A HABITAT-BASED MODEL OF STEELHEAD CARRYING CAPACITY FOR THE SKEENA RIVER

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

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INTRODUCTION

The Skeena river watershed has an international reputation as a producer of wild steelhead trout (Oncorynchus mykiss). These stocks of fish represent some of the last runs of indigenous wild stocks in the world, and contain populations with unique timing, large size, and renowned sporting ability. They are highly valued as sport fish, and in their own right as natural populations adapted to surviving on or near the range of the species.

For decades these stocks have been subjected to a mixed stock commercial fishery targeting on salmon. Steelhead are caught incidental to the target species, but are still intercepted at high rates. In recent years the development of enhancement facilities on Babine lake, an increasing interception in Alaska and in the approaches to the Nass, combined with the potential for increasing native catches, have heightened concern for the long term future of these stocks.

To be better able to manage these stocks, an understanding of the carrying capacity of the Skeena system is essential. Carrying capacity has been defined by Burns (1971) as the greatest weight of fishes that a stream can naturally support during the life history stage when habitat is limiting (ie, least available).

In steelhead and other salmonids with extensive freshwater rearing, carrying capacity is generally associated with the freshwater rearing period. Thus, for practical purposes, the carrying capacity is defined as the average number of smolts produced annually from a given river system under conditions of no exploitation. Using stock recruit terminology, carrying capacity is the replacement value in a recruitment curve.

The carrying capacity is an important number for sport fisheries, particularly when catch and release regulations are in effect. By adopting an escapement goal equal to the carrying capacity, the maximum number of spawners return to the river. This maximum can arguably be considered an optimum for steelhead anglers where the intention is not to maximize the number of fish killed. Even in sport fisheries where catch and release is not the predominate ethic, the optimum escapement probably lies somewhere between the carrying capacity value and the escapement associated with the more traditional optimum of maximum sustained yield.

Since most summer run steelhead stocks undergo some form of exploitation, it is impossible to obtain direct estimates of carrying capacity by assessing spawners or juvenile populations. Furthermore, the nature of the mixed stock fishery precludes using a stock recruit approach unless better methods of stock identification and reporting are developed.

The alternative approach involves quantifying the amount of habitat associated with carrying capacity, and using a model based on biological theory and intensively studied systems.

The habitat modelling process involves the development of a number of different subcomponents. These represent either physical and biological processes which interact in ways governed by general biological or biophysical laws. The calculations leading to estimation of carrying capacity are generated using a spreadsheet model. The paper is organized to represent each column of the spreadsheet in order.

While it may be argued that the number of steps and assumptions may limit the accuracy of the results, it is has also been demonstrated that models provide a useful tool for integrating a variety of information in a logically consistent structure.

The basic components of the carrying capacity model used in this paper involve

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

2) estimating the total area and total usable area of steelhead bearing streams

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

STUDY AREA

The Skeena drainage is roughly 42,200 km2 with a mean annual discharge of 912 m3·s-1·100 km2. Water yields (mean annual discharge per 100 km2) range from 0.7 m3·s-1·100 km2 (Buck Cr.) to 11.5 (Exchamsiks). The flow regime of the Skeena is typical of interior watersheds 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).

METHODS

STREAMS CONTAINING STEELHEAD

Streams and rivers are organized in hierarchical networks based on well defined laws. Platts(1979) examined the relationship between the network structure and the distribution of salmonid species and demonstrated a relationship between stream order and the presence of salmonids.

Stream orders for upper Skeena tributaries were determined using a method developed by Horton (1945) and later modified by Strahler (1957). The method uses stream order and water yield to classify streams according to steelhead productivity (fry rearing potential).

Stream orders were determined from the MOE Stream Atlas which consists of digitized blue lines taken from 1:50000 topographic maps. The stream atlas does not include streams designated as intermittent at the 1:50000 scale. Average water yield was determined from Water survey of Canada records by dividing mean annual discharge by watershed area.

In the data set used to generate the 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). Exceptions were allowed if this biomass was represented by small numbers of large fish, or if this condition occurred at only a single site in a reach suspected to contain steelhead based on other criteria (eg. a large stream size, presence of juvenile chinook). Streams that supported significant numbers of steelhead spawners were only included in the model if they also supported juvenile rearing populations.

These criteria were applied to the entire Skeena dataset to determine stream order and water yield categories. The output of this model component is a list of Skeena River reaches and tributaries that support significant populations of rearing steelhead fry. Glacial streams are not included as streams considered important for steelhead.

TOTAL AND USABLE AREA

Total Area

Following the identification of the reaches containing steelhead, the next step in the process was the estimation of total wetted area during the summer low flow period and calculating total area as the product of estimated width and length. It is generally agreed that most compensatory mortality takes place during this period (Chapman 1966, Burns 1971, LeCren 1973; Gee et al., 1978).

As with stream order, there are a number of well described physical relationships which describe the change in water surface width, mean depth, and mean velocity in relation to stream discharge. Authors generally agree that the response of stream width to discharge is a power function, and Leopold demonstrated an empirical relationship between stream width and mean annual discharge(Hynes 1970). The width exponent is usually 0.5. It is also accepted that summer stream width also varies with baseflows.

The model uses water yield (WY) to determine mean annual discharge (MAD) and calculate average stream width. An analysis of 119 reaches from 47 different streams in British Columbia revealed the following relationship between MAD and stream width (Sebastian et al., unpub):

$$WIDTH = 5.42 \cdot MAD^{0.523} \tag{1}$$

The adjusted R2 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 (MOE assessment reports). For large streams, average widths were determined from large scale aerial photos (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.

Adjusted mean annual discharge estimates for stream reaches in the Skeena watershed were determined using the following equation:

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

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 endorsed by the Inland Waters Directorate of Environment Canada (Howard 1990) 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.

Usable area

A number of studies have demonstrated that only a certain percentage of the area of a stream can be used by rearing salmonids. Many studies have examined fish density at a given age or size within reaches and have constructed habitat suitability curves to account for this variability (cf Bovee 1982; Sheppard and Johnson 1985; Rubin, Bjornn, and Dennis 1991). Fish prefer specific hydraulic conditions during different phases of their life cycles (Giger 1974).

Habitat suitability curves were described for steelhead fry from a large B.C. data set. These curves are for juvenile fish from 0.5 to 4.0 gms or 37 to 74 mm fork length. These curves are comparable to other published curves which associate steelhead fry with low velocity shallow habitats in large streams.

This component of the model predicts the usable habitat based on the estimated fraction of stream width that is hydraulically suitable for steelhead fry rearing Hydraulically suitable fry habitat was expressed as a percentage of stream width and determined from depth-velocity probability-of-use curves (Bovee 1978). An analysis of 628 stream reaches in the province of British Columbia revealed the following relationship between percent useable width (%UW), MAD_{adj} and low flow stage (LFS):

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

The adjusted R2 for this relationship was 0.59 with a CV of 11.9.
Once %UW was determined for reaches in the Skeena, total useable area was calculated by multiplying %UW by stream width and stream length. Stream length was determined using digitized stream atlas data.

CARRYING CAPACITY

Index systems

Steelhead carrying capacity for the Skeena cannot be estimated directly. Consequently a modelling approach has been used to define relative capability for the Skeena systems, and to prorate these values against known production for the Keogh River and Atlantic salmon. The Keogh river has been monitored since 1976 and production parameters have been relatively well defined (Ward and Slaney 1992, in prep). In addition, Symons (1979) has summarized information relevant to the production of Atlantic Salmon.

