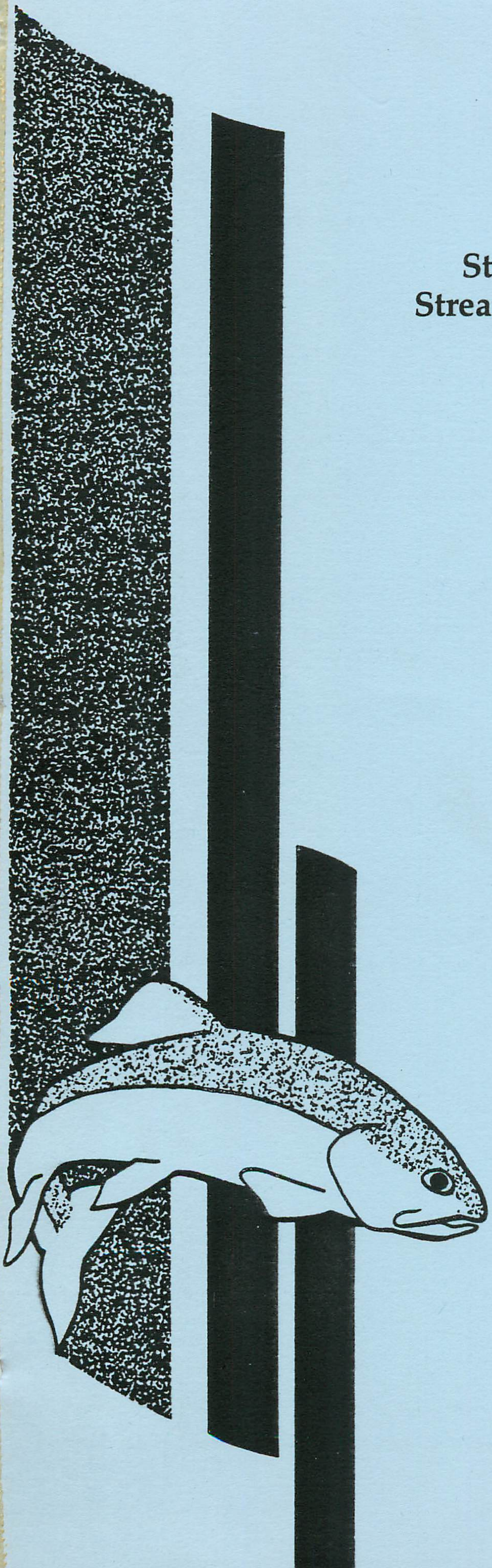

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PSARC WORKING PAPER S92-6 AND 8
Pacific Stock Assessment Review Committee

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B.R. Ward[1]
R.A. Ptolemy[2]

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[1]Ministry of Environment, Lands and Parks, Fisheries Branch,
Fisheries Research and Development Section, 2204 Main Mall,
University of British Columbia, Vancouver, B.C. V6T 1Z4

[2]Ministry of Environment, Lands and Parks, Fisheries Branch,
Conservation Section, Stock Management Unit, 780 Blanshard Street,
Victoria, B.C. V8V 1X4

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S92-6 AND 8.

STEELHEAD TROUT PRODUCTIVITY AND STREAM CARRYING CAPACITY FOR RIVERS OF THE SKEENA DRAINAGE

SUMMARY

The Skeena River contains the major proportion of British Columbia's summer-run steelhead trout. These fish are a highly-prized sports fish which are intercepted in commercial fisheries targeting mainly on sockeye and pink salmon. To manage steelhead more effectively, estimates are required of (1) the capacity of the freshwater habitat to produce smolts, as well as (2) stock productivity, expressed as the number of spawners required to sustain each of the Skeena's many steelhead populations.

Carrying Capacity

Habitat-based models of carrying capacity were examined to determine the potential of the Skeena drainage for the production of adult steelhead. Estimates were based on a) smolt production per **stream area**, b) smolt production per **stream length**, and c) a **process model** that considered variation in stream productivity, growing season, and space required to produce a smolt, for smolts of varying ages.

There are several distinct populations of steelhead which inhabit streams in the Skeena River drainage basin. The streams likely to contain steelhead were identified using stream order (from the MOE stream atlas; 1:50,000 scale maps) and water yield, as criteria. Glacial streams were excluded.

Estimation of the total area and total useable area of streams containing steelhead was calculated for the summer low-flow period. Mean annual discharge was used to estimate average stream width, and usable width was derived from habitat suitability curves based on samples of steelhead populations from many streams in B.C.

Skeena values for smolt production were estimated by calibrating the physical characteristics against those of the Keogh River, which has served as an intensively studied index system for British Columbia steelhead.

Throughout the analysis, a constant smolt-to-adult survival of 14% was used to convert smolt production to adult production.

The Skeena River was estimated to contain 2,062 km of steelhead habitat. At 40 adults$\cdot$km^{-1} (Keogh standard), 82,500 adults were predicted at capacity for the Skeena system (linear model). Useable area in the Skeena was estimated as 11,400,000 m^2. Based on 0.058 smolts$\cdot$m^{-2} of usable area at Keogh, Skeena adult

production was estimated as 92,500 fish. Estimates based on total area of the Skeena River ($4.6 \cdot 10^7 m^2$) produced an unacceptably high estimate of adult production in excess of 400,000 adults. Using conservative assumptions and excluding a significant amount of mainstem area, an estimated upper limit of approximately 200,000 fish was obtained. This result points to the desirability of using usable area as opposed to total area as a parameter, particularly for large systems. However, Symons (1979) used a total area model for Atlantic salmon, but adjusted for smolt age and survival. Using his estimates for 4+ smolts per m^2 and applying the values to the Skeena resulted in an estimate of 115,000 adults.

Using a more detailed process model, an adult capacity of 80,500 fish was derived for the Skeena River. The model incorporated the usable area concept, calibrated for the Keogh, but made adjustments based on productivity differences between streams, differences in smolt age and survival, and space required per smolt.

Overall, the models produced estimates of maximum potential production in the range of 80,000 to 300,000 fish, with the most likely value in the range from 80,000 to 120,000 adults. The value represents what could be expected in an average year under conditions of no exploitation.

Productivity

Stock productivity refers to the ability of a population to withstand a particular level of harvest on a sustained basis. Alternatively, it may be considered as the number of spawners required in order to achieve a given level of recruitment (i.e., more productive stocks produce more recruits per spawner).

The Skeena River contains a number of distinct populations of steelhead inhabiting a variety of habitat types. These populations are likely genetically distinct and vary in characteristics such as smolt age and fecundity, which directly influence their productivity.

Productivity for individual Skeena stocks was estimated based on their fecundity and on the survival patterns established from the literature and for the Keogh River. These values were used to adjust fry-to-smolt survival for the older smolt ages characteristic of the Skeena tributaries. Overall, each additional year of freshwater rearing was considered to add a 50% mortality factor.

Maximum Sustainable Yield (MSY) was estimated from stock-recruitment analyses using Beverton-Holt equations (Ricker 1975). A Beverton-Holt stock-recruit curve was fitted to the long term data available for steelhead of the Keogh River. This exercise produced an allowable harvest of 72% at MSY, for a system which produces smolts averaging 2.8 years old. The annual juvenile mortality at MSY was 48.8%. Survival rates for Skeena River steelhead were calculated at MSY by adding additional mortality based on the mean smolt age. Mean smolt age for Skeena populations varied from 3.5 to 4.5 years, indicating a lower productivity relative to the Keogh. On the other hand, the number of eggs per fish was higher in the Skeena for most stocks. Overall, and taking the stock-specific factors into account, Skeena stocks appeared to be able to withstand exploitation rates ranging from 31% to 72% at MSY. With the exploitation rate at MSY established, it was then possible to estimate the number of spawners at MSY, the number of recruits at MSY, and other stock-recruit characteristics using standard equations from the literature.

Results of this analysis indicated that some unproductive Skeena stocks could be exploited at rates in excess of their conservation requirements in most years. Of particular concern were the Sustut, Kluatantan, and Morice Rivers, and several other minor upper tributaries.

Summing the stock-specific requirements indicated a total of 23,000 spawners at MSY. However, this cannot be equated with the number of fish which must pass the Tyee test fishery, other than to say that the number past Tyee must exceed 23,000 by a factor which takes into account the native fishery, additional mortality, distribution, and weak-stock requirements.

INTRODUCTION

The Skeena River watershed is known internationally for its wild steelhead trout (Oncorhynchus mykiss). Streams in the Skeena River watershed contain some of the last major runs of indigenous wild summer-run steelhead in the world. The fish have unique run timing, large size, renowned fighting ability and represent a genetic resource which, once lost, can never be replaced.

For decades, summer-run steelhead of the Skeena River have been incidentally intercepted in a mixed-stock commercial fishery targeting on salmon (Sprout and Kadowaki 1987; Hilborn and Walters 1977). In recent years, concern for the long-term future of these stocks has heightened due to the development of enhancement facilities for sockeye salmon on Babine Lake, increasing interception in a number of commercial fisheries (Skeena River and approaches, Alaska, Nass River approaches) and the potential for increased native catch without corresponding reductions in the commercial fishery.

To better manage the many steelhead populations found within the Skeena River system, an understanding of both the carrying capacity and the productivity of the various individual populations is required.

Estimation of carrying capacity and stock productivity are separate and distinct problems. Carrying capacity is related to the maximum size of the population, while productivity is related to recruits per spawner (survival rates) and allowable harvest. For the purpose of this paper, the two problems are treated separately, but finally combined to estimate the stock-recruit characteristics of the individual Skeena steelhead populations.

Carrying Capacity Estimation

Carrying capacity refers to the average number of fish produced from a system when the habitat is fully utilized (Burns 1971). In steelhead, the limiting habitat is generally considered to be associated with the freshwater rearing period (e.g., Elliott 1989; Symons 1979). More specifically, carrying capacity may be defined approximately as the average number of smolts produced under conditions of no exploitation, or, in stock recruit terms, it is the point where the replacement line intersects the recruitment curve (Ricker 1975).

Summer-run steelhead stocks of the Skeena River undergo significant levels of exploitation in a mixed-stock fishery (Sprout and Kadowaki 1987). Therefore, populations would rarely be expected to reach the asymptotic levels of production associated with carrying capacity as defined above. Further, it is currently impossible to identify distinct stocks in the commercial catch to obtain population-specific catch and escapement data from which to calculate stock-recruit curves. Therefore, an alternative approach was required.

Our approach involved quantifying the amount of habitat for steelhead rearing associated with the various Skeena tributaries and subsequently using a variety of models to estimate smolt production. The process involved the development of several steps organized as follows:

1) distribution - identifying the number of streams in the drainage likely to contain steelhead,

2) fish use - estimating the total area and total usable area of steelhead-bearing streams, and

3) production - estimating the number of smolts produced from the usable areas.

Fish distribution may be based on ground surveys or in relation to known factors which limit distribution (e.g., temperature, flow regime, gradient). Fish use refers to physical criteria in streams (e.g., depth, velocity, substrate) which govern the positions preferred by salmonids in streams (e.g., Bovee 1982). Fish production relates to the average number that a system may produce under conditions where the habitat is fully used.

Productivity Estimation

Stock productivity is determined by fecundity and the survival rates characteristic of the various life history stages. By estimating stock productivity, other useful population statistics are obtained, including the parameters of the recruitment curve and allowable harvest at MSY. If the number of adults at carrying capacity is known, it is also possible to estimate the spawners required for conservation, number of recruits at MSY, etc.

Direct estimation of the productivity of the Skeena River tributaries was not possible, thus we used an indirect modelling approach. Life history information from intensively studied systems such as the Keogh River (Ward and Slaney 1992 in press; 1988; Ward and Wightman 1989) was used along with life history and productivity information from the literature (e.g., Symons 1979) to estimate the productivity of the Skeena's streams.

Skeena systems have shorter growing seasons and older smolts, than more southerly systems. Smolt age and fecundity are key factors which vary among Skeena tributaries. It is expected that as smolt age of anadromous populations increases, survival from egg to smolt decreases, with a corresponding decline in productivity (cf Shackley and Donaghy 1992). Chadwick (1987) noted that, with

Atlantic salmon, populations that differ in smolt age have different vulnerabilities to exploitation.

METHODS

I. Study Areas

The Skeena drainage in northwestern British Columbia is ca. 42,200 km^2 with a mean annual discharge (MAD) of 912 $m^3 \cdot s^{-1}$. Water yields (MAD per 100 km^2) vary from 0.7 $m^3 \cdot s^{-1} \cdot 100km^{-2}$(Buck Cr.) to 11.5 $m^3 \cdot s^{-1} \cdot 100km^{-2}$ (Exchamsiks). The flow regime of the Skeena is typical of interior watersheds on the west coast, with high flows occurring in June (300% of MAD) and lowest flows during March (16% of MAD). The Skeena River and its tributaries cross several geoclimatic zones (Fig. 1). Only systems which contain summer-run populations were included in the analysis.

