Gerrard Rainbow Trout Growth and Condition with Kokanee Prey at Low Densities

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Final Report

Gerrard Rainbow Trout Growth and Condition with Kokanee Prey at Low Densities

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Prepared for

Fish and Wildlife Compensation Program – Columbia

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The Fish and Wildlife Compensation Program is a -partnership of BC Hydro, the Province of BC,) Fisheries & Oceans Canada (DFO), First Nations, and public stakeholders to conserve and enhance fish and wildlife impacted by the construction of BC Hydro dams.

Cover Photo: 'A 710 mm Rainbow Trout captured in Kootenay Lake recreational fishery.' Photograph taken on the 21st of November 2014 by Kerry Reed of Reel Adventures.

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EXECUTIVE SUMMARY

Condition and growth of Gerrard Rainbow Trout (*Onchorynchus mykiss*) that inhabit Kootenay Lake were examined during a substantial decline in their primary prey, Kokanee (*Onchorynchus nerka*). Comparisons of current condition and growth were made with previous data that spans nearly three decades from 1966-2014. The recent collapse of the Kokanee population on Kootenay Lake has created a severe imbalance in the predator-prey dynamics within the lake and their abundance is an important determinant of growth, condition of predators within the lake.

An allometric mass-length model was used to assess Gerrard Rainbow Trout condition and the analysis determined that their condition had been relatively stable over time on Kootenay Lake until 2013-2014. The model output indicated a substantial and significant decline ($p<0.05$) in weight (22%) for a given length of fish for these years compared to all other year's data. Data analysis also suggests the highest conditioned fish for all years' was in 2004 when there was a 7% increase in weight for a given length. The relative growth in any given year was modeled from the back-calculated scale increments. The model output indicated that growth was slightly higher but not significantly ($p>0.05$) in the late 1980s compared to the 2000s data. However, the 2013-2014 data indicated the poorest growth for the period of record.

A dynamic factor analysis (DFA) model with a Bayesian inference was utilized to detect patterns in the time series data (>25 years) for annual trout condition, growth and Kokanee abundance estimates. The DFA model outputs indicated substantially similar trends between condition and growth of Gerrard Rainbow Trout over time until 2013-2014. This analysis also revealed that Kokanee abundance at select age classes were important predictors of condition and growth of Gerrard Rainbow Trout > 50 cm. Abundance of age 2 Kokanee, and age 1 to a lesser extent, appears to be the most important explanatory variables in predicting the patterns in observed condition and growth of Gerrard Rainbow Trout. Meanwhile, age 0 kokanee abundance were not an important predictor of condition and growth of Gerrard Rainbow Trout. The model results also clearly indicated poor growth and condition of the trout sampled during 2013 and 2014.

The implications to the predators of the current very low abundance of Kokanee in Kootenay Lake are discussed. Rebuilding the Kokanee population that is now < 0.2 million spawners may involve at least two Kokanee cycles. i.e. 4-8 years. Meanwhile the predator populations are predicted to undergo significant declines based on the condition and growth indices generated from the 2013-2014 samples. There is growing evidence from predator spawner counts that this predicted decline is already underway.

The anticipated delay in rebuilding the prey population does not bode well for the predators and it may take 10-15 years to rebalance the predator populations. A number of recommendations are made including closure of the Kokanee fishery, foregoing any attempt to increase Kokanee size for the fishery and establishing a minimal Kokanee escapement target of one million spawners.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Fish and Wildlife Compensation Program – Columbia (FWCP). The Fish and Wildlife Compensation Program is a partnership of BC Hydro, the Province of BC, Fisheries & Oceans Canada (DFO), First Nations, and public stakeholders to conserve and enhance fish and wildlife impacted by the construction of BC Hydro dams.

In-kind support was also provided by several BC Ministry of Forests, Lands and Natural Resource Operations (MFLNRO) employees. Tyler Weir (MFLNRO Large Lake specialist, Victoria BC) and David Johner (MFLNRO Victoria BC) are thanked for providing the acoustic data from Kootenay Lake for this study. Matt Neufeld (MFLNRO Fisheries biologist Nelson BC) provided some invaluable advice.

Kerry Reed (Kootenay Lake angling guide) is acknowledged for the collection of samples within the fishery.

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INTRODUCTION

Growth and condition are two metrics that are commonly used to evaluate the impact of various environmental factors on fish populations (Isley and Grabowski 2007) . Fundamentally, growth and condition are the result of bioenergetic mass balance equations that balance off energy acquisition (consumption) versus assimilation efficiency and metabolic costs (Kitchell et al. 1977, Walters and Post 1993). However, interpreting these metrics requires a good understanding of the ecology and life history of the species of focus. The amount of energy consumed, then allocated to growth, maturation and reproduction can be highly dependent the time of year (season), behavioural traits, intrinsic individual variation and environmental variation (Shelton and Mangel 2012). Nonetheless, assessment of fish growth and condition often provide an insight into environmental conditions such as food availability during specific life stages or throughout their entire life expectancy.

Availability of resources (prey) is a major factor influencing growth and condition of fish populations (Essington et al. 2001). Changes in the relative densities of predator vs prey species is expected to directly influence growth and condition indices for piscivorous fish populations over time (Hansen et al. 2010). Therefore, management of trophy fisheries for large bodied piscivores will rely on maintaining target abundances of prey populations. In aquatic ecosystems where there is a single primary prey species, prey management becomes even more critical.

Mass–length relations and condition indices often provide the basis for studying physiological condition of fish populations (Anderson and Neumann 1996). In recent years use of a Hierarchical Bayesian approach has improved the ability to model mass-length as an index of fish condition over time (He et al. 2008). This new approach has improved the ability to account for variation and uncertainty in individual, annual condition which is considered superior to conventional indices of fish condition (He et al. 2008). Likewise, the von Bertalanffy (1938) growth function (VBGF) is often used to describe the lifetime pattern of somatic growth in fishes that exhibit indeterminate growth (Ricker 1975, Walters and Martell 2004). Use of time variant VBGF growth models have also provided a better approach in assessing annual and individual variation in in fish growth over time (Pilling et al. 2002, He and Bence 2007).

Dynamic factor analysis (DFA) provides a relatively simple technique which has become an important tool for high-dimensional modelling of time series data (Zuur et al. 2003b). DFA is a multivariate time-series analysis technique used to estimate underlying common patterns in a set of non-stationary time series (Calder et al. 2003) . In fisheries, such models can provide flexibility and parsimony for underlying latent processes such as stochastic volatility and time-variation (Cressie et al. 2009). These models therefore are more flexible for assessing over time the complex multivariate factors related to fish growth and condition. Assessment of fish growth and condition often provide an insight into environmental conditions such as food availability during specific life stages or throughout their entire life expectancy.

Our current study focused on the growth and condition of the Gerrard Rainbow Trout (*Onchorynchus mykiss)* population in Kootenay Lake considered a unique ecotype (Keeley et al. 2007). These trout are the dominant large piscivore in the lake that rely almost exclusively on their prey Kokanee (*Onchorynchus nerka)* to attain such a large size (Andrusak and Parkinson 1984). We utilized nonlinear random effects models with a Hierarchical Bayesian approach to assess their condition and growth over time. We developed indices of fish condition from the individual variation in the mass-length relationship for this ecotype, similar to that described by He et al. (2008). In relation to growth, we assessed growth histories from individual fish using back-calculation of length at age based on scales collected from the recreational fishery, similar to that detailed Pilling et al. (2002). The dynamic factor analysis was used to assess the influence of Kokanee prey abundance on both condition and growth of Gerrard Rainbow Trout over time.

Quantitative modelling of growth and condition in the Gerrard Rainbow Trout population over time are key metrics used in assessing the benefits of the large scale nutrient restoration program on Kootenay Lake (FWCP 2012, Schindler et al. 2014), a primary mandate for the the Fish and Wildlife Compensation Program – Columbia (FWCP 2012).

Project Objectives

- Assess mean annual growth patterns from individual variability in growth using back-calculated growth increments from the Von Bertalanffy growth curve (Pilling et al. 2002, He and Bence 2007). i.e. determine if growth varies by year.

- Assess fish condition from individual variation in mass-length of Gerrard Rainbow Trout over same time period of growth (He et al. 2008) and determine if body condition varies by year.

- Assess measurement error associated with ageing and back-calculated of length at age used in growth modelling (Cope and Punt 2007).

- Use DFA to assess variation in prey density and abundance over time to determine if there is any effect on growth and condition of Gerrard Rainbow

Trout. Determine if trends in growth and condition are linked to trends in kokanee abundance.

- Discuss impacts of reduced Kokanee densities upon Kootenay Lake fisheries

STUDY AREA

Kootenay Lake is a large oligotrophic lake located in the upper Columbia River drainage of Southeast British Columbia. The lake supports a large and intensive recreational fishery that can generate > 200,000 rod hours annually (Andrusak and Andrusak 2012). The majority of fishing effort is primarily directed at Rainbow Trout and Bull Trout (*Salvelinus confluentus*). Gerrard Rainbow Trout represent a genetically and eco-typically distinct population of piscivorous trout within the lake and are the primary focus for this study (Keeley et al. 2007). More detail on the physical and biological attributes of Kootenay Lake can be found in numerous technical reports including Daley et al. (1981) and more recently in Schindler et al. (2014).

BACKGROUND

Gerrard Rainbow Trout juveniles emigrate from the Lardeau River at age 1-2 and recruit to the fishery as they increase in age and size (Irvine 1978, Andrusak 2010). Following their migration to the lake, these trout undergo an ontogenetic shift to piscivory described by Keeley and Grant (2001) in which a rapid increase in size at age is attained. They become vulnerable to angling near 300-350 mm in length which usually approximate ages 2-4 (Andrusak and Andrusak 2012). After attaining this size range they become increasingly piscivorous as they grow and increase in size (Cartwright 1961, Andrusak and Parkinson 1984). During most of their lifetime, these trout are almost entirely dependent upon Kokanee as their primary prey source (Andrusak and Parkinson 1984). Subsequently, these trout can attain a large size at age (>7 kg) which are highly sought by anglers in the recreational fishery that is world renown.

The Kokanee population has been monitored for over three decades using hydroacoustics and trawl surveys to determine their abundance (Schindler et al. 2014). These surveys were initiated after the lake experienced major perturbations due to a series of hydro developments within the watershed (Daley et al. 1981). A dramatic decline in lake productivity and kokanee abundance during the late 1980s promoted experimental lake fertilization commencing in 1992 that rapidly increased the lakes' productivity and kokanee abundance (Ashley et al. 1997, Schindler et al. 2014). For over twenty years this fertilization program has successfully improved in-lake conditions that have benefited piscivore populations and a prominent recreational fishery (Andrusak and Andrusak 2006, 2012). Most recently, the lakes' Kokanee population has collapsed to historic levels not observed over the past 50 years (MFLNRO data on file). It is believed that the variation in prey abundance has a profound influence on growth and condition of the predators in the lake, especially the Gerrard Rainbow Trout

METHODS

Length at age data

Length at age data for Gerrard Rainbow Trout was available for select years from 1978 to 2014. Samples were obtained from angler captured fish from various seasons and months within the recreational fishery (March-July and September to January) for years available including; 1978-1980, 1988-1992, 2003-2004, and 2008-2014 (Appendix 1). Samples were collected over periods of differential growth i.e. winter/spring and summer/fall. An underlying assumption with all the data analysis presented below is that all records of lengths and weights were accurately measured consistently over time. A second assumption is that only Gerrard Rainbow Trout that (> 50 cm) were included in the analysis to ensure exclusion of non-piscivorous (insectivorous) stocks.

