AN OVERVIEW OF THE ALGORITHMS AND PARAMETERS USED IN THE SKEENA STEELHEAD CARRYING CAPACITY MODEL

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Abstract

The Skeena steelhead (*Oncorhynchus mykiss*) carrying capacity model (Tautz *et al.* 1992), algorithms and parameters were reviewed to provide fisheries biologists with a comprehensive understanding of the three model components. For interpretative purposes, the model was described by the three model components (i.e. habitat, biological and stock-recruitment) used by Tautz *et al.* (1992). Bocking and English (1992) reviewed the Skeena steelhead carrying capacity model, but provided different algorithms for the biological component than Tautz *et al.* (1992). Therefore the biological component described by Bocking and English (1992) was also described. In addition, the data sources and origins for the different parameters were described to assist fisheries biologists in refining the model parameters, which will probably be used in a similar model under development for Nass River steelhead.

Table of Contents

List of Tables

List of Figures

1.0.0 Introduction

Tautz *et al.* (1992) developed three types of steelhead (*Oncorhynchus mykiss*) carrying capacity models based on habitat and biological parameters for the Skeena River and its tributaries. Similar models are being developed for summer and winter steelhead in the Nass River watershed. Therefore a thorough review of the Skeena steelhead carrying capacity model components was necessary to identify areas and parameters that could be refined in order to improve the efficacy of the Nass habitat capability model. Improvements may result from the collection of Nass River specific data or by refining the parameters of the model based on the addition of recent data.

The Skeena steelhead carrying capacity model was divided into three components: habitat, biological and stock-recruitment (Tautz *et al.* 1992). LGL Ltd. (Bocking and English 1992) reviewed the Skeena steelhead carrying capacity model, however Bocking and English (1992) provided a different algorithm for the biological component and performed a limited evaluation of the stock-recruitment component of Tautz *et al.*'s (1992) models.

The objective of this report is to provide a comprehensive overview of the model and identify the sources of the parameters used in the model. The overview will assist fisheries biologists in making the Nass habitat capability model more characteristic of the Nass River by identifying the mechanisms to refine the parameters and biostandards with recent information or Nass River specific data.

The paper begins with a description of the three types of models (linear, area, biological) developed by Tautz *et al.* (1992), followed by a description of the three model components (i.e. habitat, biological, stock-recruitment) and finally a summary of the sources of the parameters, biostandards and data. The description of the habitat component discusses the parameters necessary to calculate the linear and area based models and one of the parameters necessary for the biological based model. The description of the biological component discusses the remainder of the parameters necessary to calculate the biological based model developed by Tautz *et al.* (1992) and Bocking and English (1992). Each component begins with a flow diagram indicating where the parameters were used in the model and was followed by a description of the parameters and their involvement in the model.

2.0.0 Study Area

The Skeena River originates in the Skeena Mountains of north-western British Columbia and flows south-west for approximately 530 km into Chatham Sound (Figure 1). The Skeena River watershed is the second largest watershed entirely contained within British Columbia and drains approximately 51 200 km^2 (Koski *et al.* 1995). The Skeena River has six main tributaries: Sustut, Babine, Kispiox, Bulkley, Zymoetz and Kitsumkalum rivers. Common fish species in the Skeena River watershed include sockeye salmon (*O. nerka*), chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), steelhead trout, cutthroat trout (*O. clarki*), Rocky Mountain whitefish (*Prosopium williamsoni*), bull char (*Salvelinus confluentus*), Dolly Varden char (*S. malma*), largescale sucker (*Catostomus macrocheilus*), redside shiner (*Richardsonius balteatus*), peamouth chub (*Mylocheilus caurinus*) and northern squawfish (*Ptychocheilus oregonesis*; McPhail and Carveth 1994). The upper Skeena River watershed also contains lake trout (*S. namaycush*), lake whitefish (*Coregonus clupeaformis*), pygmy whitefish (*Prosopium coulteri*), lake chub (*Couesius plumbeus*), longnose dace (*Rhinichthys cataractae*), white sucker (*Catostomus commersoni*) and burbot (*Lota lota*; McPhail and Carveth 1994). The Skeena River watershed lies within three ecoprovinces (Coastal Mountains, Central Interior and Sub-Boreal Interior) and contains seven biogeoclimatic zones: Alpine Tundra, Spruce-Willow-Birch, Engelmann Spruce-Subalpine Fir, Sub-Boreal Spruce, Interior Cedar-Hemlock, Mountain Hemlock, Coastal Western Hemlock (Pojar and Nuzsdorfer 1988).

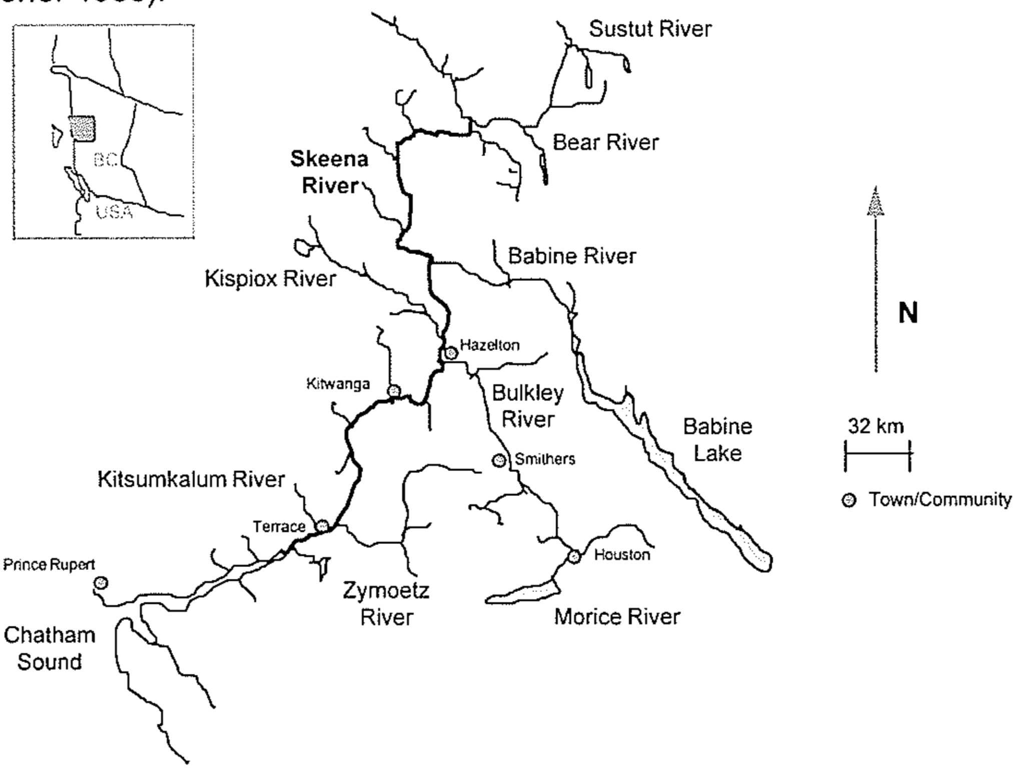


Figure 1. The Skeena River watershed and major tributaries.

3.0.0 Three Carrying Capacity Models

Tautz *et al.* (1992) developed linear, area and biological models to predict steelhead carrying capacity in Skeena River tributaries (Figure 2). The three models produced four estimates of steelhead carrying capacity for Skeena River tributaries. The three model components were used to develop inputs for the carrying capacity models and to estimate production characteristics of the different tributary populations. The habitat component estimated inputs for the linear, area and biological based models, whereas the biological component estimated inputs for the biological based model only. The stock-recruitment component estimated steelhead population production characteristics and none of the stock-recruitment outputs were used in either of the three carrying capacity models. The stock-recruitment component estimated stock productivity, allowable harvest rates and the required adult escapement for steelhead populations at maximum sustainable yield.

The linear model required two outputs from the habitat component and a provincial biostandard to estimate carrying capacity (Figure 2). From the habitat component, the distribution of steelhead streams and the total stream length of steelhead habitat were determined. Then the number of adult spawners per km at capacity was multiplied by the stream length to estimate the number of adults at carrying capacity (Figure 2). The number of adults per km at capacity (40) was estimated from Keogh River winter steelhead because a similar estimate did not exist for any Skeena River steelhead streams and the Keogh River data was the best available information.

The area based carrying capacity model produced two separate carrying capacity estimates and each required different outputs from the habitat component (Figure 2). The first area based model used the total stream area available to steelhead, an estimate of the number of smolts produced per m^2 at capacity and an estimate of smolt-to-adult survival. Total stream area was estimated in the habitat component. Since the number of smolts produced per m^2 and smolt to adult survival were unknown in the Skeena River, the biostandards measured for Keogh River winter steelhead were used because it was the best available data. The second area based model differed from the first by using the estimated total useable stream area instead of the total stream area. The total useable area was a fraction of the total stream area because only a portion of the total stream area was assumed to be suitable for steelhead rearing (Tautz *et al.* 1992). The total useable area was estimated in the habitat component and the number of smolts per m^2 and smolt-to-adult survival were estimated from Keogh River winter steelhead biostandards.

The biological based carrying capacity model was similar to the second area based model, since it required total useable area, number of smolts per m^2 at capacity and smolt-to-adult survival (Figure 2). However, the biological model differed by using biological parameters to adjust the number of smolts per m^2 at the Keogh River in order to make it more characteristic of the Skeena River. The adjustments accommodated differences in stream productivity and the length of the growth season.

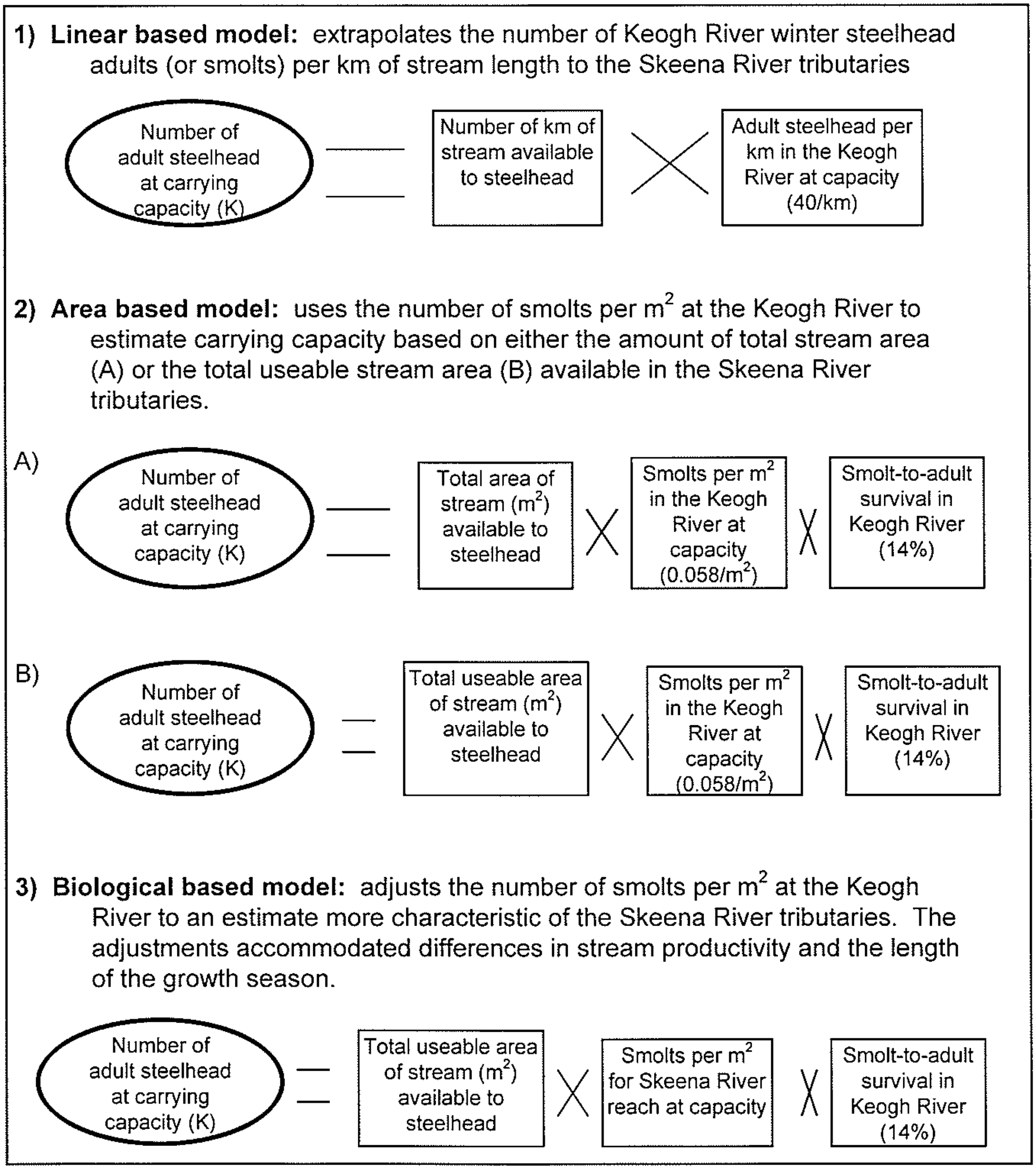


Figure 2. Linear, area and biological carrying capacity models for Skeena River summer steelhead.

4.0.0 Habitat Component

The habitat component estimated the total stream length of steelhead habitat (for the linear model), the total stream area available to steelhead (for the first area based model) and the total useable area available to summer steelhead in the Skeena River watershed (for the second area based model and biological based model; Figure 3). The main inputs to the model were the distribution of steelhead within the watershed and the total stream length of steelhead habitat. Mean Annual Discharge was used to estimate both the average width and the percentage of useable width.

