

**What Happened to the West Arm Burbot Stock in Kootenay Lake?
Use of an Age-Structured Population Model to Determine the Possible Causes
for Recruitment Failure**

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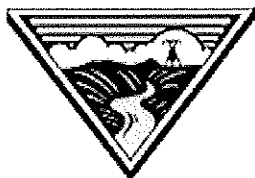
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Summary

The West Arm of Kootenay Lake once supported a significant burbot (*Lota lota*) fishery with an annual harvest of up to 20,000 fish in the late 1960's to early 1970's. Catches declined precipitously beginning in the mid 1970's and by the mid-1980's catches were typically less than 400 fish resulting in the fishery being closed to angling in 1997. As a consequence of the low numbers of burbot in Kootenay Lake and the Kootenai River, fisheries agencies in B.C. and Idaho initiated activities to review the status of this species in the Kootenay drainage and identify recovery options. A team of biologist led by the Ministry of Water, Land and Air Protection initiated a modeling exercise to address two main questions with regards to the West Arm burbot stock: 1) What were the principal factors that caused the stock to decline? and 2) What are the most feasible options for rebuilding the stock.

An age-structured population dynamics model incorporating standard methods for representing recruitment, survival, and vulnerability was used to predict natural population age structure and track possible changes in stock size associated with fishery removals and apparent recruitment (modeled as age 1 individuals) failure in recent decades for the Kootenay Lake West Arm burbot. Predicted recruitment anomalies were compared to various environmental indices to see if such indices matched the trend estimated for recruitment failure. The of environmental indices explored encapsulated: changes in nutrient loading, shifts in the zooplankton communities, variation in lake elevation and flow associated with changes in dam operations, variation in juvenile habitat and changes in the fish community composition.

Modeling results suggested that the burbot population size prior to 1967 was approximately 200,000 individuals. The estimated trend in age 1 recruitment indicated a substantial increase of recruits in the early 1960's, peaking in 1964 and failing by the late 1960's. It seem reasonable to assume the burbot fishery collapsed as a result of the recruitment failure but, the collapse was accelerated, substantially, by unsustainable harvest rates. Recruitment anomalies did not correlate well with environmental indices that changed as a result of dam operations. Recruitment failure occurred before 1970 and changes in the lake environment due to dam operations did not occur until after 1975. Changes in nutrient loading to the lake were also a poor correlate with recruitment since nutrient loads peaked in 1967, three years after the predicted recruitment peak. The best correlation resulted when cladoceran densities were used. It is likely that changes in the West Arm community structure, most noticeably the increases in mysid densities, resulting from increased productivity (via nutrient loading) caused a substantial reduction in the cladoceran community through competition and predation. The increase and subsequent collapse, in 1964, of the cladoceran community likely resulted in a catastrophic reduction in juvenile burbot food resources resulting in recruitment failure. The exact mechanism, which resulted in recruitment failure, can only be speculated.

All participants at the workshops acknowledged that establishing a West Arm burbot population will require, in the short term, an experimental stocking or transplant program. Mature individuals could be captured in Duncan Lake and/or Trout Lake and transplanted into the West Arm. There were a number of uncertainties associated with stocking or transplanting burbot. There was a reasonable amount of scepticism about whether stocking or transplanting would result in a viable, self-sustaining West Arm stock. There was

considerable uncertainty as to whether juvenile burbot can survive in the West Arm given the large biomass of northern pikeminnow and largescale sucker that have been observed in recent years as well as uncertainty as to the current cladoceran density. It was also hypothesized that the original stock had unique local adaptations cuing it to spawn on shoals near Balfour and rear in West Arm habitats downstream of the spawning area, and that it may be wishful thinking to assume that individuals from a hatchery or transplanted from another system will adopt the necessary life history characteristics.

1.0 Introduction

The West Arm of Kootenay Lake once supported a significant burbot (*Lota lota*) fishery with an annual harvest of up to 20,000 fish in the late 1960's to early 1970's. Catches declined precipitously beginning in the mid 1970's and by the mid-1980's catches were typically less than 400 fish. The fishery was eventually closed to angling in 1997 (Andursak 1998). As a consequence of the low numbers of burbot in Kootenay Lake and the Kootenai River, fisheries agencies in B.C. and Idaho initiated activities to review the status of this species in the Kootenay drainage and identify recovery options. With regards to the West Arm burbot stock, two questions remain: 1) What were the principal factors that caused the stock to decline? and 2) What are the most feasible options for rebuilding the stock? A team of biologist led by the Ministry of Water, Land and Air Protection initiated a modeling exercise to address these questions. Results from the exercise were presented and discussed at a workshop held in Nelson B.C. on Dec. 5-6, 2001. This report summarizes the modeling results and workshop discussions.

A number of hypotheses regarding the causes for the collapse of the West Arm burbot population were reviewed and discussed at the workshop.

1. **Overfishing.** Excessive harvest of the adult component of the population reduced spawning biomass to the point where recruitment was severely limited (recruitment overfishing).
2. **Nutrient Loading.** Reductions in total phosphorous (TP) loading to Kootenay Lake due to changes in production from the Cominco fertilizer plant in Kimberley and impoundment of the Kootenai and Duncan rivers by Libby and Duncan dams, led to a reduction in food availability for juvenile burbot, leading to reduced growth and survival rates.
3. **Mysid Transport.** Increases in water clarity in Kootenay Lake resulting from impoundment of the Duncan and Kootenai rivers has resulted in a deeper distribution of mysids in the main lake, leading to a reduction in transport rates over the west arm sill. Reduced mysid transport led to reduced growth and survival rates for juvenile burbot.
4. **Kootenay Lake Discharge.** Operation of Libby and Duncan Dams has increased discharge in the West Arm during winter months, and decreased discharge during the spring and summer. Increased flow during the winter was hypothesized to increase the energetic requirements of young-of-the-year (YOY) and age 1 burbot, potentially reducing their growth and survival rates. Decreases in summer discharge were hypothesized to reduce transport of mysids over the west arm sill, potentially reducing growth and survival rates for young burbot. Increased discharge through the West Arm may also have transported larval burbot out of Kootenay Lake.
5. **Kootenay Lake Elevation.** Operation of Libby and Duncan Dams has altered the seasonal pattern in lake levels, potentially reducing habitat availability for YOY and juvenile burbot, ultimately leading to reductions in growth and survival rates.
6. **Habitat Loss in Kootenay Lake.** Shoreline development on the West Arm has reduced the area and quality of YOY and juvenile burbot habitat, leading to a reduction in growth and survival rates.
7. **Community Shift.** Burbot likely dominated the demersal fish community in the West Arm in the late 1960's and mid 1970's. Reductions in the burbot population by other

factors resulted in an expansion in populations of northern pikeminnow and largescale sucker, leading to an increase in predation and competition on YOY and juvenile burbot.