While the focus of the report is on the Skeena River, the analysis relied heavily on the Keogh River as an index system. The Keogh River is a coastal stream located on the northeastern end of Vancouver Island. The river is 32 km long and drains a watershed of about 130 km^2. Ambient nutrient concentrations are low, mean pH is 6.9, and total dissolved solids are about 30 $mg \cdot l^{-1}$. Total Alkalinity is 16 $mg \cdot l^{-1}$ during the summer base flow period. The Keogh River watershed was described in Ward and Slaney (1979), Johnston et al. (1986, 1990), and Irvine and Ward (1989).

II. Carrying Capacity

The estimation of carrying capacity involved the construction of a number of submodels organized into three general areas: distribution, fish use, and fish productivity.

Distribution

We used stream order measured from 1:50,000 scale maps as a key parameter in determining the likely presence or absence of steelhead. This approach was similar to that of Platts (1979), who examined the relationship between the network structure of streams and salmonid distribution. This system was modified for British Columbia streams by incorporating a climatic index based on annual water yield (D. Sebastian, in prep., Fish. Branch, Victoria, B.C.). Stream order of the tributaries of the Skeena River was determined using a method developed by Horton (1945) and Strahler (1957).

Stream orders were determined from the MOE Stream Atlas which consists of digitized blue lines taken from 1:50,000 topographic maps. The stream atlas does not include streams designated as intermittent at the 1:50,000 scale. Average water yield was determined from Water Survey of Canada (WSC) records by dividing the MAD by watershed area. The WSC supports 52 stations that monitor discharge in the watershed.

In the development of the distribution model, a particular stream or reach was considered important for steelhead rearing if less than 10% of the total juvenile trout and char biomass consisted of species other than rainbow (i.e.; cutthroat, Dolly Varden) based on electrofishing surveys (e.g., Sebastian 1988, and data on file, Fish. Br., Smithers and Victoria, B.C. - numerous field reports of D. Tredger et al.). Glacial streams which were <7°C and turbid (>50 ppm) during the summer were not included as streams considered important for steelhead.

The distribution model provided estimates of the lengths of the systems containing steelhead, organized by stream order.

Total and usable area

After identifying reaches containing steelhead, we estimated the total wetted area during the summer low flow period as the product of length and the average wetted width of the cross sections at the top and bottom of the reach. The low summer flow value is important since, for steelhead trout, most compensatory mortality takes place during this period (Ward and Slaney 1992 in press; Bjornn 1987, 1978), and overall production would be expected to correlate with the amount of habitat utilized during the limiting life history stage.

Changes in water surface width, mean depth, and mean velocity are related to changes in stream discharge (Hogan and Church 1989; Morisawa 1968). The response of stream width to discharge is a power function, and there is an empirical relationship between stream width and MAD (Hynes 1970). The width exponent is usually 0.5 (Hogan and Church 1989).

An analysis of 119 reaches from 47 different streams in British Columbia revealed the following relationship between MAD and stream width (Sebastian et al., unpubl. MS, Fish. Br., Victoria, B.C.):

$$WIDTH=5.42\cdot MAD^{0.523} \qquad (1)$$

The adjusted r^2 value for this relationship was 0.93 with a coefficient of variation (CV) of 12.1. In this analysis, average widths for small streams were determined by averaging point width measurements within a reach unit. For large streams, average widths were determined from large scale aerial photographs (i.e.; 1:2,000 to 10,000), either by averaging several point width measurements or by digitizing stream area and dividing by thalweg length.

The average width for a particular reach was calculated from equation (1), using the MAD value calculated from equation (2):

$$MAD_{adj}=\left(\frac{\left(LWA\cdot\frac{WY}{100}\right)^{0.5}+\left(UWA\cdot\frac{WY}{100}\right)^{0.5}}{2}\right)^{2} \qquad (2)$$

where LWA is the lower watershed area, UWA is the upper watershed area and WY is the water yield obtained from historical flow records (Water Survey of Canada) for reaches with gauging stations.

The proration method (C. Howard, pers. comm. 1990, Inland Waters Directorate, Environ. Can., Ottawa) was used to develop water yield estimates for ungauged stream reaches in the Skeena drainage. Ungauged reaches on stream courses that were gauged at upstream or downstream locations were given the same water yield. Ungauged reaches for which there were no gauge locations on the same stream course were given water yield values from the nearest stream course.

The output from this component of the model produced estimates of the total stream area at low summer flow for each of the Skeena reaches containing steelhead.

In the next step, total area was adjusted downward to estimate usable area. It is recognized that fish prefer specific hydraulic conditions during different phases of their life cycles, with the result that only a certain percentage of the width or area of a stream will be used by rearing salmonids. Many studies have developed habitat suitability curves to account for this variability in usable area (e.g., Bovee 1982; Sheppard and Johnson 1985; Rubin et al. 1991).

Habitat suitability curves were described for steelhead fry from a large B.C. data set, examples of which were presented in the assessment reports of Ptolemy (1989) for the Coquihalla River, and Sebastian (1987) for the Cranberry-Nass River system. These curves are for juvenile fish from 0.5 to 4.0g, or 37 to 74mm fork length. The curves were similar to other published curves which associated steelhead fry with low velocity, shallow habitats in large streams (e.g., Rubin et al. 1991).

Usable habitat was predicted based on the estimated fraction of stream width that is hydraulically suitable for steelhead fry rearing. An analysis of 628 stream reaches in the Province revealed the following relation between percent usable width (%UW),

MAD_{adj} and low flow stage (LFS; from WSC records):

$$\%UW=10^{(2.39-0.275\cdot LOG_{10}(MAD_{adj}+1)-0.4\cdot\log_{10}(LFS+1))}-1 \qquad (3)$$

The adjusted r^2 for this relationship was 0.59 with a CV of 11.9 (R. Ptolemy, pers. comm., Fish. Br., Victoria). Once %UW was determined for reaches in the Skeena, total useable area was calculated by multiplying %UW by stream width and stream length.

Smolt production

Having obtained estimates of usable area, carrying capacity was estimated by calculating the number of smolts expected per unit of habitat. This component of the model is complex and a number of approaches were used. The intent was to provide a range of reasonable values rather than a definitive number.

Intensively studied systems such as the Keogh River (Ward and Slaney 1988; 1992 in press) provided a basis for developing production estimates. Also, Symons's (1979) summary of the production of Atlantic salmon proved useful.

In developing the range of smolt production estimates, three approaches based on values derived from the Keogh River were used. The linear model simply extrapolated the number of Keogh adults (or smolts) produced per kilometre of stream length to the Skeena systems. Similarly, an area-based model used adults or smolts per m^2 of total habitat and usable habitat to obtain estimates for the Skeena.

The above approaches have obvious limitations given the Skeena has systems with higher nutrients, colder temperatures, and older smolts. Consequently, a third approach was developed which attempted to deal with these differences by making adjustments for two key factors, stream nutrient level and space required per smolt. The adjustments were based on principles derived from the scientific literature (e.g., Symons 1979) or regression models.

(i) adjustment for nutrient differences

A regression model of steelhead standing crop vs Total Alkalinity (TALK) provided a means to adjust for systems with varying nutrient levels. In British Columbia, TALK values for sampled steelhead streams ranged from 1.2 to 246 $mg\cdot l^{-1}$. The wide range indicated the diversity of habitats in which steelhead were found in the Province, which in part also explained the high variance about the regression line. The regression equation was

(4) $$LOG(SCROP) = 0.56 + 0.5 \cdot LOG(TALK)$$

where SCROP was standing crop of steelhead in $Kg \cdot ha^{-1}$ measured at the end of the summer, and TALK was total alkalinity measured in $mg \cdot l^{-1}$ ($r^2=0.30$, $p=0.01$; cf Ptolemy et al. 1992 draft in prep.).

To calculate the Skeena adjustment, the ratio of the predicted Skeena standing crop and the predicted Keogh standing crop was calculated, i.e.,

(5) $$Adjust_1 = SCROP_{Skeena}/SCROP_{Keogh}$$

The adjustment factor was then applied to the smolts per usable area estimated for the Keogh to obtain a Skeena value.

(ii) adjustment for space per smolt

The second adjustment used the same process as above, except using space per smolt as the variable. It is assumed that populations characterized by older smolts have lower fry-to-smolt survival rates. As a result, it requires more fish to produce a smolt, and integrated over the life history, more space. Thus smolt production per m^2 of usable area is assumed to decrease as a function of the space required per smolt. The space or territory size required to produce a smolt was the sum of the space required per fish during freshwater rearing, summed over the number of fish required to produce a smolt of a given age.

A recent review by Grant and Kramer (1990) produced a general regression for stream dwelling salmonids relating territory size to fork length ($r^2=0.87$, $n=23$). The equation:

(6) $$LOG10(AREA) = 2.61 \cdot LOG10(FLENG) - 2.83$$

represents data from 5 species and 10 different studies.

Estimates of fork length at the end of the growing season for parr of various ages were obtained from extensive field sampling of steelhead populations (Ptolemy et al. pers. comm., Fish. Br., Victoria). With these values it was then possible to estimate the space required per fish from equation 6.

The next step in the method was to multiply the space per fish by the number of fish alive in each year of the fry-to-smolt life history stage. The number of fish alive is defined as the number required at a particular stage which will result in a single smolt of a given age at the end of the fry-to-smolt period. The age-specific survival rates for smolts of various ages are summarized in the productivity section. Using these values, it was then possible to generate the number alive at each life history stage. The product of the number of fish alive and space required per fish produced the total space required per year, for each year of the life history. The yearly totals were integrated to obtain the total space required to produce a smolt, for each smolt age.

In the final step of the method, the total space values were regressed against smolt age to obtain the relationship between space required and smolt age, i.e.,

(7a) $$\text{SPACE} = 1.24(\text{SAGE}) - 1.31$$

Equation 7 provided the space required values to calibrate the Skeena against the Keogh. The adjustment factor was calculated:

(7b) $$\text{ADJUST}_2 = \text{SPACE}_{\text{keogh}}/\text{Space}_{\text{Skeena}}$$

III. Productivity Estimation

As noted above, direct estimation of the productivity of the Skeena River tributaries was not possible, and an indirect approach was required. The method consisted of three steps:

(i) development of a standard stock-recruit curve for steelhead, along with estimates of survival rates for various life history stages,

(ii) development of a method to adjust stock productivity based on variation in fry-to-smolt survival rates as a function of smolt age, and

(iii) application of the method to the Skeena systems using system-specific smolt ages and fecundities.

(i) Stock-recruit analysis

Survival rates of steelhead have been studied at the Keogh River, on northern Vancouver Island, since 1976. The Keogh River data served many purposes. By looking at a wide range of spawning escapements for a virtually unexploited population (i.e., winter-run steelhead), an estimate of the asymptotic carrying capacity was obtained. In addition, fitting a Beverton-Holt recruitment curve provided an estimate of stock productivity. Estimates of egg-to-fry, fry-to-smolt, and smolt-to-adult survival rates, fecundity, and mean smolt age were obtained and used to adjust productivity between systems.

Procedures for estimating ages of adult steelhead, and methods of enumerating and sampling smolts at the Keogh River have been described elsewhere (Slaney et al. 1990; Ward and Slaney 1988, 1990; Ward et al. 1989, 1990; Irvine and Ward 1989). Estimates of survival and age structure of steelhead smolts and adult returns have been documented (Ward 1988, 1989; Ward and Slaney 1988). Methods of determining survival rates and stock-recruit parameters are briefly summarized here due to some of the complexities of the process.

Stock-recruitment in Keogh River steelhead was based on annual estimates of the size of the spawning population (Ward and Slaney 1988) and enumeration and ageing of smolts. Smolts were tabulated into their brood years of origin and recruits were determined from a broodyear's smolt yield based on size-biased survival from smolt to adult (Ward 1992a in prep.; Ward et al. 1989).

The method of calculating Recruits (R) was preferred to the alternative of aging adult returns to determine their brood year of origin. Adults' scales frequently were regenerated or unreadable in the freshwater growth zone, and sample sizes were at times too small to provide reliable estimates over the broad age structure characteristic of steelhead (Ward and Slaney 1988). Furthermore, a method based on age would not filter out the El Niño effects of 1982/83 on four of seven broods, and would reduce the available brood years for analysis, (n = 7 <u>vs</u> 12).

The relationship between R and P was asymptotic thus the Beverton-Holt equation (Ricker 1975) was used to estimate stock-recruit parameters:

$$R = P \;/\; (1-A(1-P/P_r)) \tag{8}$$

The value A can range from 0 to 1, and describes the shape of the recruitment curve and therefore the stock productivity. P_r refers to spawning stock size at replacement.