Three basic models have been used to estimate Skeena steelhead capacity;

1. Linear
2. Areal
3. Process

The linear model simply used the adults produced per kilometre of accessible stream length for the Keogh applied to the Skeena. Similarly the areal model used adult per m2 of usable habitat to obtain the estimate. The third approach attempted to deal with the dynamics of the system by taking into account most of the physical and biological factors believed to influence production. These include

1. Stream Productivity
2. Smolt Age
3. Space required to produce a smolt

In brief, the latter model adjusts for the Skeena having streams with higher alkalinity, lower temperatures and older fish with higher space requirements than the Keogh, which we used as the standard.

Stream Productivity

Stream productivity is an important consideration in the development of estimates of smolt production, and is narrowly defined as variation in standing crop measured in relation to nutrient status of the system. Predictors of stream productivity were examined in detail in Ptolemy et al. (in prep). For present purposes the relationship between Total Alkalinity and late summer standing crop was used to estimate productivity. Other factors such as stream temperature, turbidity are also involved, but are better captured by smolt age as described in the next section.

Smolt Age Estimation

Smolt age is a key component of the process model and effects a number of calculations. It is quite variable among Skeena tributaries, and is also significantly different from Keogh values. Given its importance, two different methods were used to estimate smolt age.

Growing Season

Symons(1979) in his summary of the production dynamics of Atlantic salmon used the number of days over 7 deg C in a growing season plotted against smolt age. The problem with the suggested linear relationship is that it assumes that one day at 8 deg C (ie a day with a temperature in excess of 7 deg) was equivalent to one day at 16 deg C. Growth however, is dependant on accumulated temperature units rather than days above a threshold). Also, the suggestion that 500 days is required to grow a smolt does not fit steelhead life history, where one year old smolts are known to occur. Given the above, a curve fitted to the data seemed more appropriate than the linear relationship suggested by Symons (Fig 2). The curve was

AGE= 9.08*.9938^DAYS

The curve adequately described the properties of the relationship, but needed to be calibrated to BC conditions, essentially by altering the intercept. This was accomplished by fitting the curve to Skeena systems with well described smolt ages.

Growth increment

A second method used to estimate growth rate involved 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) by the growth added per year, with adjustments for initial size and plus growth added just prior to smolting.

Smolt age and survival

Survival during the freshwater life history phase of steelhead is also a critical component of the model. Age specific survival rates for the Skeena are not available, and would likely be difficult to obtain given the size and flow characteristics of many of the key systems. As with other parameters, a relationship was developed using the life history of the Keogh and expanding the values to the Skeena system based on variation in life history.

There were two theoretical problems associated with development of a more general model. The first was establishing the relationship between egg to smolt survival and smolt age, and the secondly determining how mortality was distributed among the various years of the life history.

The most variable life history stage in the model would be expected to be fry to smolt survival. Steelhead are unlikely to compete on the spawning grounds to any significant degree, and ocean survival is unlikely to be altered in relation to life history. However, since smolt age changes significantly among systems, and it is generally agreed that most compensation takes place during the freshwater rearing of steelhead, it is the fry to smolt survival which will be the focus of the model.

The general direction of the changes are apparent. As smolt age increases, the fry to smolt survival should decline, since fish simply remain in the stream an extra year. Also, as smolt age increases, the fish length at a given age declines. Thus, with increased smolt age, fish are exposed to mortality for an additional year, and are smaller for a longer period of time.

With regard to the distribution of mortality among years, it is generally agreed that mortality is higher early in the life history, and that as fish become larger, the instantaneous rate of mortality declines.

To examine these interactions more closely, a simple simulation model was constructed. The model involved estimating or defining length at age for each of the smolt year life histories and relating that to estimates of survival expressed as a linear function of length. This submodel was used to estimate space requirements per smolt. It is also relevant to stock productivity estimation, the subject of another paper.

Space requirements and territorial Behaviour

The final aspect of the model was treated in a manner similar to productivity and smolt age. As with survival, the number of smolts produced per m2 of habitat would be expected to decline with smolt age. This follows from the fact that more fish are initially required to produce a smolt.

How much space was required for a smolt of a given age was estimated using a similar approach to Symons (1979). Territory size per fish was estimated for the end of the growing season, then multiplied by the number of fish alive, and the individual space requirements in each year summed over the life history. These relative requirements were again calibrated against the Keogh values for smolts per m2 of usable habitat.

RESULTS

TOTAL AREA

Appendix 1 lists all the stream reaches identified as being important for steelhead use. A total of 75 streams or reaches of order 4 or larger and representing 2062 km of stream habitat were classified as being important for rearing steelhead. The total stream length (sum of all tributaries and mainstem) of the Skeena drainage is 3007 km. Therefore, those streams classified as high steelhead use represent 68.7% of the total length of the system. Table 1 summarizes the streams lengths by order.

The stream order classification analysis suggest that juvenile steelhead use 4th order and larger streams at water yields of 5 m3 per 100 km^2 and less. At water yields higher than 5 m3 per 100 km^2 steelhead primarily use 3rd order and larger streams. It would also appear from the results that steelhead require a stream size resulting from a mean annual discharge of 1.0 to 1.5 $m3 \cdot s^{-1}$ or greater. This value of 1.0 $m3 \cdot s^{-1}$ as a cutoff between anadromous trout use and non-anadromous trout and char agrees with findings in lower mainland streams (Ron

Ptolemy, pers. comm.). Since all Skeena streams upstream of Terrace (summer run stocks) fell into the less than 5 $m3 \cdot s^{-1}$ water yield category, only 4th order and larger streams were included in the habitat capability model.

In general, there was good agreement between steelhead streams as determined by the model and that based on field studies. However, there is at least one potential source of error in this component of the model. A misclassification of stream order due to errors in how the blueline data was digitized could occur. Such errors are likely to be limited to a magnitude of ± 1 order. Nevertheless, if this error occurs near the division between high use and nil use, then the result could mean erroneous inclusion or exclusion of streams or reaches in the Skeena model. Errors in stream orders of 5 or higher are not likely to affect the results because it would take an error of ± 2 orders to result in misclassification. The same is true for streams of order 4 at high water yields. Similarly misclassification of stream orders 1 and 2 (at low water yields are 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% 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 indicate that although errors in stream order classification could be important, the effect on total steelhead production for the Skeena is not likely to be very significant.

Total Area and predicted width

We evaluated the accuracy of the model by comparing predicted widths with field measured widths for a number of streams. Figure 3 illustrates how well the model predicted widths for 14 selected streams in the Skeena drainage. For small streams (<30 m 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 model equation is less applicable to large streams than small streams or that field measurements of width tend to underestimate the true width for larger streams.

Useable Area

At this level of analysis, it was useful to combine detailed reaches into stock groups relevant to a management. These groups typically represented the mainstem, and tributaries to the mainstem, with some additional stocks added in large or diverse tributaries. The physical characteristics of these stock groups are summarized in Table 2.

The total predicted useable area for steelhead fry rearing in the Skeena drainage was 11,387,600 m^2 or approximately 10% of the total drainage stream habitat. The Skeena mainstem accounted for 31.8% of this useable habitat area.

A concern for this component of the model is the availability of WSC stations in the drainage. 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 is not likely a serious problem.

CARRYING CAPACITY

Index systems

The Keogh river and Snow Creek are two winter run steelhead systems where smolt production and adult returns have been monitored for several years. The characteristics of the Keogh are important in that they form the basis for tuning model relationships used to generate estimates for the Skeena.

The Keogh river is a third-order coastal stream located on the northeastern end of Vancouver Island. The river is 32 km long and drains a watershed of about 130 km2. Mean annual discharge is 5.3 m3/s, and mean summer flows are about 1.6 m3/s. Ambient nutrient concentrations are low, mean pH is 6.9, total dissolved solids are about 30 mg/l. Total Alkalinity is 16 mg/l during the summer base flow period.