Samples from the fishery provided information on date of capture, location, species, sex, maturity, fork length (± mm) and weight (± kg). A scale sample was taken from each Rainbow Trout in order to estimate its age. Scales were taken from just above the lateral line posterior to the dorsal fin. A number of scales were cleaned and mounted onto glass microscope slides (25 x 75 mm), viewed under a AmScope © stereomicroscope at a magnification of 10-30 X. Digital images (2048 x 1536 pixels) were obtained for each scale sample using a 3MP (5 mm) AmScope © camera fitted to the stereomicroscope.

Ages determined from the scale samples were based on the number of annuli observed. Three independent ageing of the scale samples were conducted for a subset of the samples. Back calculated length at age was also obtained for each individual fish by measuring the distance from the scale focus and interannual distances (± mm) between annuli for each scale (see growth section below). Back-calculation was conducted using UTHSCSA ImageTool (IT)©, a free image processing and analysis program for Microsoft operating systems. Image analysis functions include dimensional (distance, angle, perimeter, area) and gray scale measurements (point, line and area histogram with statistics).

Statistical Analysis

Hierarchical Bayesian models were fitted to the data using R version 3.1.2 (R Core Development Team 2013) and JAGS 3.4.0 (Plummer 2012) which interfaced with each other via jaggernaut 2.2.8 (Thorley 2014). For additional information on hierarchical

Bayesian modelling in the BUGS language, of which JAGS uses a dialect, the reader is referred to Kéry and Schaub (2011). Kootenay Lake Gerrard Rainbow Trout Condition and Growth Analysis were conducted by Dr. Joe Thorley of Poisson Consulting Ltd. (URL: http://www.poissonconsulting.ca/f/723490014)

Unless specified, the models assumed vague (low information) prior distributions (Kéry and Schaub 2011). The posterior distributions of the parameters were estimated from a minimum of 1,000 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of three chains (Kéry and Schaub 2011). Model convergence was confirmed by ensuring that Rhat was less than 1.1 for each of the parameters in the model (Kéry and Schaub 2011). Model adequacy was confirmed by examination of residual plots. The posterior distributions of the *fixed* (Kéry and Schaub 2011) parameters are summarized in terms of a *point* estimate (mean), *lower* and *upper* 95% credible limits (2.5th and 97.5th percentiles), the standard deviation (*SD*), percent relative *error* (half the 95% credible interval as a percent of the point estimate) and *significance* (Kéry and Schaub 2011).

Variable selection was achieved by dropping *insignificant* fixed variables and *uninformative* random variables (Kéry and Schaub 2011). A fixed variable was considered to be insignificant if its significance was $p \geq 0.05$ while a random variable was considered to be uninformative if its percent relative error was ≥ 80%. The model results are displayed graphically by plotting the relationship between particular variables and the response with 95% credible intervals (CRIs) with the remaining variables held constant. In general, continuous and discrete fixed variables are held constant at their mean and first level values respectively while random variables are held constant at their typical values [expected values of the underlying hyper-distributions] (Kéry and Schaub 2011). Where informative the influence of particular variables is expressed in terms of the *effect size* (i.e., percent change in the response variable) with 95% CRIs (Bradford et al. 2005).

Fecundity

Fecundity samples were not obtained during 2014 primarily due to poor conditioned fish. However, fecundity data was available from the fall and winter of 2003 and 2004 (Andrusak and Andrusak 2006). The relationship between fork length and the egg count was estimated from these samples using an allometric model. A log normal transformation of the standard two parameter function $F=a\,(L^b)$ for egg-length data was utilized, detailed in Table 1. Key assumptions of the condition model include:

- The residual egg counts are log-normally distributed.

Table 1. Parameter distribution and description for Bayesian mass-length model

Variable/Parameter	Description
bAlpha	Intercept for log(eFecundity)
bBeta	Slope for log(eFecundity[i])
Fecundity[i]	Fecundity of ith fish
sFecundity	SD of residual variation in log(Fecundity)

Condition

The relationship between body weight and fork length was estimated using an allometric mass-length model similar to He et al. (2008). Specifically, our analysis modelled interannual variation and individual variation in mass at a given length. Mass-length relationship was from the standard two parameter allometric mass-length function W=a (L^b), detailed in Table 2. Key assumptions of the condition model include:

- The weight varies with the length.
- The weight varies with the day of the year as a second order polynomial.
- The weight varies randomly with the year
- The residual weight is log-normally distributed.

Table 2. Parameter distribution and description for Bayesian mass-length model

Variable/Parameter	Description
bAlpha	Intercept for eAlpha
bAlphaDayte	Effect of Dayte on bAlpha
bAlphaDayte2	Quadratic effect of Dayte on bAlpha
bBeta	Intercept for eBeta
Dayte[i]	Day of the year on which ith fish encountered
eAlpha	Predicted intercept for log(eWeight)
eBeta	Predicted effect of centred log(Length) on log(eWeight)
eWeight[i]	Prediction weight of ith fish
Length[i]	Centered log fork length of ith fish
sAlphaYear	SD of effect of Year on bAlpha
sWeight	SD of residual variation in log(Weight)
Weight[i]	Weight of ith fish
Year[i]	Year on which ith fish encountered

Age

A general time-invariant VBGF growth model was fit to length at age data to exclusively assess differences in ageing between independent scale readers. Due to assumptions in back-calculation to assess previous growth history (Francis 1990), we did not attempt to analyze the data using time variant VBGF growth models, most appropriate in assessing annual and individual variation in in fish growth over time (Pilling et al. 2002, He and Bence 2007). Moreover, general VBGF growth models often assume that all process error or variation between the model and data is due to the heterogeneity in length at age and frequently ageing error is not considered when fitting of growth curves (Cope and Punt 2007). For this study, independent assessments of age were obtained from three readers for a select number of samples. Ageing was conducted by Birkenhead Scale Analysis, Redfish Consulting Ltd (primary author) and Les Fleck (former MFLNRO fisheries technician).

A general time-invariant 3 parameter nonlinear model VBGF function was fit to length at age data.

$$L_{i\,j}=L_{\infty i}*(1-\exp(-k(age-t_0)))+\varepsilon$$

Where $L_{i\,j}$ is the length at age for individual fish, L_∞ is the asymptotic average maximum body size, k is a growth rate (Brody) coefficient that determines how quickly the asymptotic maximum is attained, t_0 is the hypothetical age at which the species has zero length and Є are assumed to be independent normally distributed error terms. Parameterization of the model is detailed in Table 3.

Table 3. Parameter distribution and description for Bayesian length at age model

Variable/Parameter	Description
Age[i]	Age for ith scale reading
bK	Intercept for eK
bKReader	Effect of Reader on log(bK)
bLinf	Mean maximum length
bT0Reader	Effect of Reader on t0
eK[i]	Expected growth coefficient for ith scale reading
eT0[i]	Expected length at time zero
Length[i]	Fork length at capture for ith scale reading
Reader[i]	Reader for ith scale reading
sKReader	SD of effect of Fish on bK
sLength	SD of residual variation in Length
t0	Intercept for eT0

Growth

VBGF growth models are the most common assessment of fish growth in the literature, however, their assumptions are often violated and their results can be difficult to interpret (Pilling et al. 2002, Lester et al. 2004, Cope and Punt 2007, He and Bence 2007, Quince et al. 2008b, Shelton and Mangel 2012). Most notably, assessment of previous growth history from back-calculated scale increments relies on a fundamental principle that scale radius is proportional to fish length (Francis 1990).

In this study we assess the relative growth in any given year from the back-calculated scale increments using a polynomial model since our preliminary analysis indicated that scale radius was not proportional to fish length. Each back-calculated length at age was also given a probability (0.1 = low certainty, 0.9 = high certainty) of correctly identifying the annulus to account for uncertainty with back-calculated scale increments. Parameterization of the model is detailed in Table 4. Key assumptions of the polynomial model include:

- The scale increment varies with the scale radius as a second order polynomial.
- The scale increment varies randomly by year.
- The residual variation which is log-normally distributed varies with the reader's minimum confidence in the two annuli.

Preliminary analyses indicated that the fork length of the fish at capture and fish ID as a random effect were not informative predictors of scale increment.

Table 4. Parameter distribution and description for Bayesian growth model from back-calculated scale increments

Variable/Parameter	Description
bInc	Intercept for log(eInc)
bIncScaleRadius	Effect of ScaleRadius on bInc
bIncScaleRadius2	Quadratic effect of ScaleRadius on bInc
bSDInc	Intercept for log(eSDInc)
bSDProbability	Effect of Probability on bSDInc
eInc[i]	Expected increment for ith annulus difference
eSDInc[i]	Expected SD for for ith annulus difference
Increment[i]	Measured annulus difference
Probability[i]	Readers minimum confidence in ith annulus difference
sIncYear	SD of effect of Year on bInc
Year[i]	Inferred year of second annulus for ith annulus difference

Kokanee

Kokanee abundance, size and juvenile age data from Kootenay Lake was obtained from government hydroacoustic and trawl surveys conducted from 1985-2013 detailed in Appendix 2 and Appendix 3. Abundance estimates by Kokanee age class were used as variables in a time series model to determine if they were predictors of growth and condition of Gerrard Rainbow Trout. Relative survival was estimated from hydroacoustic information for each age class. However in some instances survival for a cohort indicated relative survival that exceeded 100% for that cohort. In these instances, due to the uncertainty in estimates they were removed from the data set.

Dynamic Factor Analysis

The DFA model with a Bayesian inference was utilized to detect patterns in time series data of 15-20 years, which include significant sources of stochasticity (Zuur et al. 2003b, Calder et al. 2003, Cressie et al. 2009). The relative similarities between the annual condition and growth (scale increment) estimates and the yearly kokanee abundance estimates, available in, were estimated using DFA model. Due to the *rotation problem* the underlying trends were indeterminate (Abmann et al. 2014) and therefore growth estimates were lagged by one year. Full details of DFA modelling is detailed in Zuur et al. (2003a)

Key assumptions of the DFA model include:

- The time series are described by two underlying trends.
- The random walk processes in the trends are normally distributed.
- The residual variation in the standardized variables is normally distributed

Table 5. Parameter distribution and description for Bayesian DFA model

Variable/Parameter	Description
bDistance[i,j]	Euclidean distance between ith and jth Variable
bTrendYear[t,y]	Expected value for tth trend in yth Year
eValue[v,y,t]	Expected standardised value for vth Variable in yth Year considering tth trends
sTrend	SD in trend random walks
sValue	SD for residual variation in Value
Value[i]	Standardised value for ith data point
Variable[i]	Variable for ith data point
Year[i]	Year of ith data point
Z[v,y]	Expected weighting for vth Variable in yth Year

RESULTS

Fecundity

A primary objective of this project was to obtain egg samples from mature females to improve on the limited amount of data on Gerrard Rainbow Trout fecundity. Unfortunately, no samples of gravid female Gerrard Rainbow Trout were obtained in 2014. The precipitous decline in the rainbow trout fishery during 2014 caused severe problems for data collection. Resorbed eggs, poor fishing conditions and factors related to declining fish condition proved problematic in obtaining samples. Furthermore, many anglers chose not to retain their fish increasing the difficulty in obtaining samples. Consequently recent fecundity data (n=21) obtained in the fall and winter of 2003 and 2004 (Andrusak and Andrusak 2006) were used in this analysis. Three of these samples were considered to be outliers since eggs had been damaged or were indistinguishable when counting, demonstrated as outliers in Figure 1. Log normal transformation of egg-length data was determined from a linear regression and posterior predictions for parameters estimates are summarized in Appendix 4.