Given A and P_r, it is possible to calculate several other recruitment statistics (Ricker 1975), including the number of spawners needed (P_s) for MSY, the recruitment (R_s) at MSY, the maximum sustainable yield (MSY), maximum recruits (R_{max}), and the rate of exploitation at MSY (μ_s).

(ii) Fry-to-smolt survival rate and the relation to smolt age

The Keogh data provided estimates of egg-to-fry, fry-to-smolt and smolt-to-adult survivals for steelhead (Ward and Slaney 1992 in press, 1988). In application of these survival rates to the Skeena, it was assumed that the egg-to-fry and smolt-to-adult survivals were density independent and constant, and that the major difference in productivity would be in the fry-to-smolt survival rates.

A general treatment of the problem of estimating survival rates as a function of smolt age was required, i.e., a table of age-specific survival rates estimated at MSY, for each of the possible smolt ages. The process used MSY survival rates from fry to smolt, estimated for the Keogh (average smolt age of 2.8 years), fry and parr size, and information from the literature to assist in establishing the mortality schedule.

We assumed that as smolt age increases, fry-to-smolt survival (and fish length at a given age) declined. Older smolts are exposed to mortality for additional years, and are smaller, longer (cf Shackley and Donaghy 1992). We also assumed that annual survival would be a function of fish length, with the consequence that higher annual mortality would be experienced earlier in life history.

To assist in developing the survival table, a simple model was created to generate age-specific survival rates. The model calculated age-specific survival as a linear function of fork length (measured at the end of the growing season), with the model parameters being the slope and intercept of the regression line. Various levels of dependency of survival on size could be tested by altering the slope of the relationship, which had the effect of distributing the mortality differently among the various years.

Knowing fry-to-smolt survival at MSY as a function of smolt age and combining that with egg-to-fry and smolt-to-adult survival, it was possible to calculate recruits per spawner and exploitation rate at MSY, from which the other population parameters could then be derived.

(iii) Smolt age estimation

The previous two sections established a means for determining the productivity of a stock given smolt age and fecundity. The last step in the method was to estimate the stock-specific smolt ages from physical or biological parameters measured for the Skeena system. Given its importance, two different methods were used to estimate smolt age. One method involved regressing length of the growing season against smolt age and the other used final smolt length divided by the annual growth increment in length to estimate smolt age.

Symons (1979), in his summary of the production dynamics of Atlantic salmon, used the number of days > 7° C to describe the relation between smolt age (AGE) and length of the growing season (DAYS):

$$\text{AGE} = 9.08 \cdot 0.9938^{\text{DAYS}} \tag{9}$$

This equation adequately described the properties of the relationship, but needed to be calibrated to B.C. conditions, essentially by altering the intercept. Such a correction was justified given the assertion that 500 days is required to grow an Atlantic salmon smolt. This disagrees with known steelhead life history, where one-year-old smolts are known to occur (e.g., Rempel et al. 1984). Calibration was accomplished by forcing the curve to fit a Skeena system (Babine River) where smolt age was estimated from steelhead scales. The Babine River was selected because it has the longest growing season and thus scales of fish are least likely to be missing the first annulus. The altered equation was:

$$\text{AGE} = 8.16 \cdot 0.9938^{\text{DAYS}} \qquad (10)$$

The second method estimated smolt age by sampling of juvenile fish and computing the length added during each year of life. Since the increment per year is suggested to be constant except for the year prior to smolting (Symons 1970), it is theoretically possible to roughly estimate smolt age by dividing a typical smolt length (175mm; Ward and Slaney 1988) by the growth added per year, with adjustments for initial size and "plus" growth added just prior to smolting. A recent, similar approach has been suggested for brown trout (L'Abee-Lund et al. 1989).

Growth increment was estimated as the difference in fork length among fresh water ages. The accurate estimation of these differences is confounded to some degree by sampling and size-dependent mortality; however, a large data set based on extensive juvenile sampling of the Skeena systems provided reasonable estimates of growth increments for a number of the Skeena systems. Annual growth increments for steelhead in the Skeena were calculated by averaging the values for the differences between ages.

Application of stock-recruitment analysis of Keogh River steelhead to Skeena River steelhead

To determine the number of recruits and the allowable harvest ($\underline{u}_s$) for steelhead of the Skeena River required information on the fecundity, smolt age, fry-to-smolt survival, and adult production at capacity for each of the major sub-populations of the Skeena steelhead population.

Fecundity was estimated from steelhead examined by Wilkman and Stockerl (1981MS). Using lengths of angler-caught fish and adjusting for possible differences in fish lengths in the 1991 commercial fishery (Thomas 1991), the average fecundity for each major substock was determined. The data on fecundity and the survival rates through each life stage were used to determine stock-specific productivity and the minimum required escapement.

The allowable harvest rate at MSY for the sub-stocks is therefore the number of recruits each spawner produces at MSY (R_s) above that required to replace itself:

(11) $$\underline{u}_s = (R_s-1)/R_s$$

With a "known" $\underline{u}_s$, Ricker (1975) suggested (equation 21, curve 4 of his Appendix III) that Beverton-Holt's A value can be estimated. Thus:

(12) $$A = 1-(1-\underline{u}_s)^2$$

The carrying capacity model provided an estimate of the adult production at carrying capacity for each of the sub-stocks (Table 5). Given that, it was possible to estimate P_s (spawners at MSY) and Rs (recruits at MSY) (Ricker 1975), i.e.:

(13) $$P_s / P_r = (A - 1 + \mathrm{sqrt}\{1 - A\}) / A$$

and

(14) $$R_s / P_r = (1 - \mathrm{sqrt}\{1 - A\}) / A$$

where the subscript r refers to the replacement value. Spawners and recruits produced at MSY were thus calculated for each of the major sub-populations of Skeena River steelhead.

RESULTS AND DISCUSSION

I. Carrying Capacity

Fish distribution

The stream order classification model and analysis suggested that juvenile steelhead used 4th order and larger streams at water yields of ca. 5 $m^3 \cdot 100km^{-2}$ or less. At higher water yields steelhead primarily used 3^{rd} order and larger streams. Steelhead required a stream size with a mean annual discharge of 1.0 to 1.5 $m^3 \cdot s^{-1}$ or greater. Since all Skeena streams upstream of Cedarvale (summer runs) fell into the less than 5 $m^3 \cdot s^{-1}$ water yield category, only 4^{th} order and larger streams were included in the habitat capability model.

All the stream reaches important for steelhead use were identified (Appendix 1). A total of 75 streams or reaches of order 4 or larger and representing 2,062 km of stream habitat were considered important for rearing steelhead. The total stream length (sum of all tributaries and mainstem reaches of order 4 or larger) of the Skeena drainage was 3,007 km. Streams classified as high steelhead use represented 68.7% of the total length of the system (Table 1).

For the purpose of analysis, it was useful to combine detailed reach information into summaries for stock groups relevant to management. These groups were the Skeena mainstem, tributaries to the mainstem, with further divisions of some large or diverse tributaries. The physical characteristics of these stock groups were summarized to facilitate stock comparisons (Table 5).

There was agreement between the distribution predicted by the model (Table 1) and field studies based on electrofishing throughout the watershed. However, a misclassification of stream order was possible due to errors in how the blueline data was digitized. Such errors were likely to be limited to a magnitude of ± 1 order. Errors in stream orders of 5 or higher were not likely to affect the results because it would take an error of ± 2 orders to result in misclassification. The same was true for streams of order 4 at high water yields. Similarly, misclassification of stream orders 1 and 2 (at low water yields) were not likely to affect the results.

Stream orders of 4 accounted for 25.5% of the total useable area, order 5 streams accounted for 17.5%, order 6 streams accounted for 35.0%, and order 7 streams accounted for 30.6% (Table 1). Accordingly, misclassification of 20% of the order 4 streams could result in an approximate ± 5.1% error in the total useable area. The above comparisons indicated that although errors in classification could be important, the effect on total steelhead production for the Skeena was not likely to be very significant. Nonetheless, care should be taken in applying this method where there is variation in map scale or accuracy.

Total and usable area

Total and usable area were calculated by multiplying the stream length by the estimated wetted width during summer low flow (Table 5). We evaluated the accuracy of the width model by comparing predicted values with field-measured widths for a number of streams. Predicted widths for 14 selected streams in the Skeena drainage were similar to field measurements (Fig. 2). For small streams (<30m width), the predicted width was slightly higher than the observed width. For larger streams, the predicted width tended to be considerably smaller than the observed width indicating that the equation #1 is less applicable to large streams than small streams, or that field measurements of width tended to underestimate the true width for larger streams.

Since the calculation of stream width is an important aspect of the area calculation, the accuracy of the discharge values was of some concern. Of the 75 streams or reaches included in the model, only 21 (28%) had WSC stations within the reach itself. However, these streams accounted for 74.2% of the predicted useable area. Of the remaining 54 streams, 22 used WSC station data from upstream or downstream areas within the same watercourse (15.5% of useable area) and 32 used data from adjacent waters (10.3% of the total useable area). Because streams with WSC stations on them accounted for a relatively high proportion of the predicted useable area, the absence of stations on every stream or reach included in the model was not likely a serious problem.

Total area and total usable were calculated to yield $102 \cdot 10^6$ m^2 total and $11.4 \cdot 10^6$ m^2 respectively (Table 5). Usable widths for tributaries ranged from 12% to 38% of total width, and as low as 5.5% for the lower mainstem. Overall, usable area was approximately 10% of the total area of the Skeena system. The Skeena mainstem accounted for 32% of the total usable area.

Fish production

Estimates of smolt production were developed using a variety of approaches, ranging from simple extrapolations using stream length or area to more complex adjustments which considered factors believed to influence production.

i) Production estimates based on length and area

Using the same formulas for the Keogh and Skeena to estimate width and discharge provided a standard approach from which to base extrapolations of production. Using the regression models (equations 1, 2 and 3), the Keogh had a predicted width of 9.46m, a length used by steelhead of 25 km, and a total usable area of 129,400 m^2 for fry. In practise, there were small differences between measured and predicted values, but for the purpose of this exercise, using the same method for the two systems minimized biases in the models.

The Keogh produced 7,500 smolts at capacity (Fig. 8) which resulted in 1,050 adults from 14% survival (Ward 1992a in prep.; Ward and Slaney 1988, 1992 in press). Overall, the Keogh produced 0.058 $smolts \cdot m^{-2}$ of usable area for end-of-summer fry, 0.032 $smolts \cdot m^{-2}$ total area, and 300 smolts or ca. 40 $adults \cdot km^{-1}$. Snow Creek, a smaller index system in Washington State (MAD, 0.69 $m^3 \cdot sec^{-1}$ <u>vs</u> 5.3 $m^3 \cdot sec^{-1}$ at the Keogh River), produced average values of 82 $smolts \cdot km^{-1}$ of total stream length and 0.026 $smolts \cdot m^{-2}$ total area (max. 0.035; Johnson and Cooper 1991), or 0.039 $smolts \cdot m^{-2}$ of usable fry habitat.

The Keogh steelhead production values, extrapolated to the Skeena, provided preliminary estimates to compare to more complicated models. The linear model (40 adults per km), applied to the 2,062 km of the Skeena, suggested an adult population of ca. 80,000 fish. The area-based computation of usable area ($11.4 \cdot 10^6 m^2 \cdot 0.058$ smolts$\cdot m^{-2}$) produced an estimate of 92,500 adults, while estimates based on total area exceeded 400,000 adults.

These results can be compared to Atlantic salmon. Symons (1979) used a total area model, but adjusted for smolt age and survival. Using his estimates for 4+ smolts per m^2 and applying the values to the Skeena resulted in an estimate of 115,000 adults.

The results were what might be expected intuitively. Smolts per km estimates derived from small streams, and applied as a standard to larger systems, would significantly underestimate production. Similarly, calculations based on total area would significantly overestimate production for large systems. The usable area method produced values which were between linear and total area values, and as such likely provided a better estimate of capacity. In both the linear and usable area cases, the derived values were 2 to 4 times higher than current estimates of run size (mean ca. 37,000 from 1956 to 1990; Spence et al. 1991).

ii) Physical and biological adjustments

The direct application of the Keogh values to the Skeena could arguably be of limited value since a number of factors have not been taken into account. The Skeena has higher nutrient levels, colder temperatures, more input from glacial tributaries, and older smolts than the Keogh. Based on known biological principles, adjustments to the usable area estimates can be made. The following analysis uses a series of spreadsheet calculations (Table 5) to perform the appropriate adjustments for nutrient levels and rearing space per smolt.