Using the model formulas, the Keogh has a predicted width of 9.2 meters, a length used by steelhead of 25 km, and a total usable area of 129400 m2. The Keogh produces 7500 smolts at capacity (Fig 4) resulting in 1050 adults at 14 percent survival. Overall, the Keogh produces .058 smolts/m2 of usable area or about 40 adults per km.

These values, when applied to the Skeena provide preliminary estimates to compare with more complicated models. The linear model using the 40 adults per km applied to the 2062 km of the Skeena suggests an adult population of approximately 80,000 fish. The area based computation of usable area (11.4 x 10^6 m2) produced an estimate of 92,500 adults, while estimates based on total area exceed 200,000 adults. In both the linear and usable area cases, the values are 2-4 times higher than current estimates of run size.

As noted above, the direct application of the Keogh values to the Skeena is of limited value since a number of factors have not been taken into account. Of most significance is the expected difference in productivity between the stocks and the variation in size of the systems. The following analysis attempts to take these factors into account.

Total Alkalinity and Stream Productivity

Total Alkalinity and Stream Productivity

Numerous investigators have demonstrated the relationship between indices of nutrient abundance and fish production. Recent work by Johnston et al (1990) has confirmed that nutrient additions
to streams increase periphyton standing crop and steelhead fry growth rates. In addition, the mean age of smolts declined in the more productive environment. Nutrient additions to lakes have similarly demonstrated increases in growth, survival and production (Hyatt and Stockner 1985).

Nutrient concentrations have a variety of well described correlations with easily measurable water chemistry parameters, including Total Dissolved Solids, Calcium content (LeCren 1972; Mann 1971), and Specific Conductance (Hynes(1970). Usually the various indices produce similar results. For present purposes Total Alkalinity was selected as the correlate of productivity.

The steelhead data set for British Columbia includes Total Alkalinity values ranging from 1.2 to 246 mg/l. The range indicates the diversity of habitats in which steelhead are found in the Province, which in part also explains the high variance about the regression line. The overall relationship (FIG 5) is

LOG(SCROP)=0.56 +.5*LOG(TALK)

where SCROP is standing crop of steelhead in KG/ha measured at the end of the summer and TALK is total alkalinity measured in mg/l. (r^2=.30, P=.01). Total Alkalinity estimates for the Skeena are summarized in Table 2.

The alkalinity equation is used in the model to adjust smolts per usable area in relation to the ratio of the standing crop measured relative to the Keogh. ie.

$$\frac{\text{STANDING CROP}}{\text{KEOGH STNDCRP}} \times .058 \text{ SMOLTS/M2} = 10^{(.56+.5(\text{LOG10(TALK)}))}/2.5$$

Output from this section of the model provides the first level of estimate of smolts per m2 of usable area by taking into account different alkalinities of the watersheds.

Determination of Smolt Age

Growing Season and Smolt Age

Estimating smolt age is an important component of both carrying capacity and productivity. Older age smolts experience a higher mortality due to their extended fresh water rearing, and consequently need more total rearing space when the requirements to produce a smolt are integrated over the total life history.

Two methods were used to obtain estimates of smolt age for the Skeena systems. These included growing season and growth increment. Direct estimation of age from scales was confounded by sampling problems, and indirect methods based on temperature considerations required calibration to known systems.

Scales have been collected on the Skeena system for a variety of different purposes. 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. Field observations have confirmed a late emergence and small size for a number of Skeena stocks.

To correct this problem, the shape of the curve as determined by Symons data was used when fitted to Atlantic Salmon data, but the intercept was altered to pass through the fastest growing system on the Skeena (Babine), where problems from the missing first annnulus would be a minimum. The altered equation is

$$AGE=8.16*.9938^{DAYS}$$

The effect of this is to adjust the smolt ages for the colder systems upward on the Skeena (Fig 6). Field observations have confirmed that in some systems steelhead fry do not emerge until late August, or September, making it highly unlikely that a detectable annulus will form in the first year.

This has been tested on other BC systems with known smolt ages and has proved to be a reasonable predictor.

Growth increment

Growth increment is 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 provides reasonable estimates of growth increments for a number of the Skeena systems. System increments were calculated by averaging the values for the differences between ages, on the assumption that length increase tends to be constant for each age.

Results produced increments from 28.5 to 40.75 mm per year. Lowest values were recorded in the Sustut, while high values were found in the lower Skeena, Babine and Bulkley.

There is a good correlation between the growing season estimate and the growth increment ($r2=.85$), (Fig 7) suggesting that the differences between the systems are consistent and can be adequately predicted by growing season.

The estimation of smolt age using growth increment is complicated by the need to determine starting size, non linear plus growth added in the last year and the actual smolt size as function of smolt age. Nonetheless, assuming a 175mm smolt, a 25 mm starting size, and plus growth in the order of 10-15 mm, it follows that 130 to 140 mm of linear growth is required. Slow growing Skeena smolts (30 mm per year increment) would average 4.3 to 4.7 mean smolt age; fast growing smolts (40 mm per year) would average 3.5 years.

In summary, and despite limitations of the various methods, the results clearly suggest an older age for Skeena of approximately four years old.

Smolt Age, growth and survival

There are clear theoretical relationships between smolt age, fry to smolt survival, and the space required to produce a smolt. Specifically, as smolt age increases, fry to smolt survival would be expected to decline, with the result that more fry are required per smolt. This in turn would have the overall effect of reducing the smolts produced per unit area.

There are three life history stages where survival is of interest; egg to fry, fry to smolt and smolt to adult. Estimated values for these parameters from a variety of sources are summarized in Table 3 and an overall view is provided in Fig 8).
For present purposes, egg to fry survival was assumed to be 10 % and smolt to adult 14% based on the Keogh data. Fry to smolt survival was assumed to be 25% when the stock is at MSY, again based on the Beverton Holt fit of the Keogh stock recruit data. Smolt age averaged 2.8 years, (ie 20% 2s and 80 % 3s) and annual juvenile survival averaged 50% per year at MSY.

Of particular interest is the annual juvenile survival of 50 %, since it is the key assumption in reducing the overall stock productivity in relation to smolt age. It is encouraging that the suggested relationship for Atlantic salmon by Symons(1979) is nearly identical to the results obtained from the MSY survival rates calculated for the Keogh river. Values for Snow Creek are less ie (30 % per year), and Idaho uses 40 % survival for parr in their last year of freshwater rearing.

Leaving the problem of the distribution by age of the annual mortality for a later section, the assumption of an additional 50% mortality for each additional year of freshwater rearing seems to be a conservative but supportable assumption. Overall egg to smolt survival as a function of smolt age can therefore be calculated as

F/SMLT = 0.50^SAGE

Distribution of mortality by age

To calculate the overall space required to produce a smolt, it is necessary to estimate the numbers of fish alive during each year, for each of the various smolt life history patterns.

The basic assumption of the conceptual model was that mortality rate is a function of fish size as defined by the slope of a line relating annual mortality to fish size. The curve was fitted to the Keogh data to meet conditions specific to that system. However, the equations also generated survival and estimates for other systems.

As the slope of the line relating survival to length increases, higher survival rates occur in later years. Thus for a known pattern of growth (ie fork lengths in each year), the model estimates the overall survival and the survival in each year, depending on the degree to which size and survival are correlated.

Mean fish lengths calculated from a number of electrofishing sites provided the input which defined average fish lengths at age. (Table 4). These lengths represent provincial averages but do not differ widely from lengths observed at Keogh.