Linkages between these hypotheses were also discussed. Overfishing or other factors could have reduced burbot populations in the West Arm leading a shift in the composition of the demersal fish community, which in turn led to further recruitment limitation. Effects of changes in Kootenay Lake discharge or elevation patterns on burbot recruitment could have been exacerbated by habitat loss along the shores of the West Arm. Recruitment problems associated with reduced food availability could have resulted from reductions in both TP loading and reduced mysid transport due to increased water clarity.

The main objective in developing a model of burbot population dynamics for the West Arm stock was to evaluate the likelihood of the hypotheses for the causes of recruitment failure. The model predicts population age structure and changes in stock size over time and uses standard methods for representation of recruitment, survival, and vulnerability to assessment sampling. As a dynamic model, it is "initialized" by estimating a natural or normal population structure, and changes over time are simulated by modifying the relative juvenile recruitment rates in specific years to provide the best fit between observed and predicted length-frequency and Catch per Unit Effort (CPE) data. We developed time series of nutrient loading, discharge and stage in Kootenay Lake and compared them with the reconstructed recruitment time series predicted by the model. The plausibility of the hypotheses for burbot recruitment failure was then assessed based on the compatibility between the time series of various physical changes to Kootenay Lake and the reconstructed burbot recruitment trends.

This document summarizes the main findings of the modeling exercise and discussions that occurred during the workshop regarding the plausibility of alternate hypotheses for burbot recruitment failure and recovery options. Section 2.0 reviews the model structure and assumptions. Section 3.0 provides a summary and interpretation of the length-frequency and CPE data from the West Arm fishery and summarizes model results regarding: population size; natural mortality rate; stock productivity; historical recruitment patterns; and comparisons between recruitment patterns and habitat changes in Kootenay Lake. Section 4.0 discusses recovery options for West Arm burbot and stock assessment requirements for burbot in other systems based on results from the modeling exercise.

2.0 Model Description

An age-structured population dynamics model was used to predict natural population age structure and track possible changes in stock size associated with fishery removals and apparent recruitment failure in recent decades for the Kootenay Lake West Arm burbot population. Data used to fit the model were obtained from the Ministry of Water, Land and Air Protection files in Nelson, B.C. Standard methods for representation of recruitment, survival, and vulnerability were used in the simulation. As a dynamic model, it was “initialized” by estimating a natural or normal population structure, and subjecting this structure to known removals from the fishery and various hypotheses about recruitment. The natural population predicted length-frequency structure is compared to length-frequency data from the West Arm fishery in order to estimate vulnerability to fishing as a function of age and annual survival rates. The predicted vulnerable population trend is compared to CPE and length-frequency data from 1967 to 1986 to estimate temporal changes in stock size and recruitment.

2.1 Assessment of natural population structure

We modeled 11 age classes assuming that age 1+ annual survival rates S_a (a =age, $S_a=e^{-M_a}$ where M_a =instantaneous mortality rate) were stable over time. A natural population will on average have a number N_a of age a animals equal to $R_o L_a$, where L_a is survivorship to age a defined recursively by $L_1=1$, $L_a=S_{a-1}L_{a-1}$ for $a>1$ and R_o is average natural recruitment rate of 1 yr old burbot. If the relative vulnerability of age a animals to the fishery is v_a , the average natural recruitment (age 1 individuals) R_o is then given by $R_o=N_o/\phi_L$, where ϕ_L is the survivorship “incidence function” and N_o is a leading parameter for natural population size.

$$\phi_L = \sum_a L_a \quad (2.1)$$

The natural spawning stock biomass, B_o , can be estimated as $B_o=R_o\phi_Y$. Where ϕ_Y is the fecundity “incidence function”.

$$\phi_Y = \sum_a L_a w_a p m_a \quad (2.2)$$

Where L_a is the survivorship to age a , w_a is the weight at age, and $p m_a$ is the proportion of the age class that is mature. The maturity schedule is assumed to be the same as the vulnerability schedule (see discussion below) since the fishery was targeting the spawning population.

2.2 Calculating age specific length and weight.

Age-specific mean length and weight can be calculated from data collected from the fishery. One must be careful when using fisheries data to estimate growth due to size selectivity in the harvesting process. In many cases, the fishery will capture a higher proportion of faster growing individuals for ages not fully vulnerable to the fishery. This selectivity is usually a result of fish reaching a size where they are morphologically or spatially vulnerable to the fishing gear. The selectivity problem will bias estimates of the Von-Bertalanfy metabolic constant K upwards but can be avoided if only fully vulnerable age classes are used in the estimation. The Von-Bertalanfy metabolic constant K can be calculated from the slope of a

Walford plot where length at age one year older is plotted against length at age. To estimate K for the West Arm burbot the mean length at age for ages 4 to 9 were used (Fig. 2.1).

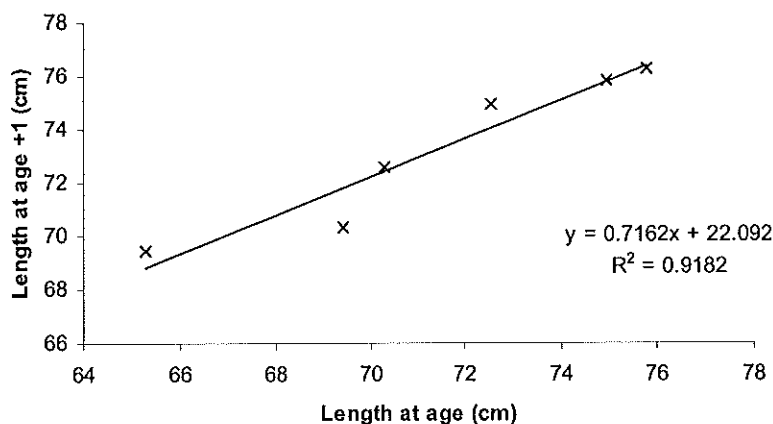


Figure 2.1. Walford plot of mean length at age +1 vs. mean length at age for West Arm burbot and linear regression (solid line).

Linear regression estimated a slope of 0.7162 resulting in an estimate of 0.295 for K ($K = -\ln(\text{slope})$). The point at which the regression line intersects the 1:1 line (intercept/(1-Slope)) is an estimate of the mean maximum length (L_∞). L_∞ was estimated at 77.9 cm. Figure 2.2 shows the resulting growth curve plotted with length age data from the fishery.

