; SR, adult spawner recruit model.

[a]Smolts in Chilko Lake, fall fry in Quesnel and Shuswap lakes.

[b]Quadratic fit.

[c]Quesnel and Shuswap smolt numbers estimated from maximum fall fry numbers (2600 and 4900/ha, respectively) and a fall–spring mortality of 7%/month (Koenings and Burkett 1987; Hume et al. 1994).

Fig. 8. Relationship between seasonal averages of photosynthetic rate (PR) and euphotic zone depth (EZD) in Fraser River lakes.



We then entered our PR data into the equation and could calculate optimum escapements and smolt outputs for Fraser system lakes. For clarity, we call the revised model the PR model.

As stated previously, Koenings and Burkett (1987) found that in the lakes they studied maximum smolt output was 23 000/EV unit and that maximum subsequent adult returns were achieved at escapements averaging 425/EV unit. We calculated optimum escapements and maximum smolt output for our study lakes and for a number of other B.C. sockeye lakes using the factors of 23 000 smolts/PR unit and 425 spawners/PR unit (Tables 2, 3). Predicted optimum total adult escapements (equivalent to S_{MAX}) for Chilko, Quesnel, and Shuswap lakes were 0.62, 1.06, and 1.85 million (18.1, 18.7, and 31.1 EFS/ha), respectively. While a true 95% confidence interval cannot be determined, a range can be estimated on the basis of the standard error of the annual variation in the PR data and the range of optimum spawning densities found in the Alaskan lakes studied. This was about 6% of the estimated optimum for each lake and overlapped the confidence range for S_{MAX} based on juvenile data in Quesnel and Shuswap lakes, but not in Chilko Lake. However, because of fertilization and limited data points at higher escapements, there is considerable uncertainty about the optimum escapements predicted by Chilko smolt data. It is worth noting that the PR model indicates that optimum escapements to Chilko are 15 EFS/ha, and existing data indicate that no more smolts were produced at densities of 25–30 EFS/ha when the lake was fertilized than were produced at densities of 15 EFS/ha when the lake was not fertilized (Table 2, Fig. 4).

If a lake's PR units are an effective indicator of a lake's rearing capacity, then the biomass of juvenile sockeye a lake can produce should be correlated to its PR units. To test this we regressed maximum observed fall fry or smolt biomass from our study lakes against PR units. Since fall fry biomass was not available for Chilko Lake and smolt biomass was not available for Quesnel and Shuswap lakes, we assumed that smolt biomass was equivalent to fall fry biomass (i.e., losses owing to mortality were offset by late fall and spring growth of surviving juveniles). We also utilized data from two additional lakes that we believe are producing maximum biomass. Fraser Lake is a relatively small (53 km^2) Fraser system lake for which we have (unpublished) fall fry data from a high-density brood year. Babine Lake was described previously and data on smolt numbers and size are available (MacDonald et al. 1987). Despite the small sample size and assumptions about growth and survival (i.e., we had to utilize both fall fry and smolt data), the data are highly correlated ($P < 0.01$, $r = 0.93$, Fig. 9). As a further test of the utility of PR units in determining lake rearing capacity, we normalized both fall fry biomass and EFS to PR units for Quesnel and Shuswap lakes. Although the data sets and fitted Ricker curves are very different when normalized to lake area (Fig. 4), they are quite similar when normalized to PR units, particularly maximum fall fry biomass (Fig.10).

Adult sockeye stock-recruitment relationships for Chilko, Quesnel, and Shuswap lakes are of limited use in predicting

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Table 3. Predicted optimum escapements and smolt output from additional B.C. lakes.

Lake	Area (km^2)	PR units	Predictions from PR model	
			Optimum escapement	Maximum smolt output
Alastair	6.7	101	4.3×10^4	2.3×10^6
Babine[a]	475	5546	2.4×10^6	1.3×10^8
Bear	19	255	1.1×10^5	5.8×10^6
Francois	247	3151	1.34×10^6	7.2×10^7
Fraser	53	1216	5.2×10^5	2.8×10^7
Fred Wright	3.9	40	1.7×10^4	9.1×10^5
Johanson	1.4	10	4.2×10^3	2.3×10^5
Kitlope	12	71	3.0×10^4	1.6×10^6
Kitsumkalum	18	95	4.1×10^4	2.2×10^6
Lakelse	13	134	5.7×10^4	3.1×10^6
Meziadin	36	438	1.9×10^5	1.0×10^7
Morice	96	796	3.4×10^5	1.8×10^7
Nimpkish	37	254	1.1×10^5	5.8×10^6
Owikeno	91	589	2.5×10^5	1.4×10^7
Swan	18	176	7.5×10^4	4.0×10^6
Woss	13	110	4.7×10^4	2.5×10^6

Note: These are B.C. sockeye lakes in which optimum escapements have not been determined and in most cases they are recruitment limited. PR data on these lakes are from Stockner and Shortreed (1979), Stockner et al. (1980), Shortreed and Stockner (1981), and K.S. Shortreed (unpublished data).