The next step in the process was to use the fitted equation to

$$ANSURV= 0.55*FLENG$$

which produced table of survivals for each life history type (Table 5).

There are clearly a number of solutions to the survival equation 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 however, that the solution is bounded by a number of constraints eg must not exceed 100% survival, must allow for 2 to 5 year smolts, must meet the Keogh survival standards, etc. In addition, there is a large body of literature which relates survival to increased fish size. Thus we feel that the tabulated values represent a best guess approximation of the distribution of mortality at MSY for the different smolt ages.

Space requirements per smolt

The objective of this section is to determine the amount of space required to produce a smolt of a given age, relate that to the Keogh values, and generate an adjustment for the smolts produced per unit area for different smolt ages. The process involves a number of assumptions, but since the objective is to obtain relative rather than specific predictions, the robustness problem is less severe.

A recent comprehensive review by Grant and Kramer (1990) produced a general regression for stream dwelling salmonids relating territory size to fork length ($r2=.87, n=23$). The equation

$$LOG10(AREA)=2.61*LOG10(FLENG)-2.83$$

represents data from 5 species and 10 different studies.

The territory size estimated for the various sizes of fish in each life history stage is calculated using the lengths provided in Table 4. Territory size per fish is summarized in Table 6.

Finally, the product of the numbers of fish alive (Table 7) and the territory size per fish, summed over the duration of stream residence gives an estimate of the space required to produce a smolt for each life history (Table 8).

To obtain estimates of space required in relation to smolt age a linear regression was fitted to the points.

$$SPACE= 1.24 -1.31*SAGE$$

As with the other parameters in the model, the adjustment in smolts/m2 was made by estimating the value for the specific system, dividing that by the value for the Keogh using (2.8 year old smolts), and multiplying by the Keogh value of smolts/m2 at capacity ie 0.058 smolts/m2 of usable area.

This set of calculations resulted in the final values for smolts per usable area, from which total smolt production and adult production at capacity were estimated.

Skeena Carrying Capacity

The overall results of the modelling exercise are summarized in the spreadsheet Table 9. The Skeena at capacity could produce approximatley 5.75 million smolts resulting in 80,400 adults. This estimate is similar to the values generated by the simpler models using length and area, ie 82,400 and 92,500 adults.

On a stream specific basis, the Bulkley has the largest capacity for adults,(22,000), if mainstem rearing is not considered.
It is important to note that the individual estimates of capacity are 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.

TABLE 1. Distribution of steelhead reaches for the Skeena watershed 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 physical characteristics of management groups for the Skeena Watershed.

SUMMARY TABLE	*MEAN ANNUAL DISCHG*	*LENGTH*	*AREA Units*	*THEOR. USABLE AREA*	*GROW SEASN*	*TOT ALKN*
MAINSTEM	*(m3/sec*	*(km)*	*m2x100*	*m2x100*	*DAYS> 7*	*(mg/l)*
LOWER SKEENA	911	152	290938	15802	137	30
MIDDLE SKEENA	354	200	233609	16268	135	15
UPPER SKEENA	99	67	40337	4179	102	15
TRIBUTARIES						
ZYMOETZ	127	242	77700	11041	113	19.2
LTRIBS	2.3	103	8381	2805	120*	30
KITWANGA	15.1	37	7390	1651	120*	35
KITSEGUECLA	12.4	37	4918	1308	120	40
BULKLEY	179	376	167219	24870	138	35.8
SUSKWA	14.8	65	10589	2113	120*	35.2
MORICE	139.4	206	24311	9255	123	27.9
KISPIOX	32.4	178	43224	8542	127	35.7
BABINE	61.7	121	48717	6185	145	35
UTRIBS	5.3	111	12431	2696	100*	20
SUSTUT	81.7	68	32356	3765	105	20
UP SUSTUT	28.5	50	14707	2258	95	20
KLUATANTAN	10.6	33	6136	1203	105*	24

Table 3. Survival values for various life history stages used in the computation of capacity and MSY values.

SOURCE	EGG/FRY	JUVENILE	SMOLT/ADLT	COMMENTS
KEOGH	10%	50% per yr	14%	At MSY
SNOW CREEK	19%	28% per yr	n/a	parr to smlt
SYMONS	13%	52% per yr	n/a	"medium values"

Table 4. Summary of estimates of length at the end of each growing season for each smolt age life history.

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 5. Annual and total survival for each life history type

	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 6. Territory sizes for fish lengths outlined in Table 2.

	TERRITORY SIZE (M2)				
SMOLT AGE	Len 0+	Len 1+	Len 2+	Len 3+	Len 4+
2+	.204	.868			
3+	.109	.432	1.676		
4+	.062	.274	.829	1.589	
5+	.041	.187	.571	1.078	1.736

Table 7. Number of fish required to produce a smolt for different smolt ages based on survival values in Table 2.

	NUMBER OF FISH ALIVE AT END OF EACH YEAR						
SMOLT AGE	START	1	2	3	4	5	SURV
2+	4.3	1.56	1				.24
3+	8.6	2.49	1.22	1			.12
4+	20.7	4.82	1.98	1.24	1		.05
5+	44.9	8.96	3.18	1.73	1.20	1	.02

Table 8. Space (m2) to produce a smolt based on the number alive at the end of the growing season (Table 5) and the territory size per fish (Table 3).

	TERRITORY REQUIREMENTS PER SMOLT					
SMOLT AGE	0+	1+	2+	3+	4+	TOTAL
2+	.32	.87				1.19
3+	.27	.53	1.68			2.47
4+	.30	.54	1.03	1.59		3.46
5+	.38	.60	.99	1.30	1.74	4.99

TABLE 9.

SKEENA PRODUCTIVITY ESTIMATES

	AREA	THEOR. USABLE AREA	THEOR. USABLE AREA		TOTAL ALKALIN.	SMOLTS PER (/100m2)	GROWTH season		SMOLT AGE	ADJUST SMOLTS (/100m2)	SMOLT YIELD at Capacity	ADULT PROD'N at CAP
MAINSTEM	(/100m2)	(/100m2)	%	%tribtot	(mg/l)	USABLE	days	sam	yrs	#	#	#
LOWER SKEENA	290938	15802	5.43		30	7.955	137.0		3.5	5.7	90652	12691
MIDDLE SKEENA	233609	16268	6.96		15	5.625	135.0		3.5	4.0	64824	9075
UPPER SKEENA	40337	4179	10.36		15	5.625	100.0	est	4.4	3.0	12355	1730
TRIBUTARIES		tributary total		77692						0.0		
ZYMOETZ	77700	11041	14.21	14.21%	19.2	6.364	113.0		4.0	3.7	41145	5760
LTRIBS	8381	2805	33.47	3.61%	30	7.955	102.0	est	4.3	4.3	11922	1669
KITWANGA	7390	1651	22.34	2.13%	35	8.592	102.0		4.3	4.6	7579	1061
KITSEGUECLA	4918	1308	26.60	1.68%	40	9.185	122.0	est	3.8	5.8	7596	1063
BULKLEY	167219	24870	14.87	32.01%	35.8	8.690	138.0		3.5	6.3	157257	22016
SUSKWA	10589	2113	19.95	2.72%	35.2	8.617	120.0	est	3.9	5.4	11315	1584
MORICE	24311	9255	38.07	11.91%	27.9	7.671	123.0		3.8	4.9	45277	6339
KISPIOX	43224	8542	19.76	10.99%	35.7	8.677	127.0		3.7	5.7	48940	6852
BABINE	48717	6185	12.70	7.96%	35	8.592	145.0		3.3	6.7	41200	5768
UTRIBS	12431	2696	21.69	3.47%	20	6.495	100.0	est	4.4	3.4	9203	1288
SUSTUT	32356	3765	11.64	4.85%	20	6.495	105.0		4.2	3.6	13394	1875
UP SUSTUT	14707	2258	15.35	2.91%	20	6.495	95.0		4.5	3.3	7400	1036
KLUATANTAN	6136	1203	19.61	1.55%	24	7.115	100.0	est	4.4	3.7	4499	630
TOTALS	1022963	113941									574557	80438
Trib totals	458079	77692										