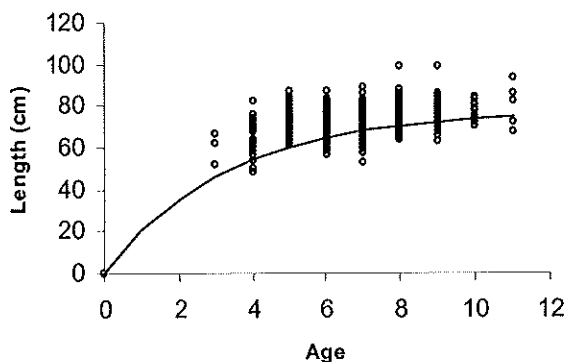


Figure 2.2. Resulting growth curve from the Walford plot (solid line) plotted with the length age data collected from the fishery (open circles).

A length weight relationship was also developed using the fisheries data assuming the relationship $W = aL^b$. From linear regression of $\ln(\text{Weight})$ vs. $\ln(\text{Length})$ (Fig. 2.3) $a=0.0000388$ and $b=2.553$.

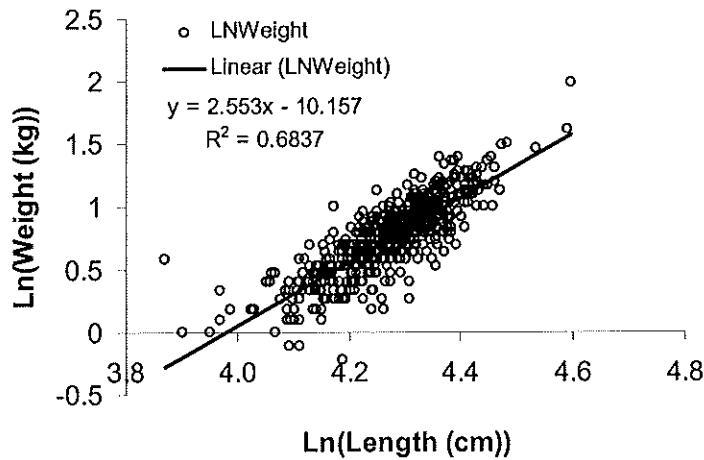


Figure 2.3. Log plot of weight vs. length for West Arm burbot and the resulting linear relationship.

2.3 Dynamic Calculations

The equilibrium recruitment rate (R_0) and spawning stock biomass (B_0) values are computed based on assumptions regarding growth, maturity, and survival (Eqn. 2.1 and 2.2). The ratio of R_0/B_0 defines the equilibrium point on the recruitment relationship. This ratio represents the number of recruits required to replace the corresponding spawning biomass at equilibrium, i.e., it is the slope of the replacement line. Myers et al. (1999) provided a meta-analysis of maximum reproductive rates in fish at low stock sizes. One of the findings of the analysis was that the initial slope of the recruitment curve, that is, stock productivity, expressed relative to the slope of the replacement line is known for many groups of fishes. One is then able to multiply the relative improvement (MyersK) in recruitment by the equilibrium slope R_0/B_0 to gain an estimate of the initial slope (α) of the recruitment relationship. Knowing the mean recruitment relationship is essential to population dynamics. Since nothing is known about the recruitment relationship for burbot in Kootenay Lake the meta-analysis done by Myers provides the best estimate of the initial slope of the recruitment relationship. The recruitment relationship for age one burbot, assuming Beverton-Holt type recruitment, can be modeled as.

$$R_t = \frac{\alpha S_t}{1 + \beta S_t} \cdot w_t | w_t \geq 0 \quad \text{where } \alpha = \frac{\text{MyersK}}{\phi_y} = S_0 \text{ and } \beta = \frac{\text{MyersK} - 1}{R_0 \phi_y} \quad (2.3)$$

Where R is the mean number of age 1 recruits produced by the spawning stock biomass S and w_t is a recruitment anomaly indicating poorer than average recruitment of $w_t < 1$ and better than average recruitment if $w_t > 1$.

The bookkeeping for numbers at age for ages 2 and older over time is straight forward using the equation:

$$N_{a+1,t+1} = e^{-M} (1 - hr_t v_a) N_{a,t} \quad (2.4)$$

where N is the number of individuals of a given age, M is the instantaneous natural mortality rate (assumed constant after age 1), hr_t is the harvest rate in year t and v_a is the age specific vulnerability. Harvest rate was calculated each year as the observed catch from the fishery divided by the model estimate of vulnerable numbers. Vulnerability was described by a continuous function (eq. 2.5).

$$v_a = \frac{1}{1 + e^{-p(l_a - l_h)}} \quad (2.5)$$

Where age specific vulnerability (v_a), ranging from 0 to 1, depends on the mean length at age (l_a) and a length at which vulnerability is 50%. The “steepness” parameter (p) for the function determines the rate of change in vulnerability (higher values of p imply closer to a “knife edge” change in vulnerability near length l_h). The vulnerability function was modeled using length instead of age so that length-frequency data could be used in parameter estimation. Age distribution was linked to length distribution assuming each size class was composed of individuals of various ages. The relative contribution of an age to a size class depends on the mean length at age and variability in growth. The predicted proportion at length can be approximated by equation 2.6.

$$p_l \propto v_l \cdot p_a (LI, L_a, \sigma_a) \quad (2.6)$$

ages

where: p_l is the proportion in a given length interval, v_l is the length specific vulnerability, p_a is the proportion at a given age and $N(LI, L_a, \sigma_a)$ is the probability mass for the length LI given the mean length at age L_a and the standard deviation σ_a . Analysis of length age data found that variance could be calculated assuming a coefficient of variation of 0.08.

2.4 Parameter Estimation

The parameters that required estimation in the burbot model were: the equilibrium stock size prior to harvesting (N_0), the recruitment parameter $MyersK$, vulnerability parameters p and l_h , instantaneous natural mortality (M) as well as the recruitment anomalies (w_t). In order to estimate the best combination of parameters an objective function was needed. The objective function allows inferences about the likelihood of parameter values to be made from the available data by comparing the models prediction, given a set of parameters, to the observed data under an assumed error structure. The best combination of parameters is found when the objective function is maximized. It is important to note that the certainty of a parameter estimates depends on the quality of the data.

Length-frequency data from 1968-78 as well as catch and effort data from 1967-86 were used in the estimation. Each data set contains information about some of the parameters and is combined using the objective function. It is worthwhile to describe how one can interpret the data since the interpretation will greatly affect the parameter estimation.