Numerous investigators have demonstrated the relationship between indices of nutrient abundance and fish production. Recent work by Johnston et al. (1990) confirmed that nutrient additions to streams increase periphyton standing crop and steelhead fry growth rates. Nutrient additions to lakes have similarly demonstrated increases in growth, survival and production (Hyatt and Stockner 1985). Current work in progess by B.C. Fisheries has led to development of a predictive relationship between maximum salmonid density in streams in relation to alkalinity, an index of nutrients, and fish size (Ptolemy et al. 1992 draft in prep.).

TALK estimates within the Skeena River varied from 15 to 40 mg•l^{-1} (Table 5), which was considerably higher than the Keogh (16 mg.l^{-1}). For the Skeena then, the adjustments in smolts per usable area ranged from no change for systems with 16 mg•l^{-1} to a 1.6 fold increase for systems with 40 mg•l^{-1}. This was a conservative assumption in that a 60 percent increase was obtained by more than doubling of nutrient levels in many of the key systems (Bulkley, lower Skeena, etc.).

The second adjustment in the model dealt with the additional rearing space required for the older smolts of the Skeena systems. Smolt age can be directly obtained from scales, and this has been done for a number of Skeena systems for a variety of reasons. Cox-Rogers (1986) examined hundreds of scales from each of the major systems for the purpose of distinguishing stocks in the commercial fishery. Average smolt ages from these studies were: Zymoetz, 3.54; Morice, 3.72; Kispiox, 3.44; Babine, 3.32; and Sustut, 3.74. Unfortunately, it is likely that the first annulus was not present for the colder systems on the Skeena, complicating the process of determining smolt age, i.e., smolts were under-aged by at least one year. (Fry in some areas of the Skeena River at the end of the growth season were too small for formation of an annulus on scales; others were within the range of formation of the intial scale placode only: cf Ward et al. 1989).

The growing season-smolt age curve established for Atlantic Salmon was adjusted to pass through the fastest growing system (Babine; Fig. 3). Using the growing-season method produced an older smolt age than was estimated by Cox-Rogers (1986). For example, the Sustut was estimated to have an average smolt age of 4.2-4.5 years compared to the estimate based on scales of 3.74. If the first annulus was missing in all fish, the Sustut age would be expected to be 4.74 years.

As a further check on the growing season calculations, smolt age was estimated by sampling of juvenile fish from the Skeena and computing the growth increment added during each year of life. Increments for each system were calculated by averaging the values for the differences between length-at-age, on the assumption that length increase tends to be constant. Skeena increments ranged from 28.5 to 40.75mm per year (cf Table 2). Lowest values were recorded for the Sustut River, while high values were found in the lower Skeena, Babine and Bulkley Rivers.

The estimation of smolt age using growth increment is complicated by the need to determine starting size, nonlinear "plus" growth added in the last year and the actual smolt size as a function of smolt age. Nonetheless, assuming a 175mm smolt, a 25mm starting size, and plus growth in the order of 10-15mm, it follows that 135 to 140mm of linear growth was required. Slowgrowing Skeena smolts (30mm per year increment) would have 4.5 to 4.7 yrs as a mean smolt age; fast growing smolts (40mm per year) would average 3.5 yrs.

A significant correlation existed between growing season and growth increment (r^2=0.85) suggesting that the differences between systems were consistent and adequately predicted by length of the growing season.

Using smolt ages as calculated above, it was then possible to develop the second adjustment for smolt production based on space required per smolt measured relative to the Keogh. These adjustments resulted in as much as a 50% reduction in smolts per m^2 for the systems with the oldest smolt ages (Table 5).

Skeena Carrying Capacity Summary

The Skeena at capacity could produce approximately 5.75 million smolts resulting in 80,400 adults (Table 5). This estimate was similar to the that of the simpler models which used stream length (82,400 adults) or area (92,500 adults).

On a stream specific basis, the Bulkley had the largest capacity for adults (22,000), if mainstem rearing was not considered. It is important to note that the individual estimates of capacity were dependent on a map exercise, with a set of rules based on stream order to establish lengths used by steelhead. Such an approach may produce statistical variation between systems, leading to high estimates in some, low estimates in another. This can only be corrected by more detailed and complete field surveys for the key systems.

III. PRODUCTIVITY ESTIMATES

(i) Keogh stock-recruit and life history analysis.

Development of productivity estimates involved analysis of stock-recruit data from the Keogh River. This analysis was complicated by a number of factors, including an El Niño event which dramatically increased survival (1982 smolts), a whole-river fertilization experiment which altered the production for a number of years (1983 to 1986; Johnston et al. 1990; Slaney et al. 1986), and returns of clipped hatchery fish from experimental net pens (e.g., Ward and Slaney 1990). Despite these complications, the data on many aspects of the life history of wild fish were quite clear, particularly for the broods of 1976 to 1981 which were unaffected by the above experiments.

A plot of the stock-recruit values for the years not influenced by fertilization or El Niño demonstrated a wide variation in number of spawners (Fig. 4) and a distinct asymptote to production. If hatchery fish were added to the analysis, the range of spawners was increased (Fig. 5), but the fundamental shape of the curve and the asymptotic value remained unchanged.

Fitting the Beverton-Holt recruitment curve resulted in a maximum production (R_{max}) of 1100 spawners, recruits at MSY of 700, spawners at MSY of 210, and an allowable exploitation rate of 70%. These values are high and dependent on a relatively small number of points for the low end of the curve. Further data collection in less productive years would result in lower allowable harvest rates. In comparison, fisheries managers in Washington State estimated an allowable harvest of 40% for their more productive steelhead stocks (Gibbons et al. 1985). In addition, the frequency of major environmental events affecting stock productivity beyond normal must also be considered (Ward 1992b in prep.).

Survival rates for each life history stage were also examined. Regression of ten years of annual smolt output (1977 to 1986) on subsequent adult return indicated a linear relationship between smolts and adults (Fig. 6; $r^2 = 0.752$, $p < 0.05$):

$$z = 0.245(x) - 497.326 \quad (15)$$

where z = the number of adults and x = number of smolts. The correlation coefficient improved to 0.878 in a multiple regression of adults vs smolt numbers and smolt length (y, in cm), where the 1982 outlier was excluded:

$$z = 0.201(x) + 377.758(y) - 6675.326 \quad (16)$$

The 1982 outlier (Ward et al. 1989; Ward and Slaney 1988, 1990) was excluded in calculation of survival rates. Thus, the arithmetic mean smolt-to-adult survival was 15.6%, while the more appropriate (skewed distribution of survival data) geometric mean survival (Ricker 1973) was 14.4%.

The relationship between fry abundance and eggs deposited at the Keogh River was found to be linear (Fig. 7) based on limited data (n = 6), where the ratio of eggs to fry was approx 10:1, except in years of much higher than (4-times) normal flow pattern (spring 1976; Ward and Slaney 1992 in press).

Plots of smolts vs eggs and smolts vs fry resembled the curve for the above spawner-recruit relationship, further indicating density dependence in fresh water (Fig. 8). Smolt yield reached an asymptote at 7,500 fish, when egg deposition was 1.5×10^6, or 1,080 spawners (Fig. 8; Ward and Slaney 1992 in press).

Overall then, egg-to-fry and smolt-to-adult stages were density independent and averaged 10% and 14%, respectively. Fry-to-smolt survival was variable and strongly density dependent.

(ii) Smolt age and fry-to-smolt survival

Steelhead smolt age is a population characteristic which varies considerably, and was the parameter we assumed would be most likely to influence stock productivity. The objective of this section was to relate fry-to-smolt survival to variation in smolt age.

From the Keogh data, it was possible to estimate the fry-to-smolt survival at MSY, for a mean smolt age of 2.8 years old. From the known overall survival it was then possible to estimate annual survival as an instantaneous rate calculation, i.e.,

(17) $$N_t/N_0 = e^{-zt}$$

Thus, for the Keogh River, -z = ln(5,843 smolts/43,556 fry)/2.8 years, or 0.7174., (average smolt age = 2.8; Ward and Slaney 1988). Annual survival was thus e^{-z}, or 48.8% or 13.4% overall. By assuming that 50% per year is a constant annual mortality, a mortality schedule as a function of smolt age (sage) could be developed; i.e.,

(18) $$\text{Mort} = 0.5^{\text{sage}}$$

However, simply adding an additional 50% annual mortality for each additional year of rearing would not accurately describe the pattern of mortality within each year of life. Survival is lower in the early life history stages and increases as a function of fish length. (e.g., Elliott 1989; Symons 1979).

To provide a more realistic representation of how mortality was distributed, we constructed a simple model where annual mortality was considered a linear function of length at age. Extensive field sampling of steelhead populations has provided a reasonably good estimate of fork lengths of fish at various ages (Table 2), and size-biased survival is common in fish populations, as demonstrated by Peterman et al. (1988).

The model was fitted to the Keogh data by using the general size-at-age values for steelhead (Table 2), and fitting the model to the Keogh data to produce an average survival rate consistent with the fry-to-smolt values derived from the stock-recruit analysis.

There are clearly a number of solutions to the size-survival relationship ranging from a 0 slope producing a constant in each cell, to the solution presented, which moves most of the mortality into the early years. Note that the solution was bounded by a number of constraints (e.g., must not exceed 100% survival, must allow for 2 to 5 year smolts, and must meet the Keogh survival standards). The fitted equation relating size (FLENG) and survival (ANSURV) during rearing in streams was:

$$\text{ANSURV} = 0.55 * \text{FLENG} \qquad (19)$$

This produced a table of survivals for each life history cell (Table 3). The product of the individual cells resulted in the estimated fry-to-smolt survival for each smolt age. These values ranged from 24.6% for 2 year old smolts to 2.5% for 5 year old smolts. These values were regressed against smolt age:

$$\text{SURV} = e^{-0.7174 * \text{age}} \qquad (20)$$

It is interesting to note that the net result of distributing the mortality among various years in relation to size results in the same conclusion as the instantaneous rate of 50% per year calculated from the stock-recruit analysis.

These survivals for average smolt ages suggested a curve that was the same shape as that found by Symons (1979) for what he termed "medium survival" (Figs. 9a,b). Besides Symons's (1979) model, other literature on Atlantic salmon agreed with the estimated shape of the relationship between survival from fry-to-smolt (or egg-to-smolt, obtained by dividing fry-to-smolt survival by 0.1) and smolt age for steelhead trout (Fig. 9a,b). Chadwick (1987) estimated egg-to-smolt survival for Atlantic salmon of Western Arm Brook, Newfoundland, and found that, except for one year class, survivals were relatively high and the relationship between eggs and smolts was linear. The exception in Chadwick's (1987) data (1980) demonstrated that the curve was likely asymptotic, and that point is close to the estimated survival curve at MSY for steelhead smolts (Fig. 9a).

Randall et al. (1987) discussed variability in freshwater residence of Atlantic salmon and considered the subsequent effects to adult production. Their model, which assumed 10% survival from egg to 1+ parr and 40% survival for each subsequent year to smolting, provided a curve for egg-to-smolt survival for four ages of smolts that is slightly higher than the curve estimated for steelhead smolts (Fig. 9a). The model developed by Evans and Dempson (1986) also provided a data point on the egg-to-smolt survival and smolt age curve that is closer to the Atlantic salmon data of Randall et al. (1987), upon which much of their assumptions were based.

Application of stock-recruitment analysis of Keogh River steelhead to Skeena River steelhead

To determine the number of recruits and the allowable harvest ($\underline{u}_s$) for steelhead stocks of the Skeena River required information on fecundity, smolt age, fry-to-smolt survival, and adult production at capacity for each of the major sub-populations. The basic steps used the above derived relations between smolt age and survival to estimate recruits per spawner at MSY to calculate allowable harvest. With $\underline{u}_s$, it is possible to derive stock-specific Beverton-Holt A values, from which the other population statistics can be derived. Carrying capacity values derived above allow the stock units to be converted into actual numbers.

The fecundity of steelhead populations migrating through the Skeena River was examined by Wilkman and Stockerl (1981MS). Based on samples of 128 females collected by gill net at the river mouth, the mean number of eggs per fish can be described by (Fig. 10; $r^2 = 0.41$, $p < 0.05$):

(21) $$\text{Mean eggs/fish} = 0.5e^{(2.099*\ln(\text{length})-5.156)}$$

These samples were obtained at the mouth of the Skeena River from steelhead incidentally intercepted in the commercial salmon fishery. The samples may have provided conservative estimates of the fecundity of spawners, since there may be attrition of eggs up to the time of spawning, some 8 to 9 months later (untested).

Lengths of adult females were estimated from angler-caught fish during years of monitoring the recreational fishery (Table 4). Measurement of female lengths of steelhead caught in the commercial fishery in 1991 provided a large sample of female lengths (n = 589). The latter indicated that angler-caught females in the past were possibly biased to larger sizes, or that the length of female steelhead has declined over time. The mean fecundity estimated from length samples obtained in 1991 (2,482 eggs/fish) was smaller than that estimated as the weighted mean fecundity from angler-caught females (3,013 eggs/fish). Thus, a correction factor of 0.824 was applied to the fecundity estimate for each sub-population (Table 5) to correct the length measurement in each.

