Reference Parameters for Headwater Stream Populations of Westslope Cutthroat Trout in Alberta

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Executive Summary

As part of the recovery planning work for westslope cutthroat trout, it is necessary to prioritize remnant populations for conservation efforts. Alberta Fish and Wildlife proposes to use its Fisheries Sustainability Index (FSI) to accomplish this task. The FSI quantifies the current status of a population in relation to a theoretical or model population that is as free as possible of anthropogenic influences.

The original intent had been to develop a theoretical reference population based on the composite data from several genetically-pure populations of westslope cutthroat trout. Aged fish were needed for critical parts of the life-history characterization. From a large file of nearly 60,000 records I produced a file of about 2500 records holding only aged fish without regard to genetic purity or habitat type. I then compared all of these elected populations to mapped locations coded by genetic purity to identify populations or sampling units with age data that were genetically pure, of which there proved to be only six.

I used the aggregated data for the six available genetically-pure populations with age data to attempt to prepare length-at-age curves for growth analysis. These demonstrated a common problem when data from stocks with widely differing growth rates or habitat conditions are aggregated in this way. Slower-growing trout commonly live longer, so the apparent growth curve turns downward at higher ages. This is theoretically not possible, except in the case of extreme starvation. It also would invalidate von Bertalanffy growth calculations, because the procedure assumes that growth in fish tends toward a length asymptote, which is true for real populations.

For these reasons the attempt to construct a composite population had to be abandoned. Instead, I selected one population with the most complete dataset: the 1978 population in Silvester Creek, Elbow drainage. I calculated reference parameters for this actual resident population of genetically-pure westslope cutthroat trout occupying a small headwater stream within the Alberta native range. These are to serve as a model for other similar native headwater stream-resident populations, the life-history type that is the most common type remaining, yet is at the greatest risk. I then compared these parameters in various ways to existing data for similar populations to determine the extent to which they were representative.

This report presents a large number of reference parameters for age and growth, sexual maturity and fecundity, population mortality and population size that can be used as standards of comparison against which other small, remnant headwater stocks of native cutthroat trout can be evaluated. It complements existing and ongoing genetic characterizations that are required for characterizing remnant stocks, and should be used in close conjunction with them.

The reference parameters developed here will be useful in planning and managing conservation efforts for the few native westslope cutthroat trout populations remaining in Alberta. They can facilitate comparisons among the remnant stocks to identify those most

able to sustain themselves if protected, and they will be helpful in designing secure archival populations.

The major problem for conserving this threatened species remains, however. Most of the last remaining native cutthroat stocks are being invaded by an overwhelming wave of non-native rainbow trout and rainbow-cutthroat hybrids. Unless they are blocked or removed, these invaders will continue to destroy native cutthroat stocks by introgressive hybridization as they move upstream into the last isolated headwater refuges of the native cutthroats. The invasion is being exacerbated by ongoing global warming, which favours rainbow and hybrid trout moving ever higher in the stream networks. These are the key problems that remain to be addressed. The reference parameters can only assist in making what ultimately are going to be hard decisions to block or remove some valuable fish stocks.

Contents

Introduction

The westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, is native to southwestern Alberta. Recent status reports (Alberta Sustainable Resource Development and Alberta Conservation Association 2006, Cleator *et al.* 2009, Mayhood and Taylor 2011, COSEWIC. 2006) have shown the subspecies to be much reduced in abundance and distribution while facing serious threats to its conservation status. The Committee on the Status of Endangered Species in Canada (COSEWIC) assessed the Alberta population of westslope cutthroat trout as Threatened in 2006 (COSEWIC 2006), a Recovery Potential Assessment has been prepared (Department of Fisheries and Oceans (DFO) 2009), and it is now being considered for listing under Canada's Species At Risk Act (SARA). The Government of Alberta has designated westslope cutthroat trout as Threatened under the provincial Wildlife Act. Alberta Fish and Wildlife has prepared a recovery plan for the subspecies.

As part of the recovery planning work for westslope cutthroat trout, it is necessary to prioritize remnant populations for conservation efforts. Alberta Fish and Wildlife proposes to use its Fisheries Sustainability Index (FSI) to accomplish this task. The FSI, modeled on a similar approach used elsewhere (Williams *et al.* 2007), quantifies the current status of a population in relation to a theoretical or model population that is as free as possible of anthropogenic influences. So far, population reference parameters have been prepared for walleye (Sullivan 2009) and are available in draft form for Arctic grayling (Coombs and Sullivan 2010).

This report presents reference parameters for an actual resident population of genetically-pure westslope cutthroat trout occupying a small headwater stream (stream order approximately 1 through 4 as determined from 1:50,000 National Topographic Service maps) within the Alberta native range to serve as a model for other similar headwater stream-resident populations. This is the life-history type at greatest immediate risk. Separate population reference parameters will need to be developed for, at a minimum, genetically-pure migratory (fluvial and adfluvial) and lake-resident life-history types at some point if these life-history forms are to be restored and managed effectively in the future.

Analytical Methods

General Procedure

The original intent was to develop a theoretical reference population based on the composite data from several genetically-pure populations of westslope cutthroat trout. I needed aged fish for critical parts of the life-history characterization. Accordingly, I sorted through a large file (nearly 60,000 records) of all cutthroat trout data held in the Fish and Wildlife Management Information System (FWMIS). From this I eventually produced a file of about 2500 records holding only aged fish from numerous populations without regard to genetic purity or habitat type.

Recently-produced maps provided by J. Earle (personal communication) showing the distribution of populations categorized by degree of genetic purity were initially consulted to match aged populations to genetically-pure locations. I abandoned this approach because the "pure" category on these maps contained populations that had either extensive low-level hybridization, or had small numbers of hybrid individuals. The reason why this had to be done is described elsewhere in this report (***Choice of Standard Populations***). Instead, I plotted all genetically-sampled populations on National Topographic Series 1:50,000-scale maps, coding them as Pure, Nearly Pure and Introgressed according to the criteria in Table 1. I then compared all of the populations with age data to the mapped locations coded by genetic purity to identify those populations or sampling units with age data that were genetically pure. There were only six of these: Ford, upper Lynx (Carbondale drainage), Silvester, "Margaret", "Goat tributary" (Carbondale drainage), and Cougar Creek between the first and second falls. At least two of these (Cougar above the first falls; Ford Creek above the falls, on top of a native stock) are known to be introduced from Job Lake/Marvel Lake/Spray Lakes stock (Stelfox, personal communication). Thus not all of these are native to the waters in which they are now found, despite being genetically pure.

For the 1978 Silvester Creek population, the one that I eventually chose as the reference population, I compared the FWMIS data cell by cell to the original datasheets (Tripp *et al.* 1979a). There had been some transcription errors, and these were corrected in the spreadsheet file, with notes in each altered cell as to the changes made in the FWMIS file. The corrected file was used in all subsequent analyses. There were also some small differences between the 1978 main report (Tripp *et al.* 1979b) and the data in the Appendix volume (Tripp *et al.* 1979a). This explains some slight differences in the findings in the present study as compared to the earlier one.

Table 1. Criteria for classifying genetic purity used in this study.

Purity criterion this study	Fish & Wildlife SARCEP Hybridization Metric (Coombs, pers. comm.)	
Pure	≥ 0.99 mean purity	no hybrids, no risk of hybridizing fish entering population
	≥ 0.99 mean purity	no hybrids known, but proximity to hybridizing fish causes concern
Nearly Pure	≥ 0.99 mean purity	hybrids rare but have been detected or are strongly suspected
Introgressed	≥ 0.95 mean purity	some hybrids in most samples
	≤ 0.95 mean purity	mostly hybrids

Statistical analyses were run in Numbers '09 V. 2.1 (apple.com), SYSTAT 5.2.1 (Wilkinson 1992). The von Bertalanffy calculations were done in Excel 2010 with the FAMS 1.0 macro add-ins (Slipke and Maceina 2010). Mortality rates were calculated in FAMS 1.0, spreadsheets, and on an HP41C scientific calculator (Mayhood, 2012b, in preparation 1). Most regressions, as well as prediction standard errors and confidence limits for ordinary least squares (OLS) and geometric mean (GM) regressions, were calculated in a purpose-built Numbers spreadsheet model (Mayhood 2012a) using the calculation methods of Ricker (1973, 1984) and Sokal and Rohlf (1969). Additional details of various methods are explained in the individual reference parameter descriptions.

Choice of Standard Population

The Silvester Creek westslope cutthroat stock was selected as the best available reference population for genetically-pure, headwater stream-resident stocks. Here are some of the major considerations that led me to this decision.

Initial attempts to build a composite reference population were thwarted by the fact that such a population proved to be too unrealistic (Appendix). It became clear that a single reference population would be needed for native cutthroat trout.

It is important that the reference population be genetically-pure, because that is the type of population that is threatened. Although it might be tempting to include "almost pure" populations with apparently low levels of introgression, such as those with high mean WCTR purity index, or those with few individual hybrids, it is unwise to do so for the following reasons (Mayhood, in preparation 2).

1. Populations showing *any* indication of introgression in the type of genetic surveys available to us probably have more widespread introgression than is indicated in the

sample (Allendorf *et al.* 2001). This is because the surveys sample only a very small part of the genome. For example, in a randomly mating hybrid swarm with as little as 1% admixture from rainbow trout, *all* individuals will be hybrids and have, on average, 1% of their alleles from the rainbow genome (Allendorf et al. 2001:621). Such a population will have over 83% of its *individuals* appearing to be pure native at all 9 diagnostic loci,[1] which is the number of diagnostic markers used in our survey (Taylor and Gow 2007, 2008). Using 9 diagnostic loci, this means that we can expect to find, on average, 25 apparently-pure specimens in a sample of 30, in a population in which *all* fish are hybrids with 1% admixture. Put another way, using 9 diagnostic markers, there is a little more than a 16% chance of detecting that such a population is hybridized in a random sample of 30 fish.