To properly interpret age/length composition data, it is important to recognize that such data contain information about mortality, recruitment, and age/length-specific vulnerability. If the population size is assumed to be stable over time, the slope of the age composition frequency distribution reflects the mortality rate from one age to the next. The steeper the slope, the greater the mortality rate (Fig. 2.4, top).

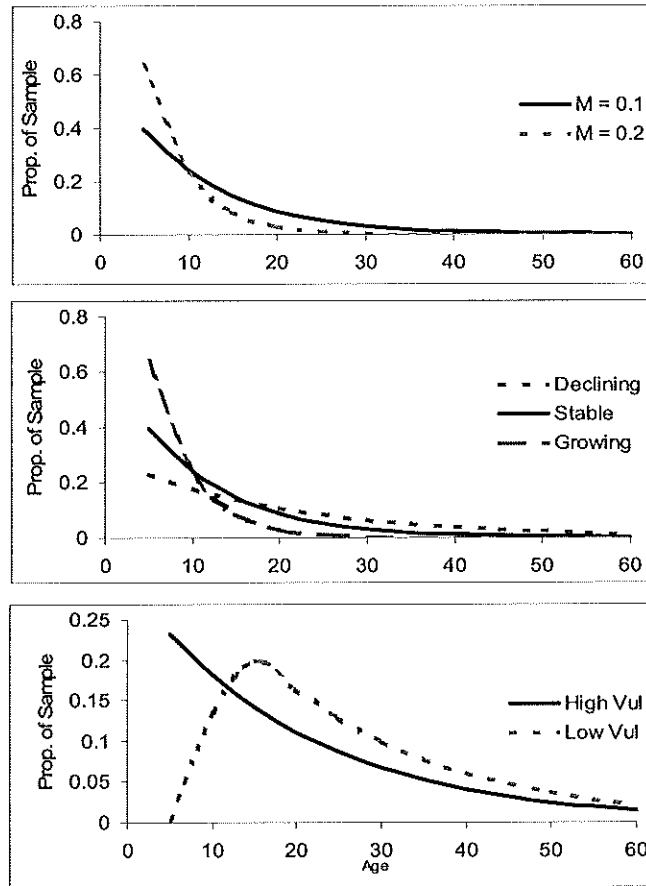


Figure 2.4. Effects of mortality rate (top), recruitment rate (middle) and age-specific vulnerability to sampling gear (bottom) on age composition data.

Differences in age/length composition between two populations may also result from trends in recruitment rates (Fig. 2.4, middle). An expanding population, where the rate of recruitment is greater than what is required to maintain current population levels, will have an overrepresentation of younger fish, which appears as a steeper slope in the age composition frequency curve. A declining population will have an under-representation of young fish, which reduces the slope of the age composition curve. The shape of age-frequency curve may also reflect differences in the vulnerability of different age fish to the sampling gear (Fig. 2.4, bottom). If young fish are underrepresented in the sampling, the age composition curve will have a right-skewed dome-shaped appearance.

It should be clear that changes observed in an age/length structure could be interpreted in a number of ways. It may be assumed that all changes in age/length structure are the result of changes in vulnerability or that recruitment variation is the main source of change. It is also possible that changes are due to sampling error/bias and have no biological significance. It was assumed that the variation in length-frequency in the burbot data resulted from changes in recruitment and depletion by the fishery. Also, it was assumed that the first year of length-frequency data (1968) came from a population at equilibrium. Given these assumption inferences can be made vulnerability parameters p and l_h , instantaneous natural mortality (M) and recruitment anomalies (w_t).

CPE data is commonly, though not always correctly, used as an index of population abundance. It is normally assumed that CPE is proportional to population abundance (eq.2.7).

$$CPE_t = qN_t \quad (2.7)$$

If proportionality holds then changes in CPE result from fishery removals compensated by recruitment. Thus CPE data can contain information about population size, recruitment and mortality. However, in many cases CPE does not change in proportion to abundance, remaining stable over a wide range of abundance. In these cases CPE is said to be hyperstable. That is, the same mean catch per effort is obtained whether total abundance is high or low, so in particular the CPE data does not warn us of population declines. There are several mechanisms that can cause hyper stability: (a) gear saturation (for example, avoidance of nets that already have fish trapped in them); (b) spacing behavior by fish that leads to similar fish densities in microhabitats that are favorable for both the fish and the sampling gear; (c) large-scale range changes in the population with changes in total abundance, so that a higher proportion of the population is concentrated in the sampled areas when total population size is lower. It was known that the majority of the effort from the burbot fishery was focused in a very small area of the West Arm and CPE data was likely hyperstable. Walters and Ludwig (1994) suggest using equation 2.8 when hyperstability is suspected and to use a value of 0.2 for q_2 to represent strong hyper stability.

$$CPE_t = q_1 N_t^{q_2} \quad (2.8)$$

Given the above assumption as to the nature of the data, estimates of the leading model parameters (θ): initial stock size (N_0), the recruitment parameter MyersK, vulnerability parameters p and l_h , instantaneous natural mortality (M) and recruitment anomalies (w_t) were estimated in two steps. First an objective function was constructed to estimate the leading parameters N_0 , MyersK, M , p and l_h from the CPE data and the first year of length-frequency data. The objective function was then modified to incorporate the remaining length-frequency data and recruitment anomalies were estimated conditional on the previous estimates of the leading parameters.

The objective function used in the first step of the estimation is described by equation 2.9. Bayes' theorem (Gelman et al.1995) states that, the posterior distribution (a measure of credibility) of the parameters is proportional to the likelihood of the data given the parameters and the prior distributions of the parameters.

$$p(\text{data} | L(\text{data})) p(\text{ }) \quad (2.9)$$

The likelihood of the data is the combined likelihood of the CPE data and the first year of length-frequency data. Walters and Ludwig (1994) recommend using equation 2.10 as the log likelihood for CPE data assuming hyperstability. Equation 2.10 assumes that CPE data is log-normally distributed but requires no assumption about the variance of the distribution since the variance has been integrated out.

$$L^{q1,q2,y} = \left[\left(\frac{1}{n-2} \right) \sum_i \left(Z_i - \left(\frac{Z_i W_i}{W_i^2} \right)^2 \right)^2 \right]^{\frac{n-1}{2}} \quad (2.10)$$

Where:

$$Z_i = \ln \text{CPE}_i \quad \hat{\theta}_1 = \frac{1}{n} \sum_i Z_i \quad \hat{\theta}_2 = \frac{\sum_i Z_i W_i}{\sum_i W_i^2} \quad W_i = \ln(N_i) - \frac{1}{n} \sum_i \ln(N_i)$$

where, N_i is the model vulnerable population estimate in year i and n is the number of data points.