From the 18 samples egg numbers per female ranged from 5,245-11,356 and the mean number was 8,048, similar to the number (8,076) derived by Irvine (1978).

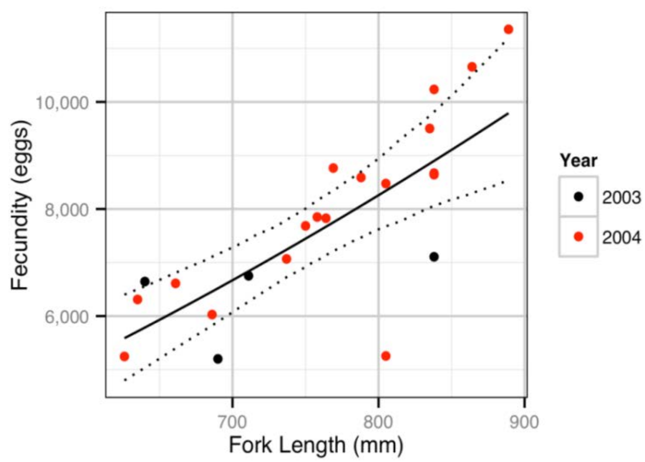

Figure 1. Predicted fecundity (eggs) by length (with 95% CRIs) from female Gerrard Rainbow Trout based on samples from Kootenay Lake fishery 2003 and 2004, as detailed in Andrusak and Andrusak (2006)

Condition

Mass-length data (n=1,360) for Gerrard Rainbow Trout (> 50 cm) that were available from samples collected from the recreational fishery during 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014. The mass-length plot demonstrates substantial variability in weight for a given length of fish compared to the model derived average estimates weight for a given length for the population over the time period (Figure 2). However, our model improved the ability to model mass-length as an index of fish condition for Gerrard Rainbow Trout since we explicitly modelled individual variation in annual condition over time, which is considered superior to conventional indices of fish condition (He et al. 2008). The model estimated an average allometric exponent of 3.26 from the mass-length relationship for all samples combined, where W is the weight in kg and L is the fork length in mm (Figure 2). The exponent or the average *b* of 3.26 (95% CRI 3.19-3.33) is well above the allometric ideal of 3 and indicates that individuals become deeper bodied as they grew. Posterior predictions for parameters estimates are summarized in Appendix 5.

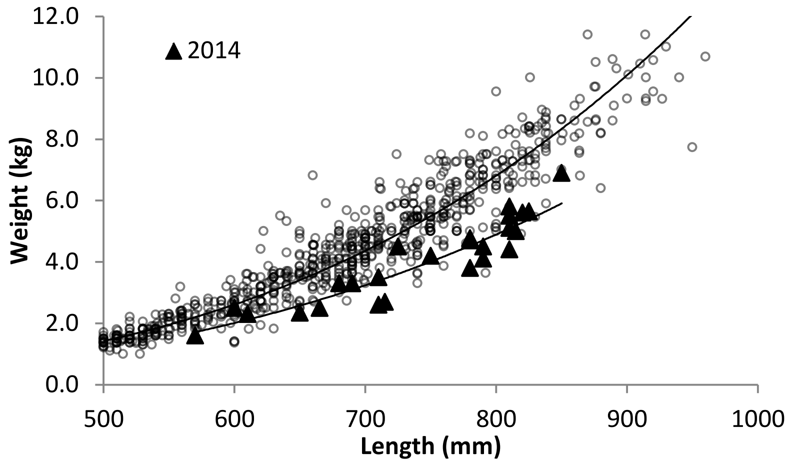

Figure 2. **Predicted mass-length relationship estimate from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including 1966-2012 compared to 2014.**

Seasonal effects were a significant predictor ($p<0.05$) of fish condition within a year (Figure 3). This may be an artifact of when samples were obtained, since the recreational fishery targeting large Rainbow Trout is quite seasonal on Kootenay Lake. Peak fishing for Rainbow Trout primarily occurs in the spring, fall and winter months (Andrusak and Andrusak 2012). Data analysis suggests that fish condition declines from the spring to summer and then increases into the fall and winter for most years (Figure 3). It is plausible that the decrease in condition may be associated with the onset of spawning.

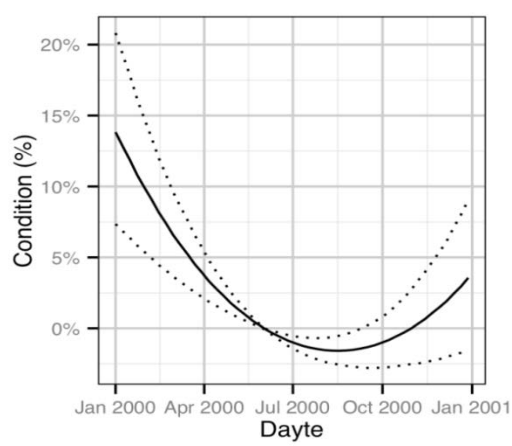

Figure 3. **Predicted seasonal deviation from mean body weight during a given year (with 95% CRIs) from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014. Dates are reflective of full calendar year (i.e. 2000 to 2001)**

In terms of percent change over the period of record based on the percent deviation from the mean, fish condition appears to have been relatively stable until 2014 (Figure 4). Data indicates a substantial and significant decline ($p<0.05$) in weight (22%) for a given length of fish in 2014 compared to all other years' data (Figure 4). The 2004 data suggests the highest condition fish over the entire time period, indicating an increase in weight (7%) for a given length. Unfortunately, higher variability due smaller sample size and other factors (biotic and abiotic) confounds comparisons.

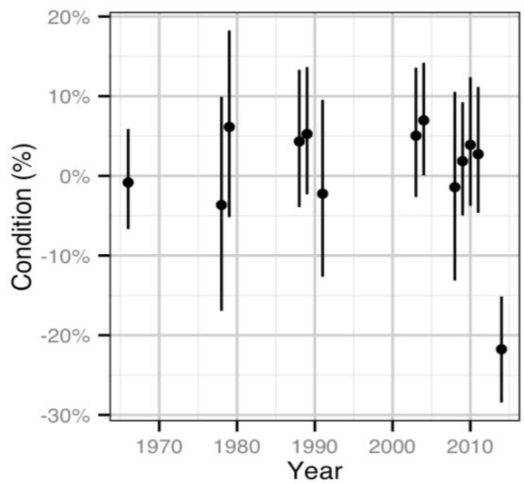

Figure 4. **Predicted percent deviation from average in body weight by year (with 95% CRIs) from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014.**

Age

An analysis of length at age (n=558) was conducted to assess differences between independent scale readers (Figure 5). The general VBGF growth model fit to length at age data indicates substantial variation in length for a given age of fish compared to model derived average estimates for growth over the time (Figure 5). Based on the results, it is apparent that the general time invariant model does not specifically account for annual and individual variation in growth over time (Pilling et al. 2002, Lester et al. 2004, He and Bence 2007). Nonetheless, the assessment of ageing from scales suggests relatively good agreement between two independent readers (Redfish [n=307] and Birkenhead [n=181]) for length at age and a significant difference ($p < 0.05$) from the third independent reader [n=339] (Figure 5). Most of the difference by the third independent reader appears to be due to difficulty in determining the first two annuli, causing an overestimation in older ages. Posterior predictions for parameters estimates from ageing modelling are summarized in Appendix 6.

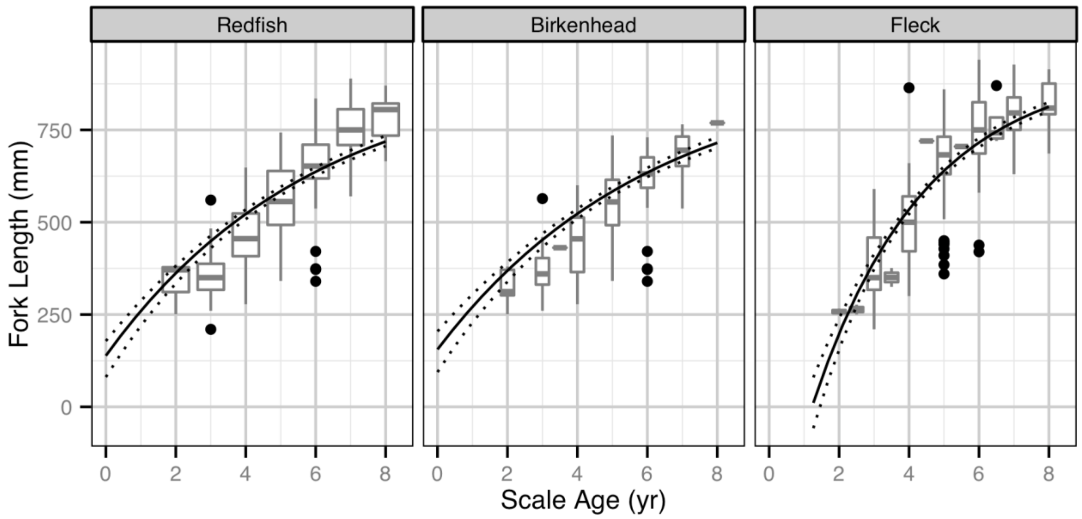

Figure 5. Predicted fork length by age (with 95% CRIs) for individual scale readers from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014. Black dots represent outliers.

Growth

Despite the relatively good agreement between scale radius and fish fork length as displayed in Figure 6, the linear relationship appears to deviate for the smallest and largest fish which violates the fundamental assumption in utilizing back-calculated length at age to assess growth, as detailed in Francis (1990).

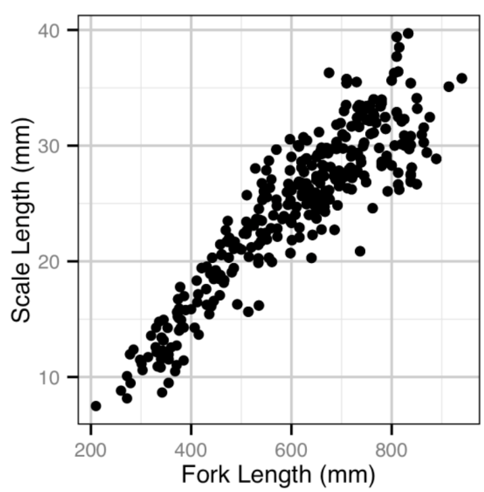

Figure 6. Relationship between scale radius and fish fork length used in back-calculation of length at age from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014.

Therefore, an assessment of scale increments on scale radius was assessed to determine the effect of changing scale increments on scale radius. The relationship between scale increment and scale radius suggest that as the scale radius increases, growth increments increase rapidly to an asymptote before declining (Figure 7). Posterior predictions for parameters estimates from ageing modelling are summarized in Appendix 7.