2. The occurrence of low numbers of individual fish with non-native markers may be evidence of an incipient invasion of a non-native genome into an otherwise pure population.
3. Different methods for managing such populations are appropriate, and may be able to recover the pure native population from the lightly-hybridized stocks.

In the first case, introgressed populations should not be used in certain kinds of recovery programs (such as reintroductions or supplementary stocking), so it is important to identify the introgressed populations and treat them separately. More to the point for present purposes, introgressed fish have different physiological (Rasmussen *et al.* 2012), reproductive (Muhlfeld *et al.* 2009b), fitness (Muhlfeld *et al.* 2009a) and behavioural (Hitt *et al.* 2003, Muhlfeld *et al.* 2009b) properties, as well as different habitat tolerances (Muhlfeld *et al.* 2009c, Rasmussen *et al.* 2012). We do not know fully at this point how much introgression it takes to produce an effect. Fitness of westslope cutthroat-rainbow hybrids, however, is reduced by 50% at an admixture of 20%(Muhlfeld *et al.* 2009a). Rasmussen et al. (2012) point out that physiological effects appear to be strongly influenced by the degree of introgression of the rainbow trout genome into that of cutthroat trout. Using introgressed stocks as standards makes it more difficult, and may even preclude, detecting introgression effects. It is comparable to using a different species as a standard.

In the second case above, a rapid response is required to protect the pure population: the signal should not be ignored. An example of where this may be going on is shown by the data for Marvel Lake, which presently has a small proportion of cutthroats with rainbow markers. This is a change from previous results; may reflect a recent, perhaps ongoing, invasion from a

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[1] The calculations follow Allendorf et al. (2001:621): 98.01% of all randomly-mating individuals will appear to be native at any one diagnostic locus (0.99 x 0.99 = 0.9801). The probability of any one fish having independently assorting, native-type markers at 9 diagnostic loci is the product of their individual probabilities of occurring independently, thus 83.45% will appear to be pure native fish at 9 loci ($0.9801^9 = 0.8345$). For comparison, using 6 diagnostic loci (Janowicz 2010), 88.6% will appear to be pure type, and using only 4 diagnostic loci (Rasmussen *et al*. 2010), over 92% will appear to be pure at all diagnostic loci, *even though all are actually hybrids*. This is why large numbers of diagnostic loci must be examined to detect hybridization in *individual* fish with a high degree of probability, as well as to detect low levels of hybridization in a population.

compromised population upstream (Gloria Lake); and should be investigated as soon as possible (Mayhood and Taylor 2011).

In the third case, ignoring evidence of light hybridization could forego an opportunity to restore the pure native genome. Recent developments in genetic methods promise the possibility of very detailed analysis of the individual genome with up to thousands of markers (Allendorf *et al.* 2010, Hohenlohe *et al.* 2011). These developments offer, for the first time, the realistic possibility that lightly-hybridized populations could be purified, or at least made more nearly pure, by identifying and selecting out all of those individuals showing the least degree of introgression. Attempts to do this based on analyses of only a few markers from survey-grade data such as that presently available to us for Alberta populations (Taylor and Gow 2007, 2008; Mayhood & Taylor 2011) were doomed to failure because the survey data cannot accurately identify the degree of introgression in individual fish, as noted above. The new genomic approach is about to be used in the Hidden Lake-Corral Creek project in Banff National Park (Humphries and Dickinson 2011). That work can serve as a pilot study with a view to more widespread use in Alberta.

Finally, it may well prove to be true that low levels of introgression are of no consequence (or are even beneficial) to the fitness of the invaded population. If so, this should be determined by a separate more detailed study. If the population proves to be minimally influenced by the invading genome, and if the situation is stable, then — and only then — it may be appropriate to consider the population as effectively pure and manage it accordingly, or even use it as a standard.

In short, we need (a) standard population(s) that are 100% pure so that we can use them for comparison to introgressed populations to detect population-level introgression effects: it is our gold-standard control. Using even a lightly-introgressed population as a standard makes it that much more difficult to detect population-level introgression effects if there are any.

The Silvester Creek population shows no evidence of genetic introgression with any other *Oncorhynchus* species, as determined by analyses of unique markers at 9 loci on a full sample of 30 individuals (Mayhood and Taylor 2011, Taylor and Gow 2008). Similarly, no hybrids were found in an additional 23-fish sample using 6 markers (Janowicz 2010). The stock is isolated above a barrier waterfall, so cannot have been invaded by natural means by non-native alleles since the population was established. Stocked rainbow (*Oncorhynchus mykiss*) fingerlings in the 1930s (Department of Fisheries 1934, 1936) evidently did not survive based on the genetic evidence. Whether the population is native to the creek is moot at this point. If introduced[2], it has since become naturalized.

The Silvester Creek stock is one of only six known genetically-pure Alberta populations with good-quality (i.e., otolith-based) age data, and the only one of those with a reasonably large

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[2] fingerling cutthroats of unknown stock were introduced in 1934-1935 from Rainbow Ranch, Troy, MT (Department of Fisheries 1935)

sample size. Age data is a critical requirement for determining life-history parameters. It also is the only aged sample of pure fish with adequate fecundity data. The population is unlikely to be fished heavily: even the largest fish are less than about 240 mm fork length, and few exceed 200 mm (Dormer and Paul 2006, Tripp *et al.* 1979b), making them not particularly attractive for angling. At the time that the reference data were gathered, the population density was very high, the highest by catch per effort (CPE) of any trout population in the region (Tripp *et al.* 1979b).

The principal negative considerations affecting the use of this population as a reference is the habitat damage (siltation, eroded streambanks) from cattle grazing and off-road vehicle use at the time of data collection, and the lack of a population estimate in the dataset (Tripp *et al.* 1979b). The habitat damage could conceivably have impacted recruitment, growth and mortality at that time. The lack of a good-quality population estimate is somewhat ameliorated by catch-per-effort (CPE) data and three estimates of electrofishing efficiency made in nearby creeks during the study, which permits rough estimates of population size to be made. Finally, there is substantial new data available for the population since the 1978 sampling that enables some tracking of changes to the population, including the cumulative effects of ongoing habitat damage (Dormer and Paul 2006, Paul and Dormer 2005, Paul *et al.*, 2008, Erdle 2011).

Reference Parameters

Age and Growth

The 1978 age determinations were made from otoliths using standard methods to identify annuli (Tripp *et al.* 1979b25), and are believed to be reliable. Cutthroats in this population reached a maximum observed age of 6. This is likely to underestimate the true maximum age because the oldest fish in any population are rare: additional sampling is likely to reveal some fish that are older than the maximum found in the smaller sample. Another estimate of maximum age can be made from a catch-curve regression (Slipke and Maceina 2010). I did this (Mayhood 2012b in preparation 1) and obtained a maximum age estimate of 9. For reasons discussed fully in that document 9 years is likely to be an overestimate, and the true maximum age must fall between 6 and 9 years.

Growth can be measured by following individual year-class cohorts throughout their lives. Those data often are unavailable, as is the case for the 1978 Silvester Creek population, so growth must be estimated from a composite of year-classes captured at one time (apparent growth), as is done here. The distinction is important to keep in mind, because in this analysis each age-group is a different cohort, and different cohorts can have somewhat different growth characteristics. The approach used here implicitly assumes that age cohorts do not differ in growth rate.

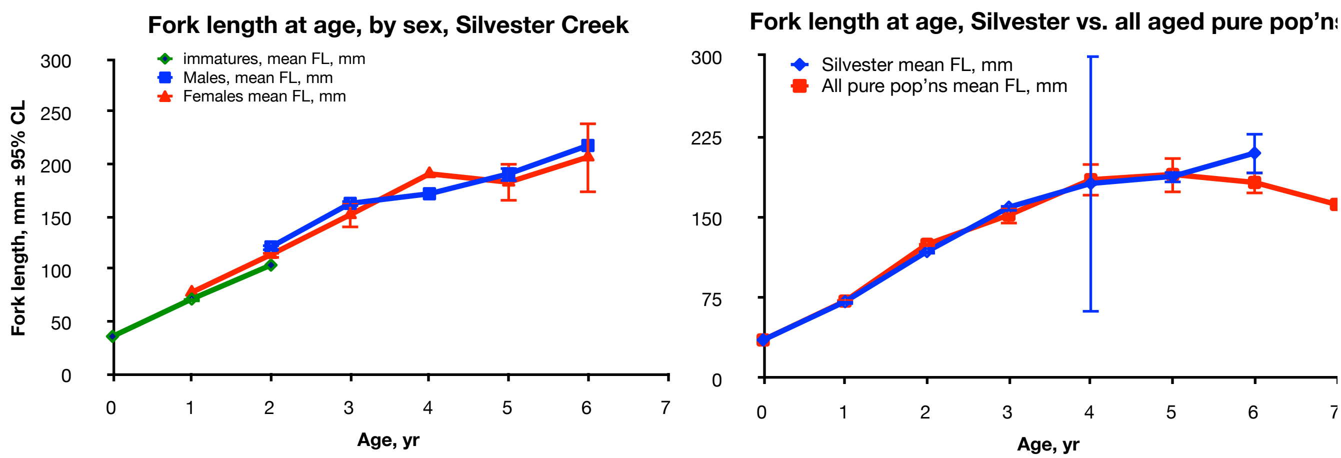
Fork-length-at-age is summarized in Table 2. Male cutthroats were identifiable at age 2 and as small as 107 mm fork length, reaching an observed maximum of 218 mm and age 6. Females were identified as early as age 1 and fork length of 78 mm, reaching a maximum of 222 mm and age 6.