The likelihood for the length-frequency is described using the multinomial likelihood (eq. 2.11).

$$L = \frac{n!}{n_1! \dots n_k!} p_{1,t}^{n_1} \dots p_{k,t}^{n_k} \quad (2.11)$$

The normalizing component $\frac{n!}{n_1! \dots n_k!}$ was approximated using Sterling's method. $p_{1,t}$ is the expected vulnerable proportion of the population in length category 1 at time t and $n_{1,t}$ is the observed number of individuals in length category 1. Initially the length-frequency component of the objective function incorporates the first year of length-frequency data.

The prior component of the objective function allows for the incorporation of previous information on the value of a parameter in the form of a probability distribution. Specifying an initial belief about the value of a parameter and the uncertainty in that belief reduces the demands placed on the data to resolve parameter values. One may argue that such an approach severely biases the assessment procedure but in many cases the available data cannot resolve all the parameters of interest. The use of prior information is particularly appealing for the burbot assessment because of the pattern in the CPE data. The CPE data from the West Arm fishery is not only hyperstable but is on average declining over time. Therefore, there is no information about the stocks ability to recover which is determined by the productivity parameter $MyersK$. The lack of resolution in the data about recruitment results in confounding between initial population size and recruitment. In other words a large unproductive population or a small productive population could have produced the observed CPE pattern. A similar argument can be made for the confounding between mortality and productivity. By using priors for natural mortality (M) and recruitment compensation ($MyersK$) the CPE data can be used mainly to estimate initial population size.

Prior distributions for natural mortality and recruitment compensation were derived from meta-analyses. Myers et al. (1999) in their analysis of maximum reproductive rates provided an estimate of the relative improvement in the slope of the recruitment relationship for Gadoids. Their reported mean value of 2.7 (with a standard deviation of 0.51) was used for burbot assuming a normal distribution. Pauly (1980) in his meta-analysis of mortality rates found that natural mortality (M) was approximately equal to the von-Bertalanffy curvature parameter (K). Although, as we will show later, M is fairly well defined by the length-frequency data, the prior distribution was assumed to be normal with a mean equal to K and a coefficient of variation of 50%. No prior information was available for the other leading parameters so uniform priors were used.

The modified objective function used in the estimation of the recruitment anomalies for 1960-1986 can be expressed using equation 2.12. The main difference between equation 2.9 and 2.12 is that the length-frequency data from 1969 to 1978 was incorporated into the multinomial likelihood.

$$p(w|data, \theta) = L(data | \theta, w)p(w) \quad (2.12)$$

Since the recruitment anomalies are being evaluated at the best estimates of the other parameters (θ') the priors for those parameters are removed and a uniform prior is used for the recruitment anomalies. With these modifications to the objective function one can obtain the best estimates, conditional on the estimates previously obtained for the leading parameters, for the recruitment anomalies.

2.5 Calculations of recruitment anomaly correlates.

As indicated in the introduction, one of the objectives of the modeling exercise was to evaluate hypotheses about the cause of the burbot collapse. This was done by calculating the correlation between a number of physical factors and the model derived recruitment anomalies in hopes that one factor would explain a large part of the pattern in recruitment. Physical data came from a number of sources. Lake levels, discharge and nutrient loading came from work done previously by Lekstrum et al. (1994). Data on changes in the zooplankton community came from Ashley et al. (1999) and Zyblut (1967). No data was available on changes in the community structure but the change in predation by burbot was calculated to see if there was a substantial decline in predation from burbot. Total consumption by burbot was used as a measure of predation pressure on the surrounding community and calculated using the numbers at age produced by the model and estimates of size dependent burbot consumption from Rudstam et al. (1995).

3.0 Results

Catch, effort (Fig.3.0) and length frequencies (Fig. 3.1) were collected from the West Arm fishery between 1967-1986. Length-frequency data was not collected after 1978.

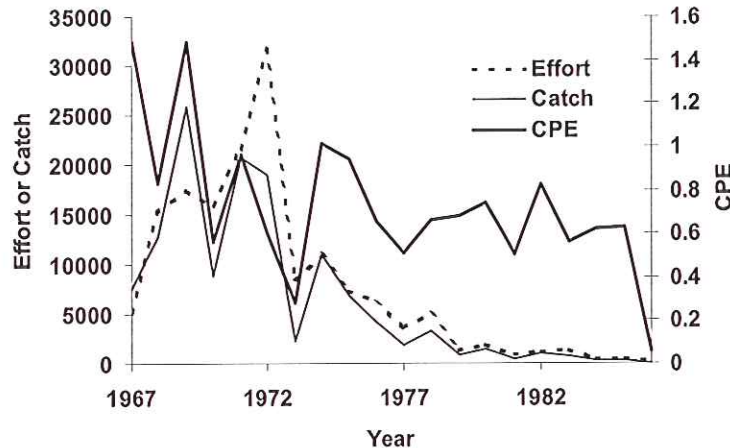


Figure 3.0. Catch, Effort and CPE data from the Kootenay Lake West Arm burbot fishery from 1967 to 1986.

CPE data indicate a decline in the burbot population from the start of the major fishery in 1967 until 1973 when the CPE appears to stabilize until 1986. During this period catch and effort declined steadily until 1986 when the fishery removed only a few fish. The lack of change in the CPE index indicates strong hyperstability in the CPE index since it is known that the stock had collapsed and that fishing pressure was focused in a very small part of the West Arm. Length frequency data indicate the loss of smaller size classes beginning in the 1970's and becoming more pronounced by the mid 70's. The loss of smaller size classes is an indication that recruitment failure may have been occurring although uncertainty in length composition during this period is very high due to the small sample size. We attempted to compensate for small sample size by including its effect in the evaluation of the length-frequency component of the objective function (eq. 2.11), thus smaller samples carry less weight, but we are still assuming that the observed changes result from a biological process and not sampling error. This causes some concern since the sample size in the length-frequency data declines in later years when we hope to gain the most information about recruitment failure from it.

3.1 Leading Parameters

The best-fit combination of leading parameters to the data is presented in Table 3.0.

Table 3.0. Best-fit estimates of leading parameters N_0 , M , l_h , p and MyersK.

Parameter	Symbol	Value
Initial population size	N_0	196703
Instantaneous natural mortality	M	0.34
Length at 50% vulnerability (cm)	l_h	63.7
Vulnerability shape parameter	p	0.28
Relative improvement in productivity at low stock size	MyersK	2.51

The data indicate the initial population size for burbot in the West Arm prior to the fishery was about two hundred thousand individuals. However there is a great deal of uncertainty in the actual value due to the hyperstability in CPE. Figure 3.2 shows part of the posterior distribution for N_0 .