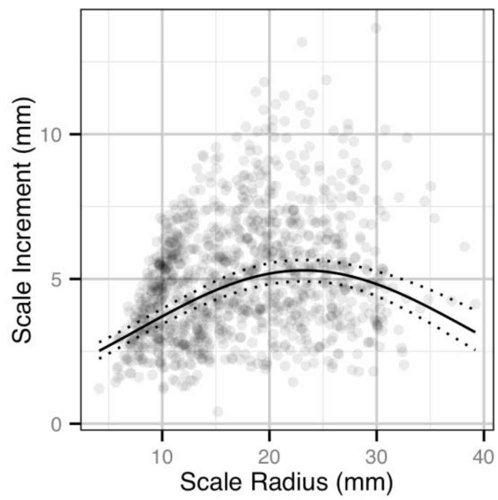

Figure 7. Relationship between scale radius and scale increments from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014.

Based on the analysis of data which indicated scale increments did not conform to a linear relationship, an assessment of the effect of scale increments by year was conducted. Subsequently, the assessment of scale increments by year suggested that scale increments could be used as a relative measure of growth over time (Figure 8). More importantly, the relative growth inferred from the scale increments provided information on previous growth within a particular year and over the time period (Figure 8). As a result, the data indicates that growth was slightly higher but not significantly ($p>0.05$) in the late 1980s compared to the 2000s data. Growth data appears to indicate a major decline starting in and around 2012 (Figure 8). Data in 2014 also indicates the poorest growth for the period of record (Figure 8). Similar to the condition indices, higher variability due smaller sample size, seasonal differences, and other factors (biotic and abiotic) may reduce confidence in comparisons of 2014 data to other years in isolation. However, Kootenay Lake benefits from substantial additional data in reference to prey availability, and so observed growth patterns can be reconciled with these data (section below).

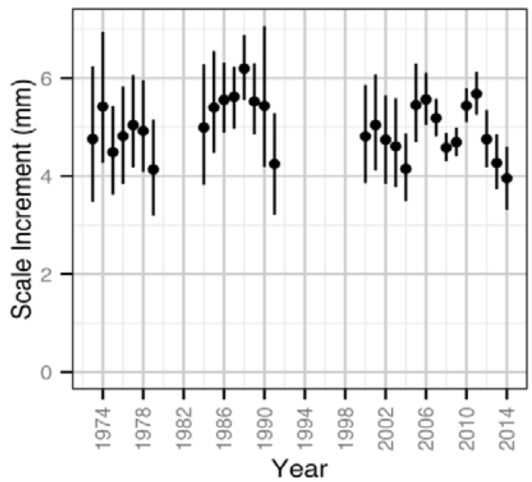

Figure 8. **Predicted effect of year on the scale increment from Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014.**

Kokanee

To understand the dynamics of Gerrard rainbow Trout growth and their condition it is instructive to review and analyze their primary prey which is Kokanee. The Kootenay Lake Kokanee time series data from hydroacoustics and trawl surveys was provided by MFLNRO from 1985 to 2013 (Appendix 2 and Appendix 3). It should be noted that hydroacoustic data presents multiple sources of variation in target strength and target interpretation that complicates the target strength–fish size relationship (Taylor et al. 2005). This uncertainty may substantially bias population size estimates due to difficulty in separation of Kokanee age classes especially between age 1-3 (Simmonds 2005). It also should be noted that estimations of fry abundance in the lake are directly related to Meadow Creek spawning channel (MCSC) production (Kurota et al. 2011, Schindler et al. 2014). Changes in fry abundance can also be influenced by variation in lake productivity that was not analyzed in this study but has been reviewed and discussed by Kurota et al. (2011) and Schindler et al. (2014).

The Kokanee hydroacoustics data combined with trawl data (since 1985) illustrated in Figure 9 indicates substantial differences by age class in annual abundance (also see Appendix 2). Age 0+ Kokanee fall fry estimates have averaged approximately 15 million during the nutrient addition era since 1992, well above the average of 6 million prior to fertilization. Their annual abundance has ranged from a low of 5 million to a high of 30 million. Similarly, age 1 Kokanee have averaged approximately 4 million since the nutrient addition era compared to approximately 1 million prior to fertilization. Their numbers have ranged from < 1 million to approximately 15 million. Age 2 Kokanee have averaged 2 million during the nutrient addition era compared to approximately 1 million prior to fertilization. Their numbers have ranged from < 0.5 million to approximately 8.0 million. While age 3 and spawner information is presented in Figure 9 and Appendix 2, our analysis of growth and condition of Gerrard Rainbow Trout focused primarily on age 0-2 Kokanee. It is noteworthy from the Kokanee time series that a substantial decline in Age 1-3 Kokanee abundance started in 2011 (Figure 9).

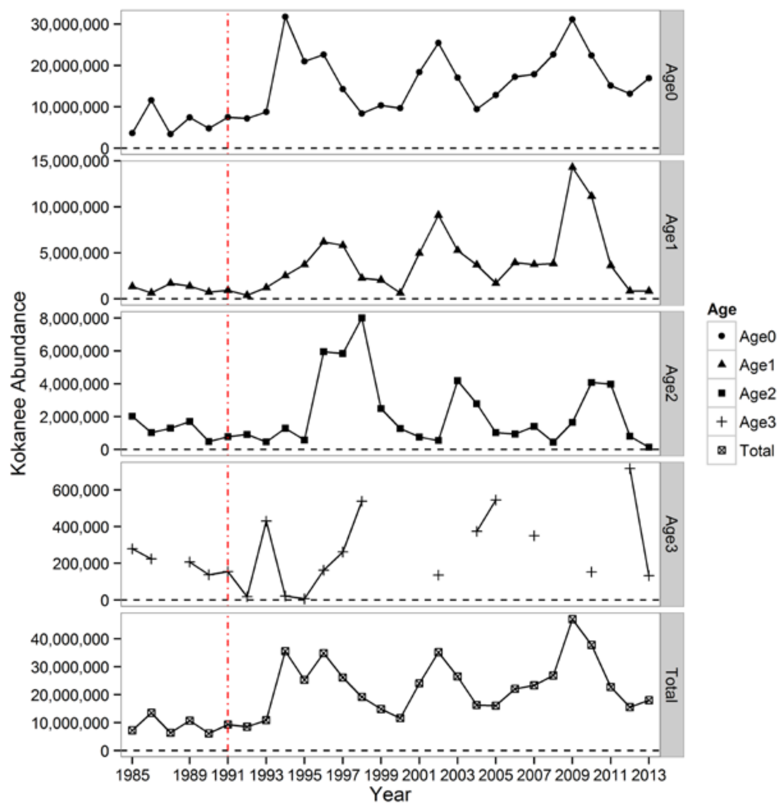

Figure 9. Kootenay Lake Kokanee abundance by age class from hydroacoustic data provided by MFLNRO from 1985-2013. Red segmented line indicates commencement of nutrient addition program on Kootenay Lake in 1992.

Similar to the abundance estimates, with the exception of spawners, size at age information obtained from trawl data is highly variable because in some years sample sizes were small possibly biasing the size at age information. Based on the best available information, Kokanee size information indicates only slight changes in age 0-2 size at age over the time series. Age 0 Kokanee have ranged in size from 48-60 mm since 1985 with little variation between years Figure 10). With the exception of 2013 (109 mm), Age 1+ size has ranged between 116-154 mm in length since 1985 but have decreased notably during the last three years. Age 2+ Kokanee have ranged between 168-246 mm in length since 1985 with the largest size recorded in 2013. Lastly, Kokanee spawners have ranged between 196-279 mm in length and have been accurately measured at MCSC since 1985 (Schindler et al. 2014). With the recent decline in abundance of ages 1-3, ages 2 and 3 Kokanee demonstrated a compensatory increase in size at age starting in 2013 (Figure 10).

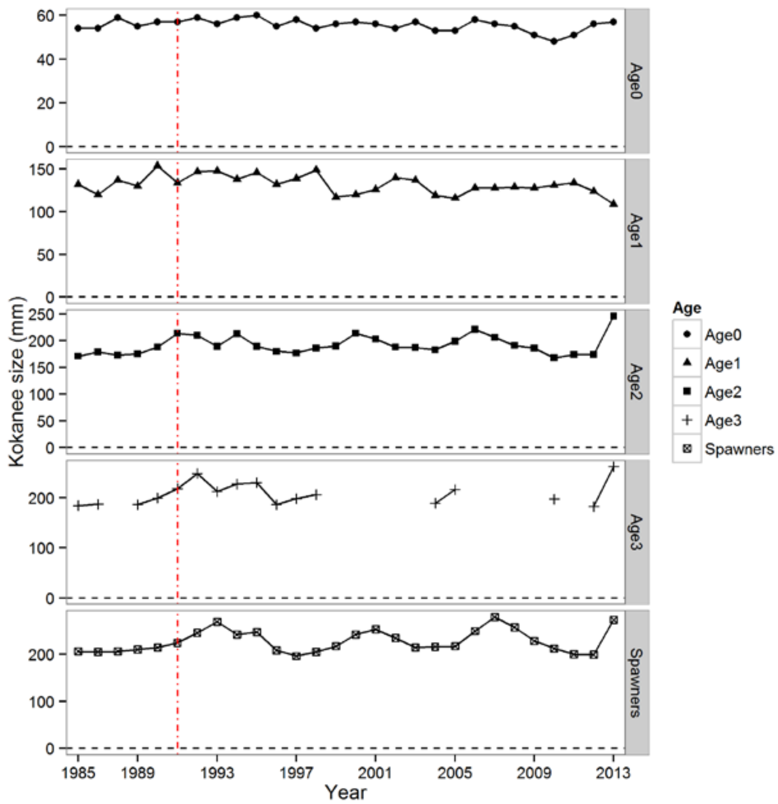

Figure 10. Kootenay Lake average Kokanee length (mm) by age class from hydroacoustic data provided by MFLNRO from 1985-2013. Red segmented line indicates commencement of nutrient addition program on Kootenay Lake in 1992.

The decline in Kokanee abundance also appears to be associated with changes in relative survival from 1985-2012 (Figure 11). Egg to fry survival based on data from MCSC appears to be relatively constant over the same time period (Figure 11) and evidenced by the stable fall age 0 abundance displayed in Figure 9. In contrast, relative survival declined substantially between age 0 and age 1, precipitously since 2009 (Figure 11). Similarly, relative survival also declined substantially between age 1 and age 2 but started 2010 and follows the lower survival experienced by the cohort one year earlier.

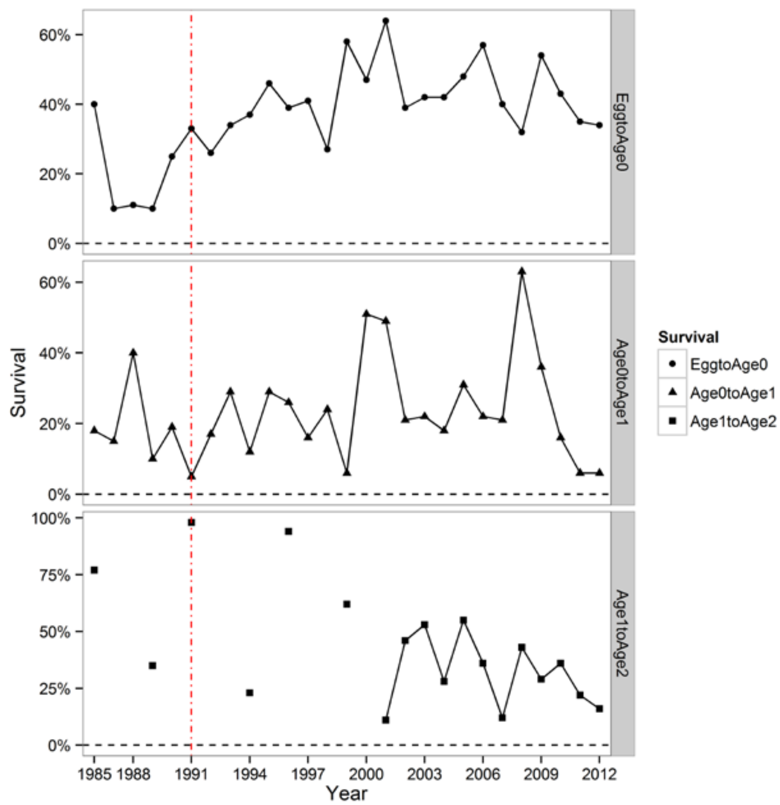

Figure 11. Kootenay Lake relative survival from egg to fry (MCSC), age 0 to age 1, and age1 to age 2 (hydroacoustic data) provided by MFLNRO from 1985-2012. Red segmented line indicates commencement of nutrient addition program on Kootenay Lake in 1992. Data has been updated to reflect survival estimates above 100%, based on inaccuracies within hydroacoustic estimates.