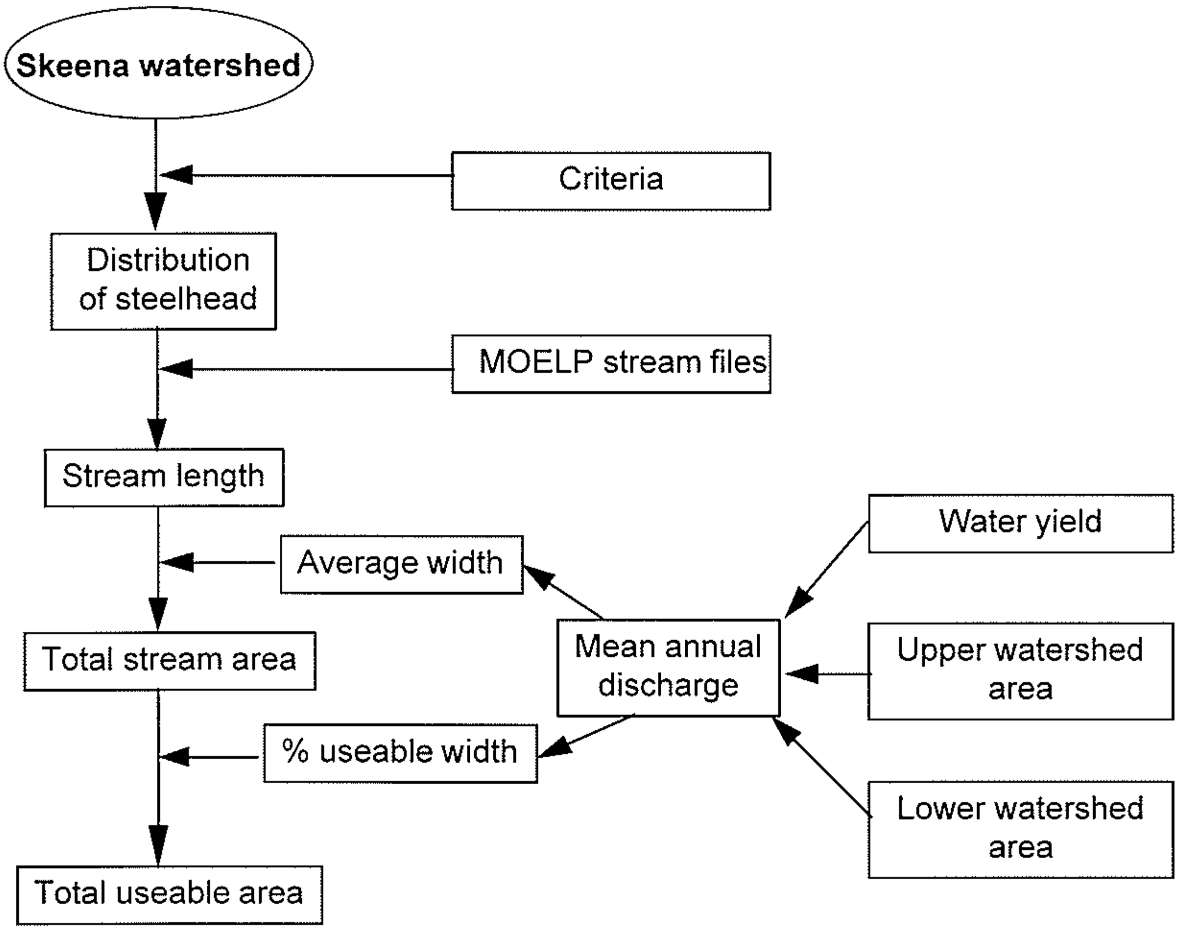


Figure 3. Flow diagram of the parameters used in the habitat component.

4.1.0 Steelhead Distribution

The distribution of steelhead in the Skeena River watershed was identified by using steelhead physical and biological criteria as well as the Ministry of Environment, Lands and Parks (MOELP) stream atlas.

Criteria: the distribution of steelhead fry was based on stream order and water yield.

- Tautz *et al.*'s (1992) stream order classification suggested juvenile steelhead used 4^{th} order streams (determined from 1:50 000 scale maps) with water yields less than 5 m^3/s / 100 km^2.
- The stream order was determined from the MOELP stream atlas and excluded ephemeral streams.
- Water yield was determined from the Water Survey of Canada (WSC) records by dividing the Mean Annual Discharge (MAD) by watershed area. Fifty-two (52) WSC stations were present in the Skeena River watershed.

Other Criteria: 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 (e.g. cutthroat, Dolly Varden). Some exceptions were made in cases where few large non-rainbows were sampled (i.e. chinook).

- Glacial streams were classified by low water temperatures ($<7^0$ C) and high turbidity (>50 PPM) and were considered unimportant for juvenile steelhead rearing (Tautz *et al.* 1992).

After the distribution of steelhead was estimated, the stream length was estimated from 1:50 000 scale topographic maps and the MOELP stream files. The total stream length of steelhead habitat was used in the linear based model (Figure 2).

4.2.0 Total Stream Area

Total stream area was calculated by estimating the average stream width and multiplying by the reach length.

(equation 1) $$\text{Total Area } (m^2) = \text{Reach Length (m)} \times \text{Average Stream Width (m)}$$

For large streams the average stream width was estimated from aerial photographs by either averaging several point width measurements or by digitizing stream area and dividing by thalweg length. Alternatively, the average stream width was estimated from a linear regression relationship developed from 119 reaches from 47 different streams in BC.

(equation 2) $$\text{Average Stream Width (m)} = 5.42 \times \text{MAD}^{0.523}$$

where MAD was the Mean Annual Discharge (m^3/s) for a reach. MAD estimates were from historical WSC records for reaches with gauging stations, whereas for ungauged reaches a proration method was used to estimate the MAD (equation 3). The proration method was endorsed by the Inland Waters Directorate of Environment Canada.

(equation 3) $$MAD_{adj} = \left[\frac{\sqrt{(LWA \times WY / 100)} + \sqrt{(UWA \times WY / 100)}}{2} \right]^2$$

where LWA was the Lower Watershed Area, UWA was the Upper Watershed Area and WY was the Water Yield. Ungauged reaches on streams that were gauged at either upstream or downstream locations were given the same water yield. Water yield values from the nearest stream course were used for ungauged reaches without gauge locations on the same stream course

4.3.0 Total Useable Area

Total useable area was calculated by estimating the percentage useable width and multiplying by the total area.

(equation 4) $$\text{Total Useable Area} = \text{Total Area} \times \text{Percentage Useable Width}$$

The percentage useable stream width (%UW) estimated the 'hydraulically suitable' habitat for steelhead fry and was estimated from a linear regression relationship of 628 stream reaches in BC.

(equation 5) $$\%UW = 10^{(2.39 - 0.275\log(\text{MAD adj}+1) - 0.4\log(\text{LFS}+1))} - 1$$

where LFS was the Low Flow Stage from WSC records.

5.0.0 Biological Component:

5.1.0 Biological Component From Tautz et al. *(1992)*

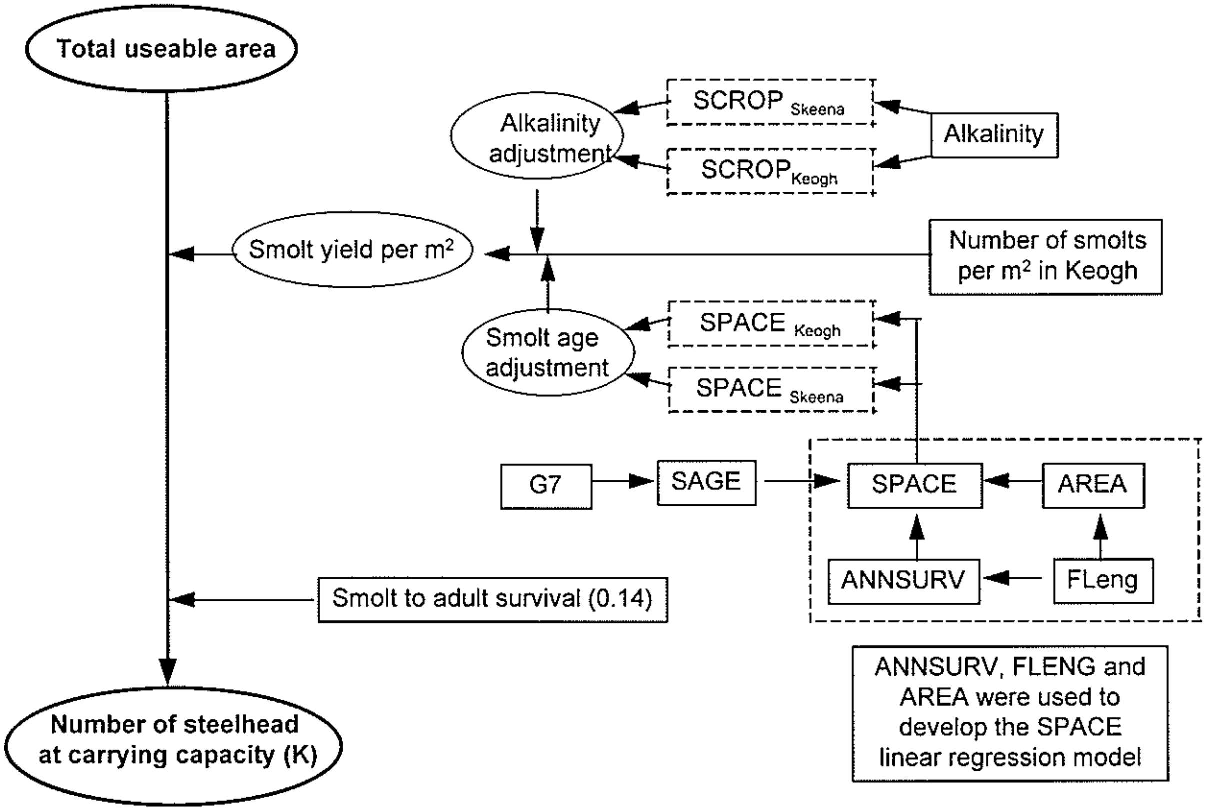
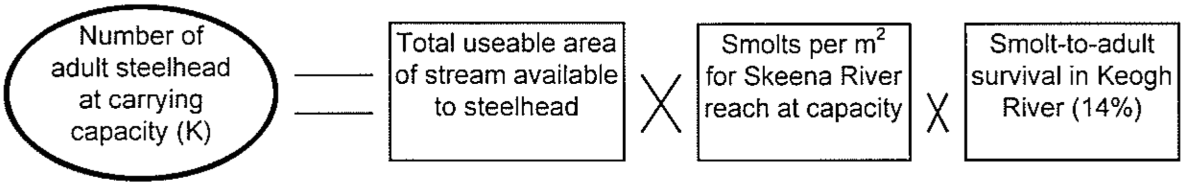


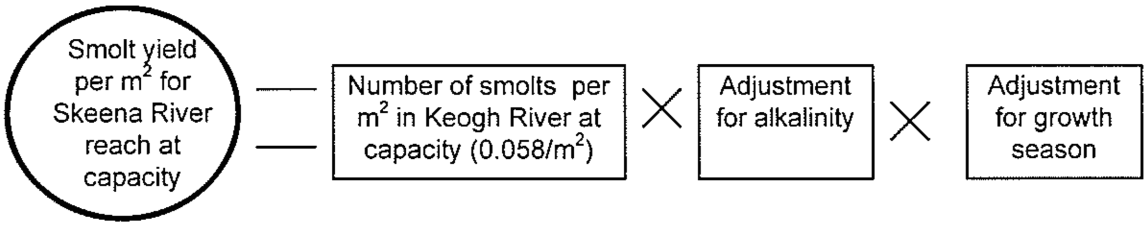
Figure 4. Flow diagram of the parameters used in the biological component from Tautz *et al.* (1992).

The biological component adjusted the number of smolts per m^2 at the Keogh River to an estimate more characteristic of the Skeena River based on biological parameters of stream productivity (SCROP) and the required rearing area to produced one smolt (SPACE). The length of the growth season (G7) was used to estimate the amount of space required to produce one smolt. The dashed box surrounding the SPACE, AREA, ANNSURV and FLENG parameters indicated the parameters used to develop a linear regression model that related mean smolt age (SAGE) and the required rearing area to produced one smolt (SPACE). The SPACE linear regression model was developed by Tautz *et al.* (1992) from Keogh River winter steelhead data. The main output of the biological component by Tautz *et al.* (1992) was an estimate of the number of smolts per m^2 based on parameters characteristic of Skeena River tributaries. The adjusted number of smolts per m^2 were used to estimate carrying capacity in the biological based model.

The number of adult steelhead at carrying capacity in the Skeena River was dependent upon the total useable area, the number of smolts per m^2 in the Skeena River and the smolt-to-adult survival. However, the number of smolts per m^2 at capacity in the Skeena River was unknown, and therefore the Keogh River biostandard was adjusted to make the estimate more characteristic of the Skeena River.



Skeena River tributaries were assumed to have higher stream productivity than the Keogh River, as indicated by higher alkalinity (Tautz *et al.* 1992). Alkalinity was used as an index of nutrient abundance for predicting salmonid densities (Ptolemy 1993). The adjustment for alkalinity increased the number of smolts produced per m^2 at capacity in the Skeena River. The Skeena River has a shorter growth season and steelhead juveniles may take longer to grow to smolt size with respect to conditions in the Keogh River. Skeena River smolts were generally older than Keogh River smolts, and thus the total stream area to produce one smolt in the Skeena River may be higher than the area required in the Keogh River. For example, an extra year of freshwater rearing (associated with an additional mortality rate of approximately 50%) may require twice the area to produce a smolt.



5.1.1 Adjustment for Alkalinity

The adjustment for alkalinity was used to accommodate the higher nutrient levels observed in the Skeena River watershed with respect to the Keogh River (Tautz *et al.* 1992).

(equation 6)
$$\text{Adjustment for Alkalinity} = \frac{\text{SCROP}_{\text{Skeena Reach}}}{\text{SCROP}_{\text{Keogh}}}$$

A regression model relating steelhead standing crop (SCROP) to total alkalinity was developed from 226 BC streams by Ptolemy *et al.* (1992 draft).