In many populations, males and females grow at significantly different rates. I examined this possibility in Figure 1 (left panel). Males and female fork lengths at the same ages do not differ significantly. Although immatures unidentified as to sex are smaller than identified males and females at the same age, the differences are quite small and it is legitimate to combine data from both sexes. For both sexes combined, the apparent growth curve well represents the apparent growth curve for all 6 pure populations combined for which age data were available, up to and including age 5 (Figure 1, right panel). Growth curves for Silvester Creek (Figures 2 and 3) therefore reasonably represent these 6 pure stocks over that range, although they will be too high at ages 6 and 7 for at least some of the non-Silvester stocks. Growth is well described by the von Bertalanffy function (Figure 3).

Table 2. Fork-length-at-age for the 1978 Silvester Creek cutthroat trout population.

Age	Immatures, sex not identifiable			Males			Females		
	mean FL, mm	range	N	mean FL, mm	range	N	mean FL, mm	range	N
0	36.0	—	1						
1	71.6	60 — 78	28				78.0	—	1
2	104.0	—	1	121.3	107 — 145	25	114.0	97 — 125	15
3				162.8	155 — 174	11	152.0	142 — 169	5
4				172.0	—	1	191.0	—	1
5				191.0	183 — 205	7	183.0	168 — 197	4
6				218.0	—	1	207.0	194 — 222	3

Figure 1. Mean length-at-age ± 95% confidence limits for the 1978 genetically-pure Silvester Creek westslope cutthroat trout population, by sex (left). Mean length-at-age for the 1978 Silvester Creek population vs. all 6 pure populations for which data are available (right). The wide confidence limits for age 4 are due to only 2 fish of that age-class being captured, which is interpreted here as a year-class failure.



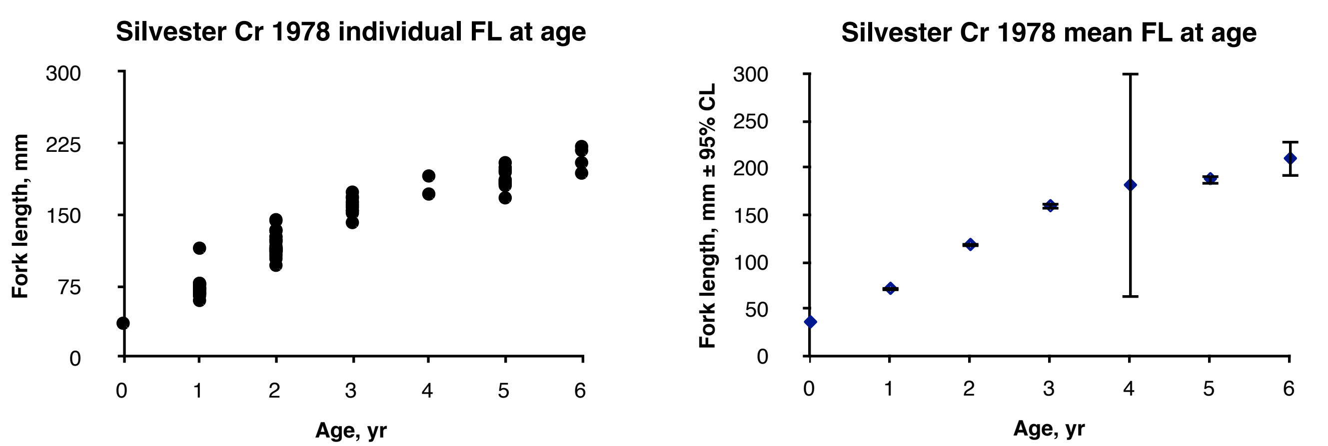


Figure 2. Individual and mean fork-length-at-age for the 1978 Silvester Creek westslope cutthroat trout population (left). N = 105. Only 2 age 4 fish were identified, suggesting a recruitment failure that year. This also accounts for the unusually wide confidence limits for mean length in that age group (right).

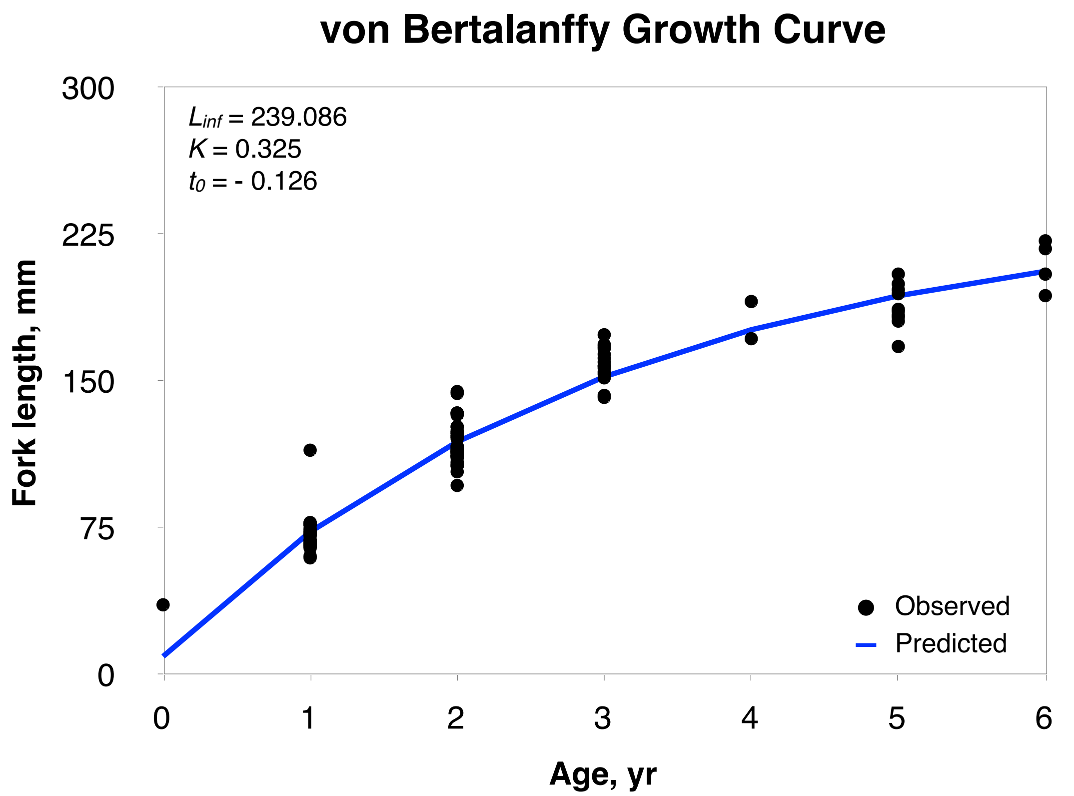
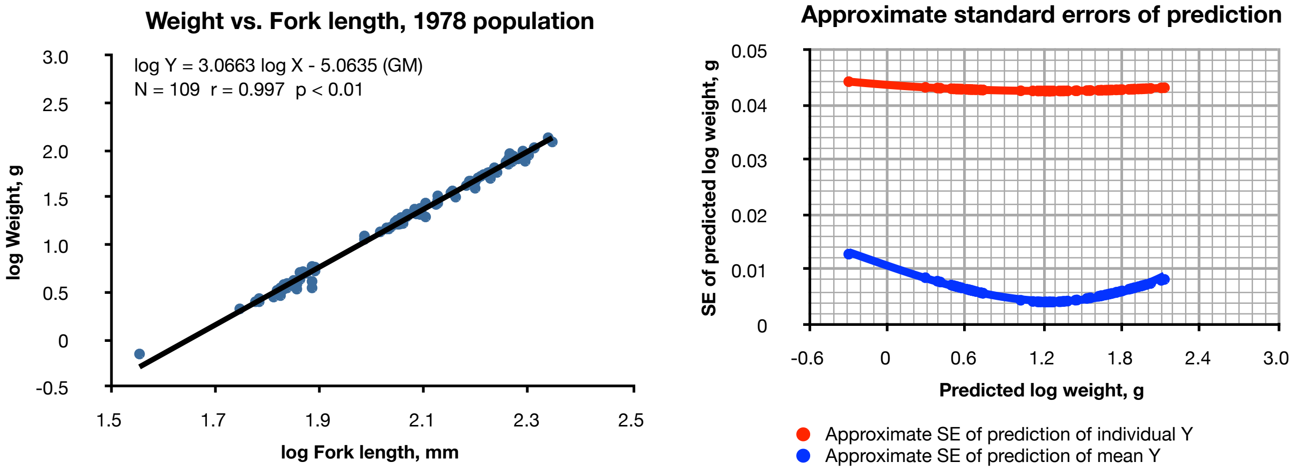


Figure 3. von Bertalanffy apparent growth curve for the 1978 Silvester Creek population, $r^2 = 0.94$.

The length - weight regression of a population is a better measure of condition than the condition factor, and can be used to estimate weight if length is known. It is presented in Figure 4.

Figure 4. Weight-length GM regression and approximate prediction standard errors for the 1978 Silvester Creek population.



Sexual Maturity & Fecundity

Most (60%) females in this populations are sexually mature by age 3, and all are mature by age 4 (Table 3). Many males mature as early as age 2 (40%), and all are mature at age 3. Of all trout identifiable as to sex, the sex ratio is 1.56:1 M:F. Notably, once all fish are fully mature at age 4 and above, the sex ratio is nearly equal at 1.13:1 M:F. This is of interest because immature fish, especially the youngest, can be easily misidentified as to sex, with many of the youngest being erroneously misidentified as male. Nevertheless, at any one time there are many more mature males to mature females (3.17:1), at least in part because males mature faster than females in this population.

Table 3. Maturation schedule for pure westslope cutthroat trout, Silvester Creek 1978. Data from Tripp *et al.* (1979a).