Dynamic Factor Analysis (DFA)

Use of the DFA was particularly important in determining the relationship and dynamics of the predator-prey interactions in Kootenay Lake, particularly between Gerrard Rainbow Trout and Kokanee. The model was able to simultaneously estimate (1) the effects of explanatory variables (prey abundance), (2) common patterns in non-stationary time series and (3) interactions between response variables (growth and condition). Posterior predictions for parameters estimates are summarized in Appendix 8.

The DFA model outputs indicated substantially similar trends between condition and growth of Gerrard Rainbow Trout over time (Figure 12). Moreover the analysis also revealed that Kokanee abundance at select age classes were important predictors of condition and growth of Gerrard Rainbow Trout > 50 cm (Figure 12). Abundance of age 2

Kokanee, appear to be the most important explanatory variables in predicting the patterns in observed condition and growth of Gerrard Rainbow Trout (also see below (Figure 12). Age 1 were a predictor, but to a lesser extent than age 2 .Meanwhile, age 0 kokanee abundance was not an important predictor condition and growth of Gerrard Rainbow Trout (Figure 12). The model results clearly indicate poor growth and condition of the fish sampled during 2013 and 2014.

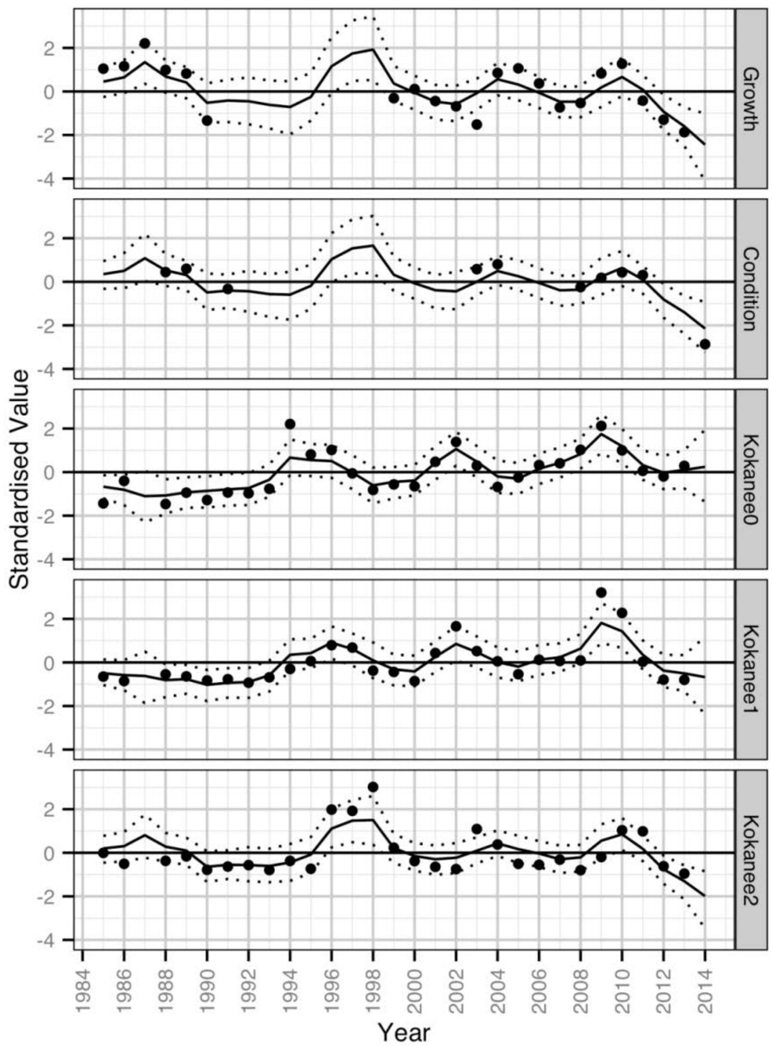

Figure 12. DFA predicted standardized variables values by year (with 95% CRIs) from time series of response variable condition and growth of Gerrard Rainbow Trout (> 50 cm) based on samples from Kootenay Lake fishery including; 1966, 1978-1980, 1988-1992, 2003-2004, and 2008-2014. As well, predictor variables that include Kokanee abundance by age class on Kootenay Lake from 1985-2013.

Somewhat similar to a principal component analysis (PCA), the DFA analysis indicates a dissimilarity/distance (correlation) matrix between response variables and explanatory variables using non-metric multidimensional scaling (NMDS). The NMDS indicated abundance of age 2 kokanee was the best explanatory variable for predicting the condition and growth of Gerrard Rainbow Trout > 50 cm (Figure 13). Abundance of age 1 Kokanee were more similar compared to age 0 Kokanee. However, both age 1 and to age 0 Kokanee were the most dissimilar or farthest distance apart from predicting the observed time series patterns in Gerrard Rainbow Trout (Figure 13). Growth, condition and age 2 Kokanee were the most similar, indicated the closest distances to each other, and were the primary predictors of the observed patterns within the time series (Figure 13).

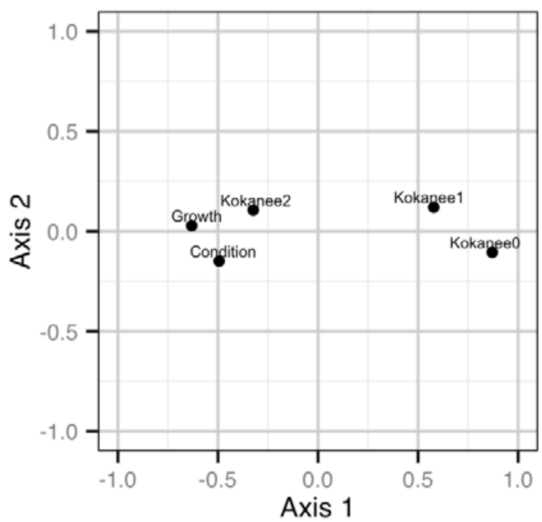

Figure 13. The non-metric multidimensional scaling (NMDS) from DFA analysis. Plot indicates a dissimilarity/distance (correlation) matrix between response variables (growth, condition) and explanatory variables (Kokanee abundance).

DISCUSSION

Obtaining data for this growth and condition study on Gerrard Rainbow Trout in Kootenay Lake was difficult. Poor fishing conditions and factors related to declining fish condition proved problematic in obtaining a good number of samples from the recreational fishery. Moreover, due to the poor condition of many of the fish encountered most anglers chose not retain their fish, increasing the difficulty in obtaining samples. As a result, no fecundity samples were collected from the recreational fishery in 2014 and the study relied upon samples collected in 2003 and 2004 (Andrusak and Andrusak 2006). Most biological samples from the recreational fishery obtained in 2013 and 2014 were obtained by a commercial guide charter licensed for the lake (Kerry Reed; Reel Adventures). Stationing a person at scheduled derbies proved to be inefficient and costly with low angler participation and very few fish harvested.

Growth and condition of fish are fundamental measures utilized in assessing factors that influence fish populations over the course of their life (Anderson and Neumann 1996). An assessment of growth and condition requires a good understanding of the ecology and life history of the focus species and the multitude of factors that affect these metrics (Saborido-Rey and Kjesbu 2012). Availability of resources (prey) is considered to a major factor influencing growth and condition (Essington et al. 2001) and variable prey density and abundance can have a profound effect on growth and condition indices for piscivorous fish populations (Hansen et al. 2010). Due to their highly piscivorous behaviour (Irvine 1978, Andrusak and Parkinson 1984, Keeley et al. 2007) Gerrard Rainbow Trout in Kootenay Lake provided an unique opportunity to assess how primary prey (Kokanee) abundance influence their growth and condition over time.

Our assessment of annual condition of Gerrard Rainbow Trout, which explicitly accounted for individual variation in the mass-length, provided reliable indices of fish condition on Kootenay Lake. Our approach makes better use of limited data and provides a statistical inference in comparison to conventional assessments of fish condition (Fulton's Condition factor; K). Conventional assessments are often limited due to differences in how body condition varies among fish of different ages and lengths, a tendency that can lead to substantial bias (He et al. 2008). Our results suggest that fish condition has been relatively stable over time on Kootenay Lake since lake fertilization commenced until 2013-2014, when condition declined significantly. The condition indices time series demonstrates patterns which appear to coincide with sharp declines in prey abundance, especially for age 1 and age 2 Kokanee illustrated in Figure 12. As a result of a rapid decline in prey abundance since the record high in 2009, Gerrard Rainbow Trout > 50 cm in 2014 were approximately 22% lighter in weight for a given length of fish compared to all other year's data. This observation has been substantiated by angler dissatisfaction with the poor fishing conditions observed on Kootenay Lake in 2013 and 2014 (Kerry Reed Angling Guide Nelson BC pers. comm.).

Use of back-calculated growth from scale increments relies on a fundamental principle that scale radius is proportional to fish length (Francis 1990) and species that exhibit a non-linear body-scale relationship require a different method for estimating historic growth information (Pierce et al. 1996). Our analysis of the Rainbow Trout body-scale relationship indicated that the assumed linear relationship appears to deviate for the smallest and larger fish which violates the fundamental assumption in utilizing back-calculated length at age to assess growth over time. We believe the observed deviation from the linear relationship may be a real phenomenon associated with this species and their life history characterized by relatively fast growth and potentially early maturation. The deviations were most evident in larger fish and it is hypothesized that as these fish grow rapidly and mature the allocation of energy from somatic growth is transferred to reproductive growth and development described by Saborido-Rey and Kjesbu (2012). Growth and reproduction requirements involve the allocation of energy over the lifetime of an individual fish, as summarized in Figure 14. As a result, allocation of energy to maturation and reproduction may elicit declines in somatic growth (Quince et al. 2008a, 2008b), as evidenced by decreasing scale increments in most older and larger fish.

Despite the shortcomings associated with back-calculation of growth (Francis 1990), scale increments can be used as a relative measure of growth when the relationship with scale radius is known (Pierce et al. 1996). In our study, scale increments by year suggested that these increments could be used as a relative measure for predicting previous growth. Our analysis revealed that growth may have been slightly higher in the late 1980s compared to the nutrient addition era, but also displayed much lower growth in 2013 and 2014. It is acknowledged that comparisons of annual growth can be somewhat misleading since underlying factors (biotic and abiotic) are difficult to assess in such analysis. To overcome such concerns, time series modelling offers an advantage which allows more effective use of the information contained in long time series across many indicators (Parkinson and Arndt 2014). Consequently, information from scale increments can be used to assess factors that drive important trends in growth in Gerrard Rainbow Trout over time.