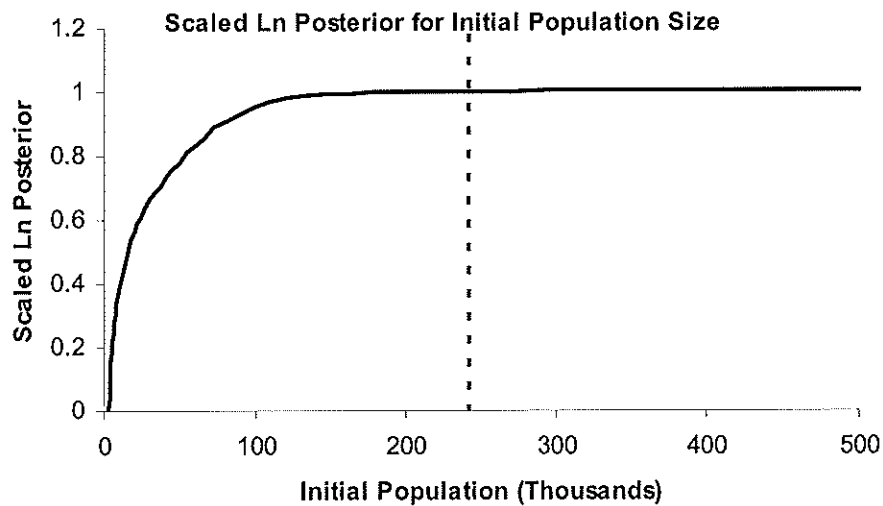


Figure 3.2. Partial conditional posterior distribution for initial population size evaluated at the best-fit estimates of the other leading parameters. Dotted line is the population estimated using a depletion estimate.

A lower bound on initial population size is well defined, there had to be at least that many fish at the start of the simulation (1949) to provide the number of fish that were removed from the fishery (~129000). However, there is little certainty in the upper bound on the initial population size. Although it is difficult to see in the figure, a maximum in the objective function occurs at ~200,000 individuals, although, the value of the objective function is similar for higher population estimates. This lack of information about initial population size in the CPE data, even when using prior information about recruitment and mortality, arises

due to the hyperstability and high variability in the CPE data. If CPE were proportional to population abundance one would expect to see the effect of the removals (fishery) on the population (e.g. a 50 % drop in CPE results from a 50% drop in population size). It is the magnitude of the decline in CPE that results from the removals which provides information about population size. When the effect of removals is obscured due to hyperstability there is a loss of information about population size. There is also confounding between the population size and q_2 parameters in the relationship between CPE and population size (eq. 2.8). It is difficult to know if the lack of decline in CPE resulted from hyperstability (low value of q_2) or a large population size. In our analysis it was assumed that there was strong hyperstability so this effect could be ignored. The final confounding resulted from the variability in CPE combined with hyperstability. The flattening of the CPE trend and the high variability resulted in horizontal straight-line fit to the data explaining almost as much of variability as the best fit line given an initial population size of ~200,000. Since the q_1 parameter in equation 2.8 is a scalar, any population size that is not impacted by the fishery removals (no change in CPE) will produce a straight-line fit through the data. All these factors result in high uncertainty about the upper bound on initial population size.

In an attempt to lend support for the N_0 estimate, a depletion estimate for the population size at the start of the fishery (1967) was computed (Fig. 3.3) and determined to be ~241,000 (the x intercept of Fig. 3.3). Application of a depletion-estimate approach for estimating the initial stock size requires the assumption that there has been no recruitment during the fishery (1967-1986). While we know this assumption is not completely valid given some evidence of recruitment from the length composition data, the approach provides an upper bound that is helpful since our model-derived profile for N_0 (Fig. 3.2) is very uninformative about higher values of N_0 .

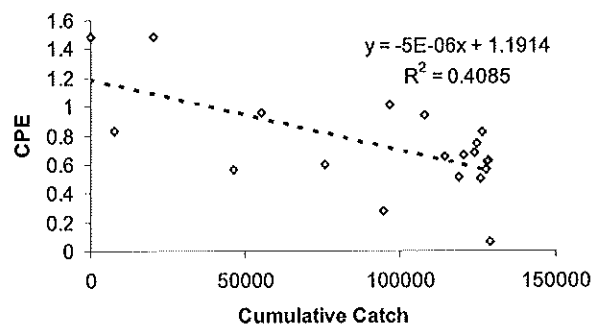


Figure 3.3. Fit of a linear trend line through CPE data from the fishery for a depletion estimate of the burbot population size in 1967. The estimate assumes that there has been no recruitment since 1967.

Natural mortality (M) for ages 1+ was estimated at 0.34 and reasonably well defined by the 1968 length-frequency data (Fig. 3.4). Although the difference is not shown, the removal of the prior on M had little effect on its distribution. A mortality rate of 0.34 is higher than that reported in the literature for burbot (Froese and Pauly 2001) but corresponds well to the K value calculated for the von-Bertalanffy growth function ($K=0.29$).

Both vulnerability parameters are well defined by the 1968 length-frequency data (Fig. 3.5). Length at 50% vulnerability was ~64 cm. with a shape parameter of 0.28. The low value of the shape parameters indicated that if the fishery is targeting a spawning population, burbot are maturing over a broad range of lengths. This might indicate that age is a more important determinant of maturity than size. However, if the fishery is targeting a feeding population then the gradual increase in vulnerability may be the result of variation in that age at which juveniles join the adult population.

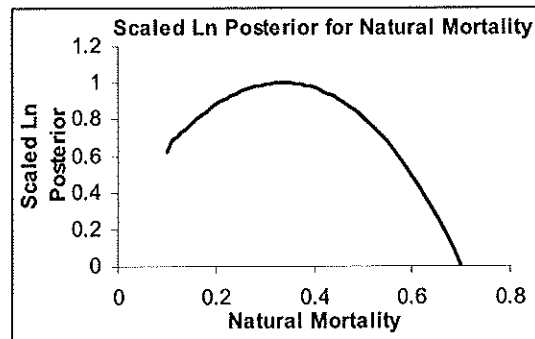


Figure 3.4. Partial conditional posterior distribution for instantaneous natural mortality evaluated at the best fit values of the other leading parameters.