Age	Unidentified sex		Male				Female				Total N	Prop'n male, by age
	Immature		Immature		Mature		Immature		Mature			
	N	%	N	%	N	%	N	%	N	%		
0	1	100.0			0	0.0			0	0.0	1	
1	28	93.3	1	100.0	0	0.0	1	100.0	0	0.0	30	0.50
2	1	2.4	10	40.0	15	60.0	15	100.0	0	0.0	41	0.63
3					11	100.0	2	40.0	3	60.0	16	0.69
4					1	100.0			1	100.0	2	0.50
5					7	100.0			4	100.0	11	0.64
6					1	100.0			3	100.0	4	0.25
Total	**30**		**11**		**35**		**18**		**11**		**105**	**0.61**

Fecundity relationships in this sample represent fall (non-spawning) conditions in 1978, when the sample was collected (Tripp *et al.* 1979b). Fecundity was significantly correlated with body weight (Figure 5), and is best predicted by the GM regression. There was also a significant relationship between egg number and fork length (Figure 6), so the GM regression provides an alternative method of estimating fecundity. Fecundity was not related to age in these data (Figure 7).

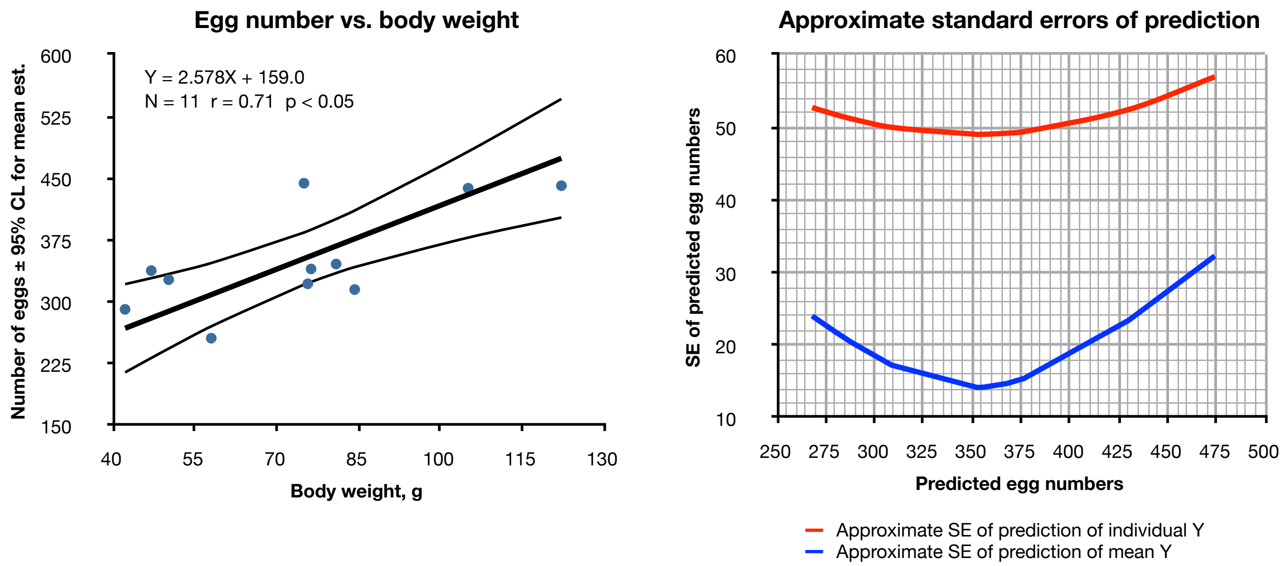


Figure 5. Correlation and functional GM regression of egg number on body weight, 1978 Silvester Creek population.

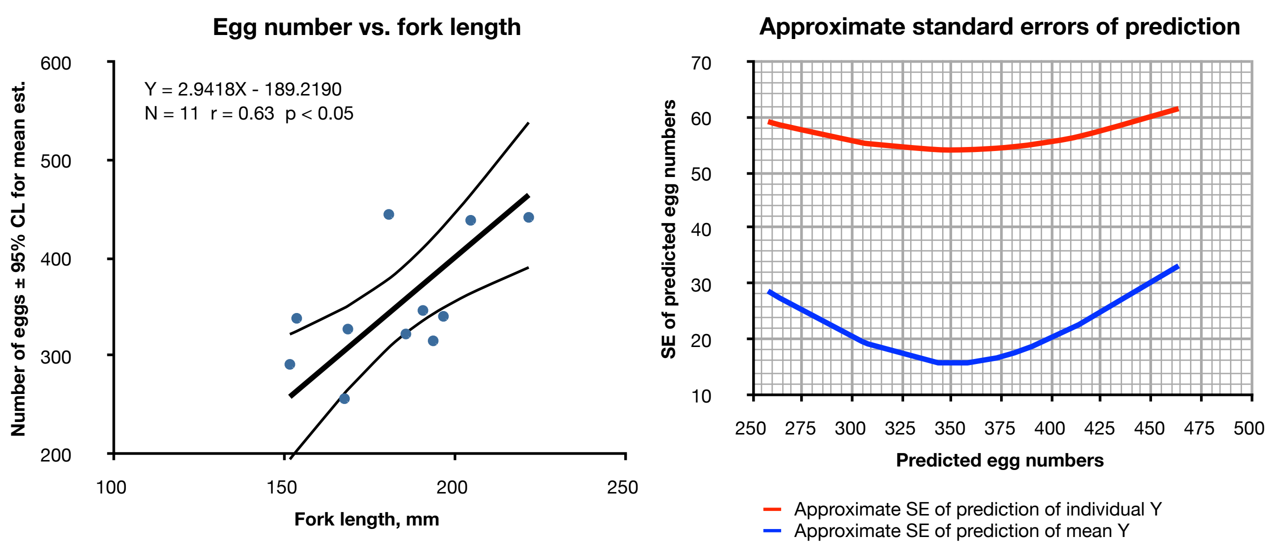


Figure 6. Correlation and functional GM regression of egg number on fork length, 1978 Silvester Creek population.

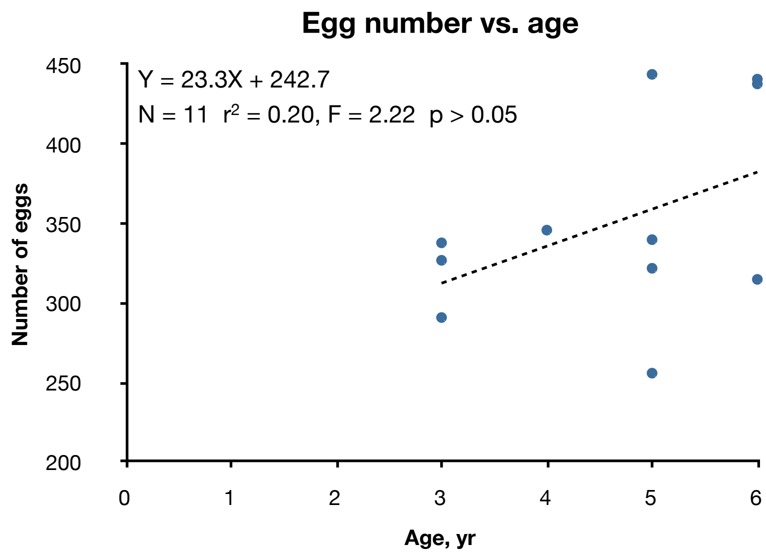


Figure 7. OLS regression of number of eggs on age, 1978 Silvester Cr population.

These estimation methods presume that the sex of the fish can be determined, which is not usually possible without sacrificing the fish [except during spawning; also see Kano (2005)]. Reasonable estimates for the population can be made by making use of the sex ratio of fully mature fish together with the above regression equations.

Ovary weight was correlated with egg numbers (Figure 8). The functional GM regression can be used for prediction if ovary weight can be obtained, although the confidence limits will be quite wide. For example, ovary weight is positively correlated with both weight and length (Figures 9 and 10), as well as age (Figure 11), so can be estimated from the relevant GM regressions for weight and length, and the OLS regression for age, if age can be obtained.

Larger egg diameter can be associated with greater survival in salmonids. Larger females on the whole produced larger eggs (Figures 12 and 13), although the correlation with length was barely significant at $p = 0.05$.

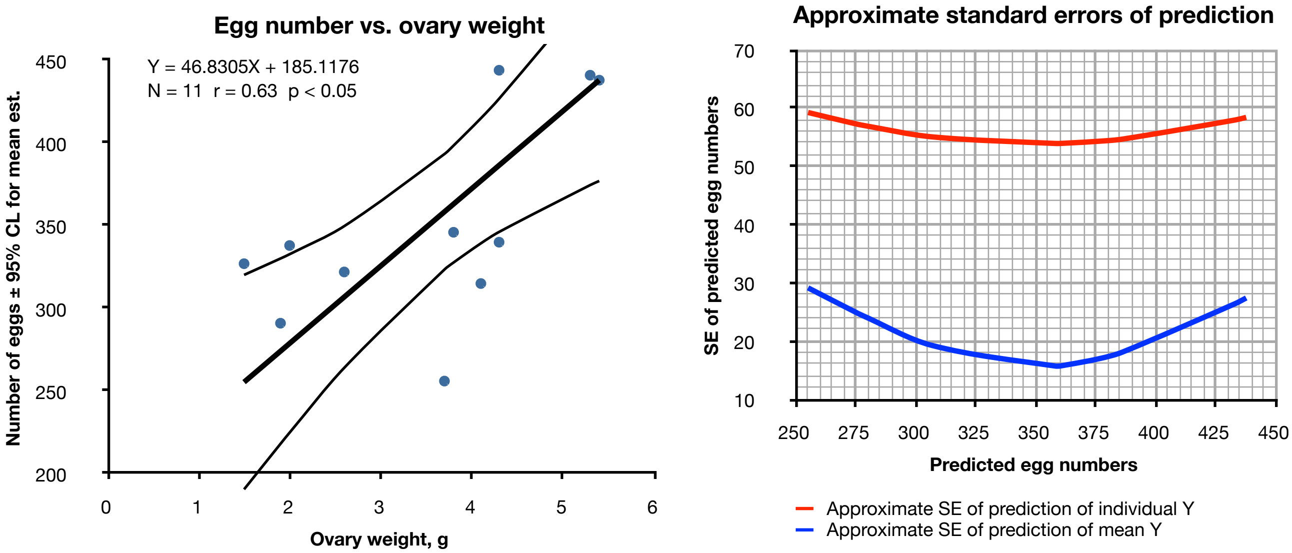


Figure 8. Correlation and functional GM regression of egg number on ovary weight, 1978 Silvester Creek population.