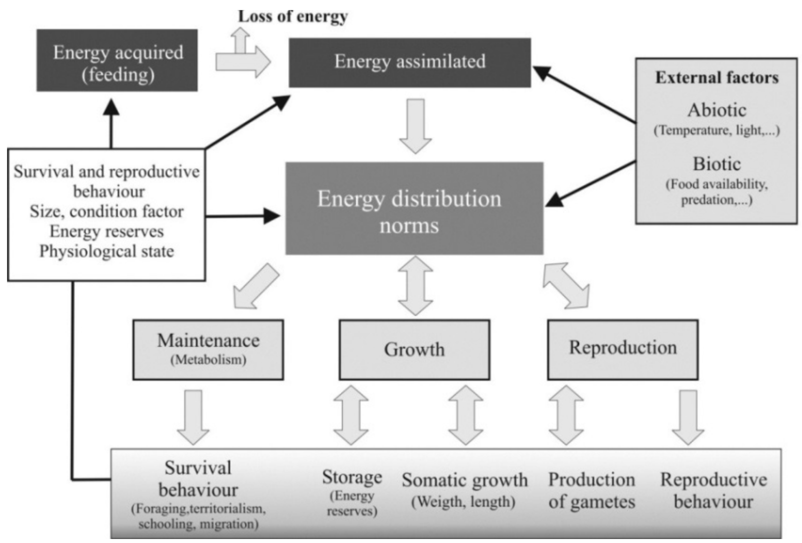

Figure 14. **Schematic representation of energy flow allocation norms. Open arrows represent energy routes while solid arrows represent factors affecting energy allocation. Energy allocated for maintenance, growth and reproduction is partitioned between survival, storage of energy reserves, somatic growth, and reproductive activity taken from Saborido-Rey and Kjesbu (2012) based on van Winkle et al. (1997) in Chambers and Trippel (1997).**

Dynamic factor analysis has provided a useful tool in assessing multivariate time series data, especially within fisheries stock assessment (Zuur et al. 2003b). But unlike traditional population dynamics modelling (i.e. growth and condition), which has difficulty in elucidating meaningful covariates to explain common patterns or trends, DFA can provide a simple statistical assessment of the most complex multivariate time series datasets. Common trends in response variables can be predicted by numerous environmental explanatory variables, similar to a regression analysis (Zuur et al. 2003b). Based on our study, Kokanee abundance was a strong predictor of the observed patterns in condition and growth of Gerrard Rainbow Trout in Kootenay Lake over the period of record. Despite the one year time lag in growth and condition estimates, the years when Kokanee abundance was high appear to have the most influence on the growth and condition of the predators. Therefore any management decisions related to varying Kokanee production at the Meadow Creek Spawning Channel (MCSC), the primary producer of Kokanee (Schindler et al. 2014), should consider the affects upon predator populations and how these factors relate to the once prominent recreational fishery (Andrusak and Andrusak 2012).

It is well understood that Kokanee are the primary prey source for Gerrard Rainbow Trout on the lake (Andrusak and Parkinson 1984). Therefore, it is not surprising that our analysis indicated that Kokanee abundance is an important predictor of growth and condition of this unique ecotype. Moreover, it is also not surprising that analysis demonstrated that that age 2+ Kokanee were the best predictor of growth and condition. Age 2+ abundance was also found to be an important predictor of condition in Bull Trout on Arrow Lakes (Parkinson and Arndt 2014). With the onset of piscivory near 30 cm, selection of prey size increases with predator size (Andrusak and Parkinson 1984, Parkinson et al. 1989; Keeley and Grant 2001). However, as prey and predator size increase, an optimal prey-size range is established that maximizes the relation between the energy obtained and the energy used to catch the prey (Harper and Blake 1988). A relative preference of piscivorous Rainbow Trout for Kokanee suggests an optimal predator-prey ratio between 0.15-0.20 (Parkinson et al. 1989), as displayed in Figure 15 . Various other studies have demonstrated similar relative preferences for Bull Trout and Rainbow Trout (Beauchamp and Van Tassell 2001, Keeley and Grant 2001, Arndt 2004). Our study only included piscivorous Rainbow Trout > 50 cm (range 50-90 cm), hence the relative preference for Kokanee prey selection ranged between 75-180 mm. Depending on the time of the year, this range falls well within the age 1 and age 2 Kokanee size range (Figure 10), which has not varied substantially since 1985.

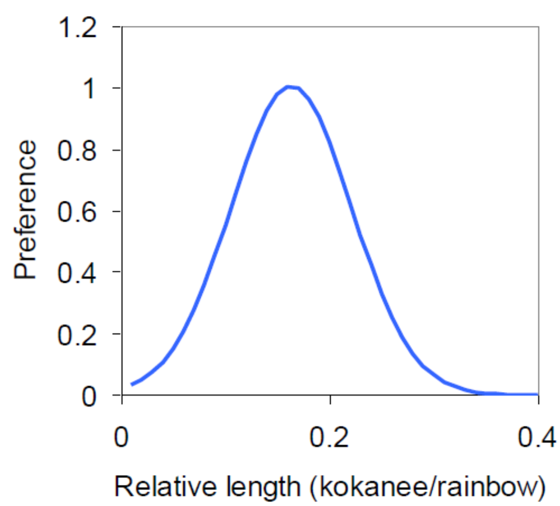

Figure 15. Relative preference of piscivorous Rainbow Trout for Kokanee as a function of relative lengths of the Kokanee and the Rainbow Trout taken from Kurota et al. (2011)

The recent collapse of the Kokanee population in Kootenay Lake appears to be associated with high predation mortality most notably by Bull Trout and Gerrard Rainbow Trout. While no direct assessment of predation induced mortality was conducted, increased predation has been implicated in the collapse of a number of prey populations, particularly related to Kokanee populations (Vidergar 2000, Hansen et al. 2010, Ellis et al. 2011). High predation mortality associated with Lake Trout (*Salvelinus namaycush*) has been implicated in the collapse of Kokanee population on Lake Pend Oreille, Idaho (Hansen et al. 2010). A similar collapse occurred on Flathead Lake where high predation rates on Kokanee were due to the non-native introduction of Lake Trout combined with direct competition with kokanee for macro-zooplankton, predominately the introduced opossum shrimp, *Mysis diluviana* (Ellis et al. 2011). On Kootenay Lake, the recent Kokanee collapse has coincided with exceptional increases in Gerrard Rainbow Trout spawner numbers during 2009-2013 that represent the highest escapements in over fifty years (Figure 16). Based on the hydroacoustics data, it appears the Kokanee collapse started in 2012 when the age 1 cohort of Kokanee declined drastically. Kurota et al. (2011) also predicted the highest predation mortality occurred within the age 1's on the lake. We believe the dramatic increase in the Gerrard Rainbow Trout population, reflected in their spawner numbers, is due to improved growth and survival conditions in the lake, a desired outcome of the nutrient restoration program described by Schindler et al (2014). As well, increased abundance could be attributed to the commencement of South Arm nutrient addition and angling regulation changes implemented in 2004. Long term increases in juvenile trout in-lake survival, translating into increased predator numbers, have been implicated in the Kokanee collapse on Flathead Lake (Ellis et al. 2011). Likewise, it is believed that long-term (10-15 years) increases in juvenile predator survival may have contributed to a surge in the predator populations within Kootenay Lake, drastically increasing predation mortality and ultimately collapsing the Kokanee population. The current situation on Kootenay Lake was also somewhat predicted from a non-equilibrium prey-predator interaction model that was constructed and fitted to a 40-year time series (Kurota et al. 2011).

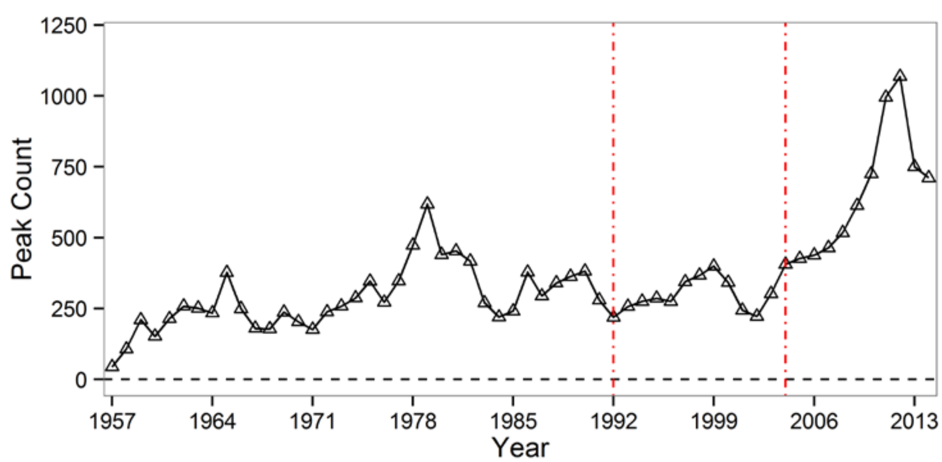

Figure 16. Gerrard rainbow trout spawner peak count from 1957-2013. Vertical lines represent the commencement of North Arm (1992) and South Arm (2004) nutrient addition (data from MNFLRO file data).

Implications

This study was aimed at determining Gerrard Rainbow Trout growth rates during a period of low Kokanee densities in Kootenay Lake. The results clearly demonstrate a decline in growth and condition of these trout at a time when Kokanee abundance is at an all-time low. Our calculations of present day growth and condition of the Gerrard Rainbow Trout strongly suggest this population is likely in rapid decline. These trout rely on fast growth to attain a large size before maturation, and will predictably experience an immediate decrease in abundance in response to deteriorating growth conditions. In the longer term, it could be expected that a decline in predator abundance could potentially provide a benefit to the Kokanee population recovery through reduced predation mortality, similar to that experienced on Lake Pend Oreille (Hansen et al. 2010). However, there is concern that predation mortality may not decline proportionally with decreasing prey densities since Gerrard Rainbow Trout are highly efficient predators even under low prey densities (Walters et al. 1991, Parkinson and Korman 1994). Therefore, until direct management actions are taken to increase Kokanee abundance, the recovery of the Gerrard Rainbow Trout population is likely to involve a long period of time, possibly 10-15 years.

Recovery of the Kokanee population itself will be difficult despite improved lake productivity due to annual nutrient additions and the ability to control the majority of Kokanee production via the MCSC. Long-term effects of a trophic cascade (middle out and top down effects) in a large lake ecosystem such as Kootenay Lake potentially could delay the recovery process. For example, reduced Kokanee densities could create a competitive response in *Mysis diluviana* and elicit “middle out effects” within the food chain (Chipps and Bennett 2000), which may further complicate the recovery of the Kokanee population. However, monitoring data indicated that Mysis did not indicate a substantial change over the time period (M. Bassett pers. comm MFLNRO) Interestingly, the “middle out effects” were originally a predicted outcome of the Kootenay Lake Response Model by Walters et al. (1991) prior to the commencement of lake fertilization, also described in Walters and Martell (2004).