Smolt ages may have been underestimated. The relationship (equation # 10) underestimated the smolt age of Keogh River steelhead based on 215 days > 7° C and a mean smolt age of 2.8 yrs, but, as discussed, was calibrated to the Babine steelhead stock. Thus, the predictor estimates a higher level of productivity than may exist; a higher intercept in the relationship between smolt age and growing season would imply lower allowable harvest rates than predicted by this model.

When the above relation between survival and smolt age was applied to Skeena steelhead smolts, estimated fry-to-smolt survivals at MSY in the Skeena River varied from 4.4% in the upper tributaries of the watershed to 9.4% in the more productive Babine River stock (Table 5). Babine stocks appeared most productive, at 3.6 recruits•spawner^{-1}, whereas the steelhead of the upper Sustut River are least productive at 1.5 recruits per spawner at MSY; although that stock displayed high fecundity, the older smolts of this system yielded a low fry-to-smolt survival (Table 5).

Allowable harvests rates (equation 11) as determined by the production model were sensitive to fecundity and the fry-to-smolt survival at MSY. Rates as low as 32% (upper Sustut) to 39% (lower tributaries, upper Skeena, and Kluatantan) were predicted (Table 5). The maximum rate was estimated for the Babine River population, at 73%, which was similar to the value for the Keogh River, but with older smolts (3.3 vs 2.8 yrs) because of higher fecundity of Babine steelhead (2,762 eggs/fish, Babine; 1,850, Keogh).

Steelhead populations in the Skeena River had a weighted mean allowable harvest rate of 55%. The majority of spawning in the Skeena River watershed occurs in the tributary rivers listed. Based on the least productive stock an allowable harvest of 32% could not be exceeded.

Calculation of harvest rates (equation 11) allowed determination of Beverton-Holt's A value (equation 12). Beverton-Holt's A values were estimated for the Skeena River sub-stocks, and varied from 0.54 (upper Sustut) to 0.93 (Babine) (Table 5), and were used to determine numbers of spawners and recruits produced per stock unit at MSY (equations 13 and 14).

The number of Skeena River spawners required at MSY was estimated as 23,000. However, to obtain this number on the spawning grounds a number of additional factors must be taken into account. These include:

- Native harvest
- Distribution effects
- Weak stocks
- Hooking and poaching mortality.

Native harvest was estimated to be approx 5,000 fish (MOE and DFO data on file), with the potential for increased rates in the future.

Distribution refers to the fact that if 23,000 fish passed Tyee (river mouth), they would not distribute themselves to produce the required number of spawners on each of the spawning grounds, even if all populations were of the same productivity.

Weak stocks escapement refers to the fact that the Skeena River has a variety of populations with different productivities. Allowing an escapement of only 23,000 would result in the weak stocks being over-harvested (such as the Sustut, Kluatantan, and upper and lower tributaries).

A loss of approx 1,000 fish is estimated due to hooking mortality in the sports fishery (Hooton 1987). There is an additional but unknown loss due to poaching.

In conclusion, trout production within the Skeena River has been simulated by combining information on maximum fry density expected in usable steelhead habitat and steelhead population dynamics from an index stream, the Keogh River. Under no exploitation, predicted maximum adult returns were 80,000 to 120,000 fish. An overall escapement requirement of 23,000 fish was determined from this analysis. However, it was based on a number of conservative assumptions.

Other models would produce higher capacity estimates and lower allowable exploitation rates. For example, Gibbons et al. (1985) provided spawning escapement goals for Washington streams based on parr densities that predicted adult requirements of from 0.03 (stream gradient from 0 to 0.25%) to 0.18 (stream gradient 1 to 3%) spawners per 100m^2 (or between 28,000 and 181,000 adults required on the Skeena). The capacity estimates are 1.5 to 2 times higher than the minimum escapement requirement, given the allowable exploitation rate of 40% (Gibbons et al. 1985). This comparison is flawed by the large difference in smolt age between Washington streams and the Skeena River and further points out the need to adjust for such differences.

As with most simulation exercises, several model components would benefit from further information. Glacial streams were deleted but we may have overestimated production from areas of partial glacial influence (e.g., mainstem reaches), or underestimated yield from some glacial streams. Large adjustments were made to carrying capacity as a result of rearing space requirements, using predicted territory size as the standard. These are untested with experiment. While rearing space during the summer period likely limits production, other limits may be imposed by winter habitat or spawning habitat requirements. When calculating smolt ages we assumed that smolts originated from their natal streams, whereas there is migration and rearing in downstream mainstem reaches. Higher stream temperatures generally prevail there at lower altitudes, thus smolt age is likely lower, but usable rearing space is limited in mainstem reaches. (Lower temperatures may occur downstream of some mainstem areas of some important lake outlets than at the outlet, where egg stages are critically dependent on relatively small areas for incubation and fry emergence; e.g., Sustut Lake, Johanson Lake).

Survival rates in the egg-to-fry and smolt-to-adult stages may be lower for summer-run steelhead of the Skeena River than for Keogh River fish. Egg incubation and fry emergence there occurs through the period of spring freshet, thus mortality is likely higher than that experienced by the winter-run stock from which the biostandards were derived (cf Ward and Slaney 1992 in press). Summer-run adults in the Skeena River system spend up to 9 months in streams prior to spawning. Mortality during the winter under ice may be higher than that of winter-run fish in the ocean, from which the smolt-to-adult survivals were determined. Our analysis excluded repeat spawners and resident spawners, whose influence in a stock-recruit analysis and on survival rates through life stages remains to be determined. Despite these and other possible sources of error, the model estimates of steelhead productivity and carrying capacity of the Skeena River may be used conservatively to manage the resource until improved methodologies are developed.

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TABLE 1. Distribution of reaches, their lengths, and composition of the total length of rivers in the Skeena River watershed containing steelhead, listed by stream order.

STREAM ORDER	NO. OF REACHES	TOTAL LEN (KM)	% OF TOTAL LEN
7	2	352	0.17
6	7	575	0.28
5	13	406	0.20
4	53	729	0.35
TOTALS	75	2,062.00	

Table 2. Summary of estimates of lengths of rearing steelhead at the end of each growing season for each smolt-age life history observed in field studies in the Skeena River watershed.

SMOLT AGE	Len 0+	Len 1+	Len 2+	Len 3+	Len 4+
2+	66	115			
3+	52	88	148		
4+	42	74	113	145	
5+	36	64	98	125	150

Table 3. Annual and total survival from fry to smolt for each life history type (smolt age) of steelhead trout.

	ANNUAL SURVIVAL					
SMOLT AGE	0+	1+	2+	3+	4+	TOTAL
2+	.38	.66				.246
3+	.30	.50	.84			.125
4+	.24	.42	.64	.83		.054
5+	.21	.36	.56	.71	.86	.025

Table 5. Estimates of the steelhead trout production in the Skeena River watershed, including total and usable area estimates, alkalinity, length of the growing season, age of smolts, adult production at capacity, population fecundities, survival rates at MSY, allowable harvest rates (Us), Beverton-Holt's A value, number of spawners at MSY (Ps), and number of recruits at MSY (Rs). Adjust1 refers to adjustment to standing crop based on alkalinity differences and adjust2 refers to rearing space requirement differences, both relative to the index stream (Keogh River) standard.

MAINSTEM	*AREA X100m2*	*THEOR. USABLE AREA X100m2*	*THEOR. USABLE AREA %*	*TOTAL ALKA-LINITY (mg/l)*	*Adjust1*	*GROWTH SEASON days*	*SMOLT AGE yrs*	*Adjust2*	*SMOLT YIELD at Capacity*	*ADULT PROD'N at Capacity*	*MEAN EGGS/ FISH*	*FRY TO SMOLT AT MSY (%)*	*RECRUITS PER FISH (no)*	*Us*	*A*	*Ps*	*Rs*
LOWER SKEENA	290938	15802	5.43	30.00	1.37	137.0	3.5	0.72	90652	12691	2615	8.37	3.07	0.67	0.89	3122	9570
MIDDLE SKEENA	233609	16268	6.96	15.00	0.97	135.0	3.5	0.71	64824	9075	2615	8.12	2.97	0.66	0.89	2285	6790
UPPER SKEENA	40337	4179	10.36	15.00	0.97	100.0	4.4	0.53	12355	1730	2644	4.41	1.63	0.39	0.62	657	1072
TRIBUTARIES																	
ZYMOETZ	77700	11041	14.21	19.20	1.10	113.0	4.0	0.59	41145	5760	2444	5.62	1.92	0.48	0.73	1971	3789
LTRIBS	8381	2805	33.47	30.00	1.37	102.0	4.3	0.53	11922	1669	2444	4.58	1.57	0.36	0.59	650	1019
KITWANGA	7390	1651	22.34	35.00	1.48	102.0	4.3	0.53	7579	1061	2615	4.58	1.68	0.40	0.64	396	665
KITSEGUECLA	4918	1308	26.60	40.00	1.58	122.0	3.8	0.63	7596	1063	2615	6.57	2.41	0.58	0.83	312	751
BULKLEY	167219	24870	14.87	35.80	1.50	138.0	3.5	0.73	157257	22016	2374	8.50	2.83	0.65	0.87	5754	16262
SUSKWA	10589	2113	19.95	35.20	1.49	120.0	3.9	0.62	11315	1584	2830	6.35	2.52	0.60	0.84	451	1134
MORICE	24311	9255	38.07	27.90	1.32	123.0	3.8	0.64	45277	6339	1868	6.68	1.75	0.43	0.67	2307	4032
KISPIOX	43224	8542	19.76	35.70	1.50	127.0	3.7	0.66	48940	6852	2906	7.14	2.91	0.66	0.88	1754	5097
BABINE	48717	6185	12.70	35.00	1.48	145.0	3.3	0.78	41200	5768	2762	9.44	3.65	0.73	0.93	1240	4528
UTRIBS	12431	2696	21.69	20.00	1.12	100.0	4.4	0.53	9203	1288	2644	4.41	1.63	0.39	0.62	490	799
SUSTUT	32356	3765	11.64	20.00	1.12	105.0	4.2	0.55	13394	1875	2853	4.85	1.94	0.48	0.73	638	1237
UP SUSTUT	14707	2258	15.35	20.00	1.12	95.0	4.5	0.50	7400	1036	2644	3.99	1.48	0.32	0.54	418	618
KLUATANTAN	6136	1203	19.61	24.00	1.23	100.0	4.4	0.53	4499	630	2644	4.41	1.63	0.39	0.62	239	390
TOTALS	1022963	113941							574557	80438						22685	57753

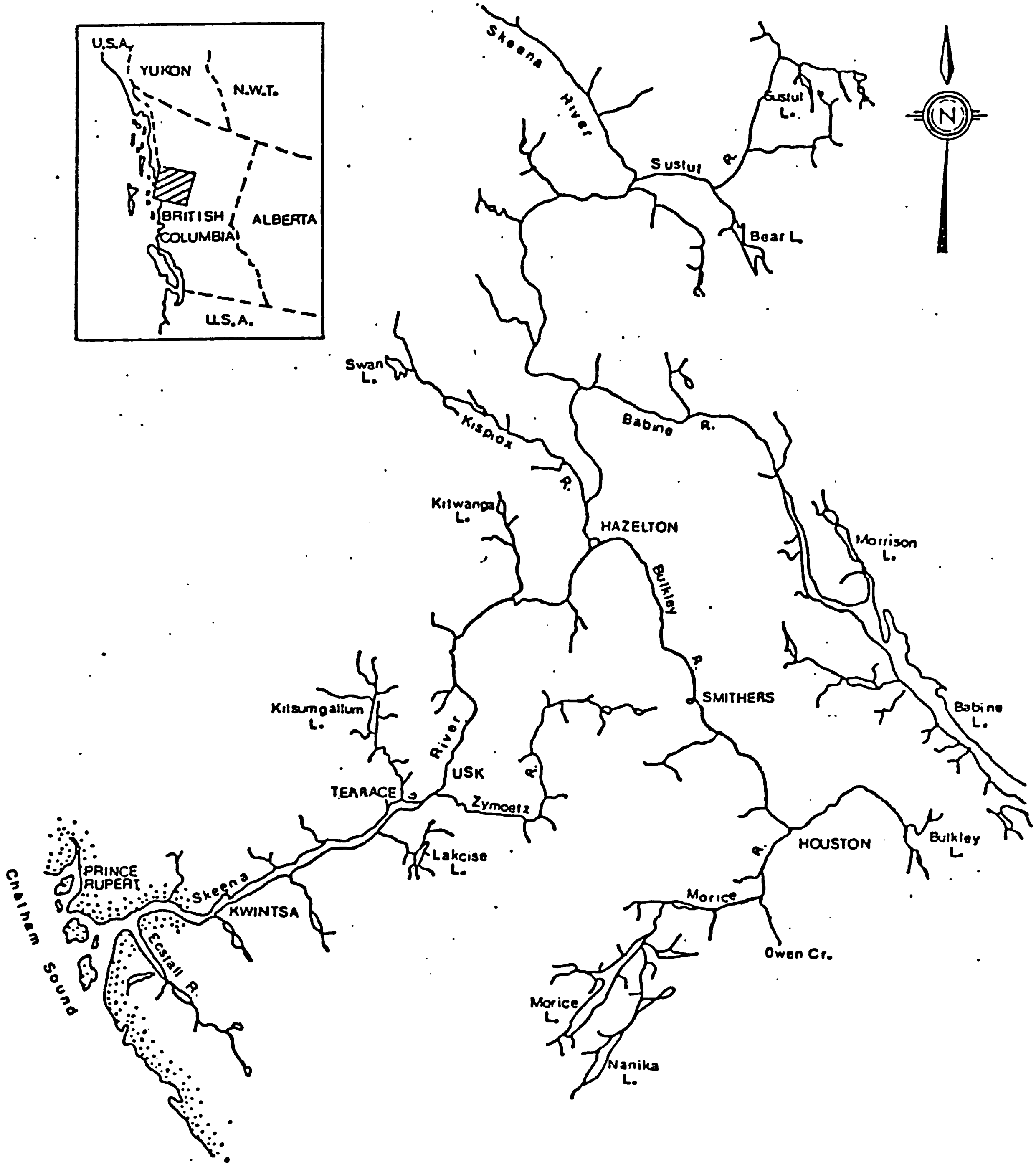


Fig. 1. The Skeena River and main tributaries.