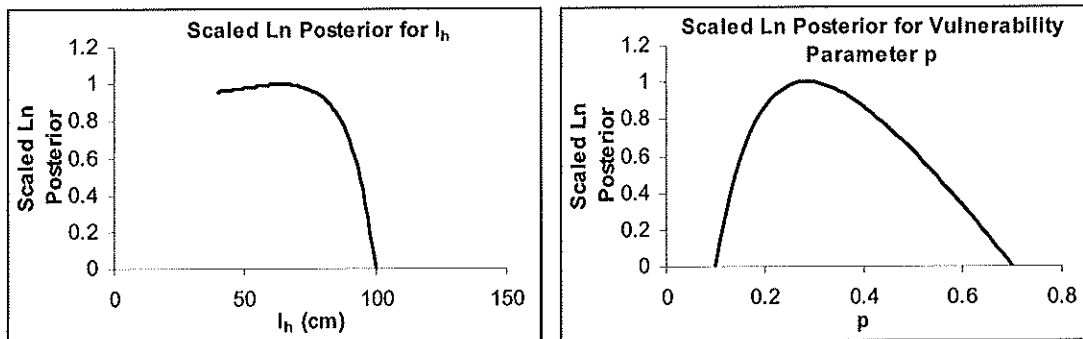


Figure 3.5. Partial conditional posterior distributions for the vulnerability parameters l_h and p evaluated at the best estimates of the other leading parameters.

The relative increase in productivity parameter $MyersK$ was reasonably well defined at a value of 2.51 when a prior distribution was used and the evaluation was conditioned on the best estimates of the other leading parameters (Fig 3.6 A). However, when the prior was not used and the conditional marginal (with respect to N_0) posterior with was calculated, the lack of information in the CPE data on productivity was clear (Fig. 3.6 B). By removing the prior there is no penalty in the objective function selecting very high or low values for recruitment compensation which when fitting to the CPE data, as discussed earlier, can be compensated for by population size. Thus by allowing N_0 to vary and not evaluating the posterior distribution of the recruitment compensation parameter conditioned on the best fit N_0 , the lack of information on $MyersK$ in the CPE data can be demonstrated.

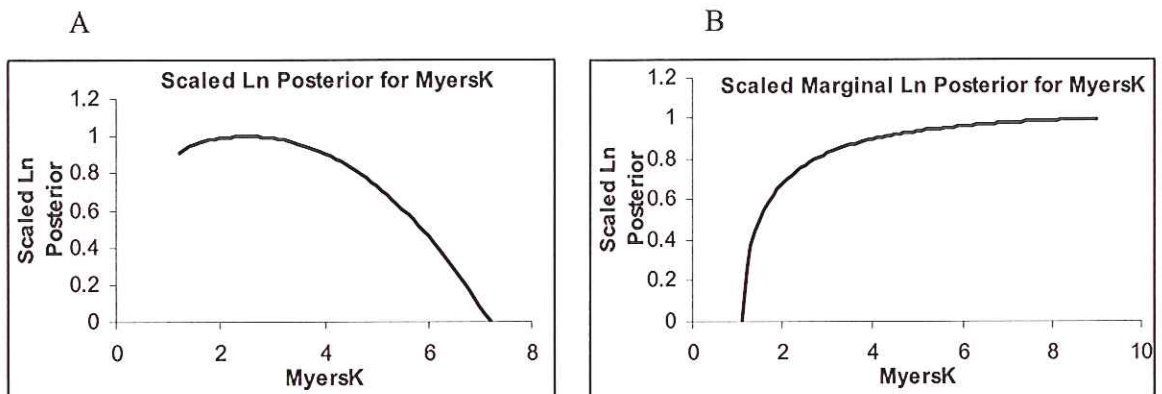


Figure 3.6. A) Scaled conditional partial posterior distribution for MyersK evaluated at the best-fit estimates of the other leading parameters and using a prior distribution. B) Scaled conditional (on the best-fit of the leading parameters except No) marginal (with respect to No) posterior for MyersK without using a prior distribution.

3.1 Recruitment Anomalies and Correlations

The calculation of recruitment anomalies, deviations from the mean recruitment relationship (Eq. 2.3) for age 1 burbot, can be quite subjective depending on how one interprets the data as well as how one treats the uncertainty in leading parameters. Calculation of anomalies for the West Arm burbot stock was done assuming that changes in the length-frequency distribution from the catch was a reflection of changes in recruitment and not the result of changing vulnerabilities or under representation of smaller length classes due to small sample size. These assumptions are problematic but without them the analysis becomes impossible. In addition to the length-frequency assumption there is conflicting information in the CPE and length-frequency data. The absence of smaller size classes beginning in the 70's in the length-frequency data indicate recruitment failure while the high CPE in the early 80's indicate a healthy population implying that there had to be some recruitment. However, assuming strong hyperstability in CPE data reduces the conflict between these data sources. These points need to be taken into consideration when examining the recruitment reconstruction from the model.

The general trend in the anomaly sequence (Fig. 3.7) is, increased (from baseline of 1) reproduction in the 1960 peaking in the mid 60's and declining in the later half of the decade. The anomaly is constantly below 1 (poor reproduction) throughout the 1970's declining to 0 in some years. The spike in the anomaly sequence in the mid 70's is a result of the fitting procedure chasing the hyperstable CPE points, even though strong hyperstability was assumed. This is an indication that the hyperstability in CPE is even stronger than that used in the fitting procedure. The increase in the anomalies in the 80's result from having no length-frequency data for the later part of the 80's resulting in no information about recruitment in the early 80's.

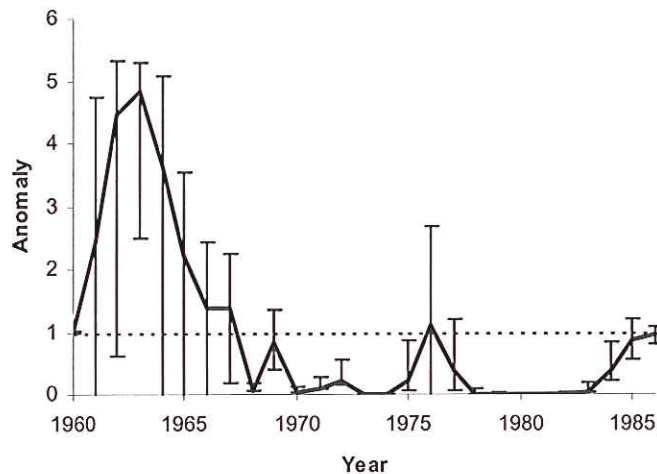


Figure 3.7. Best estimates of recruitment (age 1 burbot) anomalies from 1960 to 1986 and uncertainty in the estimates (error bars as +/- standard deviation) calculated from partial marginal distribution from MCMC over a range of values of N_0 from 22,000-1,200,000, MyersK from 2-6 and M from .2-.4.