The other primary Kootenay Lake piscivore, Bull Trout will undoubtable play a major role in how quickly Kokanee can recover. Bull Trout are likely better adapted to the current slower growing environment and lower prey densities (McPhail and Baxter 1996, McPhail 2007, Hagen and Decker 2011). With reduced prey numbers it is quite likely that the Bull Trout population will delay maturation and forgo spawning events since these require a substantial allocation of energy and resources (Johnston and Post 2009). This may already have started in Kootenay Lake based on spawner redd count indices which demonstrate severe declines beginning in 2013 (Figure 17 from Andrusak (2014). Often, environmentally induced changes in growth produce variation in the phenotypic expressions of size and age at maturation traits, known as phenotypic plasticity (Roff 1992). This phenotypic plasticity induced by environmental changes, will likely allow Bull Trout, compared to Gerrard Rainbow Trout, to endure the impact of declining Kokanee abundance in the short-term.

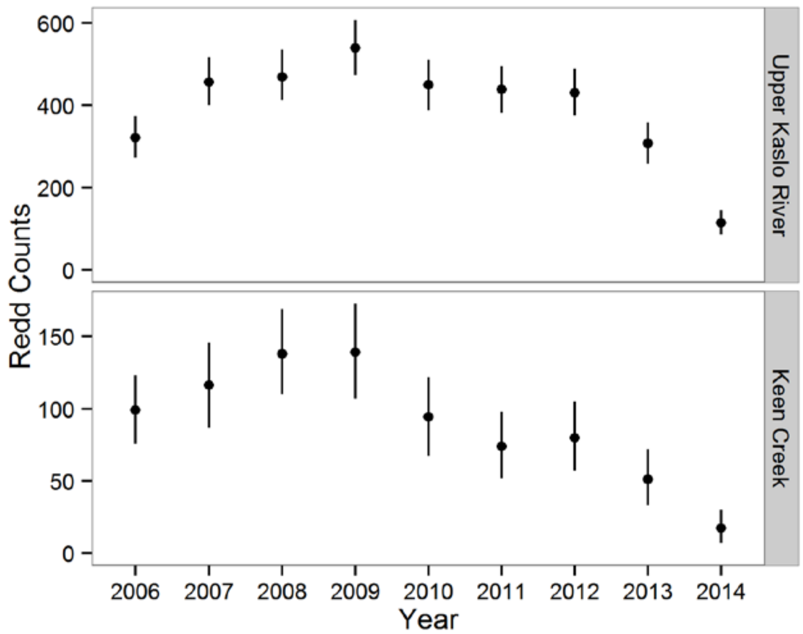

Figure 17. **Bull Trout redd count data (with 95% CRIs) on Kootenay Lake from Kaslo River and Keen Creek since 2006 taken from Andrusak 2014.**

Kootenay Lake fisheries management has historically aimed at providing an abundance of kokanee for the predators (Andrusak and Brown 1987, Andrusak and Andrusak 2012). Andrusak and Brown (1987) recognized the reliance of Kokanee by the predators and indicated the necessity of management to ensure an annual Kokanee escapement of 1 million in order to sustain the predator populations. More recently, Kurota et al. (2011) indicated that negative impacts to the predators appear at kokanee spawner abundances below 0.5 million. Current Kokanee escapements have plunged to levels well below these targets with returns of only 435,700 and 147,148 in 2013 and 2014 (MFLNRO on file).

The current decline in Kokanee abundance provides highly informative data towards the density-dependent growth relationship for Kootenay Lake Kokanee, and whether an improved angling opportunity exists for the prey species. Data from Kootenay Lake since 1992 (commencement of nutrient addition) indicates that spawner size (mm) increases as spawner density (spawner/ha) declines, especially between 10-20 fish/ha (Figure 18). These densities represent a range of fish sizes (>230 mm) that are most vulnerable to angling and are required to sustain a fishery (Rieman and Maiolie 1995, Askey and Johnston 2013). However, the growth response in Kootenay is still lower than Okanagan Lake where Askey and Johnston (2013) documented a Kokanee fishery collapse. The recent Kokanee escapements in Kootenay Lake are extremely low and spawner size is increased substantially to 28 cm in 2013 and 32 cm in 2014 (28cm in 2013). Despite the size increase, there appears to be limited opportunity to try to meet recreational angler size and catch rate preferences needed for a high effort Kokanee fishery on this lake (P. Askey pers. comm.). Therefore, managers are left only with an option to manage Kokanee as a prey resource, with a small secondary fishery for those anglers who are not dissuaded by smaller fish since there are trade-offs (Parkinson et al. 2004). Askey and Johnston (2013) suggest there would be no value in lowering bag limits or closing the main lake Kokanee fishery, as the inherent angler effort dynamics are expected to have severely reduced harvest in recent years.

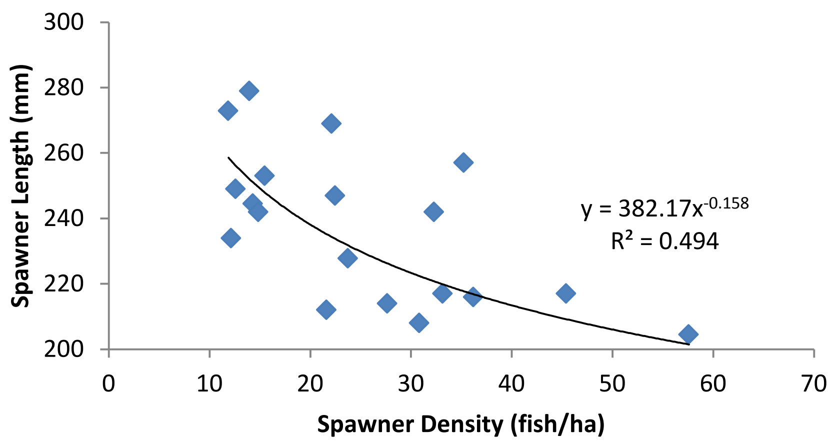

Figure 18. Relationship between spawner size (mm) and spawner density (fish/ha) on Kootenay Lake since 1992. Data from MFLNRO hydroacoustic data.

The rapid decline in Kokanee abundance appears to be associated with survival transitions from 0 to 1 and 1 to 2, since age-0 abundance has remained relatively constant (Figure 11). There are at least two alternative plausible hypotheses as to why mortality may increase after the fall fry stage: (1) predation mortality: increased predation as Kokanee recruit to a size preferred by predators, or (2) competition mortality: a change in in-lake conditions whereby fry abundance is overshooting the new lake capacity. The second hypothesis does not seem likely given there is a notable growth response among the same cohorts experiencing increased mortality, however, a careful check of fertilization protocols and results from recent years should be conducted. If the increased mortality rate is due to predation, as opposed to competition, then one option is to simply try and overcome the poor survival by compensating with enhanced fry densities. Therefore, assuming that survival is lower, but that older age classes are still positively correlated to fry abundance, then management efforts could be to maximize fry production at MCSC despite decreases in survival.

Hydroacoustic data supports the fact that age 1+ and age 2 + abundance is typically a function of increasing fry abundance (cohort strength), as displayed in Figure 19 and Figure 20. As an example, Table 6 demonstrates the importance of the numerical abundance within a cohort (10 million vs 20 million fry) at differing levels of assumed survival: 1) annual survival at 0.35 yr^{-1} for smaller cohort) 2) annual survival at 0.20 yr^{-1} for larger cohort. This example clearly demonstrates the importance of providing high abundance of fry despite the decreased survival the cohort would experience.

Table 6. Example of varying levels of annual survival (exponential) of a cohort based on two fry production targets from MCSC.

Survival	Age0	Age1	Age2	Age3	Spawners
35%	10,000,000	5,220,458	2,725,318	1,422,741	742,736
20%	20,000,000	8,986,579	4,037,930	1,814,359	815,244

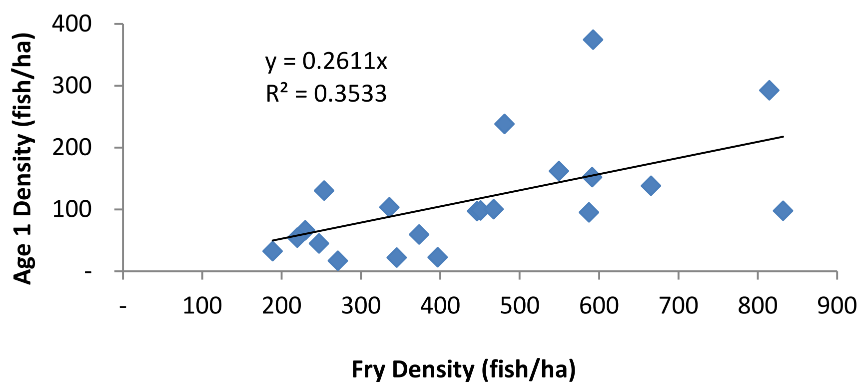

Figure 19. Relationship between Age 1+ density (fish/ha) and fall fry density (fish/ha) in Kootenay Lake since 1992. Data from MFLNRO hydroacoustic data.

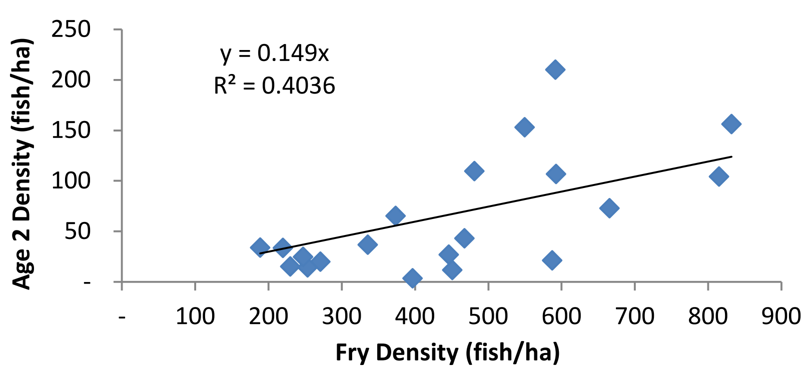

Figure 20. Relationship between Age 2+ density (fish/ha) and fall fry density (fish/ha) in Kootenay Lake since 1992. Data from MFLNRO hydroacoustic data.

In summary, the recent collapse of the Kokanee population on Kootenay Lake has created a serious imbalance in the predator-prey dynamics within the lake. Kokanee are known to be a keystone species in this ecosystem, and their abundance is an important determinant of growth, condition and ultimately survival of predators within the lake. The recent poor growth and condition of Gerrard Rainbow Trout is likely related to a substantial top down effect by the top predators that have driven prey densities to unprecedented low numbers. Currently, it is unknown, but expected that lower returns of Gerrard and Bull Trout to spawning grounds represents energy conservation (skipping/delaying a reproductive event) as opposed to actual mortality. If predation is the causal factor, predation mortality on Kootenay Lake appears to act as depensatory mechanism directly affecting the abundance, distribution, and age or size structure of prey (Hilborn and Walters 1992, Walters and Kitchell 2001, Liermann and Hilborn 2001). Therefore, as recent weak year classes of kokanee grew in the lake they were likely subject to increasingly high predation pressure. Low recruitment by particular cohorts, coupled with stochastic increases in mortality ultimately created an imbalance causing a precipitous decline in the kokanee population. Re-building the Kokanee population should be considered the highest priority, and could be a challenge given the notable predator populations in Kootenay Lake. While the link between Rainbow trout condition in large piscivores and survival is not known, given the severe decline in Gerrard Rainbow Trout condition and growth to unprecedented levels, it is plausible that the population will decline to a level not observed in over fifty years. The Bull trout population may also be expected to decline but owing to differences in their ability to adapt to a slower growing environment they will likely fare better than Gerrard Rainbow Trout. All these factors will undoubtable create substantial declines in effort and angling quality in recreational fishery on Kootenay Lake in the foreseeable future (Redfish Consulting Ltd 2007, Andrusak and Andrusak 2012). Moreover, the decline effort and associated the downturn in the fishery may have a negative implications upon the local economy that rely on the fishery.