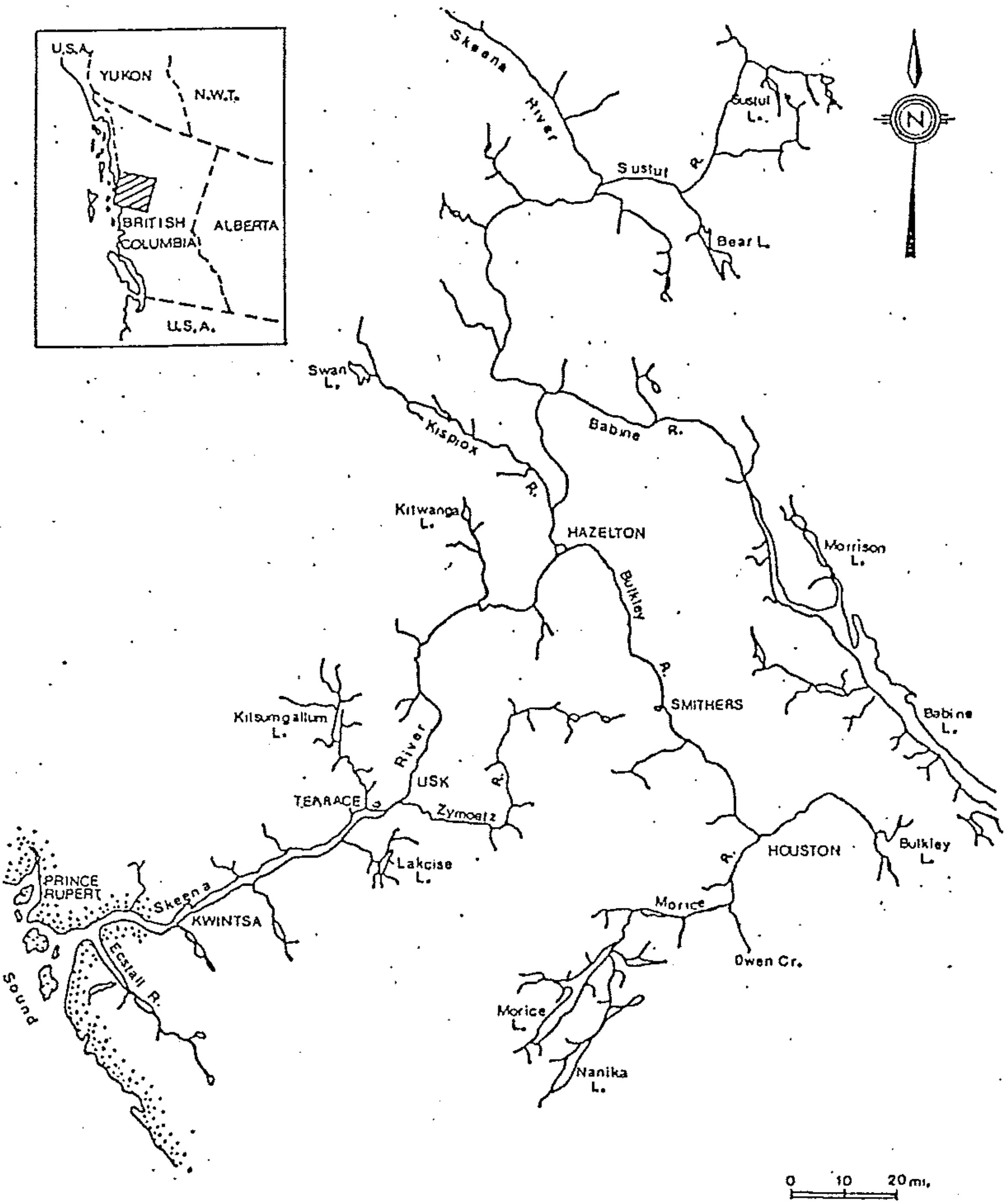

Fig. 1. The Skeena River and main tributaries.

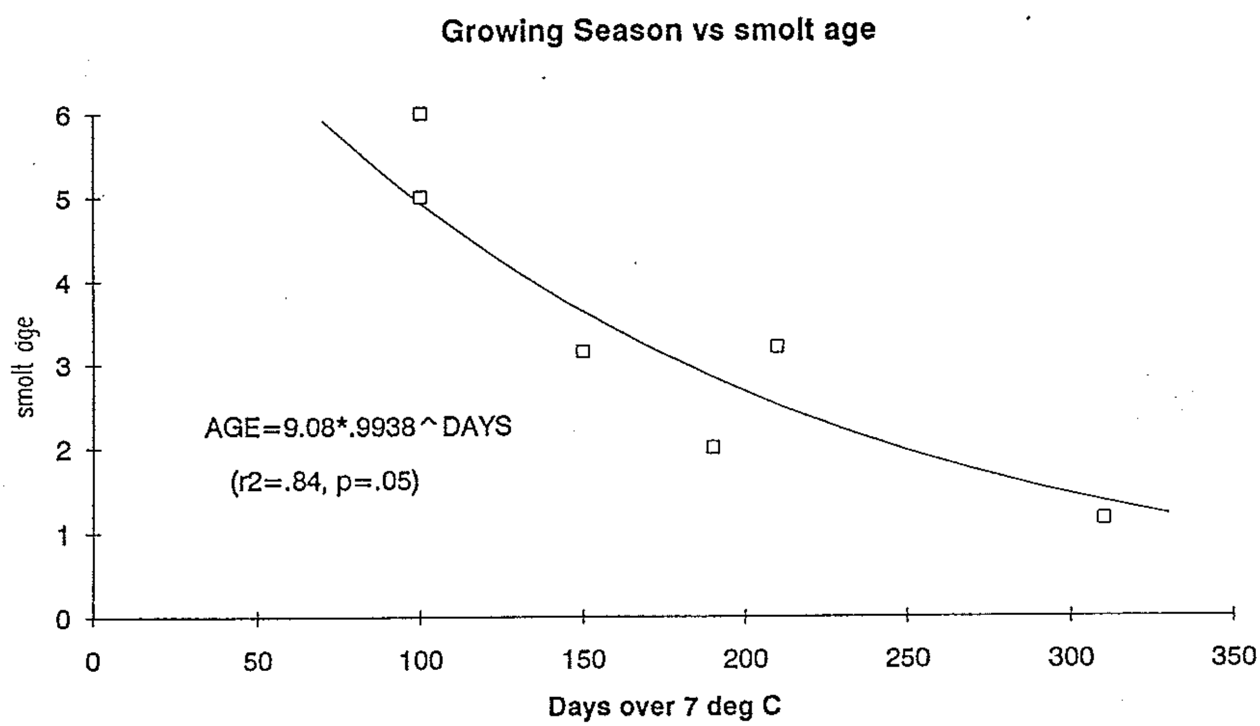

Fig 2. Curvilinear fit to Atlantic Salmon Data Symons (1979)