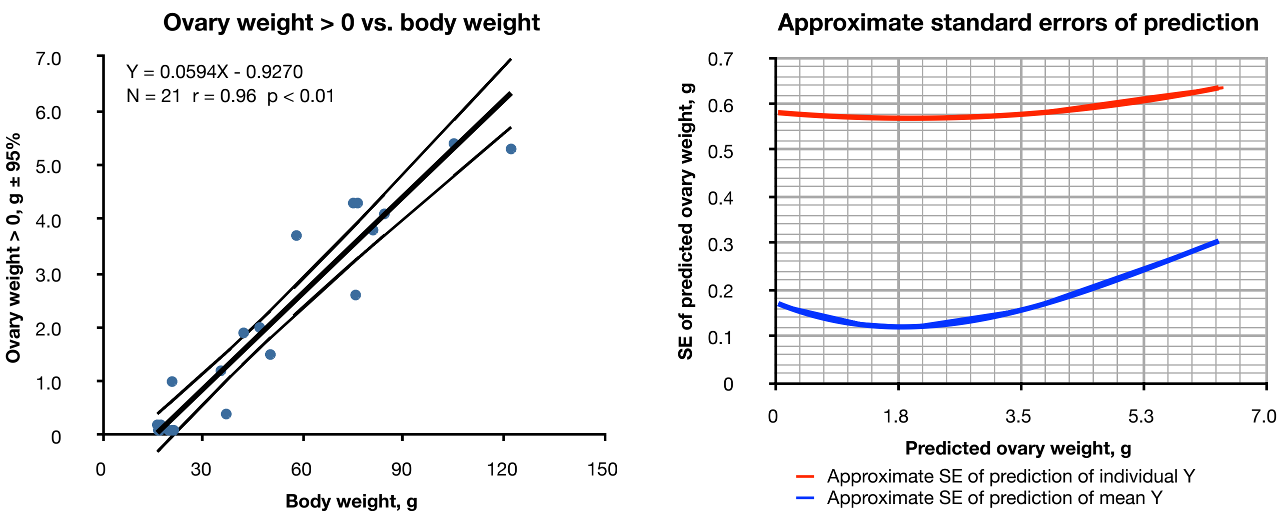


Figure 9. Correlation and functional GM regression of ovary weight > 0 g on body weight, 1978 Silvester Creek population.

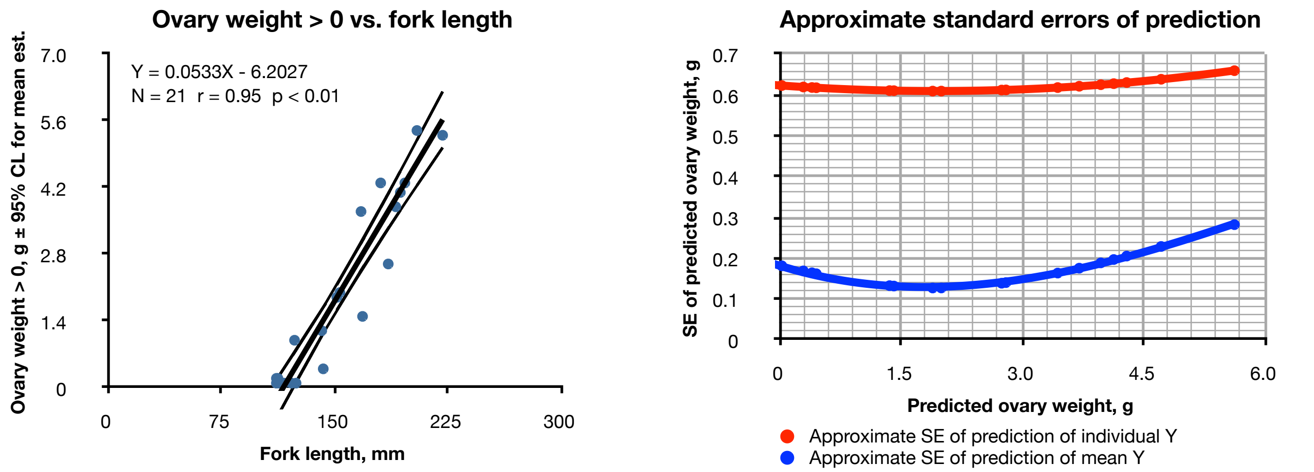


Figure 10. Correlation and functional GM regression of ovary weight > 0 g on fork length, 1978 Silvester Creek population.

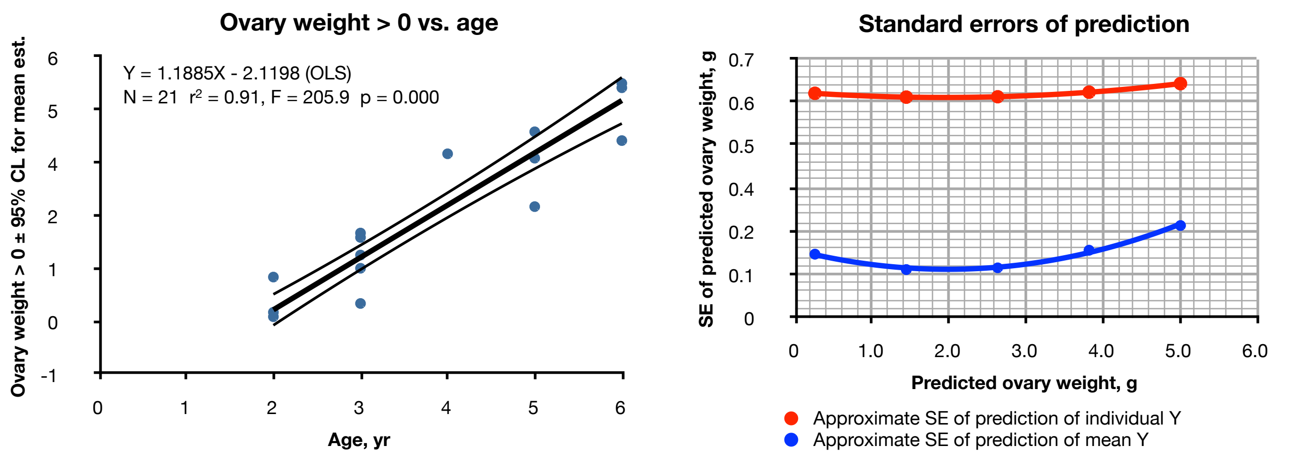


Figure 11. OLS regression of ovary weight > 0 g on age, 1978 Silvester Creek population.

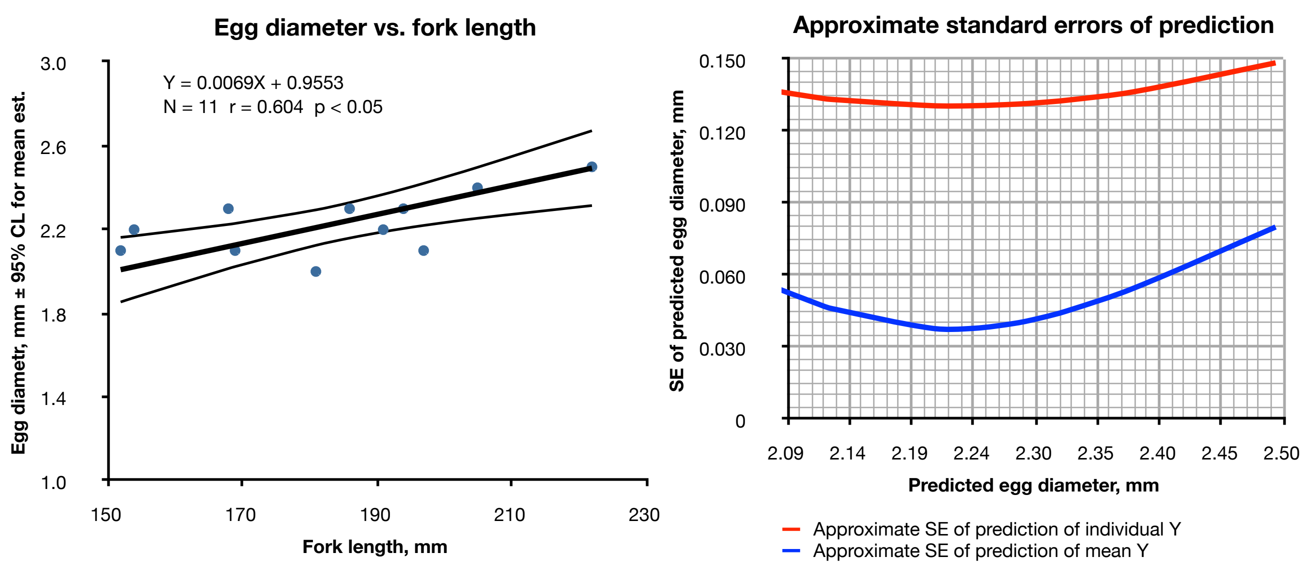


Figure 12. Correlation and functional GM regression of egg diameter on fork length, 1978 Silvester Creek population. The correlation is just significant at p = 0.05.