Recommendations

1. Increase kokanee numbers in Kootenay Lake to ensure a minimal escapement of >1.0 million Kokanee spawners.

2. Implement management actions to increase Kokanee abundance (egg plants, predator reductions through regulations)

3. Assess biphasic growth models (Quince et al. 2008b). separation of growth into two phases, early juvenile growth and sub-adult/adult growth phases

4. Determine if changes in somatic growth are due to maturation and growth and energy allocated to reproduction.

5. Instruct local guides to record length and weight statistics, and recover scales, so that sample sizes and time series can be maintained

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Appendix 1. Summary Data

ID	Year	Age	N	Length	± SD	Weight	±SD
1	1966	3	20	388	86.4	0.7	0.6
2	1966	4	35	481	72.0	1.4	0.7
3	1966	5	23	619	78.9	NA	NA
4	1966	6	11	710	82.8	4.4	1.2
5	1966	7	12	750	49.5	5.3	1.6
6	1966	8	2	795	7.1	6.6	2.2
7	1966	NA	584	539	174.8	2.5	2.3
8	1978	6	1	610	NA	3.4	NA
9	1978	7	1	838	NA	5.9	NA
10	1978	8	1	870	NA	8.6	NA
11	1979	5	1	698	NA	4.9	NA
12	1979	6	1	686	NA	4.1	NA
13	1979	7	3	794	50.6	6.4	1.6
14	1979	8	1	749	NA	7.3	NA
15	1979	NA	1	762	NA	7.1	NA
16	1980	7	1	0	NA	6.4	NA
17	1988	4	3	714	129.9	5.3	2.5
18	1988	5	10	740	68.2	5.5	1.5
19	1988	6	3	830	69.9	NA	NA
20	1988	7	2	841	13.5	8.3	0.2
21	1988	NA	7	776	57.6	6.2	1.8
22	1989	4	4	645	60.8	3.3	1.0
23	1989	5	13	734	65.3	5.3	1.4
24	1989	6	6	806	49.3	7.4	1.1
25	1989	7	3	838	67.2	NA	NA
26	1989	NA	12	633	235.7	5.3	2.4
27	1990	4	1	432	NA	0.8	NA
28	1991	6	3	864	66.0	8.4	1.6
29	1991	NA	3	745	80.3	5.3	2.6
30	1992	7	1	0	NA	6.8	NA
31	2003	3	3	482	51.7	1.5	0.2
32	2003	4	3	575	70.7	1.7	0.3
33	2003	5	9	644	126.8	4.5	2.5
34	2003	6	11	754	87.2	6.1	1.1
35	2003	7	3	800	104.0	7.3	1.7
36	2003	NA	6	695	168.8	4.9	2.9
37	2004	2	4	261	13.2	0.2	0.0
38	2004	3	14	339	95.7	NA	NA
39	2004	4	30	475	141.9	NA	NA
40	2004	5	34	645	162.4	4.2	1.8
41	2004	6	38	733	99.9	5.8	2.3
42	2004	7	27	808	74.4	7.6	1.9
43	2004	8	8	822	80.4	7.6	2.6
44	2004	NA	4	727	123.7	6.6	2.6
45	2008	3	21	328	42.1	NA	NA
46	2008	4	4	350	62.9	NA	NA
47	2008	5	11	511	84.8	NA	NA
48	2008	6	9	550	118.0	NA	NA

49	2008	7	6	665	38.4	NA	NA
50	2008	NA	8	318	44.3	NA	NA
51	2009	2	2	311	84.9	0.4	0.3
52	2009	3	7	398	31.9	0.7	0.2
53	2009	4	13	420	70.2	NA	NA
54	2009	5	18	564	93.7	2.2	1.2
55	2009	6	18	608	89.9	3.0	1.2
56	2009	7	9	685	69.8	4.5	1.4
57	2009	NA	10	433	137.0	NA	NA
58	2010	2	3	331	42.4	NA	NA
59	2010	3	10	430	58.3	NA	NA
60	2010	4	14	503	73.9	NA	NA
61	2010	5	20	558	75.3	NA	NA
62	2010	6	9	684	31.1	4.1	0.8
63	2010	7	6	715	44.1	5.0	1.1
64	2010	8	1	769	NA	6.6	NA
65	2010	NA	26	404	105.8	NA	NA
66	2011	NA	104	561	156.8	NA	NA
67	2012	NA	27	656	93.5	NA	NA
68	2013	6	3	682	85.2	NA	NA
69	2013	7	3	767	110.2	NA	NA
70	2013	8	1	720	NA	NA	NA
71	2013	NA	9	661	104.3	NA	NA
72	2014	6	6	745	57.1	3.7	0.8
73	2014	7	13	743	88.5	4.3	1.6
74	2014	8	4	749	73.1	4.2	1.4
75	2014	NA	7	720	85.2	3.7	1.2

Appendix 2. Kootenay Lake Kokanee Abundance (MFLNRO Hydroacoustics)

ID	Year	Age 0	Age 1	Age 2	Age 3	Total all ages	Spawners
1	1985	3,630,000	1,334,103	2,016,667	279,231	7,260,000	1,501,100
2	1986	11,603,512	648,799	1,023,105	224,584	13,500,000	697,600
3	1988	3,400,660	1,685,283	1,294,057		6,380,000	767,900
4	1989	7,423,643	1,368,605	1,700,388	207,364	10,700,000	523,000
5	1990	4,808,922	732,788	480,892	137,398	6,160,000	475,000
6	1991	7,479,751	930,124	775,104	155,021	9,340,000	347,100
7	1992	7,212,801	390,618	908,413	18,168	8,530,000	547,200
8	1993	8,790,000	1,218,451	460,634	430,915	10,900,000	845,000
9	1994	31,780,000	2,510,286	1,287,886	21,829	35,600,000	1,233,000
10	1995	21,000,000	3,721,029	572,466	6,505	25,300,000	858,100
11	1996	22,600,000	6,181,282	5,956,053	162,665	34,900,000	1,178,000
12	1997	14,270,000	5,807,355	5,840,165	262,479	26,180,000	1,444,200
13	1998	8,400,000	2,248,680	8,012,903	538,416	19,200,000	2,200,000
14	1999	10,360,000	2,050,323	2,489,677		14,900,000	1,734,700
15	2000	9,690,000	636,667	1,273,333		11,600,000	567,700
16	2001	18,380,000	4,967,368	752,632		24,100,000	591,300
17	2002	25,430,000	9,091,528	542,778	135,694	35,200,000	464,000
18	2003	17,049,000	5,263,848	4,187,152		26,500,000	1,056,100
19	2004	9,450,000	3,692,578	2,782,813	374,609	16,300,000	1,382,600
20	2005	12,830,000	1,703,125	1,021,875	545,000	16,100,000	1,266,700
21	2006	17,230,000	3,933,462	936,538		22,100,000	481,000
22	2007	17,859,000	3,735,840	1,400,940	350,235	23,346,015	533,700
23	2008	22,644,000	3,827,896	445,104		26,917,000	1,346,000
24	2009	31,130,000	14,295,903	1,642,097		47,068,000	907,500
25	2010	22,443,000	11,157,397	4,075,762	152,841	37,829,000	825,958
26	2011	15,162,366	3,622,974	3,978,167		22,763,507	1,764,000
27	2012	13,197,000	851,057	806,264	716,679	15,571,000	1,255,860
28	2013	16,933,171	838,940	132,464	132,464	18,037,040	453,700

Appendix 3. Kootenay Lake Kokanee Mean Size (MFLNRO Hydroacoustics)

Year	Age 0	Age 1	Age 2	Age 3	Spawners
1985	54	132	171	184	206
1986	54	120	179	187	205
1988	59	137	173		206
1989	55	130	175	186	210
1990	57	154	188	199	214
1991	57	134	214	218	224
1992	59	147	210	248	245
1993	56	148	189	212	269
1994	59	138	213	227	242
1995	60	146	189	230	247
1996	55	132	180	186	208
1997	58	139	177	198	196
1998	54	149	186	206	205
1999	56	117	190		217
2000	57	120	214		242
2001	56	126	203		253
2002	54	140	188		234
2003	57	137	187		214
2004	53	119	183	189	216
2005	53	116	199	216	217
2006	58	128	221		249
2007	56	128	206		279
2008	55	129	191		257
2009	51	128	186		228
2010	48	131	168	197	212
2011	51	134	174		200
2012	56	124	174	182	199
2013	57	109	246	262	273

Appendix 4. Fecundity

Parameter	Estimate	Lower 95% CRI	Upper95% CRI	SD	Error	Significance
bAlpha	8.97314	8.93770	9.00968	0.01825	0	7e-04
bBeta	1.75510	1.40700	2.10020	0.17130	20	7e-04
sFecundity	0.07817	0.05534	0.11306	0.01483	37	7e-04

Convergence	Iterations
1	1000

Appendix 5. Condition

Parameter	Estimate	Lower 95% CRI	Upper95% CRI	SD	Error	Significance
bAlpha	1.31830	1.25770	1.37980	0.03170	5	0.0010
bAlphaDayte	-0.01216	-0.02547	0.00051	0.00667	110	0.0619
bAlphaDayte2	0.02217	0.01006	0.03423	0.00616	55	0.0010
bBeta	3.26200	3.18840	3.34160	0.03870	2	0.0010
sAlphaYear	0.10080	0.06310	0.16610	0.02640	51	0.0010
sWeight	0.15757	0.14981	0.16548	0.00406	5	0.0010

Convergence	Iterations
1	1.0E+05

Appendix 6. Age

Parameter	Estimate	Lower 95% CRI	Upper95% CRI	SD	Error	Significance
bK	0.16708	0.15351	0.18307	0.00793	9	0.0010
bKReader[2]	-0.03040	-0.08680	0.02220	0.02740	180	0.2555
bKReader[3]	0.62150	0.51260	0.71200	0.05310	16	0.0010
bLInf	925.64000	907.44000	947.37000	10.43000	2	0.0010
bT0Reader[2]	-0.17060	-0.49070	0.11740	0.15280	180	0.2615
bT0Reader[3]	2.20110	1.71600	2.60940	0.25130	20	0.0010
Convergence	**Iterations**					
1.09	10000					

Appendix 7. Back-calculated Growth

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bInc	1.5957	1.5217	1.6634	0.0359	4	0.001
bIncScaleRadius	0.16301	0.1371	0.1906	0.0141	16	0.001
bIncScaleRadius2	-0.09404	-0.1167	-0.0717	0.012	24	0.001
bSDInc	-0.96241	-1.0017	-0.92	0.0214	4	0.001
bSDIncProbability	0.02379	-0.0214	0.0688	0.0228	190	0.2955
sIncYear	0.1468	0.0954	0.2182	0.0321	42	0.001
Convergence	**Iterations**					
1.01	1.00E+05					

Appendix 8. Dynamic factor Analysis

Parameter	Estimate	Lower 95% CRI	Upper95% CRI	SD	Error	Significance
sTrend	0.7764	0.4964	0.9841	0.1296	31	0.001
sValue	0.6228	0.5035	0.786	0.0723	23	0.001
Convergence	**Iterations**					
1.07	1.00E+05					