(equation 7) $$Log(SCROP) = 0.56 + 0.5 \times Log(\text{Total Alkalinity})$$

The adjustment for alkalinity increased the number of smolts at capacity per m^2 because the Skeena River tributaries had higher alkalinity values than the alkalinity of the Keogh River.

5.1.2 Adjustment for Growth Season

The length of the growth season was inversely related to the duration of the freshwater rearing period. Thus, short growth seasons were associated with long freshwater rearing periods and high mean smolt ages. Longer freshwater residence periods led to additional mortality and therefore a larger number of individual steelhead were required in order to have one steelhead survive to smolt age. A larger amount of rearing space was required to produce one smolt in rearing streams with short growth seasons, since more individuals were required to produce one smolt. The adjustment for space per smolt in a Skeena River reach involved a number of separate calculations.

(equation 8) $$\text{Adjustment for Growth Season} = \frac{\text{SPACE}_{\text{Keogh}}}{\text{SPACE}_{\text{SkeenaReach}}}$$

The space required to produce a smolt was dependent on the mean smolt age. Mean smolt age can be estimated from out-migrating smolts, the length of the growth season, adult scales and yearling fork length (Bocking and English 1992). The space required per smolt (SPACE) was related to the mean smolt age (SAGE) by:

(equation 9) $$\text{SPACE} = 1.24 \times (SAGE) - 1.31$$

Tautz *et al.* (1992) estimated the mean smolt age (SAGE) from the length of the growth season. The growth season was estimated as the number of days with mean water temperatures over 7° C (G7). Symons (1979) developed a model relating the length of the growth season (G7) to the mean smolt age of Atlantic salmon (*Salmo salar*; equation 10). Tautz *et al.* (1992) used Symons' (1979) model because it was not subject to the negative biases associated with estimating the freshwater age from scales (Jensen and Johnsen 1982; Hooton *et al.* 1987). Water temperature data was obtained from WSC stations in the Skeena River and tributaries.

(equation 10) $$SAGE = 9.08 \times 0.9938^{G7}$$

Tautz *et al.* (1992) recalibrated the equation to data collected from the Babine River because the Babine 'had the longest growth season and thus scales of fish were least likely to be missing the first annulus'. The recalibrated equation was (Tautz *et al.* 1992):

(equation 11) $$SAGE = 8.16 \times 0.9938^{G7}$$

Tautz *et al.* (1992) compared the mean smolt age estimates produced from the length of the growth season to estimates from the yearling fork length to judge the adequacy of the growth season method.

The amount of space required to produce 1 smolt was related to the mean smolt age (Tautz *et al.* 1992):

(equation 12) $$\mathrm{SPACE} = 1.24 \times (SAGE) - 1.31$$

Tautz *et al.* (1992) developed the regression by estimating the total amount of space required to produce an age 1+ smolt, age 2+ smolt, age 3+ smolt, age 4+ smolt and age 5+ smolt and then calculated a line of best fit.

The total area required to produce a smolt was estimated by summing the total area used by each age class to produce one smolt. In order to calculate the area used by each age class, Tautz *et al.* (1992) had to determine the number of steelhead within each age class required to produce one smolt.

e.g. for a 3+ smolt which has little growth after the end of the growth season for age 2+:

(equation 13) $$\text{Total Area} = (N_{0+} \times AREA_{0+}) + (N_{1+} \times AREA_{1+}) + (N_{2+} \times AREA_{2+})$$

However, Tautz *et al.* (1992) had to determine the age specific survival rates (S) in order to estimate the number of fish in each age class (i.e. N_{0+}, N_{1+}, N_{2+}) that would be required to produce a smolt of a specific freshwater age (for a 3+ smolt). Age specific survival rates were calculated for smolts of different freshwater ages because the incremental growth (yearly) differs between smolts of different ages (i.e. age 2+ smolts have higher incremental growth than age 5+ smolts from the same tributary; Table 2 in Tautz *et al.* 1992).

e.g. for a 3+ smolt

$$N_{1+} = N_{0+} \times S_{0\text{-}1+\ (\text{for 3+ smolt})}$$
$$N_{2+} = N_{1+} \times S_{1\text{-}2+\ (\text{for 3+ smolt})}$$
$$1\ \text{smolt} = N_{2+} \times S_{2\text{-smolt}\ (\text{for 3+ smolt})}$$

thus, $$1\ \text{smolt} = N_{0+} \times S_{0\text{-}1+\ (\text{for 3+ smolt})} \times S_{1\text{-}2+\ (\text{for 3+ smolt})} \times S_{2\text{-smolt}\ (\text{for 3+ smolt})}$$

Life history tables of Keogh River winter steelhead were analysed and produced a fitted equation relating size (FLENG) and annual survival (ANNSURV; Tautz *et al.* 1992):

(equation 14) $$ANNSURV = 0.55 \times FLENG / 100$$

Note: data from Table 3 in Tautz *et al.* (1992) suggested the slope (0.55) was approximately 0.575 to 0.578.

The annual survival rates differed for smolts of different ages because of the differences in the incremental growth (yearly; Table 3 in Tautz *et al.* 1992). After the survival rates were calculated, the number of fish in a given age class required to produce a smolt of a given age was calculated (i.e. N_{0+}, N_{1+}, N_{2+}).

Next, the area required for an age specific steelhead smolt was estimated using the empirical data for size at age of juvenile steelhead collected from extensive field sampling of BC steelhead populations (Tautz *et al.* 1992). The relationship between territory size (AREA) and fork length (FLENG) was described by Grant and Kramer (1990) for stream dwelling salmonids (data from 5 species and 10 different studies):

(equation 15) $$Log(AREA) = 2.61 \times Log(FLENG) - 2.83$$

The regression was used to estimate the area required for an age 0+, 1+, 2+, 3+ and 4+ steelhead and was then used to estimate the total area required to produce different aged smolts.

5.2.0 Biological Component From Bocking and English (1992)

Yearling size ($FLENG_{1+}$) was used to calculate the mean weight of fry (SIZE) and the mean smolt age (SAGE). The main output of the biological component by Bocking and English (1992) was an estimate of steelhead carrying capacity stratified by Skeena River tributary.

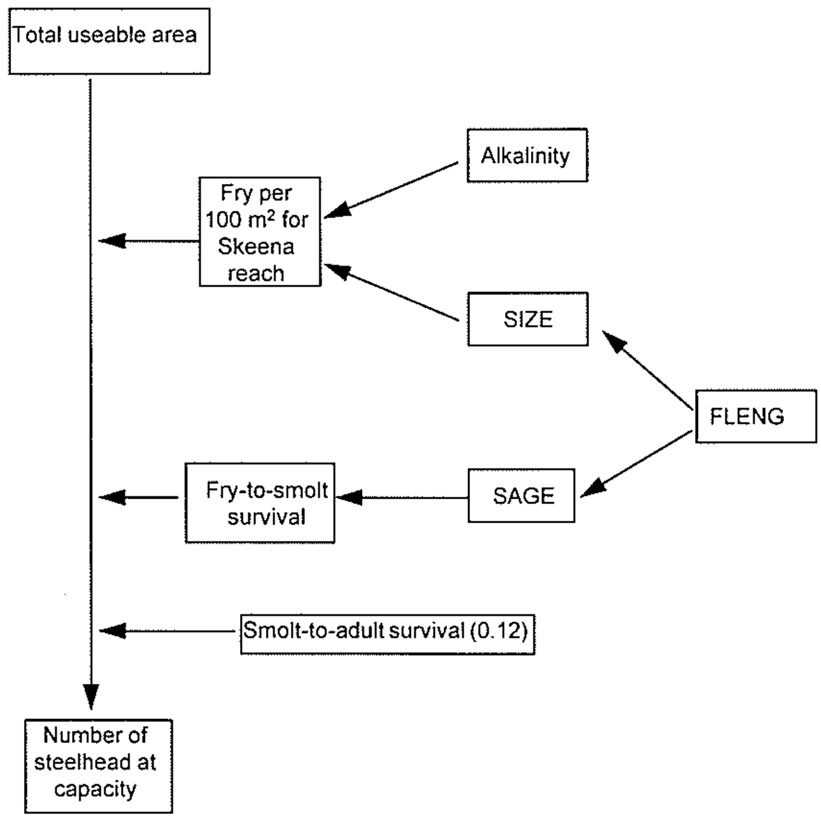
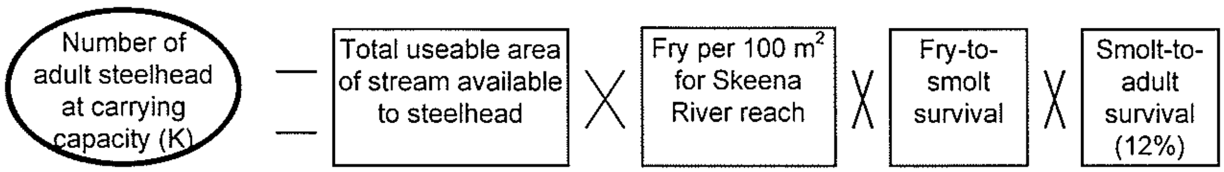


Figure 5. Flow diagram of the parameters used in the biological component from Bocking and English (1992).

Bocking and English (1992) calculated the number of fry (age 0+) per 100 m^2 at capacity maximum at the end of the growth season in addition to fry-to-smolt survival. The estimated fry density at capacity was then multiplied by the estimated fry-to-smolt survival, smolt-to-adult survival and the total useable area.



The fry per 100 m^2 at capacity for the end of the growth season was calculated using the total alkalinity of a tributary (measured at the end of the growth season or near the fall low flow stage; ALK) and the mean weight of fry (SIZE) at the end of the growth season. The relationship was based on 216 observations from resident and anadromous rainbow trout in 37 BC streams.

(equation 16) $$\text{Fry per 100 m}^2 \text{ for Skeeana River Reach} = \frac{36.3 \times \sqrt{ALK}}{SIZE}$$

The mean weight of fry (SIZE) was related to the yearling fork length (age 1+; FL_{1+}) by:

(equation 17) $$SIZE = 10(3.1 \times Log(FL_{1+}) - 5.85$$

Fry-to-smolt survival was estimated from a regression described by Symons (1979) for Atlantic Salmon:

(equation 18) $$\text{Fry - to - Smolt Survival} = \frac{10^{(-0.78-(0.38 \times SAGE))}}{0.13}$$

The denominator (0.13) implied an egg-to-fry survival of 13%. This value could be changed to 0.10, which was Tautz *et al.*'s (1992) estimated egg-to-fry survival for Keogh River winter steelhead. The mean smolt age (SAGE) was calculated from the yearling fork length (FL_{1+}) using a regression developed by Symons (1979) for Atlantic salmon.

(equation 19) $$SAGE = 10^{(3.58-(1.59 \times Log(FL_{1+}))}$$

Note:

Tautz *et al.* (1992) determined fry-to-smolt survival as a function of mean smolt age from Keogh River winter steelhead data, whereas Bocking and English (1992) estimated fry-to-smolt survival as a function of mean smolt age from Atlantic salmon data.

Tautz *et al.* (1992) estimated smolt-to-adult survival (14%) from Keogh River winter steelhead, whereas Bocking and English (1992) applied a 12% smolt-to-adult survival.

6.0.0 Stock-Recruitment Component

The stock-recruitment component produced estimates of steelhead population production characteristics and the number of spawners required at MSY. The steelhead life history model estimates (i.e. recruits per spawner, allowable harvest rates and Beverton-Holt's A value) were calculated using life history model parameters (Figure 6). The dashed box surrounding the SURV, ANNSURV and FLENG parameters indicates a sub-component of the life history model which was used to develop the linear regression relating mean smolt age (SAGE) and survival (SURV). The SURV linear regression model was developed by Tautz *et al.* (1992) from Keogh River winter steelhead data.

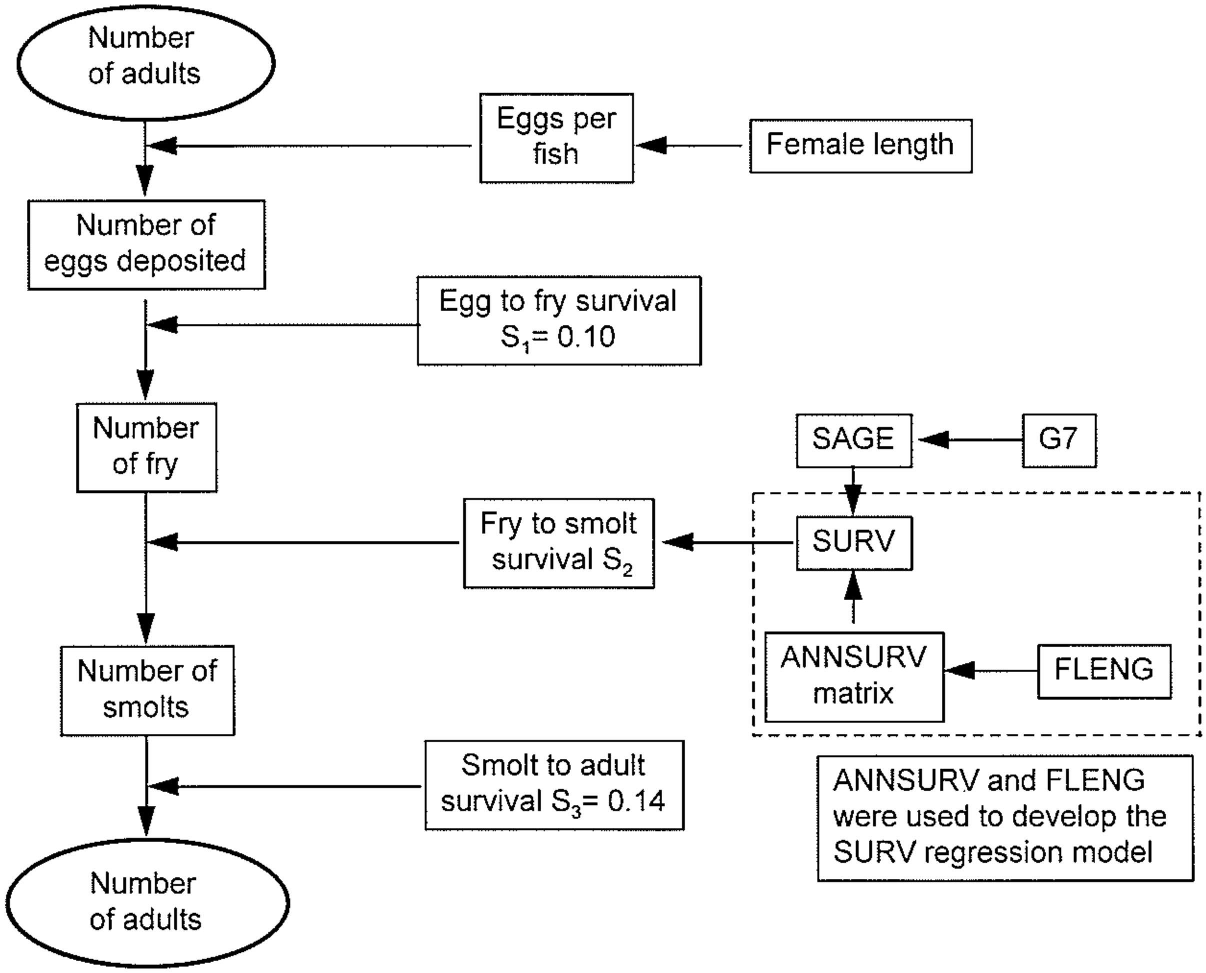


Figure 6. Flow diagram of the parameters used in the stock-recruitment component.