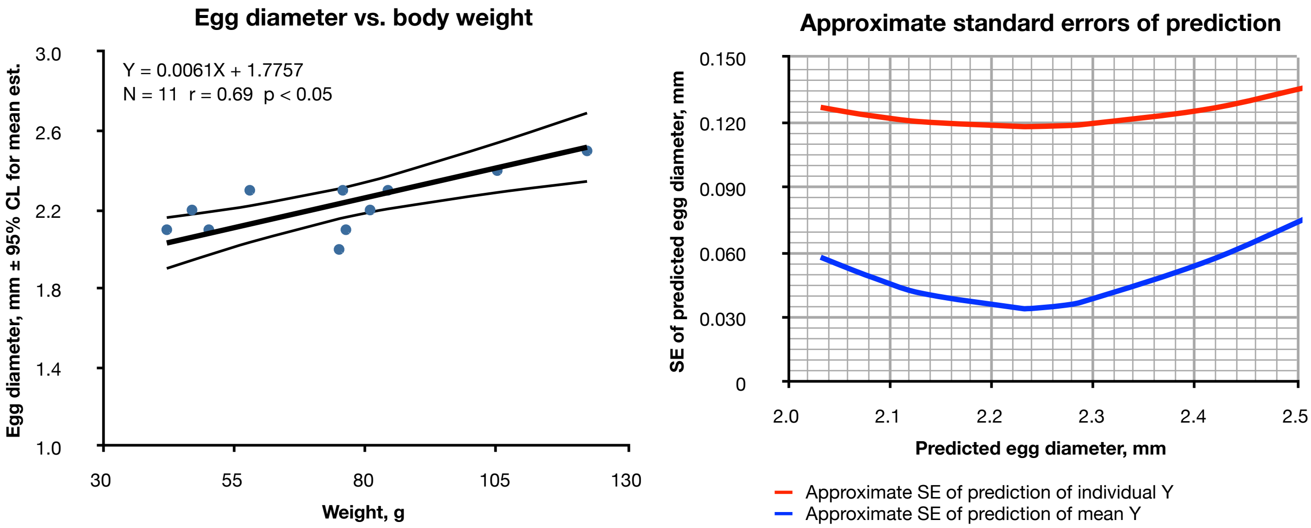


Figure 13. Correlation and functional GM regression of egg diameter on body weight, 1978 Silvester Creek population.

Mortality Rates

Changes in abundance of fish populations are defined by the balance among reproduction, immigration, emigration and mortality (Beverton and Holt 1957). Modeling populations requires estimates of all four parameters. I have addressed reference parameters for reproduction elsewhere in this report. Immigration and emigration rates are specific to each population. In Silvester Creek, immigration is 0 because impassable falls block movements from the Elbow River. Emigration rates in the Silvester Creek population are unknown, but fish undoubtedly pass over the falls without any possibility of return. Again, these would need to be estimated with additional field work. Here I attempt to provide reference data for the final main parameter, mortality.

There are actually several kinds of mortality rate, any of which may be important depending on the purpose of the modeling project, but the two large classes are natural mortality and total mortality. Natural mortality is usually defined as the rate of death due to all causes except fishing (Ricker 1975). It is often treated as intrinsic to a species and stock, or to life-history type within species, varying with basic life-history parameters but within rather narrow limits. If so, it is realistic to use it as a reference parameter. Total mortality is that due all causes combined; i.e., natural mortality plus fishing mortality. Fishing mortality can be divided up among various types of "fishing," which may be defined to include other causes of death if that is important to the question. Total mortality varies widely among populations due to differences in exploitation rates. Subtracting instantaneous rates of natural mortality from instantaneous total mortality provides an estimate of fishing mortality.

In an unexploited population, total mortality equals natural mortality so that methods for the former can be used to estimate the latter. It seems likely that angling mortality is negligible in

Silvester Creek because the fish are very small, and the watershed is heavily used by off-road vehicles, creating highly turbid flows much of the time. Both features would dissuade anglers from using this stream to any great extent. If the stock is significantly exploited, however, it should show up in a difference between natural and total mortality estimates.

I used a total of 16 methods for estimating mortality, both total and natural, for the 1978 cutthroat population in this study. Estimated natural mortality rates ranged widely (Table 4), and were widely overlapped by the somewhat narrower estimates for total mortality. With such a wide range of credible estimates, there is no justification for simply averaging them. Instead, modeling efforts should explicitly recognize this uncertainty and use the range of best estimates. I am working to narrow these ranges somewhat with further analysis (Mayhood 2012b, in preparation 1), but at this point it appears that a substantial reduction in the range of best estimates is not likely.

Table 4. Mortality estimates for the 1978 Silvester Creek population. Methods from numerous sources (Chen and Watanabe 1989; Miranda and Bettoli 2007; Peterson and Wroblewski 1984; Quinn and Deriso 1999; Smith *et al.* 2012; Gulland 1969; Pauly 1980; Hoenig 1983; McGurk 1986, 1987; Jensen 1996)

Mortality measure	**Range of best estimates**	**Range of single estimates**	**Number of methods**
instantaneous natural M y^{-1}	0.333 - 0.951	0.239 - 1.01	10
conditional natural cm y^{-1}	0.28 - 0.61	0.21 - 0.83	10
instantaneous total Z	0.328 - 0.687	0.328 - 0.687	6
annual total A	0.28 - 0.50	0.28 - 0.50	6

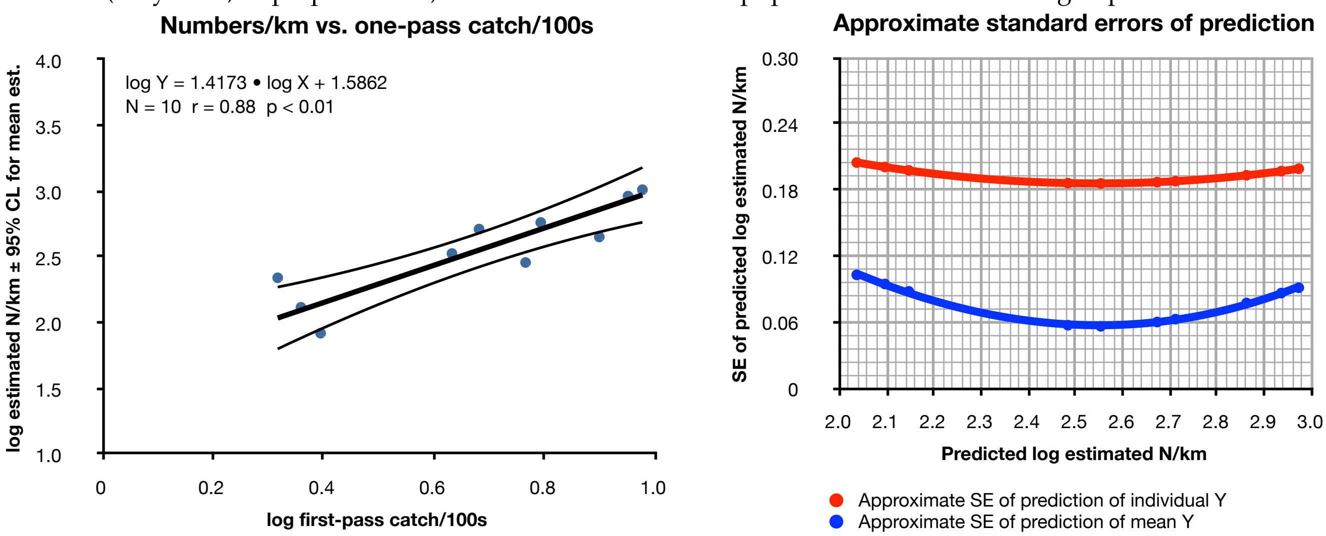
With regard to possible angling mortality, if anything the natural mortality estimates often exceeded the total mortality estimates. The most that can be said about this is that there is no evidence that fishing mortality is significant in this dataset.

Population Size

The size of the population is the best single predictor of vertebrate extinction risk, and along with trend is the most important measure to use in evaluating conservation status in vertebrate populations (O'Grady *et al.* 2004). For westslope cutthroat trout this statement is true for populations that are isolated from invading *Oncorhynchus* spp., especially rainbow trout. Rainbows — if they successfully invade cutthroat habitat — are effectively certain to drive westslope cutthroats to extinction through introgressive hybridization (Allendorf and Leary 1988, Allendorf *et al.* 2001) regardless of population size. Population size might also be an important factor in making westslope cutthroat resistant to brook trout invasions. Brook trout sometimes — but not always — eliminate westslope cutthroats after invading their streams and lakes (Mayhood 2009). Isolating populations from invaders is one of the principal tactics needed for conserving this species, the size of the population will largely determine the probability of the isolated population surviving, so population estimates are a critical reference parameter for planning to conserve native cutthroats.

An estimate of abundance was not provided for the 1978 Silvester Creek population, but some basic catch data are available (Tripp *et al.* 1979b). Tripp et al. captured cutthroats from the mouth to approximately 4.5 km upstream at the rate of 32.15 cutthroat trout per 100 seconds. In a preliminary analysis I found that, for small eastern slopes streams in southwestern Alberta, one-pass electrofishing capture rate per unit time could be related with reasonable precision to the numbers of trout per kilometre as estimated by depletion-removal and mark-recapture estimates (Figure 14). Unfortunately, Tripp et al.'s capture rate for 1978 Silvester Creek cutthroats, 32.15•100 s^{-1}, was well beyond the range to which this relationship could be safely applied.