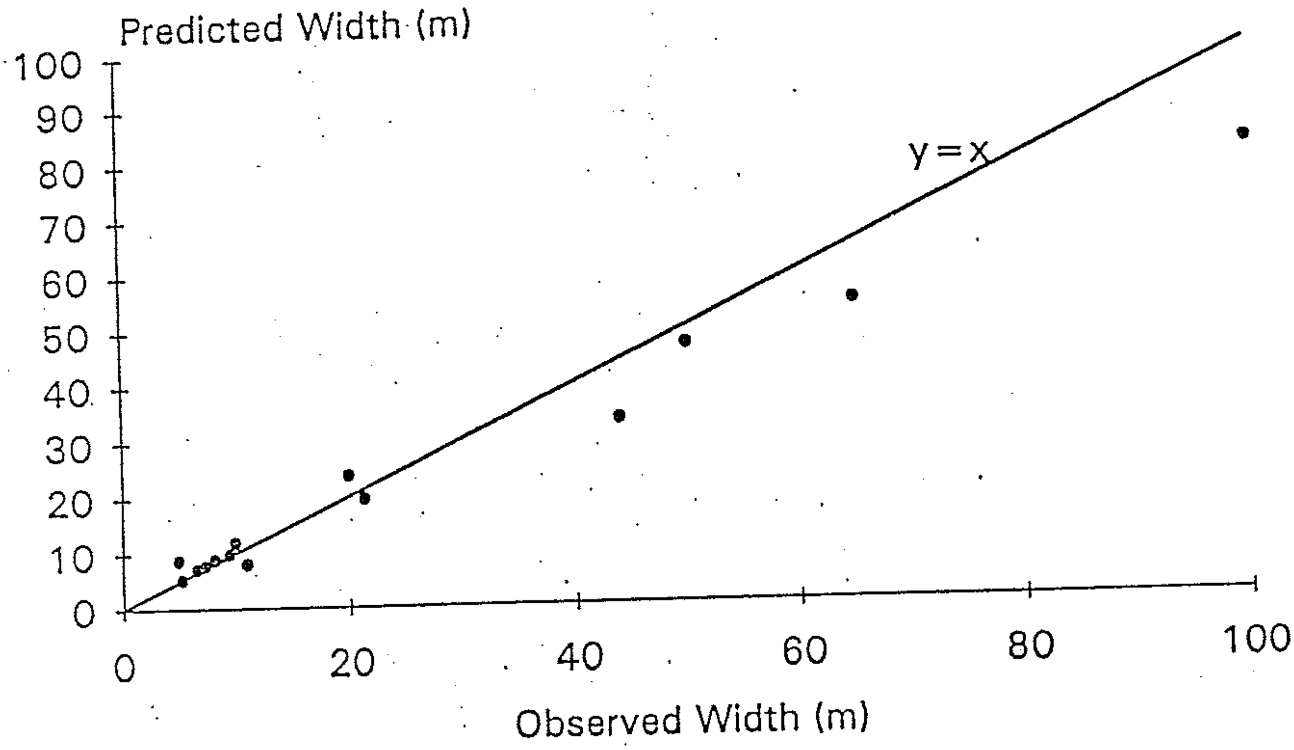

Fig 3. Predicted vs observed widths for Skeena tributaries based on model regression equation

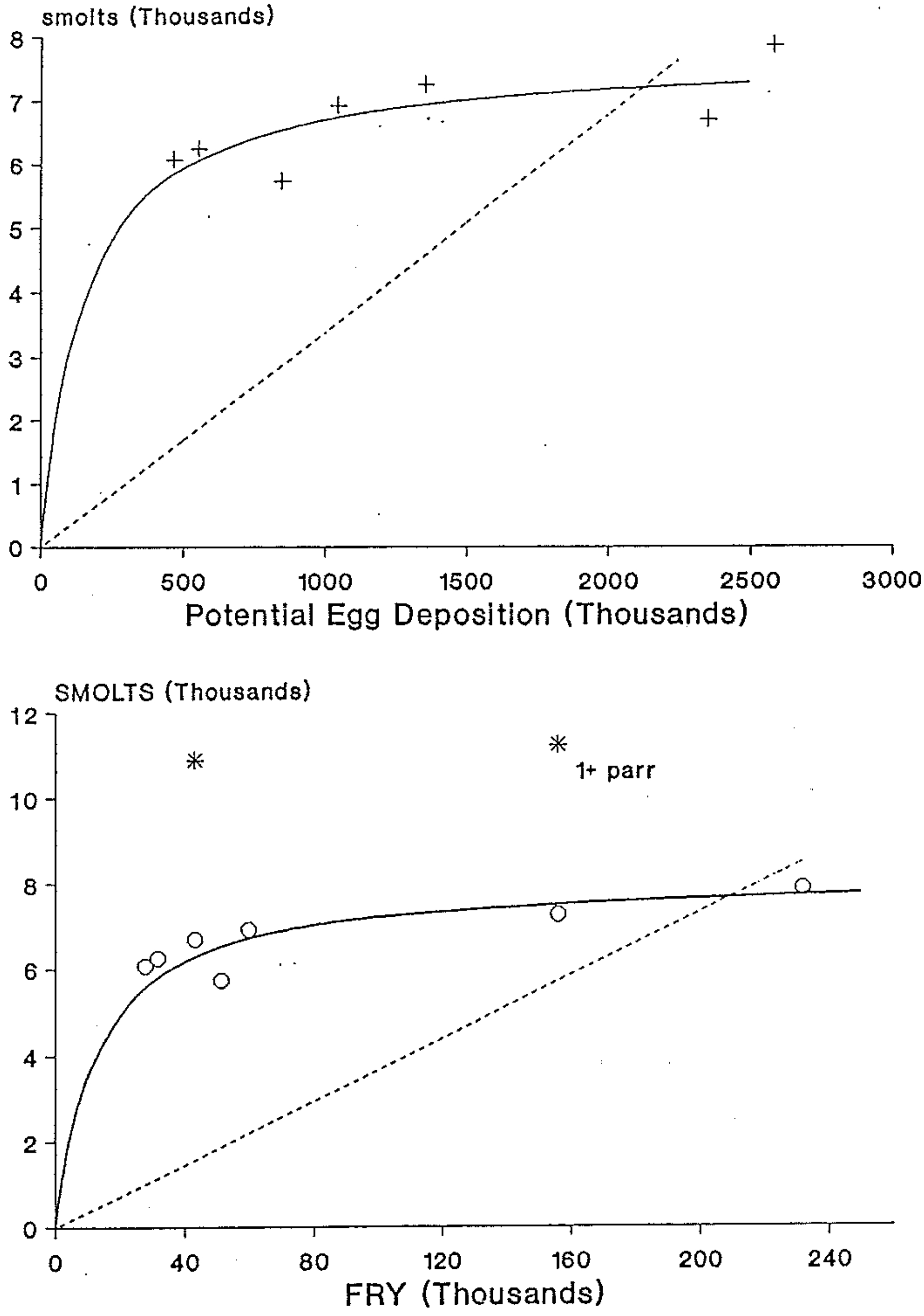

Figure 4. Beverton-Holt recruitment curves for freshwater rearing stages of steelhead trout, from Ward and Slaney (1992 in prep.). a.) The relationship between smolt yield from brood years 1976 to 1982 and the potential egg deposition of Keogh River steelhead. The dashed line is replacement assuming 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.