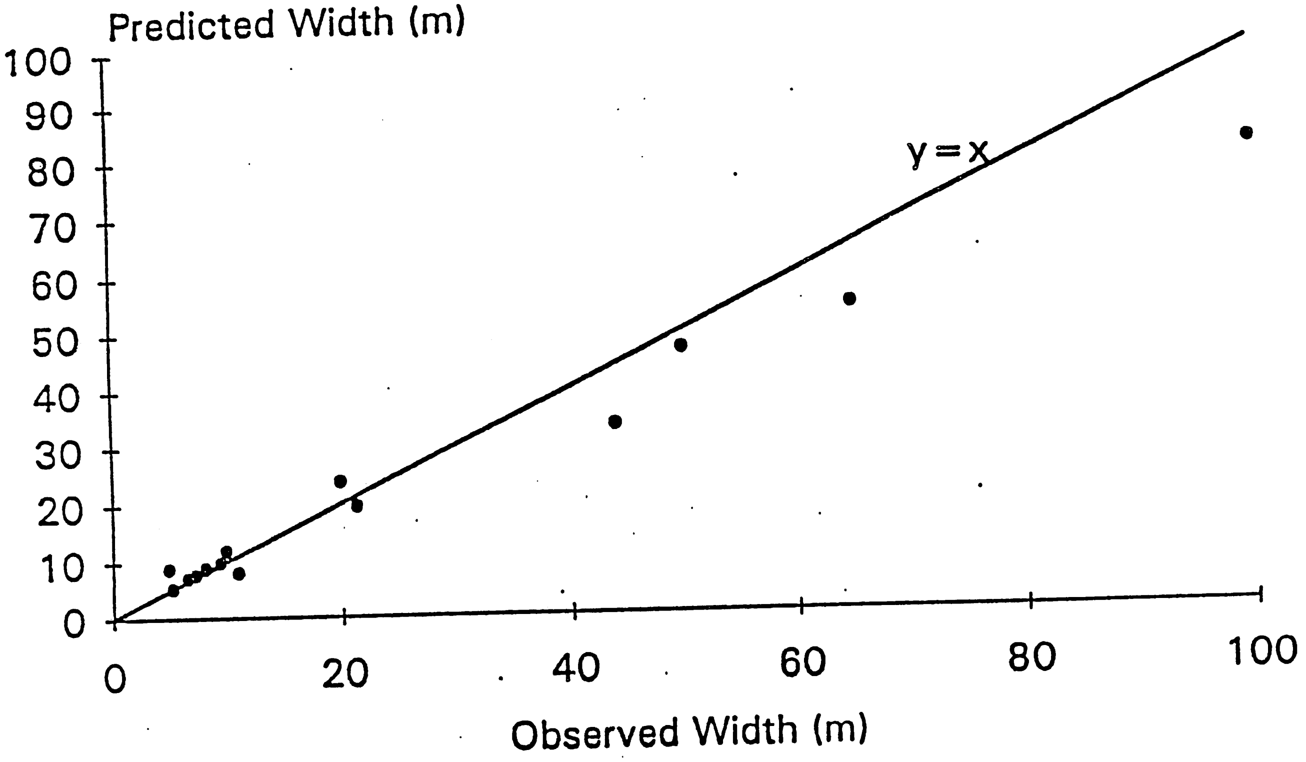


Figure 2. The relationship between predicted stream width (equation 1) and observed width based on field measurements in tributaries of the Skeena River.

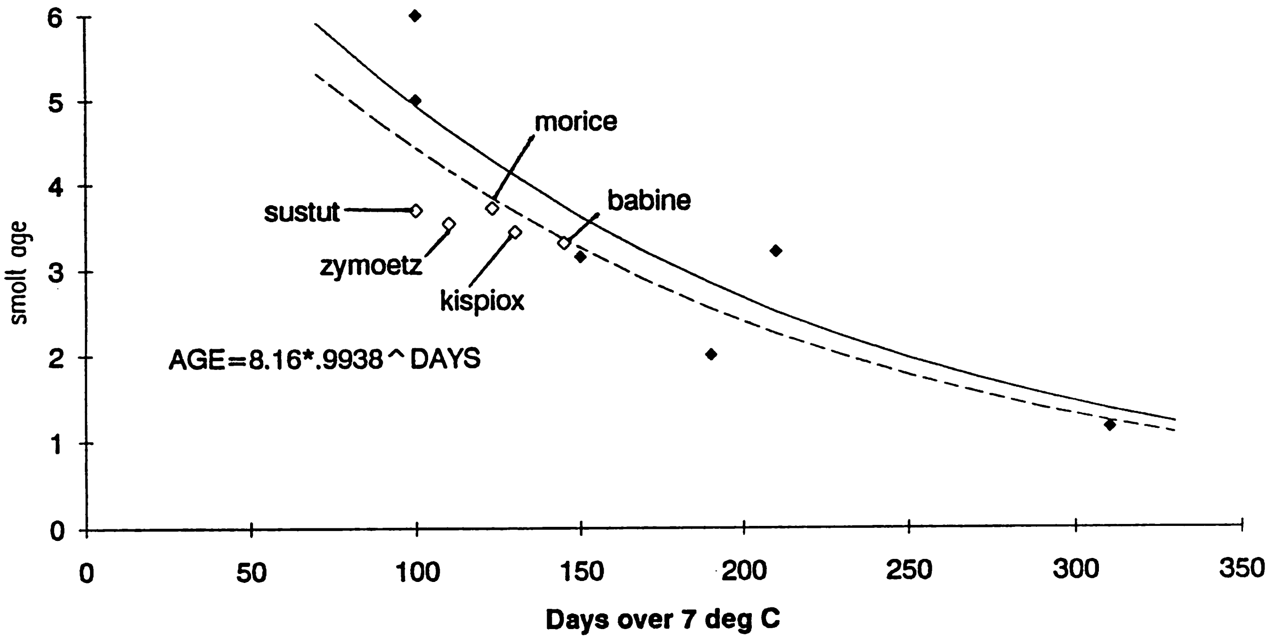


Figure 3. The relationship between steelhead smolt age and length of the growing season (days > 7°C.). The solid line is from Symons (1979) for Atlantic salmon (equation 9), and the dashed line is the result of changing the slope to force the line through the datum for smolt age of Babine River steelhead (equation 10).

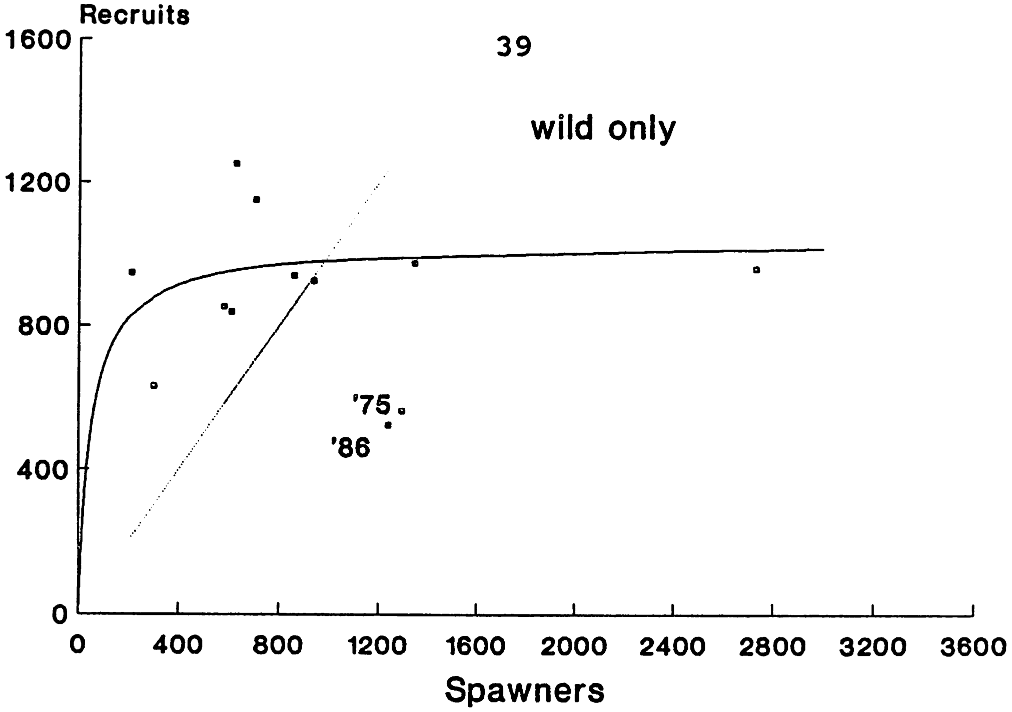


Figure 4. The relationship between Keogh River steelhead spawners and their subsequent recruits based on smolt size and survival (see text) for wild fish. The curved line is the Beverton-Holt curve fit to the data; the straight line represents replacement values.

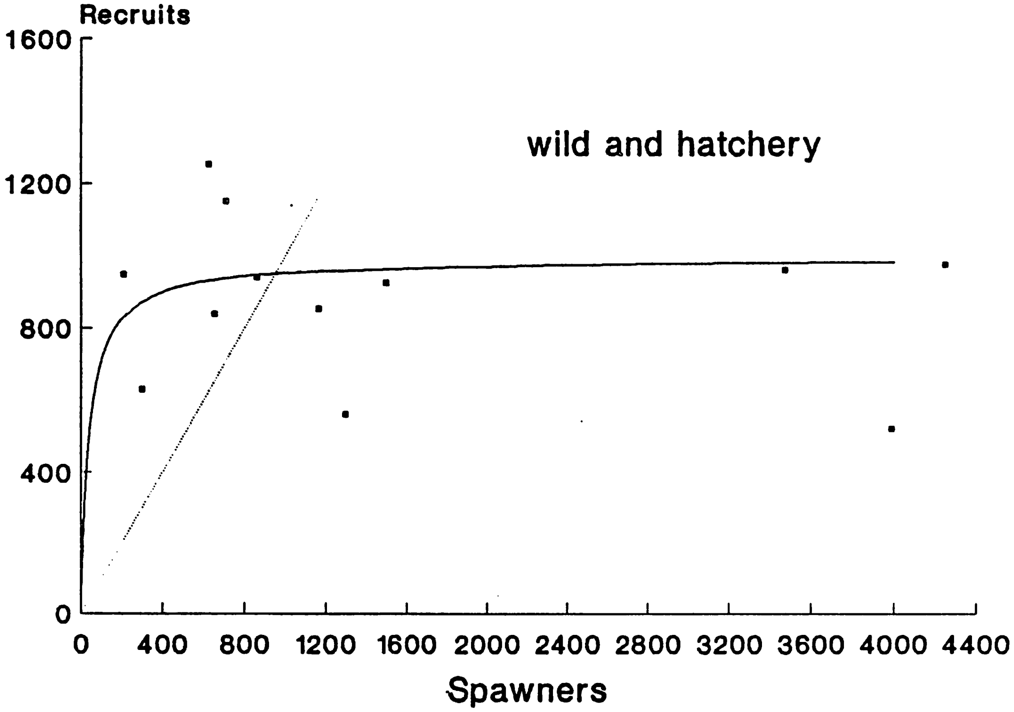


Figure 5. The spawner-recruit relationship for Keogh River steelhead including wild and hatchery spawners. The curved line is the Beverton-Holt curve fit to the data; the straight line represents replacement values.