6.1.0 Stock-Recruitment Parameters

Skeena River summer steelhead were modelled with a semelparous life history (Figure 7). The life history of a steelhead population at MSY was modelled to predict the stock-recruitment estimates (i.e. recruits per spawner, allowable harvest rate and Beverton-Holt's A value). The parameters of the number of eggs/adult (fecundity), egg-to-fry survival and smolt-to-adult survival were assumed density independent (Tautz *et al.* 1992). However, fry-to-smolt survival was assumed density dependent and was estimated from the mean smolt age using a regression developed from Keogh River winter steelhead (Tautz *et al.* 1992).

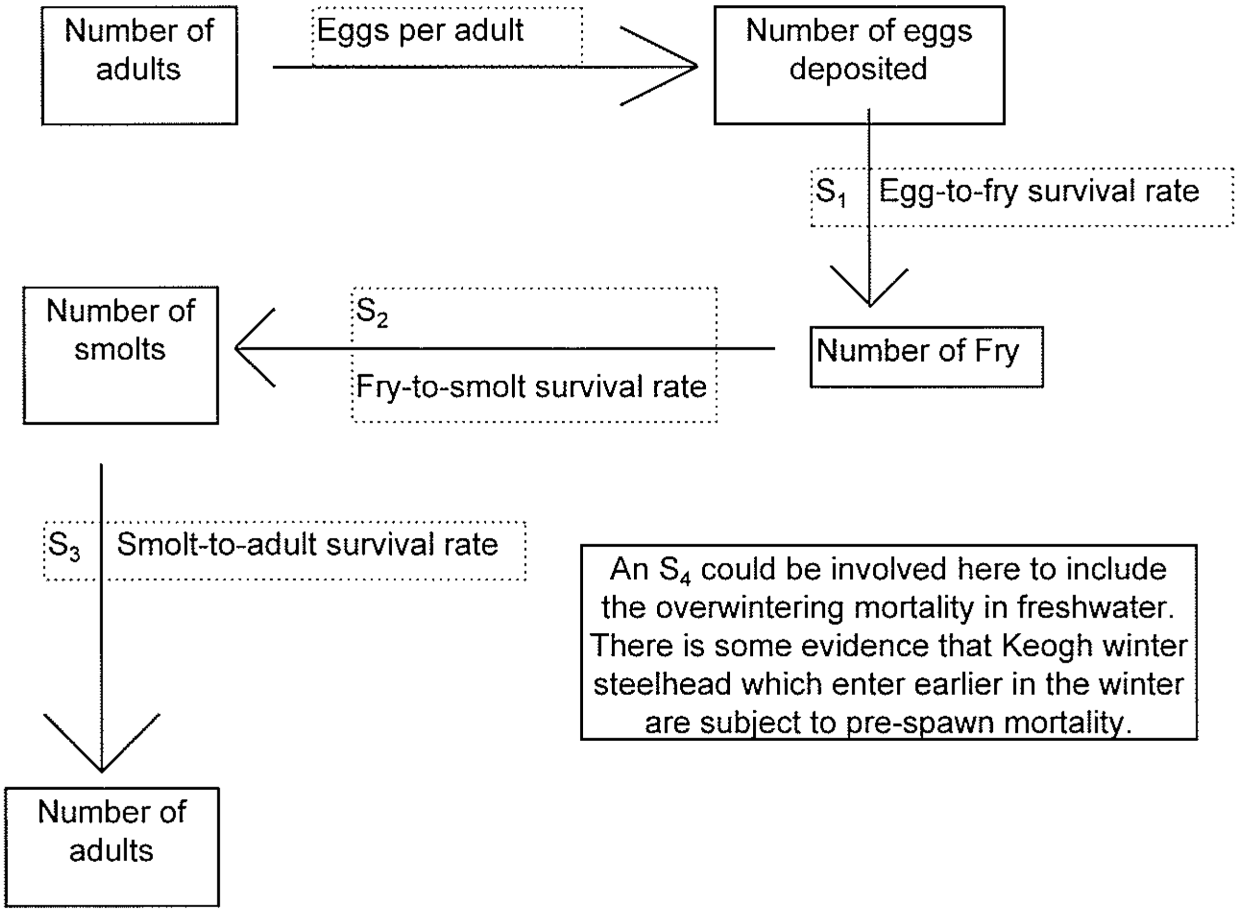


Figure 7. Semelparous steelhead life history model used to estimate steelhead productivity and allowable harvest rates by Tautz *et al.* (1992).

Fecundity was estimated using a regression developed for Skeena River summer steelhead by Wilkman and Stockerl (1981). The mean number of eggs per adult (fecundity) was determined from a linear regression model of the number of eggs per fish and length from 128 females captured in gillnets at the Skeena River mouth (Wilkman and Stockerl 1981; Figure 10 in Tautz *et al.* 1992).

(equation 20) $$\text{Mean Eggs / Adult} = 0.5 \times e^{(2.099 \times \ln(\text{Mean Length}) - 5.156)}$$

In 1991, the mean female length of 589 female steelhead (sampled from the Tyee test fishery at the Skeena River mouth) was smaller than the weighted mean female length of angler caught steelhead in the tributaries. Thus, the mean fecundity for 1991 steelhead was 82.4% of the weighted mean fecundity of angler caught females from previous studies. Tautz *et al.* (1992) applied a correction factor (0.824) to the fecundity estimate for each tributary. Female steelhead length may have been smaller in 1991 than when the tributaries were sampled, however the difference may have been a result of variation in the proportion of different ocean aged females.

Tautz *et al.* (1992) estimated egg-to-fry survival (S_1) from Keogh River winter steelhead (10%; Figure 7 in Tautz *et al.* 1992) from six data points. Seven years of data were available (1976-1982), however one year (1976) was excluded from the regression analysis because of unusually high river discharge (three times the 10 year average) during the incubation period (Tautz *et al.* 1992). Considerable variability existed between years and additional monitoring may provide a better distribution of egg-to-fry survival in the Keogh River. A wide range of egg-to-fry survival estimates exist in the literature and egg-to-fry survival was reported to be influenced by characteristics such as habitat quality (substrate composition) and environmental factors (floods and drought; Chapman 1988; Bradford 1995).

Fry-to-smolt survival (S_2) was estimated as a function of mean smolt age (from Tautz *et al.* 1992). The product of the annual survival estimates (ANNSURV) from the life history matrix (described in the biological component section from Tautz *et al.* 1992) were also used to develop the regression relating mean smolt age (SAGE) and fry-to-smolt survival (SURV):

(equation 21) $$SURV = e^{(-0.7174 \times SAGE)}$$

The product of the annual survivals (ANNSURV) for each smolt age class was the estimated fry-to-smolt survival for a smolt of a specific age. Steelhead egg-to-smolt survivals at MSY were compared to other estimates from the literature (Tautz *et al.* 1992). The steelhead regression estimates of egg-to-smolt were similar to Symons' (1979) medium survival estimates for Atlantic salmon (Figure 9 in Tautz *et al.* 1992). Tautz *et al.* (1992) also illustrated how fry-to-smolt survival at carrying capacity was lower than fry-to-smolt survival at MSY (Figure 9 in Tautz *et al.* 1992). Mean smolt age was estimated from the length of the growth season, as previously described in the biological component section (from Tautz *et al.* 1992).

Smolt-to-adult survival (S_3) was estimated from Keogh River winter steelhead (Figure 6 in Tautz *et al.* 1992). Data were available from 1977 to 1986, however 1982 was excluded from the calculation of the arithmetic and geometric mean of survival rates because it was considered an outlier (Tautz *et al.* 1992). Tautz *et al.* (1992) calculated yearly survival rates and reported the arithmetic mean (15.6%) and the geometric mean (14.4%), and used the geometric mean for productivity calculations.

6.2.0 Stock-Recruitment Estimates

The stock-recruitment relationship for Keogh River steelhead was assumed to follow the theoretical Beverton-Holt type stock-recruitment curve (Figures 4 and 5 in Tautz *et al.* 1992). The Beverton-Holt stock recruitment curve was described by Ricker (1975) as:

(equation 22)
$$R = \frac{P}{1 - A(1 - \frac{P}{P_r})}$$

where R was the abundance of returning adults (recruits), P was the abundance of Parents (spawners), A was Beverton-Holt's A value, and P_r was the abundance of Parents at replacement (capacity).

The number of recruits per spawner (RPS) at MSY was calculated from the life history model with fry-to-smolt survival estimated at MSY. The number of recruits per spawner at MSY was also a measure of the relative steelhead productivity of a Skeena River tributary population.

(equation 23)
$$RPS = 1 \times \text{Number of Eggs / Fish} \times S_1 \times S_2 \times S_3$$

The model excluded repeat spawners and therefore tributaries with a high frequency of repeat spawners may actually be more productive than estimated by the Skeena steelhead carrying capacity model (Tautz *et al.* 1992). In the absence of commercial harvest repeat spawners may have composed a higher proportion of the returning adults because repeat spawners are subject to additional harvest mortality when they emigrate from the Skeena River as kelts and then subject to harvest again when they re-enter for their second spawning migration. If the proportion of repeat spawners was historically (pre-commercial harvest) higher, mean length also may have been higher due to additional growth (approximately 3.45 cm/yr in the ocean, unpublished Sustut River steelhead data).

After determining RPS, the allowable harvest rate at MSY (μ_{msy}) was calculated as :

(equation 24)
$$\mu_{msy} = \frac{(RPS-1)}{RPS}$$

and then Beverton-Holt's A value was calculated as:

(equation 25)
$$A = 1-(1-\mu_{msy})^2$$

Next, the number of spawners at MSY (P_{msy}) and the number of recruits at MSY (R_{msy}) could be determined using the following equations from Ricker (1975).

(equation 26)
$$P_{msy} / P_r = \frac{A-1+\sqrt{(1-A)}}{A}$$

or

(equation 27)
$$P_{msy} = \frac{P_r \times (A-1+\sqrt{(1-A)})}{A}$$

and

(equation 28)
$$R_{msy} / P_r = \frac{1-\sqrt{(1-A)}}{A}$$

or

(equation 29)
$$R_{msy} = \frac{P_r \times (1-\sqrt{(1-A)})}{A}$$

7.0.0 Parameter Summary

The summary of the parameters and their data sources indicated a high reliance on data from Keogh River winter steelhead (Table 1). Many of the provincial biostandards and regressions were based on the Keogh River winter steelhead, since it was the best available data set. Water Survey of Canada data were also widely used in the model. The presence of a large number (52) of WSC stations in the Skeena River watershed aided the development of the model. Watersheds with fewer WSC stations may have to rely on other data or extrapolate from the nearest WSC stations. However, large assumptions are required to extrapolate data between watersheds because of differences in characteristics such as basin aspect, elevation, precipitation, snow pack levels and hydrograph characteristics. BC data and literature sources were involved with a similar number of parameters. BC data was used mainly in the habitat component, whereas literature data was involved mainly in the biological component. Tributary and watershed specific data (excluding WSC data) were used for fewer parameters than the other data sources and origins.

Table 1. Summary of the parameters used in the Skeena steelhead carrying capacity model components and their data sources.

Parameters	Data Origin/Source					
Habitat Component	Tributary Specific	Watershed Specific	Keogh River	Literature	BC Data	Other Sources
Criteria		x				
Water yield						WSC
Up/low watershed area						WSC
Mean annual discharge					x	WSC
Average width					x	
% useable width					x	
Low flow stage						WSC
Biological Component Tautz *et al.* (1992)						
Alkalinity	x					
SCROP					x	
Number of smolts/m^2			x			
G7 (water temperature)						WSC
SAGE				x (adjusted to BC)		
SPACE			x			
ANNSURV			x			
AREA				x		
FLENG			x			
Biological Component Bocking and English (1992)						
$FLENG_{1+}$	x					
SIZE					x	
Fry - $Smolt_{LGL}$				x		
$SAGE_{LGL}$				x		
Stock-Recruitment Component						
Female length	x					
Eggs/fish		x				
Egg -fry survival			x			
Fry - smolt survival			x			
SAGE				x (adjusted to BC)		
G7						WSC
SURV			x			
ANNSURV (matrix)			x			
FLENG			x			
Smolt - adult survival			x			

8.0.0 Acknowledgements

I thank Dana Atagi for assistance with interpreting the Skeena steelhead carrying capacity model and for many useful comments and critical reviews. I thank Krista Morten and Mark Beere for critical reviews. I thank Dr. Ted Down for securing funding for the preparation of this review. Funding for the preparation of this review was provided by the Common Land Information Base.