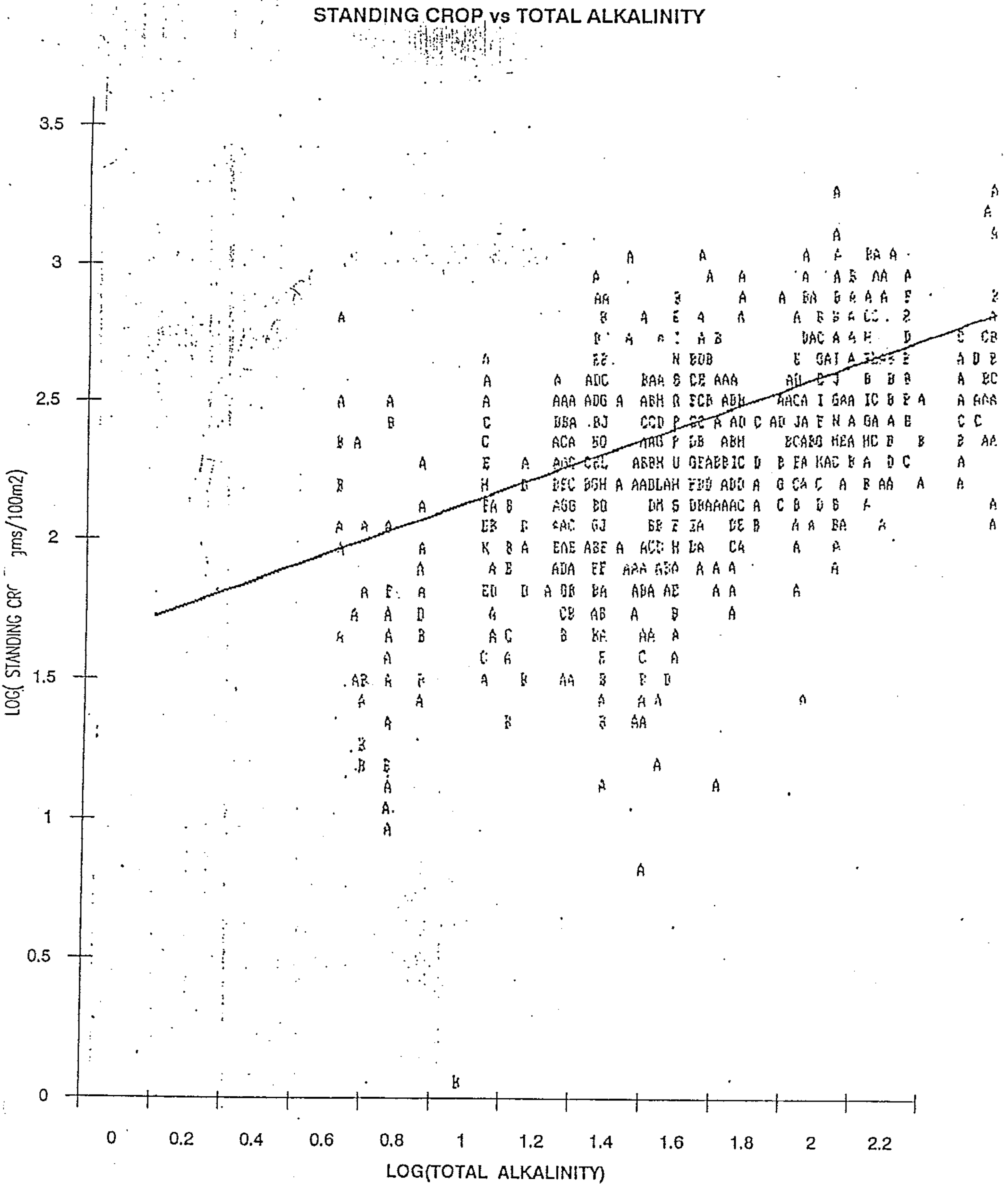

Fig 5. Scatter plot of Standing crop vs Total Alkalinity for provincial data set

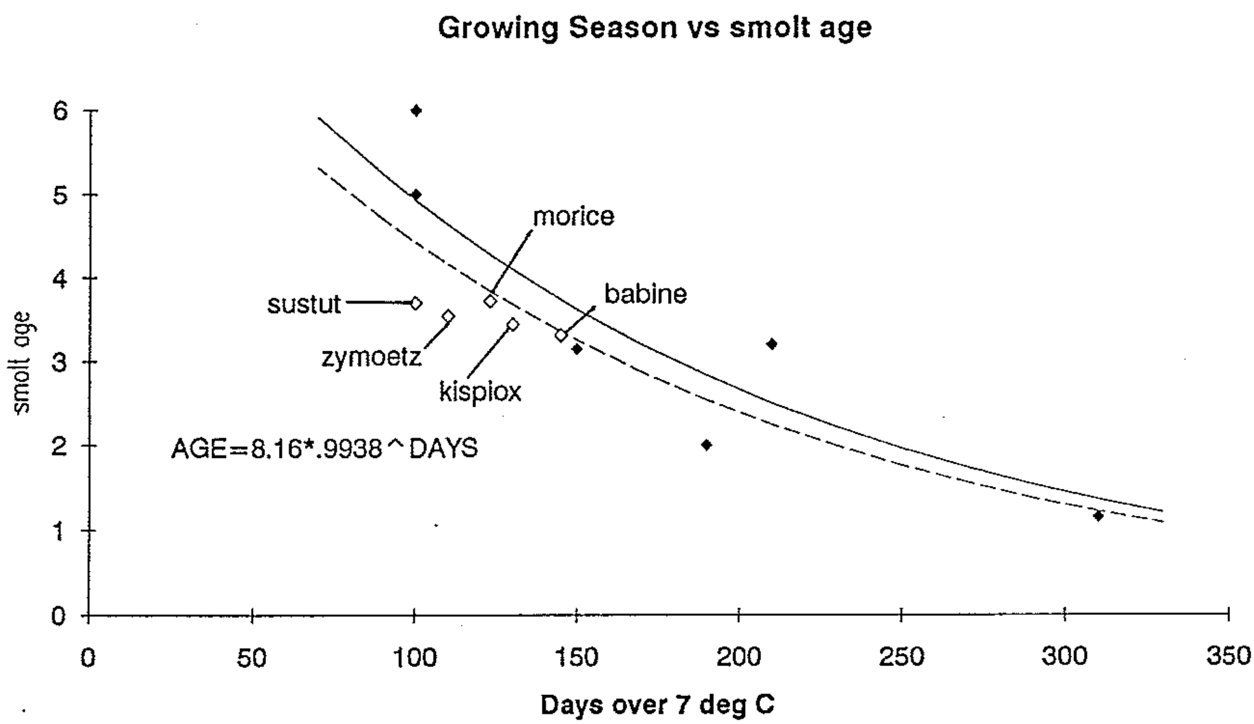

Fig 6. Adjusted curve fitted to Babine, compared with original

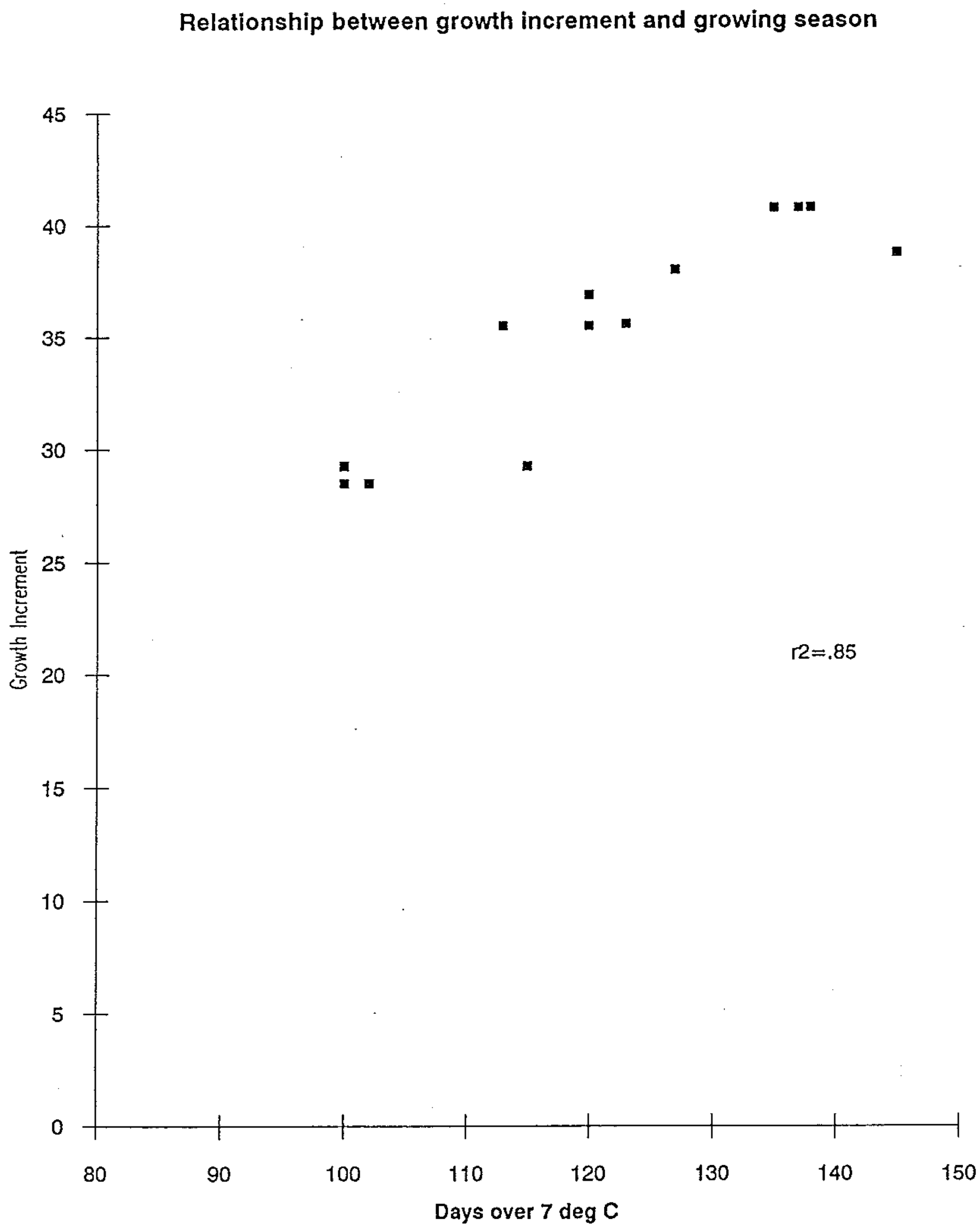

Fig 7. Skeena growth increments vs growing season

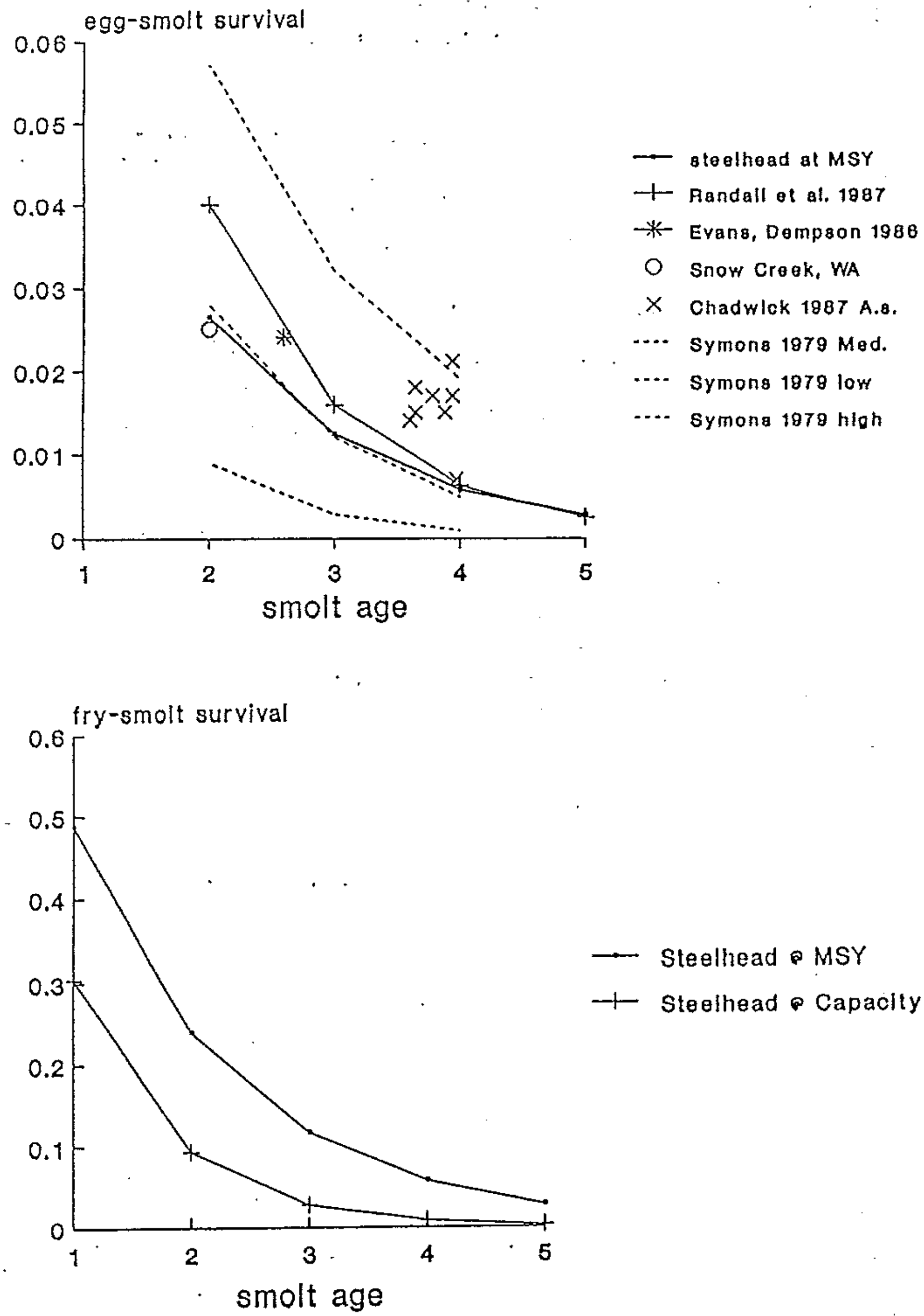

Figure 2. a.) The relationship between egg-to-smolt survival and smolt age for steelhead and Atlantic salmon. The bold line is the egg-to-smolt survival at maximum sustainable yield (MSY) based on Keogh River steelhead, as explained in the text. b.) Fry-to-smolt survival and the relationship to smolt age at MSY and at capacity production levels for steelhead trout.

Appendix I

TABLE 2 USABLE REARING AREA FOR STEELHEAD FRY										
STREAM	ORDER	KM	LOA	UPA	WY	CPMM		MAD	PWID	%UWID
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

TABLE 2 USABLE REARING AREA FOR STEELHEAD FRY										
STREAM	ORDER	KM	LOA	UPA	WY	CPMM		MAD	PWID	%UWID
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
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 TOMMY	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

TABLE 2 USABLE REARING AREA FOR STEELHEAD FRY										
STREAM	ORDER	KM	LOA	UPA	WY	CPMM		MAD	RWID	%UWID
TOTAL SKEENA		2,062								