[a]Most spawning in Babine Lake occurs in spawning channels where egg to fry survival is higher than in natural streams (MacDonald and Hume 1984). Consequently, the PR model overestimates the optimum escapement to Babine Lake.

Fig. 9. Maximum observed fall fry or smolt biomass in British Columbia lakes that are at or near optimum escapement. Data for Fraser Lake are the authors' and those for Babine Lake are from MacDonald et al. (1987).

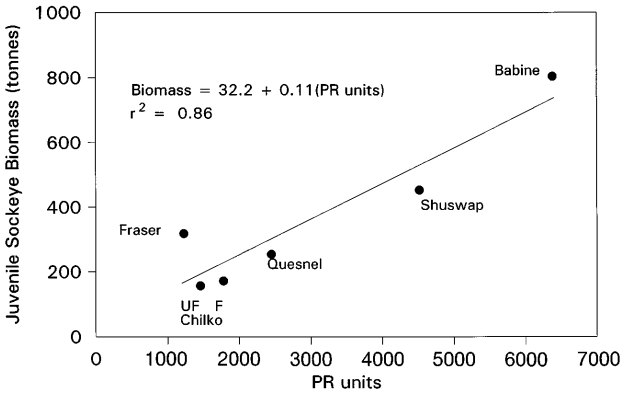
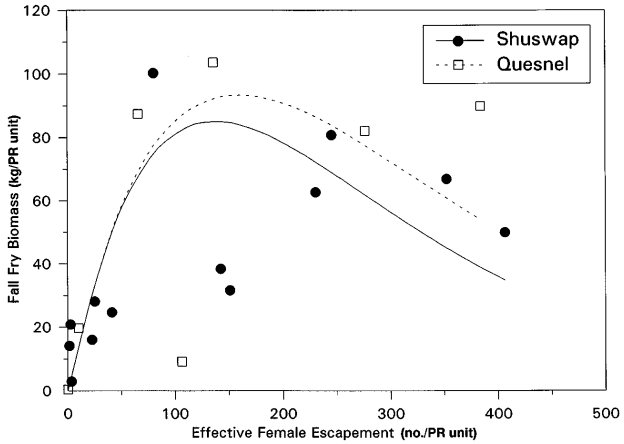


Fig. 10. Relationship between fall fry and effective female spawners in Shuswap and Quesnel lakes, normalized by photosynthetic rate (PR) units. Ricker stock-recruit curves have been fitted to the data.



optimum escapements because of the considerable scatter and because of the paucity of escapements beyond S_{MAX} (Fig. 3). With current data, juvenile sockeye (fall fry or smolt) numbers from these lakes provide a better estimate of escapements that maximize smolt production (Fig. 4). Current data indicate that fall fry or smolt numbers do not increase beyond total adult escapements of 1.4 million to Shuswap, 0.9 million to Quesnel, and 0.5 million to Chilko lakes. Predicted optimum escapements generated by the PR model agree reasonably well with those that produced maximum fry numbers (Fig. 4, Table 2).

In the Alaskan lakes studied, the EV model is an effective tool in predicting a lake's rearing capacity. We suggest that our PR model, which is a simple modification of the Alaskan EV model, will be a useful tool in B.C. lakes. When sufficient data are available, relationships between EFS and fall fry or smolt numbers provide a direct estimate of the optimum escapement to a lake. In addition, they are useful in predicting adult returns. Reliable PR data can be obtained in monthly surveys carried out from spring to fall for 1–2 years. There are many lakes in British Columbia for which we have PR data and for which sockeye production is currently recruitment limited (Table 3). Enhancement through catch management or other techniques is being considered or attempted on a number of these lakes. The PR model provides an estimate of the rearing capacity of these lakes that is based on actual lake

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productivity and that enables a manager to determine the amount of stock rebuilding that is desirable (Table 3).

Clearly, however, other factors can affect a lake's ability to produce sockeye and must be considered when setting escapement goals. Thermal regime, plankton community structure or productivity, and predator–competitor populations (Burgner 1987) all affect rearing capacity. Further, implicit in the use of the PR model to predict optimum escapements is the assumption that the relationship between spawners and fry recruitment is similar in B.C. and Alaskan lakes and that there is no spawning ground limitation. Another factor to be considered is how our estimates of optimum escapements relate to the cycles exhibited by some Fraser system sockeye stocks. Can the lakes sustain continuous optimum escapements or are lower nondominant returns necessary within each 4-year cycle? Further research is needed to better understand these factors and perhaps incorporate them together with zooplankton productivity in an improved version of the PR model. However, we conclude that in its current simple form the PR model will be a useful tool in calculating optimum escapements in British Columbia sockeye nursery lakes.

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