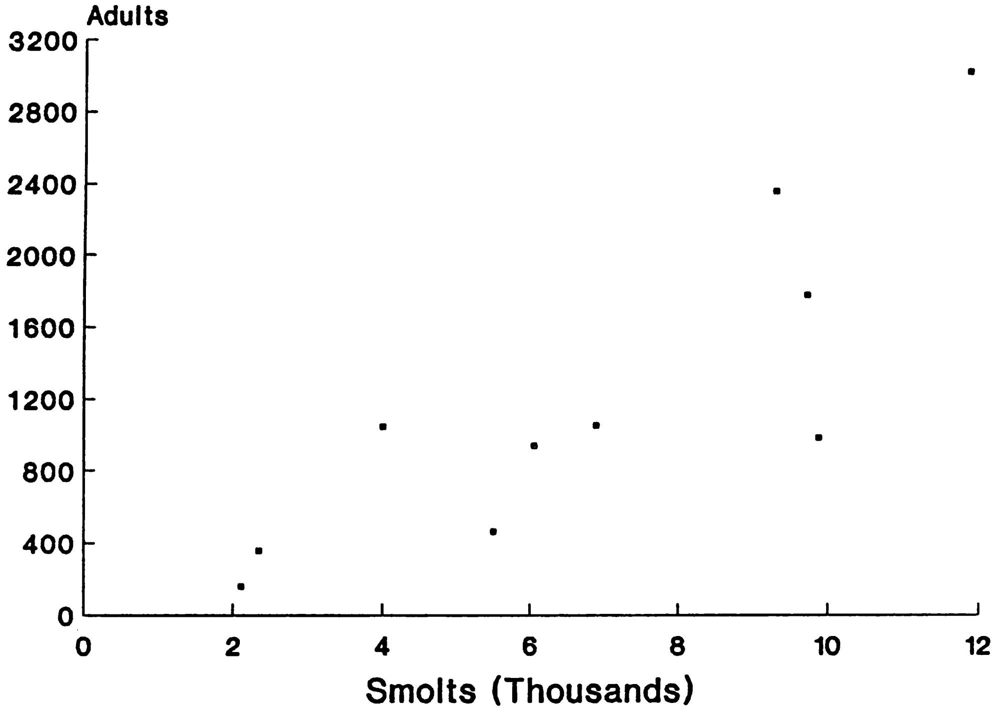


Figure 6. The number of adult returns of steelhead to the Keogh River in relation to the number of smolts counted from 1977 to 1986.

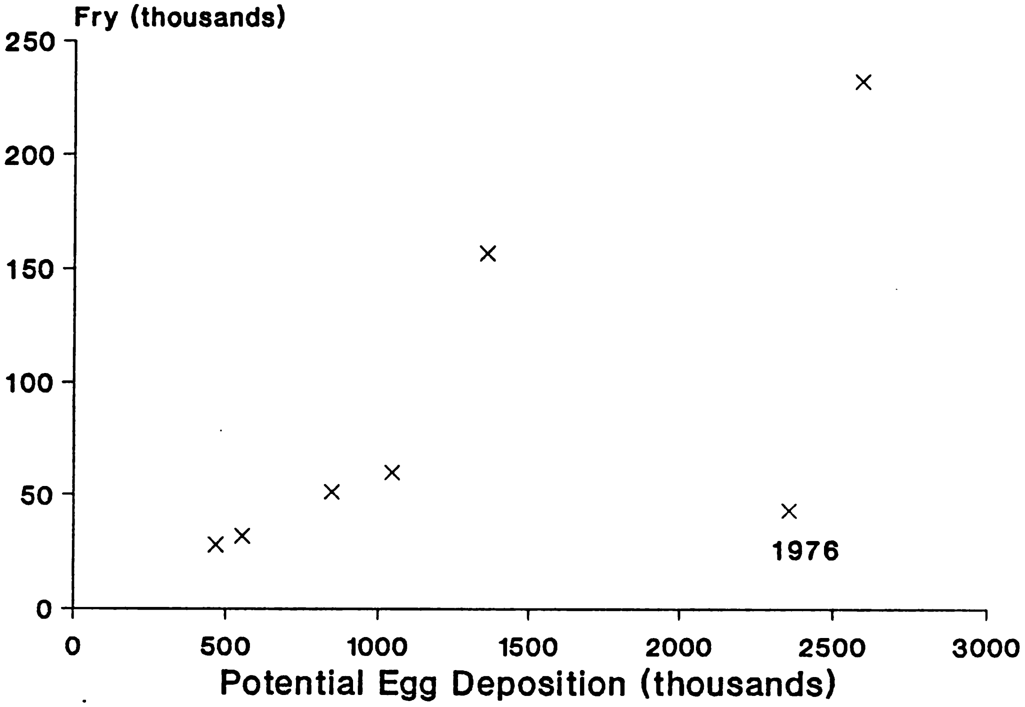


Figure 7. Steelhead fry population estimates in the Keogh River from 1976 to 1982 in relation to the number of eggs deposited that spring by spawning adults.

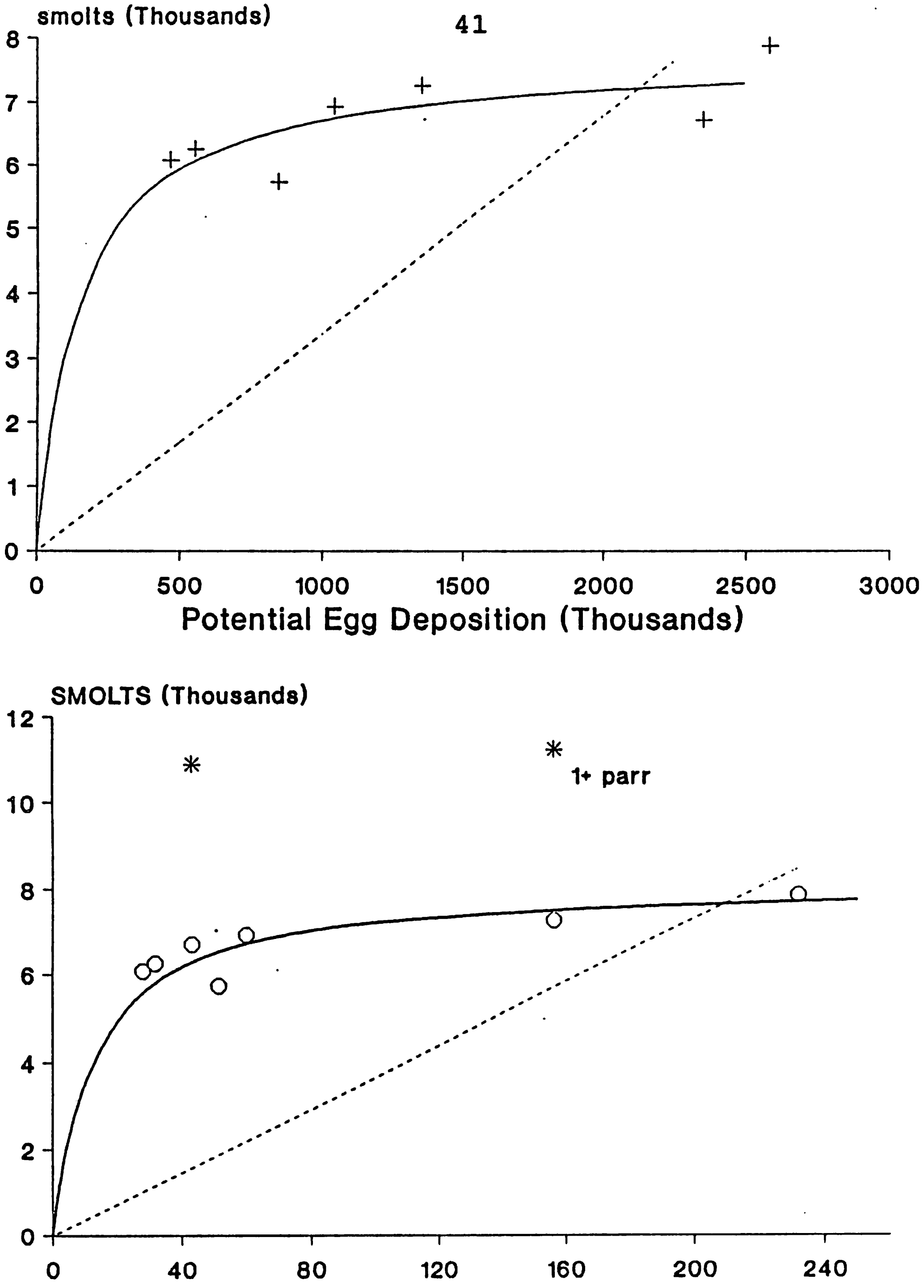
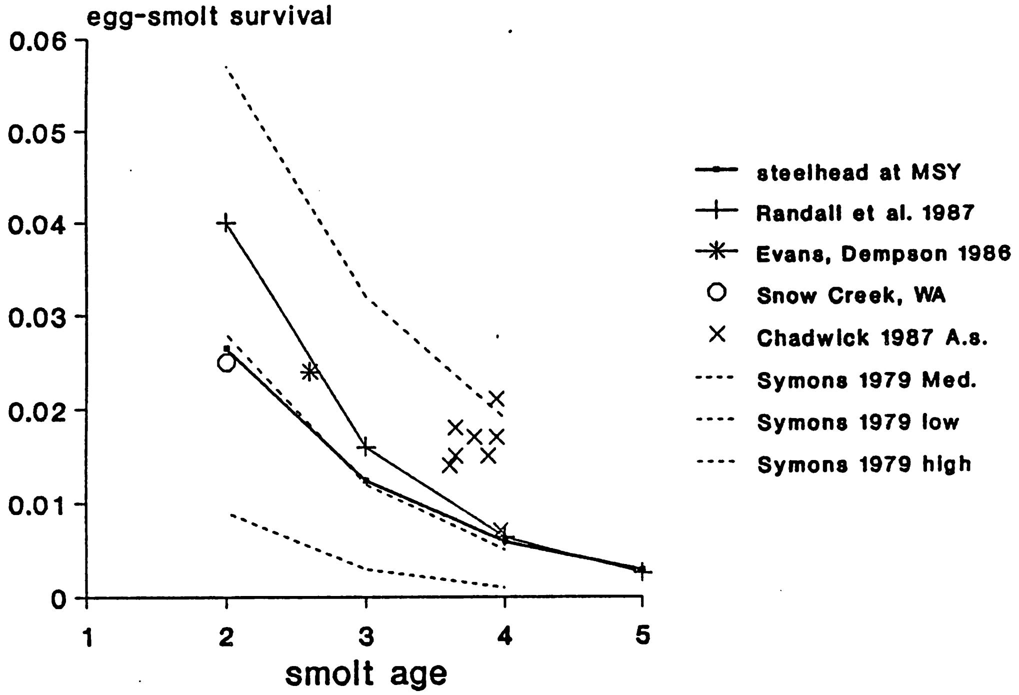


Figure 8. Beverton-Holt recruitment curves for freshwater rearing stages of steelhead trout, from Ward and Slaney (1992 in prep.). a.) The relationship between smolt yield from brood years 1976 to 1982 and the potential egg deposition of Keogh River steelhead. The dashed line is replacement assuming average average smolt-to-adult survival and fecundity. b.) The relationship between fry and subsequent parr abundance (star-shaped points, n = 2 yrs) and smolt yield (open circles, n = 7 yrs) for the Keogh River. The replacement line (dashed) was based on average smolt-to-adult survival, fecundity, and egg-to-fry survival.