Figure 14. Preliminary GM regression analysis of data relating capture rate in one-pass electrofishing to numbers km^{-1} in small East Slopes streams, southwestern Alberta over the capture rate range of approximately 2 — 10 fish • 100 s^{-1} (Mayhood, in preparation 3). Error estimates relate to population estimators using depletion-removal



and mark-recapture methods, not to the true population size itself.

An alternative method of estimation is possible, however. Tripp *et al*. (1979b:Table 34) electrofished for a total of 1664 seconds at 11 quite regular intervals over a channel distance of approximately 4.5 km as measured on a 1:50,000-scale National Topographic Service map. At a maximum, therefore, they sampled about 400 m per station — effectively the entire stream. This seems unlikely, however: more likely they would have remarked on such a high intensity of sampling. Yet they did not. A hint of a more reasonable average distance electrofished per location is given by their habitat sampling stations. Electrofishing sites were located at each of 11 habitat assessment sites (Tripp et al. 1979:Figure 2). Habitat was assessed over a distance of about 100 m, centred on the site (Tripp et al. 1979:8). It seems reasonable that they would have sampled fish in the same reach. Similarly, their electrofishing efficiency estimates in 3 other streams in the same study were conducted over 60 — 180 m sections, with a mean of 113 m. One hundred metres therefore seems to me to provide a reasonable lower limit for the average distance fished at each sampling station, giving a possible range of 1100 — 4500 m over which they captured trout at their reported rate. That is, they captured fish at a rate of

$$0.3215 \text{ cutthroats s}^{-1} \bullet 1664 \text{ s} = 535 \text{ cutthroats, or } 0.19 — 0.49 \text{ cutthroats m}^{-1}.$$

Tripp *et al*. (1979b) did not estimate their electrofishing efficiency in Silvester Creek, but they made estimates in three other creeks in their study area. Total efficiencies ranged rather narrowly in diverse habitats, from 0.49 — 0.69, mean 0.60. These correction factors applied to the above estimated linear capture rates suggest that the 1978 cutthroat population was within the range of approximately 1200 — 4500 catchable fish (Table 5).

Table 5. Population estimates for the 1978 Silvester Creek cutthroat trout stock. Sampling was conducted at 11 intervals estimated at 100 — 400 m each, over 4.5 km of channel from the mouth to the headwater forks.

Capture rate, trout m^{-1}	Estimated electrofishing efficiency	Population
0.19	0.49	1745
	0.69	1239
0.49	0.49	4500
	0.69	3196

Discussion

Age and Growth

Maximum age in the 1978 Silvester Creek population, more than 6 and less than 9 years, is consistent with that known for those in other small headwater streams. It was similar to the maximum age of 8 found in a survey of 33 headwater stocks in Montana (Downs *et al.* 1997). All of these populations were genetically-pure westslope cutthroats aged by otoliths. Montana headwater populations with maximum ages of 6 to 8 ranged from 159 to 246 mm in mean fork length at maximum age (overall mean 197.5, N = 8), similar to the 209.8 mm (n = 4) found for maximum-age 6 fish found in the present study, but not unexpectedly they were considerably shorter that the von Bertalanffy fork length L_{inf} of 239 mm in the Silvester Creek population.

The 1978 Silvester Creek population was among the slowest-growing cutthroat populations of the 6 surveyed by Tripp *et al.* (1979b). The comparative populations, however, are known, or are strongly suspected to be, hybrids with rainbow trout, *O. mykiss*, so are not really comparable cutthroat stocks. The Silvester Creek cutthroats were also as slow-growing as the slowest-growing westslope cutthroats summarized by Rieman and Apperson (1989) and McIntyre and Rieman (1995). These populations were from large fluvial and adfluvial systems, and depending on exactly where in the identified systems these fish were studied, at least some populations may be hybridized. In any case they were aged using scales, which often underestimate ages when compared to otolith determinations, (e.g., Downs *et al.* 1997, Hining *et al.* 2000, and references therein). On average, lengths-at-age in Silvester Creek cutthroats were higher from age 1 through 3, about the same at age 4, and much lower at ages 5 and 6 in comparison to populations in the North Fork Flathead River summarized by Shepard *et al.* (1984); but again these fish were scale-aged. As noted above, the Silvester Creek cutthroats had a growth rate very similar to that of five other Alberta East Slopes streams for which there are comparable otolith-based age data (Figure 1, right panel). Though comparable data are sparse, there is at least no strong evidence that the Silvester population is slower-growing than other comparable stocks, and may even grow faster than several others in the first three years.

The weight-length relationship slope of 3.07 in this study is within the range of 3.05 to 3.15 found for the same species in USA waters (Rieman and Apperson 1989). Erdle (2011), using weight-length regressions, found a greater weight for a given length in the 1978 population than that in 2005, especially at smaller lengths, indicating poorer condition for the youngest fish in the more recent year. Several possible explanations exist, but the difference is at least consistent with reduced recent habitat quality. Suspended solids loading from all-terrain vehicle use in this catchment was high enough to cause mortality and reduced growth in salmonids, especially eggs and larvae (Erdle 2011).

Sexual Maturity & Fecundity

Silvester Creek cutthroats generally matured earlier than those in 11 Montana headwater pure populations (Downs *et al.* 1997). In the Montana headwaters maturity rates were, on average, about 40% at age 2, 55% at age 3, and 100% at age 4 for males. For females, the comparable figures were 0% at age 2, 25% at age 3, 70% at age 4, 90% at age 5, and 100% at age 6. In contrast, Silvester Creek males were all mature by age 3, and all females were mature by age 4.

Fecundities were not significantly different at given fork lengths in the Silvester Creek population and in two Montana headwaters, as shown in Table 6.

Table 6. Average fecundity of female westslope cutthroat trout. Silvester Creek figures are calculated from the regression of Figure 6 and provide the standard error of prediction for the mean (N = 11). Montana data are from Downs *et al.* (1997).

Mean fork length, mm	Egg number per female ± SE of predicted mean	
	Silvester Creek	2 Montana headwaters
162	287 ± 23	227
189	367 ± 16	346
218	452 ± 30	459

Mortality Rates

Estimates of conditional natural mortality in five westslope cutthroat populations from lakes and larger streams in the northwestern USA ranged from 0.31 to 0.54, while total annual mortality in eight populations ranged from 0.57 to 0. 78 (Rieman and Apperson 1989). The USA conditional natural mortality figures are reasonably similar to the range of "best" estimates in Table 4, but the total mortality estimates are definitely higher than the comparable figures for Silvester Creek, probably reflecting the exposure to significant angling pressure in most of the stocks summarized by Rieman and Apperson (1989). The comparisons suggest that the Silvester Creek total mortality estimates are reasonable, or at least are in the expected range.

In a recent modeling study of westslope cutthroats in southwestern Alberta, Sullivan (2007) employed a natural mortality estimate of 0.35, and total mortalities of 0.35, 0.44 and 0.60. Based on the 1978 Silvester Creek data in Table 4 these appear to be reasonable, although the natural mortality estimate is near the low end of the likely range. In future work it would probably be advisable to investigate results using a somewhat larger natural mortality rate as well, and adjust total mortality rates accordingly. Paul *et al.* (2003) modeled a nearby hybrid cutthroat population in Quirk Creek using natural mortalities over the range 0.30 — 0.70, which is within the range of all single estimates but slightly wider than the range of best estimates in Table 4, and would seem to cover all of the likely true values.

Population Size

Paul and Dormer (2005:37) could not explain the large difference between the catch-per-effort figure of 32.15 cutthroats • 100 s^{-1} reported by Tripp *et al.* (1979b) and catch rates found in their own and other recent studies in the same stream. They pointed out that Tripp *et al*.'s figure was five-fold greater than the highest catch reported from a single section in their study, 20-fold higher than their own average catch rate, and four-fold greater than the highest value reported in three previous studies conducted on Silvester Creek from 1996 to 2002. If Tripp *et al*.'s figure is seriously in error, then so is the population estimate made in the present study.

Several considerations suggest that the catch-per-effort figure reported by Tripp *et al.* (1979b) is reliable. Although the Silvester Creek CPE of 32.15 • 100 s^{-1} was the highest those authors found in the 15 streams of their study, it was comparable in magnitude to that found for total salmonids in their lower Elbow River (19.99 • 100 s^{-1}) and Threepoint Creek (21.43 • 100 s^{-1}) study sections, and for rainbow trout in their Muskeg Creek study section (25.90 • 100 s^{-1}). Total CPE reported for 10 other streams in their study ranged from approximately 1 — 5 • 100 s^{-1}, similar to that reported for Silvester Creek in recent years (Paul and Dormer 2005:37) as well as for many other southwestern Alberta East Slopes streams (Mayhood, unpublished data). This suggests that a systemic error, such as a mistake in calculation method or an inaccurate timer on the electrofisher, was unlikely. Additionally, only a subsample of the trout population was used for life-history studies in Silvester Creek (Tripp *et al.* 1979a). This would be done only if catches were too large to process efficiently, as the calculated total catch of 535 cutthroats certainly would be in a survey study of this type. Finally, the estimated range of likely population size made from Tripp *et al*.'s CPE is only, at most, 4.5 times larger than Paul and Dormer's more recent estimate of about 1000, not the 20 times larger that comparison of the CPEs for the two studies would suggest. This is yet another example of how CPE can be misleading as an index of population size.

A population of the size range in Table 5 has an estimated probability of 0.67 — 0.90 of persisting over 40 generations (essentially in perpetuity; Mayhood 2009:Figure 4B). It should be noted, however, that the population may have declined somewhat since 1978. More recent population studies have provided estimates of approximately 1000 fish ≥ 70 mm fork length, and less than 500 for the number of adults (≥ 150 mm; Paul *et al.* 2008). These correspond to probabilities of persistence of 0.51 — 0.63 for 40 generations. Both the recent absolute population size and the apparent trend over the nearly three decade interval suggest that the Silvester Creek cutthroat trout population is at significant risk of eventual extinction.