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AN OVERVIEW OF THE ALGORITHMS AND PARAMETERS USED IN THE SKEENA STEELHEAD CARRYING CAPACITY MODEL

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Abstract

The Skeena steelhead (*Oncorhynchus mykiss*) carrying capacity model (Tautz *et al.* 1992), algorithms and parameters were reviewed to provide fisheries biologists with a comprehensive understanding of the three model components. For interpretative purposes, the model was described by the three model components (i.e. habitat, biological and stock-recruitment) used by Tautz *et al.* (1992). Bocking and English (1992) reviewed the Skeena steelhead carrying capacity model, but provided different algorithms for the biological component than Tautz *et al.* (1992). Therefore the biological component described by Bocking and English (1992) was also described. In addition, the data sources and origins for the different parameters were described to assist fisheries biologists in refining the model parameters, which will probably be used in a similar model under development for Nass River steelhead.

Table of Contents

List of Tables

List of Figures

1.0.0 Introduction

Tautz *et al.* (1992) developed three types of steelhead (*Oncorhynchus mykiss*) carrying capacity models based on habitat and biological parameters for the Skeena River and its tributaries. Similar models are being developed for summer and winter steelhead in the Nass River watershed. Therefore a thorough review of the Skeena steelhead carrying capacity model components was necessary to identify areas and parameters that could be refined in order to improve the efficacy of the Nass habitat capability model. Improvements may result from the collection of Nass River specific data or by refining the parameters of the model based on the addition of recent data.

The Skeena steelhead carrying capacity model was divided into three components: habitat, biological and stock-recruitment (Tautz *et al.* 1992). LGL Ltd. (Bocking and English 1992) reviewed the Skeena steelhead carrying capacity model, however Bocking and English (1992) provided a different algorithm for the biological component and performed a limited evaluation of the stock-recruitment component of Tautz *et al.*'s (1992) models.

The objective of this report is to provide a comprehensive overview of the model and identify the sources of the parameters used in the model. The overview will assist fisheries biologists in making the Nass habitat capability model more characteristic of the Nass River by identifying the mechanisms to refine the parameters and biostandards with recent information or Nass River specific data.

The paper begins with a description of the three types of models (linear, area, biological) developed by Tautz *et al.* (1992), followed by a description of the three model components (i.e. habitat, biological, stock-recruitment) and finally a summary of the sources of the parameters, biostandards and data. The description of the habitat component discusses the parameters necessary to calculate the linear and area based models and one of the parameters necessary for the biological based model. The description of the biological component discusses the remainder of the parameters necessary to calculate the biological based model developed by Tautz *et al.* (1992) and Bocking and English (1992). Each component begins with a flow diagram indicating where the parameters were used in the model and was followed by a description of the parameters and their involvement in the model.

2.0.0 Study Area

The Skeena River originates in the Skeena Mountains of north-western British Columbia and flows south-west for approximately 530 km into Chatham Sound (Figure 1). The Skeena River watershed is the second largest watershed entirely contained within British Columbia and drains approximately 51 200 km^2 (Koski *et al.* 1995). The Skeena River has six main tributaries: Sustut, Babine, Kispiox, Bulkley, Zymoetz and Kitsumkalum rivers. Common fish species in the Skeena River watershed include sockeye salmon (*O. nerka*), chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), steelhead trout, cutthroat trout (*O. clarki*), Rocky Mountain whitefish (*Prosopium williamsoni*), bull char (*Salvelinus confluentus*), Dolly Varden char (*S. malma*), largescale sucker (*Catostomus macrocheilus*), redside shiner (*Richardsonius balteatus*), peamouth chub (*Mylocheilus caurinus*) and northern squawfish (*Ptychocheilus oregonesis*; McPhail and Carveth 1994). The upper Skeena River watershed also contains lake trout (*S. namaycush*), lake whitefish (*Coregonus clupeaformis*), pygmy whitefish (*Prosopium coulteri*), lake chub (*Couesius plumbeus*), longnose dace (*Rhinichthys cataractae*), white sucker (*Catostomus commersoni*) and burbot (*Lota lota*; McPhail and Carveth 1994). The Skeena River watershed lies within three ecoprovinces (Coastal Mountains, Central Interior and Sub-Boreal Interior) and contains seven biogeoclimatic zones: Alpine Tundra, Spruce-Willow-Birch, Engelmann Spruce-Subalpine Fir, Sub-Boreal Spruce, Interior Cedar-Hemlock, Mountain Hemlock, Coastal Western Hemlock (Pojar and Nuzsdorfer 1988).

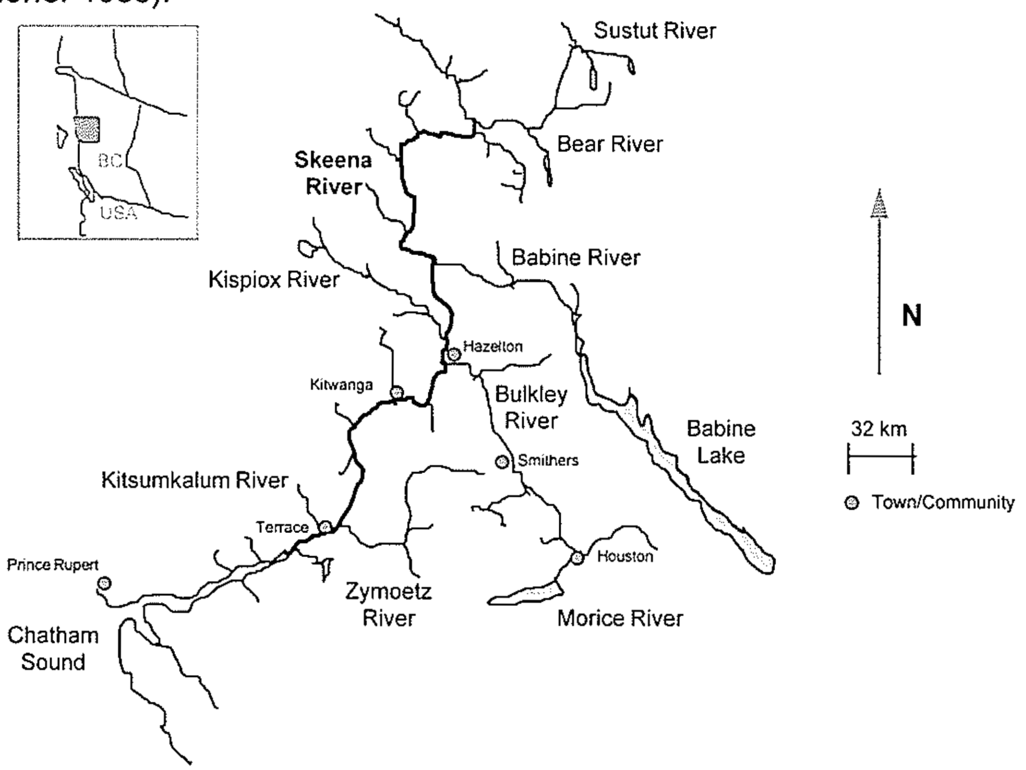


Figure 1. The Skeena River watershed and major tributaries.

3.0.0 Three Carrying Capacity Models

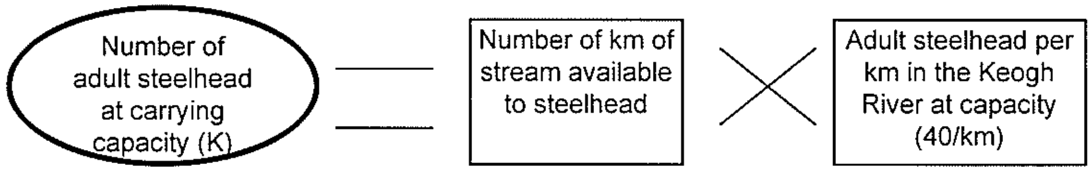
Tautz *et al.* (1992) developed linear, area and biological models to predict steelhead carrying capacity in Skeena River tributaries (Figure 2). The three models produced four estimates of steelhead carrying capacity for Skeena River tributaries. The three model components were used to develop inputs for the carrying capacity models and to estimate production characteristics of the different tributary populations. The habitat component estimated inputs for the linear, area and biological based models, whereas the biological component estimated inputs for the biological based model only. The stock-recruitment component estimated steelhead population production characteristics and none of the stock-recruitment outputs were used in either of the three carrying capacity models. The stock-recruitment component estimated stock productivity, allowable harvest rates and the required adult escapement for steelhead populations at maximum sustainable yield.

The linear model required two outputs from the habitat component and a provincial biostandard to estimate carrying capacity (Figure 2). From the habitat component, the distribution of steelhead streams and the total stream length of steelhead habitat were determined. Then the number of adult spawners per km at capacity was multiplied by the stream length to estimate the number of adults at carrying capacity (Figure 2). The number of adults per km at capacity (40) was estimated from Keogh River winter steelhead because a similar estimate did not exist for any Skeena River steelhead streams and the Keogh River data was the best available information.

The area based carrying capacity model produced two separate carrying capacity estimates and each required different outputs from the habitat component (Figure 2). The first area based model used the total stream area available to steelhead, an estimate of the number of smolts produced per m^2 at capacity and an estimate of smolt-to-adult survival. Total stream area was estimated in the habitat component. Since the number of smolts produced per m^2 and smolt to adult survival were unknown in the Skeena River, the biostandards measured for Keogh River winter steelhead were used because it was the best available data. The second area based model differed from the first by using the estimated total useable stream area instead of the total stream area. The total useable area was a fraction of the total stream area because only a portion of the total stream area was assumed to be suitable for steelhead rearing (Tautz *et al.* 1992). The total useable area was estimated in the habitat component and the number of smolts per m^2 and smolt-to-adult survival were estimated from Keogh River winter steelhead biostandards.

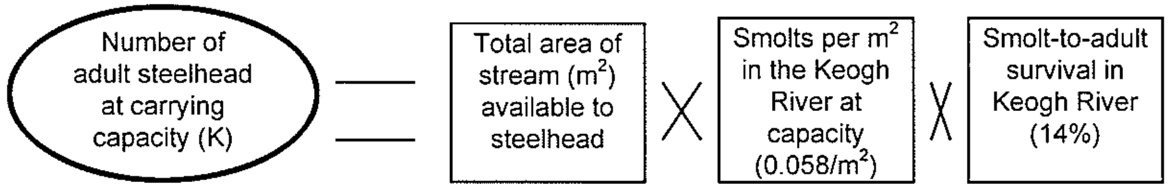
The biological based carrying capacity model was similar to the second area based model, since it required total useable area, number of smolts per m^2 at capacity and smolt-to-adult survival (Figure 2). However, the biological model differed by using biological parameters to adjust the number of smolts per m^2 at the Keogh River in order to make it more characteristic of the Skeena River. The adjustments accommodated differences in stream productivity and the length of the growth season.

1) Linear based model: extrapolates the number of Keogh River winter steelhead adults (or smolts) per km of stream length to the Skeena River tributaries

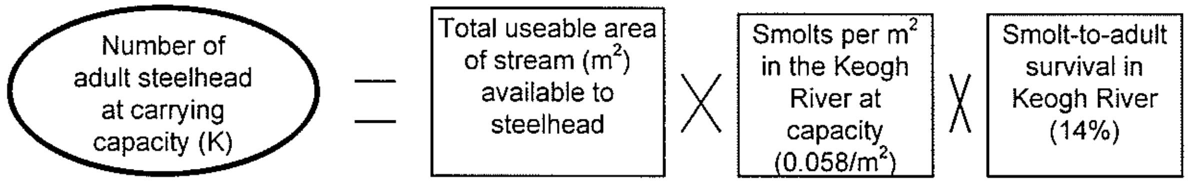


2) Area based model: uses the number of smolts per m^2 at the Keogh River to estimate carrying capacity based on either the amount of total stream area (A) or the total useable stream area (B) available in the Skeena River tributaries.

A)



B)



3) Biological based model: adjusts the number of smolts per m^2 at the Keogh River to an estimate more characteristic of the Skeena River tributaries. The adjustments accommodated differences in stream productivity and the length of the growth season.

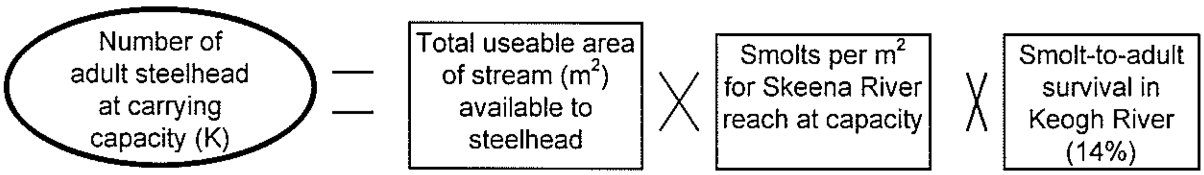


Figure 2. Linear, area and biological carrying capacity models for Skeena River summer steelhead.

4.0.0 Habitat Component

The habitat component estimated the total stream length of steelhead habitat (for the linear model), the total stream area available to steelhead (for the first area based model) and the total useable area available to summer steelhead in the Skeena River watershed (for the second area based model and biological based model; Figure 3). The main inputs to the model were the distribution of steelhead within the watershed and the total stream length of steelhead habitat. Mean Annual Discharge was used to estimate both the average width and the percentage of useable width.