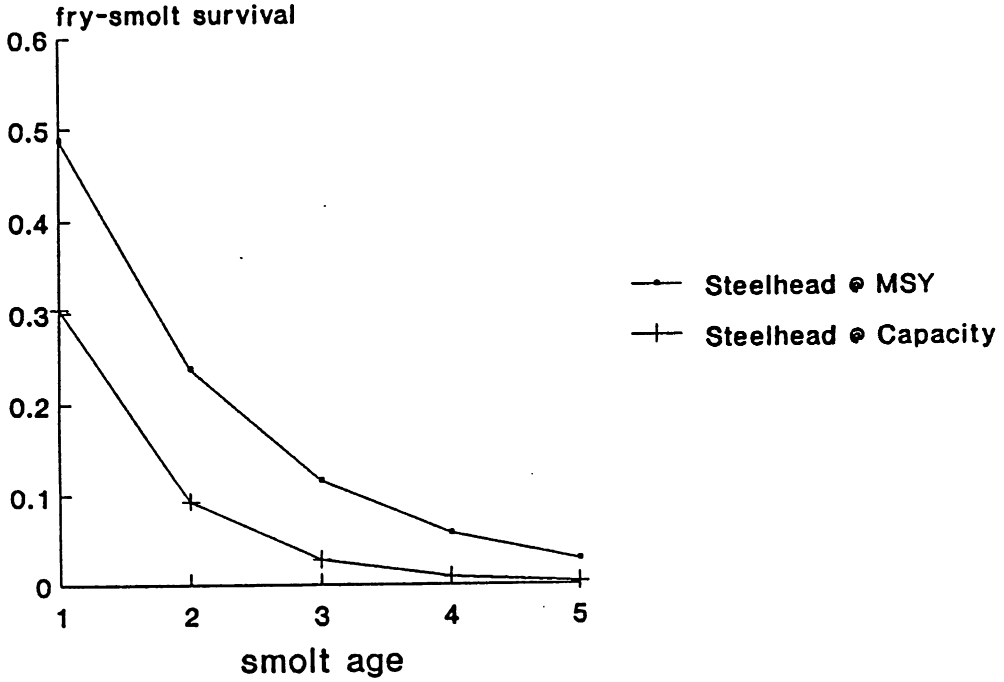


Figure 9. a). The relationship between egg-to-smolt survival and smolt age for steelhead and Atlantic salmon. The bold line is the egg-to-smolt survival at Maximum Sustainable Yield based on Keogh River steelhead, as explained in the text. b.) Fry-to-smolt survival and the relationship to smolt age at MSY and at Capacity production levels for steelhead trout.

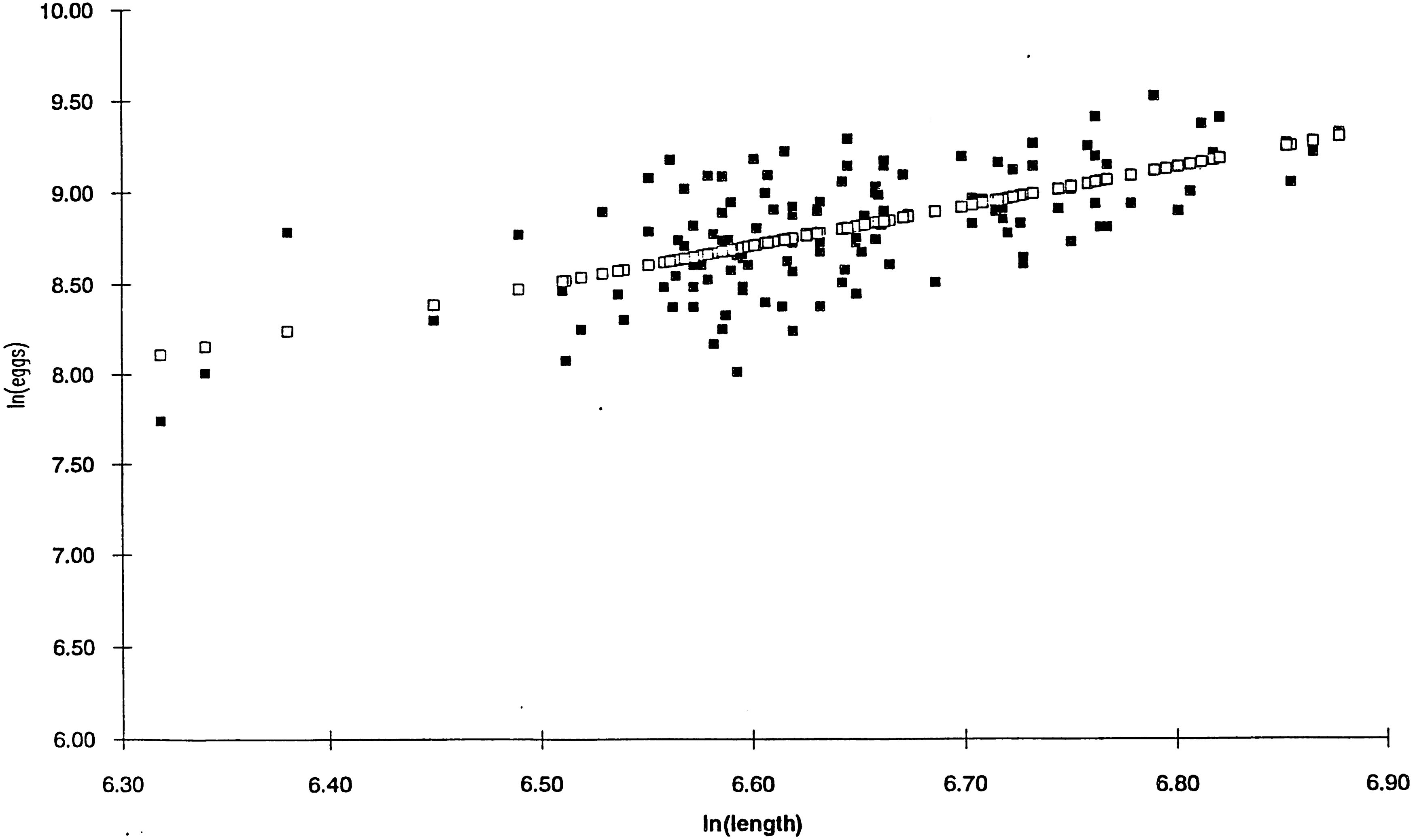


Figure 10. The relationship between female length and fecundity in Skeena River steelhead sampled at the river mouth (from Wilkman and Stockerl 1981).

Appendix 1. Stream order, length, flow characteristics, width, and usable width for Skeena River areas used by steelhead fry.

STREAM	ORDER	Length (km)	Lower Catchment Length (m)	Upper Catchment Length (m)	Water Yield (cm/km)	Critical Period Monthly Mean Flow (cms)		Mean Annual Discharge (cms)	Predicted Width (m)	Usable Width (%)
SKEENA	7	152	42200	42200	2.16	82.0	Y	911.5	191.4	5
ZYMOETZ	6	35	3000	2680	4.48	88.0	Y	127.1	68.3	10
ZYMOETZ	5	85	1730	185	4.48	88.0	I	34.1	34.3	14
ZYMOETZ	4	10	143	45	4.48	88.0	I	3.9	11.0	25
SALMONRUN	4	4	44	34	4.48	88.0	I	1.7	7.2	30
CLORE	5	43	950	510	4.48	88.0	I	31.9	33.2	15
CLORE	4	19	170	116	4.48	88.0	I	6.3	14.2	23
KITNAYAKWA	4	28	285	54	4.48	88.0	I	6.6	14.5	22
TREASURE	4	1	36	14	4.48	88.0	I	1.1	5.6	32
RED CANYON	4	6	93	76	4.48	88.0	I	3.8	10.9	26
'440-6382	4	5	142	126	4.48	88.0	I	6.0	13.8	23
'440-8913	4	6	55	40	4.48	88.0	I	2.1	8.0	29
PASSBY	4	4	42	37	4.48	88.0	I	1.8	7.3	30
KLEANZA	4	24	207	47	2.1	59.0	A	2.4	8.5	33
LEGATE	4	5	139	131	2.1	59.0	A	2.8	9.3	32
L OLIVER	4	6	76	57	2.1	59.0	A	1.4	6.4	37
OLIVER	4	20	151	40	2.1	59.0	A	1.8	7.4	35
FIDDLER	4	11	172	127	2.1	59.0	A	3.1	9.8	31
INSECT	4	12	196	174	2.1	59.0	A	3.9	11.0	30
SEDAN	4	14	119	25	2.1	59.0	A	1.3	6.3	37
MILL	4	11	88	51	2.1	59.0	A	1.4	6.5	36
KITWANGA	5	26	828	620	2.1	59.0	A	15.1	22.4	21
KITWANGA	4	7	364	328	2.1	59.0	A	7.3	15.3	26
KITWANCOOL	4	3	257	250	2.1	59.0	A	5.3	13.0	28
MOONLIT	4	1	145	140	2.1	59.0	A	3.0	9.6	32
KITSEGUECLA	5	14	711	485	2.1	59.0	Y	12.4	20.3	22
KITSEGUECLA	4	23	173	88	2.1	59.0	I	2.7	9.1	32
BULKLEY	6	162	12000	7922	1.82	78.0	Y	179.4	81.8	9
BULKLEY	5	10	2240	2220	0.76	15.0	I	16.9	23.8	36
BULKLEY	4	78	1313	427	0.76	8.0	Y	6.2	14.0	58
TROUT	4	1	90	89	1.96	93.0	A	1.8	7.3	29
TOBOGGAN	4	3	110	100	1.96	93.0	A	2.1	7.9	28
REISETER	4	8	168	148	0.84	29.0	A	1.3	6.3	49
CANYON	4	12	276	244	0.84	29.0	Y	2.2	8.2	45
TELKWA	5	27	1227	735	3.78	108.0	I	36.5	35.6	13
TELKWA	4	18	499	219	3.78	108.0	Y	13.0	20.8	17
HOWSON	4	14	234	167	3.78	108.0	I	7.5	15.6	20
BUCK	4	30	565	328	0.71	15.0	Y	3.1	9.8	54
MAXAN	4	13	400	327	0.7	11.0	Y	2.5	8.8	63
SUSKWA	5	24	1320	920	1.33	98.0	A	14.8	22.2	17
SUSKWA	4	12	166	102	1.33	98.0	A	1.8	7.3	29
HAROLD PRICE	5	25	762	600	1.33	98.0	A	9.0	17.1	20
NATLAN	4	4	226	222	1.33	98.0	A	3.0	9.6	26

Appendix 1. Stream order, length, flow characteristics, width, and usable width for Skeena River areas used by steelhead fry.

STREAM	ORDER	Length (km)	Lower Catchment Length (m)	Upper Catchment Length (m)	Water Yield (cm/km)	Critical Period Monthly Mean Flow (cms)		Mean Annual Discharge (cms)	Predicted Width (m)	Usable Width (%)
MORICE	6	76	4340	2900	3.89	109.0	Y	139.4	71.7	9
MORICE	5	15	1960	1830	3.89	109.0	Y	73.7	51.4	10
HOUSTON TOMM	4	17	253	160	1.33	71.0	A	2.7	9.1	30
LAMPREY	4	12	166	127	1.33	71.0	A	1.9	7.7	32
PIMPERNEL	4	6	80	60	1.33	71.0	A	0.9	5.2	36
THAUTIL	5	23	420	263	1.33	71.0	A	4.5	11.9	27
THAUTIL	4	5	150	132	1.33	71.0	A	1.9	7.5	32
GOSNELL	4	17	525	396	1.33	71.0	A	6.1	13.9	25
005-283	4	13	205	149	1.33	71.0	A	2.3	8.5	31
NANIKA	4	22	911	746	3.81	80.0	Y	31.5	32.9	15
SKEENA	7	200	25900	7922	2.27	92.0	Y	354.5	116.8	7
KISPIOX	6	81	1870	913	2.4	67.0	Y	32.4	33.4	16
KISPIOX	5	37	671	372	2.4	67.0	I	12.3	20.1	21
KISPIOX	4	15	225	150	2.4	67.0	I	4.5	11.8	27
MCCULLY	4	24	177	54	2.4	67.0	I	2.6	8.9	31
CULLON	4	21	115	35	2.4	67.0	I	1.7	7.1	34
SHEGUNIA	4	27	275	140	2.4	67.0	A	4.8	12.4	27
BABINE	6	99	10400	7130	0.71	92.0	Y	61.7	46.8	12
HANAWALD	4	2	175	168	0.71	92.0	I	1.2	6.0	31
NICHYESKWA	4	20	340	270	0.71	92.0	I	2.2	8.1	28
BOUCHER	4	12	149	126	0.71	92.0	I	1.0	5.3	32
KULDO	5	34	461	245	2.92	90.0	I	10.1	18.1	20
KULDO	4	8	113	54	2.92	90.0	I	2.4	8.5	28
CALAMITY	4	3	152	145	2.92	90.0	I	4.3	11.7	24
5903-687	4	12	137	92	2.92	90.0	I	3.3	10.1	26
CANYON	4	27	266	209	2.92	90.0	I	6.9	14.9	22
SKEENA	6	67	4350	2600	2.92	90.0	Y	99.8	60.2	10
SUSTUT	6	55	3570	2120	2.92	90.0	Y	81.7	54.2	11
SUSTUT	5	43	1540	540	2.92	90.0	Y	28.5	31.3	15
BEAR	4	13	453	345	2.92	90.0	Y	11.6	19.5	19
SUSTUT	4	7	366	324	2.92	90.0	Y	10.1	18.1	20
KLUATANTAN	4	33	569	201	2.92	90.0	Y	10.6	18.6	20
TOTAL SKEENA		2,062								