Applying the Reference Parameters

The reference parameters developed here will be useful in planning and managing conservation efforts for the few native westslope cutthroat trout populations remaining in Alberta. They can facilitate comparisons among the remnant stocks to identify those most able to sustain themselves if protected, and they will be helpful in designing secure archival populations.

The major problem for conserving this threatened species remains, however. Most of the last remaining native cutthroat stocks are being invaded by an overwhelming wave of non-native rainbow trout and rainbow-cutthroat hybrids. Unless they are blocked or removed, these invaders will continue to destroy native cutthroat stocks by introgressive hybridization as they move upstream into the last isolated headwater refuges of the native cutthroats. The invasion is being exacerbated by ongoing global warming, which favours rainbow and hybrid trout moving ever higher in the stream networks (Robinson 2007, Rasmussen *et al*. 2010). These are the key problems that remain to be addressed in conserving native cutthroats in Alberta. The reference parameters can only assist in making what ultimately are going to be hard decisions to block or remove some valuable fish stocks.

Summary of Key Reference Parameters

Table 7. Life-history parameters of a genetically-pure, headwater stream-resident population of westslope cutthroat trout on Alberta's Eastern Slopes, Silvester Creek (Tripp *et al.* 1979a, 1979b). As at the time of sampling, the population is presumed to be lightly-exploited, but is believed to have been at least moderately affected by negative anthropogenic influences on habitat.

Parameter	Values	Data Source
von Bertalanffy K	0.325	Tripp *et al*. (1979a, 1979b)
von Bertalanffy L_{inf}	239.1 mm fork length 250.4 mm total length	Tripp *et al.* (1979a) Mayhood (2012a)
von Bertalanffy t_0	-0.126	Tripp *et al*., (1979a, 1979b)
maximum age, years	6 observed 1978 9 estimated from catch curve 1978 8 observed 2004-2006	Tripp *et al.* (1979a) Mayhood, in prep. 1, A. Paul, unpublished data
weight-fork length relationship	geometric mean regression $\log_{10}W_g = 3.0663 \bullet \log_{10}L_{mm} - 5.0635$, SE prediction of an individual estimate ± 0.04	Tripp *et al*. (1979a, 1979b)
age at maturity, males	YOY through 1 yr, 0% 2 years, 60.0% 3+ years, 100%	Tripp *et al*. (1979a, 1979b)
age at maturity, females	YOY through 2 yr, 0% 3 years, 60% 4+ years, 100%	Tripp *et al*. (1979a, 1979b)
sex ratio, all fish in which sex determinable	M : F = 1.56 : 1 no apparent trend with age	Tripp *et al*. (1979a, 1979b)
sex ratio, mature fish only ≥ age 4	M : F = 1.13 : 1	Tripp *et al*. (1979a, 1979b)
total length to fork length	$L_{T\ mm} = 1.040 \bullet L_{F\ mm} + 1.697$	Mayhood (2012a)
population estimates	1978: ~ 1200 - 4500 2004-2006: ~ 1000	Mayhood, in prep. 3, Dormer and Paul (2006), Paul *et al.* (2008)

Mortality estimates for the 1978 Silvester Creek population. Methods from numerous sources (Chen and Watanabe 1989; Miranda and Bettoli 2007; Peterson and Wroblewski 1984; Quinn and Deriso 1999; Smith *et al.* 2012; Gulland 1969; Pauly 1980; Hoenig 1983; McGurk 1986, 1987; Jensen 1996)

Mortality measure	**Range of best estimates**	**Range of single estimates**	**Number of methods**
instantaneous natural M y^{-1}	0.333 - 0.951	0.239 - 1.01	10
conditional natural cm y^{-1}	0.28 - 0.61	0.21 - 0.83	10
instantaneous total Z	0.328 - 0.687	0.328 - 0.687	6
annual total A	0.28 - 0.50	0.28 - 0.50	6

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Appendix

I used the aggregated data for the six available genetically-pure populations with age data to attempt to prepare length-at-age curves for growth analysis (Figures A1 and A2). These demonstrated a common problem when data from stocks with widely differing growth rates or habitat conditions are aggregated in this way. Slower-growing trout commonly live longer, so the apparent growth curve turns downward at higher ages. This is theoretically not possible, except in the case of extreme starvation. It also would invalidate von Bertalanffy growth calculations, because the procedure assumes that growth in fish tends toward a length asymptote, which is true for real populations.

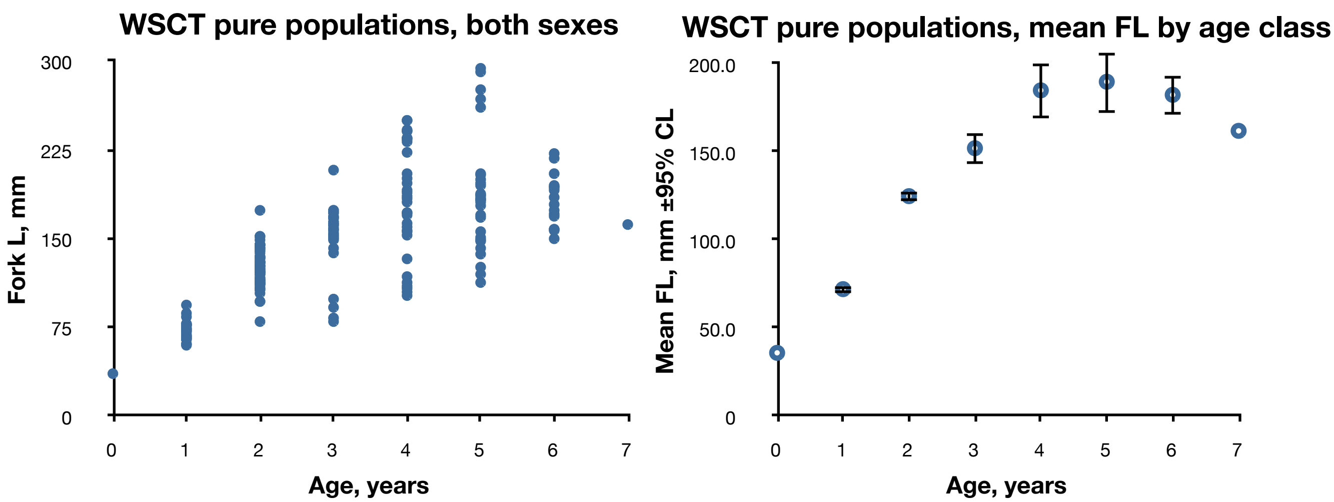

Figure A1 (left panel). Individual length-at-age of genetically-pure westslope cutthroat trout from 6 headwater stream populations in Alberta.

Figure A2 (right panel). Mean length-at-age of genetically-pure westslope cutthroat trout from 6 headwater stream populations in Alberta**.**

To try to estimate the near-maximum growth of fish possible among these six populations, I then plotted the 95th percentiles of lengths in each age class (Figure A3). Again, the resulting curve showed lower sizes in the larger age groups.

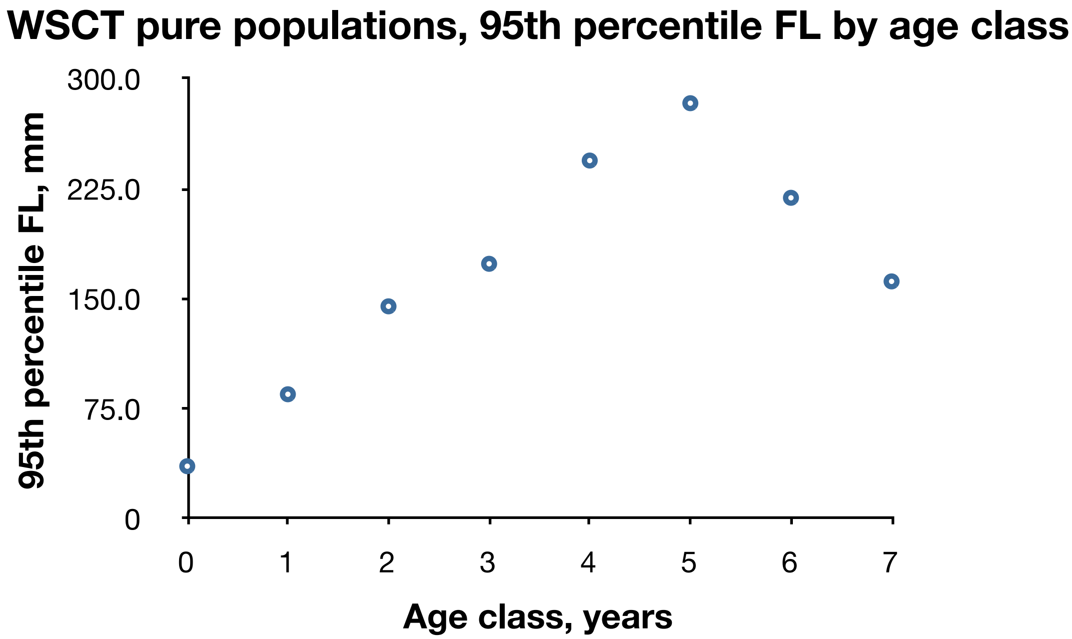

Figure A3. 95th percentile of length-at-age of genetically-pure westslope cutthroat trout from 6 headwater stream populations in Alberta.

These data could not be used to produce a composite theoretical population, so I chose the 1978 Silvester Creek population from above the falls, the best single-population dataset out of the collection as the reference population (Tripp *et al.* 1979a, 1979b) (see ***Choice of Standard Population***). Age-at-length plots for Silvester Creek westslope cutthroat trout produced more realistic apparent growth curves (Figures 1 to 3).