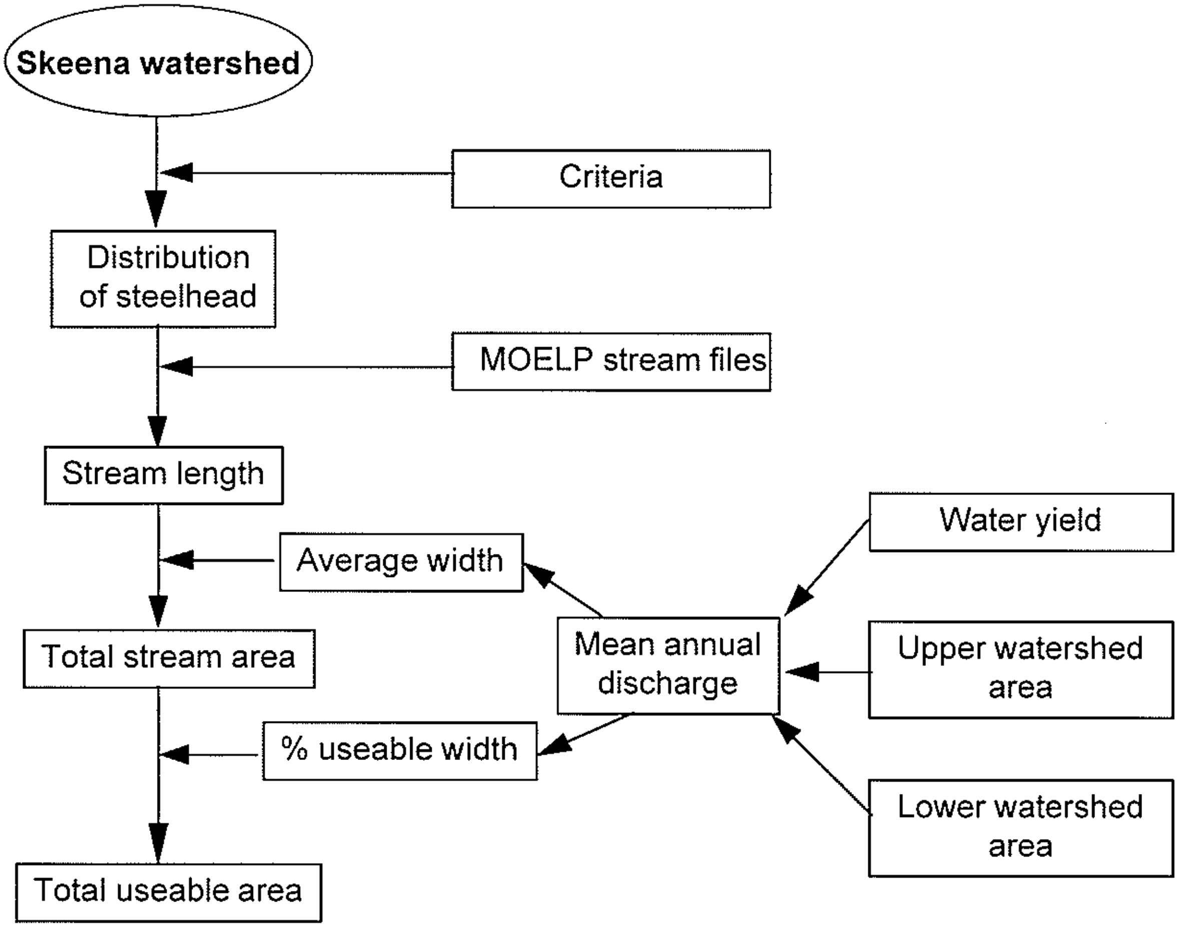


Figure 3. Flow diagram of the parameters used in the habitat component.

4.1.0 Steelhead Distribution

The distribution of steelhead in the Skeena River watershed was identified by using steelhead physical and biological criteria as well as the Ministry of Environment, Lands and Parks (MOELP) stream atlas.

Criteria: the distribution of steelhead fry was based on stream order and water yield.

- Tautz *et al.*'s (1992) stream order classification suggested juvenile steelhead used 4^{th} order streams (determined from 1:50 000 scale maps) with water yields less than 5 m^3/s / 100 km^2.
- The stream order was determined from the MOELP stream atlas and excluded ephemeral streams.
- Water yield was determined from the Water Survey of Canada (WSC) records by dividing the Mean Annual Discharge (MAD) by watershed area. Fifty-two (52) WSC stations were present in the Skeena River watershed.

Other Criteria: 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 (e.g. cutthroat, Dolly Varden). Some exceptions were made in cases where few large non-rainbows were sampled (i.e. chinook).

- Glacial streams were classified by low water temperatures ($<7^0$ C) and high turbidity (>50 PPM) and were considered unimportant for juvenile steelhead rearing (Tautz *et al.* 1992).

After the distribution of steelhead was estimated, the stream length was estimated from 1:50 000 scale topographic maps and the MOELP stream files. The total stream length of steelhead habitat was used in the linear based model (Figure 2).

4.2.0 Total Stream Area

Total stream area was calculated by estimating the average stream width and multiplying by the reach length.

(equation 1) $$\text{Total Area (m}^2\text{)} = \text{Reach Length (m)} \times \text{Average Stream Width (m)}$$

For large streams the average stream width was estimated from aerial photographs by either averaging several point width measurements or by digitizing stream area and dividing by thalweg length. Alternatively, the average stream width was estimated from a linear regression relationship developed from 119 reaches from 47 different streams in BC.

(equation 2) $$\text{Average Stream Width (m)} = 5.42 \times \text{MAD}^{0.523}$$

where MAD was the Mean Annual Discharge (m^3/s) for a reach. MAD estimates were from historical WSC records for reaches with gauging stations, whereas for ungauged reaches a proration method was used to estimate the MAD (equation 3). The proration method was endorsed by the Inland Waters Directorate of Environment Canada.

(equation 3) $$MAD_{adj} = \left[\frac{\sqrt{(LWA \times WY / 100)} + \sqrt{(UWA \times WY / 100)}}{2}\right]^2$$

where LWA was the Lower Watershed Area, UWA was the Upper Watershed Area and WY was the Water Yield. Ungauged reaches on streams that were gauged at either upstream or downstream locations were given the same water yield. Water yield values from the nearest stream course were used for ungauged reaches without gauge locations on the same stream course

4.3.0 Total Useable Area

Total useable area was calculated by estimating the percentage useable width and multiplying by the total area.

(equation 4) $$\text{Total Useable Area} = \text{Total Area} \times \text{Percentage Useable Width}$$

The percentage useable stream width (%UW) estimated the 'hydraulically suitable' habitat for steelhead fry and was estimated from a linear regression relationship of 628 stream reaches in BC.

(equation 5) $$\%\text{UW} = 10^{(2.39 - 0.275\log(\text{MAD adj}+1) - 0.4\log(\text{LFS}+1)} - 1$$

where LFS was the Low Flow Stage from WSC records.

5.0.0 Biological Component:

5.1.0 Biological Component From Tautz et al. *(1992)*

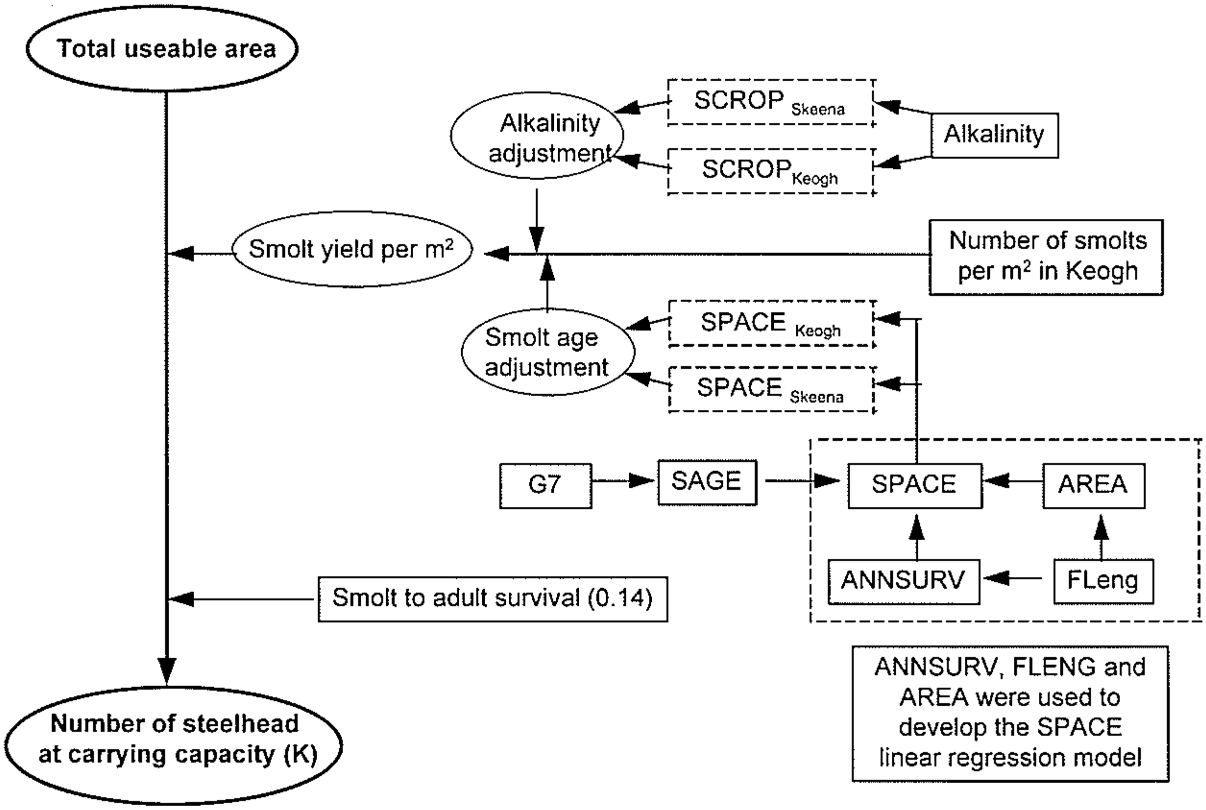
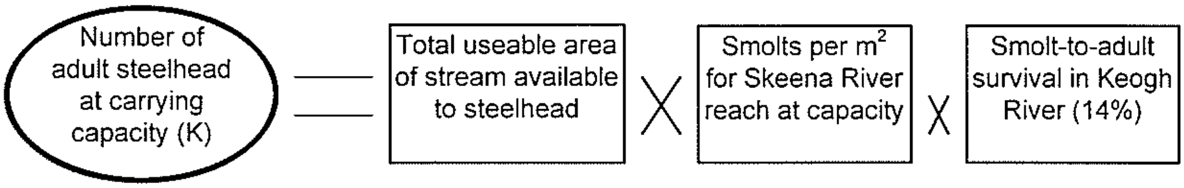


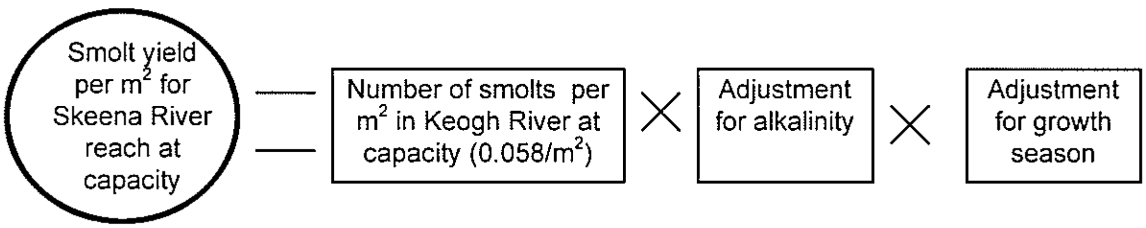
Figure 4. Flow diagram of the parameters used in the biological component from Tautz *et al.* (1992).

The biological component adjusted the number of smolts per m^2 at the Keogh River to an estimate more characteristic of the Skeena River based on biological parameters of stream productivity (SCROP) and the required rearing area to produced one smolt (SPACE). The length of the growth season (G7) was used to estimate the amount of space required to produce one smolt. The dashed box surrounding the SPACE, AREA, ANNSURV and FLENG parameters indicated the parameters used to develop a linear regression model that related mean smolt age (SAGE) and the required rearing area to produced one smolt (SPACE). The SPACE linear regression model was developed by Tautz *et al.* (1992) from Keogh River winter steelhead data. The main output of the biological component by Tautz *et al.* (1992) was an estimate of the number of smolts per m^2 based on parameters characteristic of Skeena River tributaries. The adjusted number of smolts per m^2 were used to estimate carrying capacity in the biological based model.

The number of adult steelhead at carrying capacity in the Skeena River was dependent upon the total useable area, the number of smolts per m^2 in the Skeena River and the smolt-to-adult survival. However, the number of smolts per m^2 at capacity in the Skeena River was unknown, and therefore the Keogh River biostandard was adjusted to make the estimate more characteristic of the Skeena River.



Skeena River tributaries were assumed to have higher stream productivity than the Keogh River, as indicated by higher alkalinity (Tautz *et al.* 1992). Alkalinity was used as an index of nutrient abundance for predicting salmonid densities (Ptolemy 1993). The adjustment for alkalinity increased the number of smolts produced per m^2 at capacity in the Skeena River. The Skeena River has a shorter growth season and steelhead juveniles may take longer to grow to smolt size with respect to conditions in the Keogh River. Skeena River smolts were generally older than Keogh River smolts, and thus the total stream area to produce one smolt in the Skeena River may be higher than the area required in the Keogh River. For example, an extra year of freshwater rearing (associated with an additional mortality rate of approximately 50%) may require twice the area to produce a smolt.



5.1.1 Adjustment for Alkalinity

The adjustment for alkalinity was used to accommodate the higher nutrient levels observed in the Skeena River watershed with respect to the Keogh River (Tautz *et al.* 1992).

(equation 6)
$$\text{Adjustment for Alkalinity} = \frac{\text{SCROP}_{\text{Skeena Reach}}}{\text{SCROP}_{\text{Keogh}}}$$

A regression model relating steelhead standing crop (SCROP) to total alkalinity was developed from 226 BC streams by Ptolemy *et al.* (1992 draft).

(equation 7) $$Log(SCROP) = 0.56 + 0.5 \times Log(\text{Total Alkalinity})$$

The adjustment for alkalinity increased the number of smolts at capacity per m^2 because the Skeena River tributaries had higher alkalinity values than the alkalinity of the Keogh River.

5.1.2 Adjustment for Growth Season

The length of the growth season was inversely related to the duration of the freshwater rearing period. Thus, short growth seasons were associated with long freshwater rearing periods and high mean smolt ages. Longer freshwater residence periods led to additional mortality and therefore a larger number of individual steelhead were required in order to have one steelhead survive to smolt age. A larger amount of rearing space was required to produce one smolt in rearing streams with short growth seasons, since more individuals were required to produce one smolt. The adjustment for space per smolt in a Skeena River reach involved a number of separate calculations.

(equation 8) $$\text{Adjustment for Growth Season} = \frac{\text{SPACE}_{\text{Keogh}}}{\text{SPACE}_{\text{SkeenaReach}}}$$

The space required to produce a smolt was dependent on the mean smolt age. Mean smolt age can be estimated from out-migrating smolts, the length of the growth season, adult scales and yearling fork length (Bocking and English 1992). The space required per smolt (SPACE) was related to the mean smolt age (SAGE) by:

(equation 9) $$\text{SPACE} = 1.24 \times (SAGE) - 1.31$$

Tautz *et al.* (1992) estimated the mean smolt age (SAGE) from the length of the growth season. The growth season was estimated as the number of days with mean water temperatures over 7° C (G7). Symons (1979) developed a model relating the length of the growth season (G7) to the mean smolt age of Atlantic salmon (*Salmo salar*; equation 10). Tautz *et al.* (1992) used Symons' (1979) model because it was not subject to the negative biases associated with estimating the freshwater age from scales (Jensen and Johnsen 1982; Hooton *et al.* 1987). Water temperature data was obtained from WSC stations in the Skeena River and tributaries.

(equation 10) $$SAGE = 9.08 \times 0.9938^{G7}$$

Tautz *et al.* (1992) recalibrated the equation to data collected from the Babine River because the Babine 'had the longest growth season and thus scales of fish were least likely to be missing the first annulus'. The recalibrated equation was (Tautz *et al.* 1992):

(equation 11) $$SAGE = 8.16 \times 0.9938^{G7}$$

Tautz *et al.* (1992) compared the mean smolt age estimates produced from the length of the growth season to estimates from the yearling fork length to judge the adequacy of the growth season method.

The amount of space required to produce 1 smolt was related to the mean smolt age (Tautz *et al.* 1992):

(equation 12) $$\mathrm{SPACE} = 1.24 \times (SAGE) - 1.31$$

Tautz *et al.* (1992) developed the regression by estimating the total amount of space required to produce an age 1+ smolt, age 2+ smolt, age 3+ smolt, age 4+ smolt and age 5+ smolt and then calculated a line of best fit.

The total area required to produce a smolt was estimated by summing the total area used by each age class to produce one smolt. In order to calculate the area used by each age class, Tautz *et al.* (1992) had to determine the number of steelhead within each age class required to produce one smolt.

e.g. for a 3+ smolt which has little growth after the end of the growth season for age 2+:

(equation 13) $$\text{Total Area} = (N_{0+} \times AREA_{0+}) + (N_{1+} \times AREA_{1+}) + (N_{2+} \times AREA_{2+})$$

However, Tautz *et al.* (1992) had to determine the age specific survival rates (S) in order to estimate the number of fish in each age class (i.e. N_{0+}, N_{1+}, N_{2+}) that would be required to produce a smolt of a specific freshwater age (for a 3+ smolt). Age specific survival rates were calculated for smolts of different freshwater ages because the incremental growth (yearly) differs between smolts of different ages (i.e. age 2+ smolts have higher incremental growth than age 5+ smolts from the same tributary; Table 2 in Tautz *et al.* 1992).

e.g. for a 3+ smolt

$$N_{1+} = N_{0+} \times S_{0\text{-}1+\ (\text{for 3+ smolt})}$$
$$N_{2+} = N_{1+} \times S_{1\text{-}2+\ (\text{for 3+ smolt})}$$
$$1\ \text{smolt} = N_{2+} \times S_{2\text{-smolt}\ (\text{for 3+ smolt})}$$

thus, $$1\ \text{smolt} = N_{0+} \times S_{0\text{-}1+\ (\text{for 3+ smolt})} \times S_{1\text{-}2+\ (\text{for 3+ smolt})} \times S_{2\text{-smolt}\ (\text{for 3+ smolt})}$$

Life history tables of Keogh River winter steelhead were analysed and produced a fitted equation relating size (FLENG) and annual survival (ANNSURV; Tautz *et al.* 1992):

(equation 14) $$ANNSURV = 0.55 \times FLENG / 100$$

Note: data from Table 3 in Tautz *et al.* (1992) suggested the slope (0.55) was approximately 0.575 to 0.578.

The annual survival rates differed for smolts of different ages because of the differences in the incremental growth (yearly; Table 3 in Tautz *et al.* 1992). After the survival rates were calculated, the number of fish in a given age class required to produce a smolt of a given age was calculated (i.e. N_{0+}, N_{1+}, N_{2+}).

Next, the area required for an age specific steelhead smolt was estimated using the empirical data for size at age of juvenile steelhead collected from extensive field sampling of BC steelhead populations (Tautz *et al.* 1992). The relationship between territory size (AREA) and fork length (FLENG) was described by Grant and Kramer (1990) for stream dwelling salmonids (data from 5 species and 10 different studies):

(equation 15) $$Log(AREA) = 2.61 \times Log(FLENG) - 2.83$$

The regression was used to estimate the area required for an age 0+, 1+, 2+, 3+ and 4+ steelhead and was then used to estimate the total area required to produce different aged smolts.

5.2.0 Biological Component From Bocking and English (1992)

Yearling size ($FLENG_{1+}$) was used to calculate the mean weight of fry (SIZE) and the mean smolt age (SAGE). The main output of the biological component by Bocking and English (1992) was an estimate of steelhead carrying capacity stratified by Skeena River tributary.

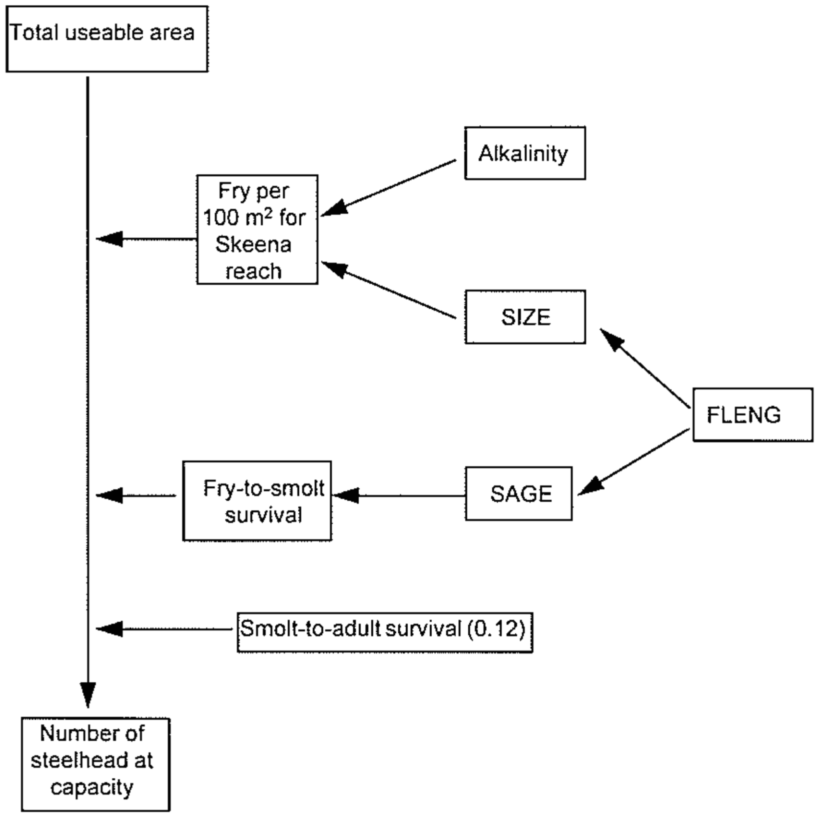
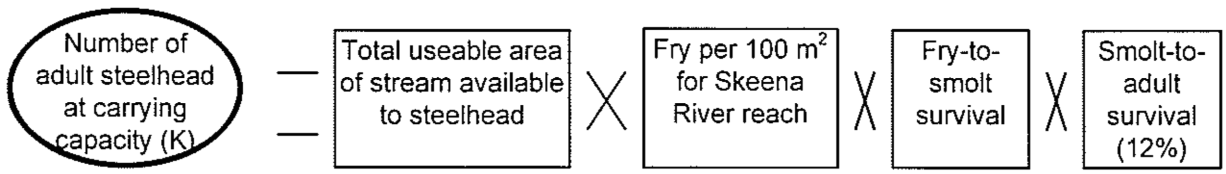


Figure 5. Flow diagram of the parameters used in the biological component from Bocking and English (1992).

Bocking and English (1992) calculated the number of fry (age 0+) per 100 m^2 at capacity maximum at the end of the growth season in addition to fry-to-smolt survival. The estimated fry density at capacity was then multiplied by the estimated fry-to-smolt survival, smolt-to-adult survival and the total useable area.



The fry per 100 m^2 at capacity for the end of the growth season was calculated using the total alkalinity of a tributary (measured at the end of the growth season or near the fall low flow stage; ALK) and the mean weight of fry (SIZE) at the end of the growth season. The relationship was based on 216 observations from resident and anadromous rainbow trout in 37 BC streams.

(equation 16) $$\text{Fry per 100 m}^2 \text{ for Skeeana River Reach} = \frac{36.3 \times \sqrt{ALK}}{SIZE}$$

The mean weight of fry (SIZE) was related to the yearling fork length (age 1+; FL_{1+}) by:

(equation 17) $$SIZE = 10(3.1 \times Log(FL_{1+}) - 5.85$$

Fry-to-smolt survival was estimated from a regression described by Symons (1979) for Atlantic Salmon:

(equation 18) $$\text{Fry-to-Smolt Survival} = \frac{10^{(-0.78-(0.38 \times SAGE))}}{0.13}$$

The denominator (0.13) implied an egg-to-fry survival of 13%. This value could be changed to 0.10, which was Tautz *et al.*'s (1992) estimated egg-to-fry survival for Keogh River winter steelhead. The mean smolt age (SAGE) was calculated from the yearling fork length (FL_{1+}) using a regression developed by Symons (1979) for Atlantic salmon.

(equation 19) $$SAGE = 10^{(3.58-(1.59 \times Log(FL_{1+}))}$$

<u>Note:</u>

Tautz *et al.* (1992) determined fry-to-smolt survival as a function of mean smolt age from Keogh River winter steelhead data, whereas Bocking and English (1992) estimated fry-to-smolt survival as a function of mean smolt age from Atlantic salmon data.

Tautz *et al.* (1992) estimated smolt-to-adult survival (14%) from Keogh River winter steelhead, whereas Bocking and English (1992) applied a 12% smolt-to-adult survival.

6.0.0 Stock-Recruitment Component

The stock-recruitment component produced estimates of steelhead population production characteristics and the number of spawners required at MSY. The steelhead life history model estimates (i.e. recruits per spawner, allowable harvest rates and Beverton-Holt's A value) were calculated using life history model parameters (Figure 6). The dashed box surrounding the SURV, ANNSURV and FLENG parameters indicates a sub-component of the life history model which was used to develop the linear regression relating mean smolt age (SAGE) and survival (SURV). The SURV linear regression model was developed by Tautz *et al.* (1992) from Keogh River winter steelhead data.

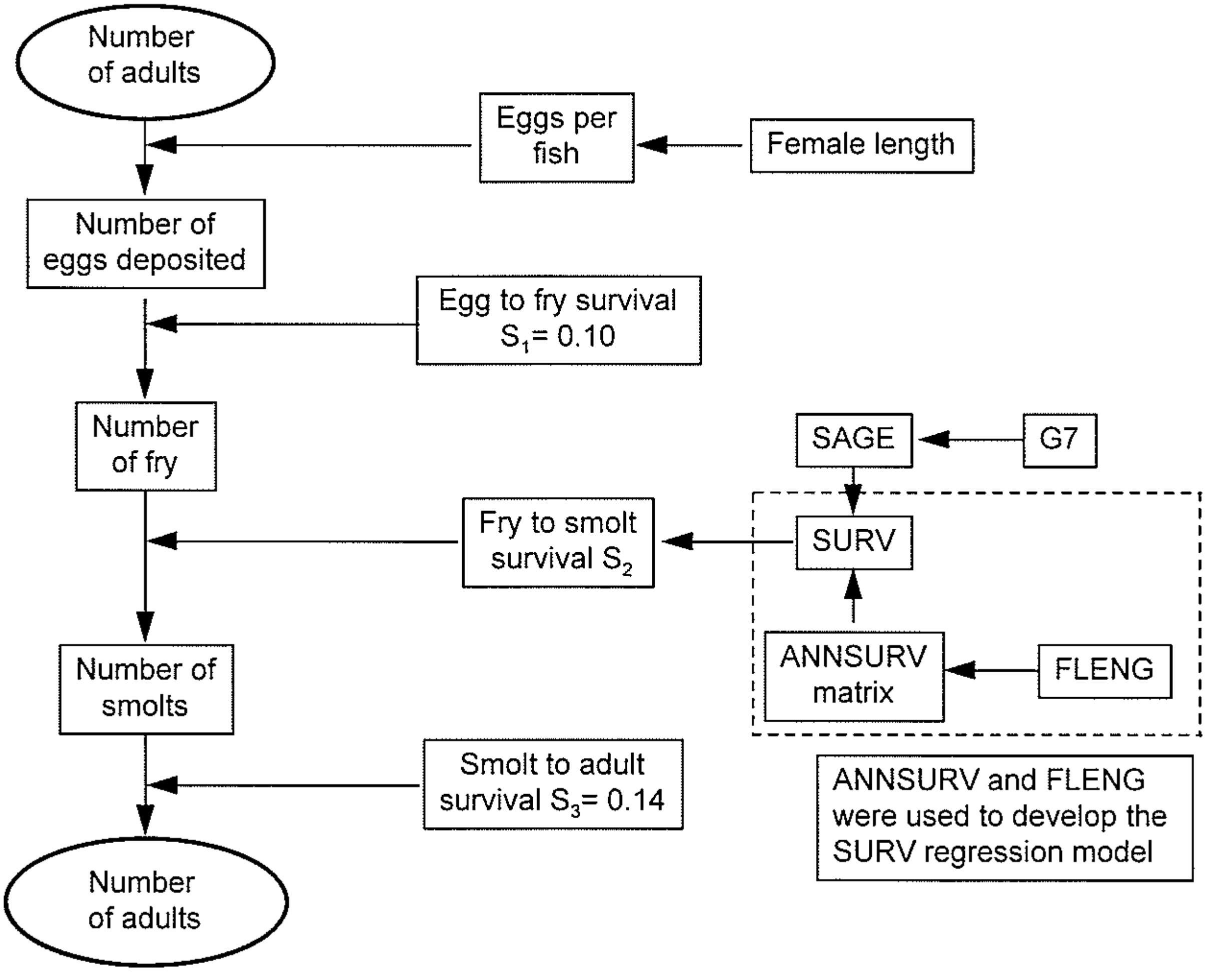


Figure 6. Flow diagram of the parameters used in the stock-recruitment component.

6.1.0 Stock-Recruitment Parameters

Skeena River summer steelhead were modelled with a semelparous life history (Figure 7). The life history of a steelhead population at MSY was modelled to predict the stock-recruitment estimates (i.e. recruits per spawner, allowable harvest rate and Beverton-Holt's A value). The parameters of the number of eggs/adult (fecundity), egg-to-fry survival and smolt-to-adult survival were assumed density independent (Tautz *et al.* 1992). However, fry-to-smolt survival was assumed density dependent and was estimated from the mean smolt age using a regression developed from Keogh River winter steelhead (Tautz *et al.* 1992).

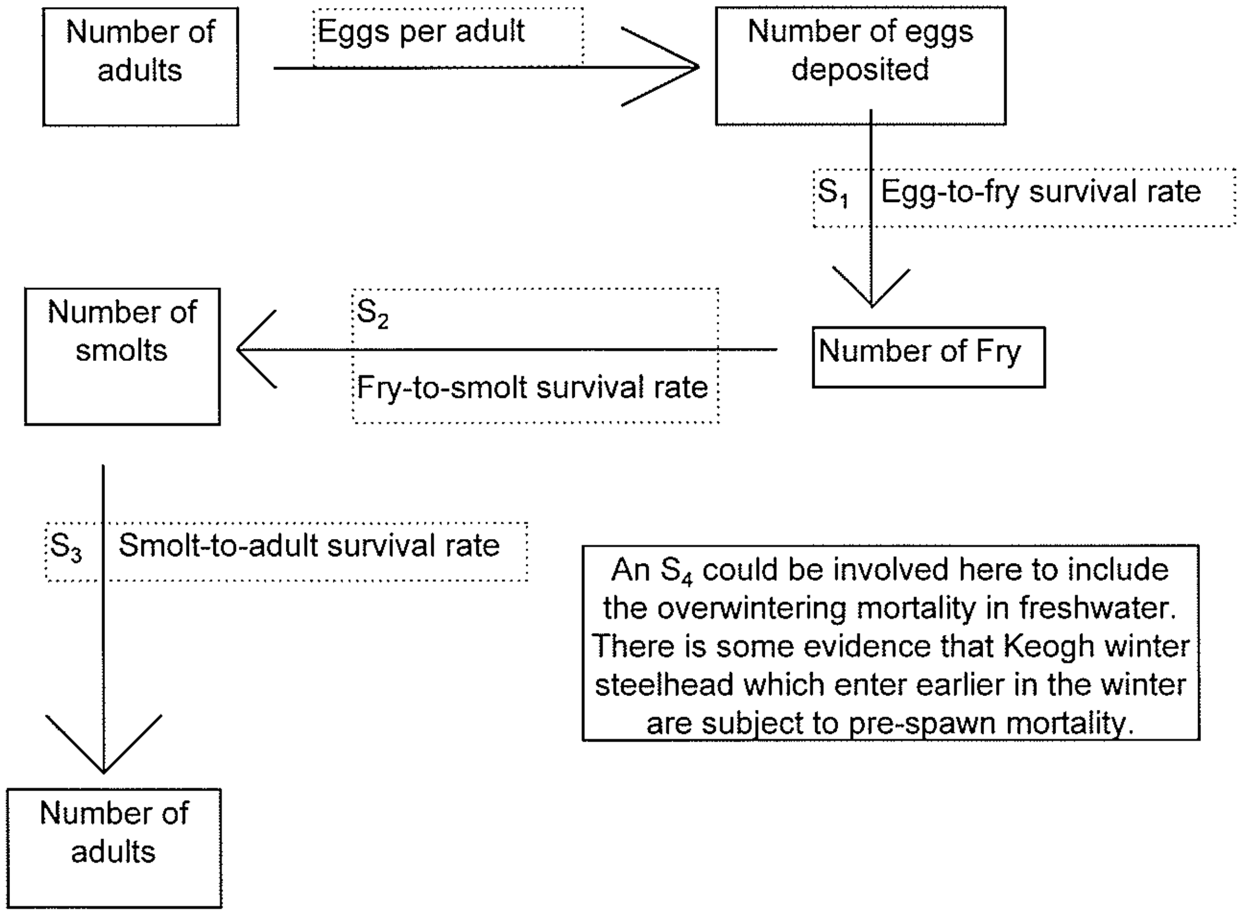


Figure 7. Semelparous steelhead life history model used to estimate steelhead productivity and allowable harvest rates by Tautz *et al.* (1992).

Fecundity was estimated using a regression developed for Skeena River summer steelhead by Wilkman and Stockerl (1981). The mean number of eggs per adult (fecundity) was determined from a linear regression model of the number of eggs per fish and length from 128 females captured in gillnets at the Skeena River mouth (Wilkman and Stockerl 1981; Figure 10 in Tautz *et al.* 1992).

(equation 20) $$\text{Mean Eggs / Adult} = 0.5 \times e^{(2.099 \times \ln(\text{Mean Length}) - 5.156)}$$

In 1991, the mean female length of 589 female steelhead (sampled from the Tyee test fishery at the Skeena River mouth) was smaller than the weighted mean female length of angler caught steelhead in the tributaries. Thus, the mean fecundity for 1991 steelhead was 82.4% of the weighted mean fecundity of angler caught females from previous studies. Tautz *et al.* (1992) applied a correction factor (0.824) to the fecundity estimate for each tributary. Female steelhead length may have been smaller in 1991 than when the tributaries were sampled, however the difference may have been a result of variation in the proportion of different ocean aged females.

Tautz *et al.* (1992) estimated egg-to-fry survival (S_1) from Keogh River winter steelhead (10%; Figure 7 in Tautz *et al.* 1992) from six data points. Seven years of data were available (1976-1982), however one year (1976) was excluded from the regression analysis because of unusually high river discharge (three times the 10 year average) during the incubation period (Tautz *et al.* 1992). Considerable variability existed between years and additional monitoring may provide a better distribution of egg-to-fry survival in the Keogh River. A wide range of egg-to-fry survival estimates exist in the literature and egg-to-fry survival was reported to be influenced by characteristics such as habitat quality (substrate composition) and environmental factors (floods and drought; Chapman 1988; Bradford 1995).

Fry-to-smolt survival (S_2) was estimated as a function of mean smolt age (from Tautz *et al.* 1992). The product of the annual survival estimates (ANNSURV) from the life history matrix (described in the biological component section from Tautz *et al.* 1992) were also used to develop the regression relating mean smolt age (SAGE) and fry-to-smolt survival (SURV):

(equation 21) $$SURV = e^{(-0.7174 \times SAGE)}$$

The product of the annual survivals (ANNSURV) for each smolt age class was the estimated fry-to-smolt survival for a smolt of a specific age. Steelhead egg-to-smolt survivals at MSY were compared to other estimates from the literature (Tautz *et al.* 1992). The steelhead regression estimates of egg-to-smolt were similar to Symons' (1979) medium survival estimates for Atlantic salmon (Figure 9 in Tautz *et al.* 1992). Tautz *et al.* (1992) also illustrated how fry-to-smolt survival at carrying capacity was lower than fry-to-smolt survival at MSY (Figure 9 in Tautz *et al.* 1992). Mean smolt age was estimated from the length of the growth season, as previously described in the biological component section (from Tautz *et al.* 1992).

Smolt-to-adult survival (S_3) was estimated from Keogh River winter steelhead (Figure 6 in Tautz *et al.* 1992). Data were available from 1977 to 1986, however 1982 was excluded from the calculation of the arithmetic and geometric mean of survival rates because it was considered an outlier (Tautz *et al.* 1992). Tautz *et al.* (1992) calculated yearly survival rates and reported the arithmetic mean (15.6%) and the geometric mean (14.4%), and used the geometric mean for productivity calculations.

6.2.0 Stock-Recruitment Estimates

The stock-recruitment relationship for Keogh River steelhead was assumed to follow the theoretical Beverton-Holt type stock-recruitment curve (Figures 4 and 5 in Tautz *et al.* 1992). The Beverton-Holt stock recruitment curve was described by Ricker (1975) as:

(equation 22)

$$R = \frac{P}{1 - A(1 - \frac{P}{P_r})}$$

where R was the abundance of returning adults (recruits), P was the abundance of Parents (spawners), A was Beverton-Holt's A value, and P_r was the abundance of Parents at replacement (capacity).

The number of recruits per spawner (RPS) at MSY was calculated from the life history model with fry-to-smolt survival estimated at MSY. The number of recruits per spawner at MSY was also a measure of the relative steelhead productivity of a Skeena River tributary population.

(equation 23)

$$RPS = 1 \times \text{Number of Eggs / Fish} \times S_1 \times S_2 \times S_3$$

The model excluded repeat spawners and therefore tributaries with a high frequency of repeat spawners may actually be more productive than estimated by the Skeena steelhead carrying capacity model (Tautz *et al.* 1992). In the absence of commercial harvest repeat spawners may have composed a higher proportion of the returning adults because repeat spawners are subject to additional harvest mortality when they emigrate from the Skeena River as kelts and then subject to harvest again when they re-enter for their second spawning migration. If the proportion of repeat spawners was historically (pre-commercial harvest) higher, mean length also may have been higher due to additional growth (approximately 3.45 cm/yr in the ocean, unpublished Sustut River steelhead data).

After determining RPS, the allowable harvest rate at MSY (μ_{msy}) was calculated as :

(equation 24) $$\mu_{msy} = \frac{(RPS-1)}{RPS}$$

and then Beverton-Holt's A value was calculated as:

(equation 25) $$A = 1-(1-\mu_{msy})^2$$

Next, the number of spawners at MSY (P_{msy}) and the number of recruits at MSY (R_{msy}) could be determined using the following equations from Ricker (1975).

(equation 26) $$P_{msy} / P_r = \frac{A-1+\sqrt{(1-A)}}{A}$$

or

(equation 27) $$P_{msy} = \frac{P_r \times (A-1+\sqrt{(1-A)})}{A}$$

and

(equation 28) $$R_{msy} / P_r = \frac{1-\sqrt{(1-A)}}{A}$$

or

(equation 29) $$R_{msy} = \frac{P_r \times (1-\sqrt{(1-A)})}{A}$$

7.0.0 Parameter Summary

The summary of the parameters and their data sources indicated a high reliance on data from Keogh River winter steelhead (Table 1). Many of the provincial biostandards and regressions were based on the Keogh River winter steelhead, since it was the best available data set. Water Survey of Canada data were also widely used in the model. The presence of a large number (52) of WSC stations in the Skeena River watershed aided the development of the model. Watersheds with fewer WSC stations may have to rely on other data or extrapolate from the nearest WSC stations. However, large assumptions are required to extrapolate data between watersheds because of differences in characteristics such as basin aspect, elevation, precipitation, snow pack levels and hydrograph characteristics. BC data and literature sources were involved with a similar number of parameters. BC data was used mainly in the habitat component, whereas literature data was involved mainly in the biological component. Tributary and watershed specific data (excluding WSC data) were used for fewer parameters than the other data sources and origins.

Table 1. Summary of the parameters used in the Skeena steelhead carrying capacity model components and their data sources.

Parameters	Data Origin/Source					
Habitat Component	Tributary Specific	Watershed Specific	Keogh River	Literature	BC Data	Other Sources
Criteria		x				
Water yield						WSC
Up/low watershed area						WSC
Mean annual discharge					x	WSC
Average width					x	
% useable width					x	
Low flow stage						WSC
Biological Component Tautz *et al.* (1992)						
Alkalinity	x					
SCROP					x	
Number of smolts/m^2			x			
G7 (water temperature)						WSC
SAGE				x (adjusted to BC)		
SPACE			x			
ANNSURV			x			
AREA				x		
FLENG			x			
Biological Component Bocking and English (1992)						
$FLENG_{1+}$	x					
SIZE					x	
Fry - $Smolt_{LGL}$				x		
$SAGE_{LGL}$				x		
Stock-Recruitment Component						
Female length	x					
Eggs/fish		x				
Egg -fry survival			x			
Fry - smolt survival			x			
SAGE				x (adjusted to BC)		
G7						WSC
SURV			x			
ANNSURV (matrix)			x			
FLENG			x			
Smolt - adult survival			x			

8.0.0 Acknowledgements

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