The recruitment anomalies did not correlate well with most of the physical habitat factors tested (Table 3.1). The lack of correlation with physical factors is not surprising. Many of the flow and elevation changes (Fig. 3.8), which could have contributed to the decline in burbot, occurred after Libby Dam became operational in 1975, well after the data indicated recruitment failure.

Table 3.1. Squared Pearson correlation coefficients for trends in potential habitat indices of Kootenay Lake compared against calculated recruitment anomalies.

Factor	Correlation (r^2)
Minimum June lake elevation (index of juvenile habitat Figure 3.8 A)	0.21
Minimum July lake elevation (index of juvenile habitat Figure 3.8 B)	0.12
Winter discharge from Kootenay lake (index of juvenile winter energetic expenditure Figure 3.8 C)	0.46
Summer stage difference (index of habitat variability Figure 3.8 D)	0.18
Total P load (index of productivity Figure 3.9 A)	0.12
Average summer cladoceran density (index of juvenile food Figure 3.9 B)	0.85

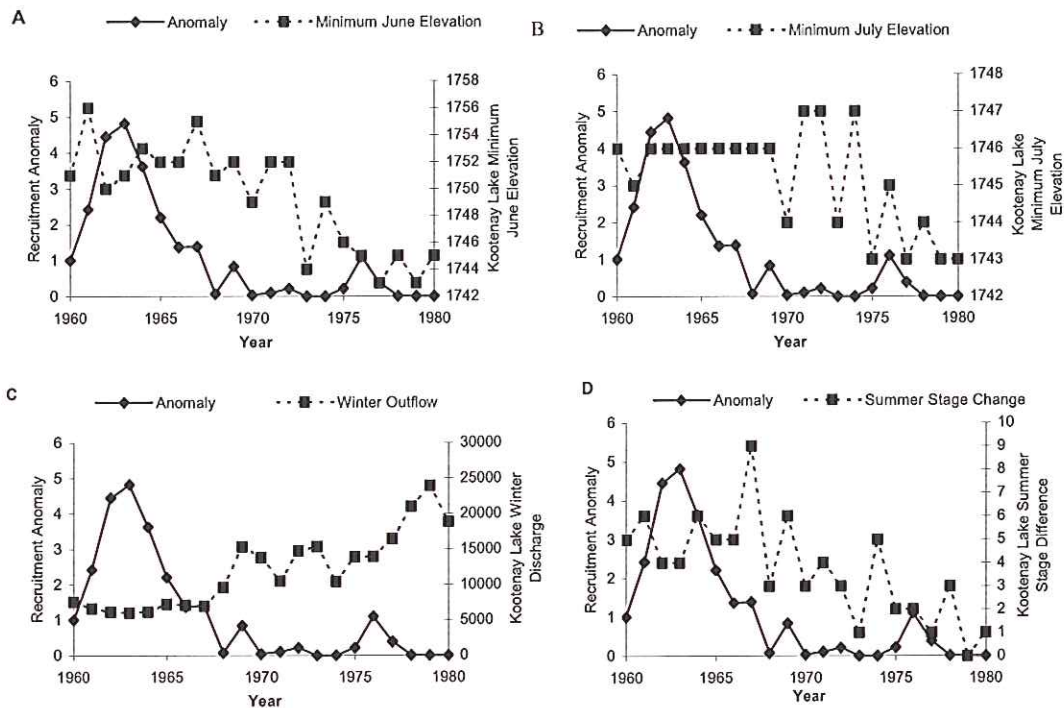


Figure 3.8 Correlations between calculated recruitment anomalies and various measures of juvenile environment affected by changes in dam operations. A) Minimum June lake elevation (r^2 0.12). B) Minimum July lake elevation (r^2 0.12). C) Kootenay Lake winter discharge (r^2 0.46). D) Kootenay Lake summer elevation change (r^2 0.18).

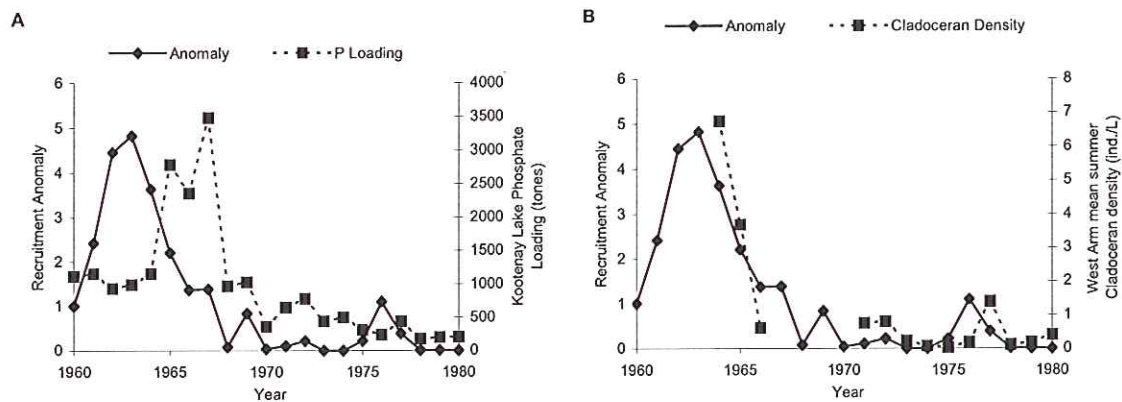


Figure 3.9 Correlations between calculated recruitment anomalies and productivity. A) Total phosphorous loading into Kootenay lake (tonnes per year) (r^2 0.12). B) Mean summer cladoceran density (individuals per liter) in the West (r^2 0.84).

The lack of correlation between nutrient loading and recruitment (Fig. 3.9 A) is somewhat troubling since this seemed to be the best hypothesis for recruitment failure based on an

anecdotal description of the timing of changes in loading. However on closer inspection, peak nutrient loads occurred in the late 1960's (Northcote 1972, Ashley et al. 1999) four years after the model prediction of peak juvenile production. The recruitment anomalies correlated well with the mean summer cladoceran density in the west arm (Fig. 3.9 B.)

3.2 Overall Fit to Length-Frequency and CPE Data, Resulting Biomass Trends and Potential Recovery Times

The model was able to fit both the CPE (Fig. 3.10) and length-frequency data (Fig 3.11) reasonably well when recruitment anomalies were incorporated into the model. It was not possible to fit the model to the substantial drop in CPE from 1985 to 1986 nor effectively capture the apparent very strong hyperstability in CPE from the late 1970's to 1985 even though hyperstability was included in the model. Incorporating recruitment failure through anomalies provided a reasonable fit to the length-frequency data.

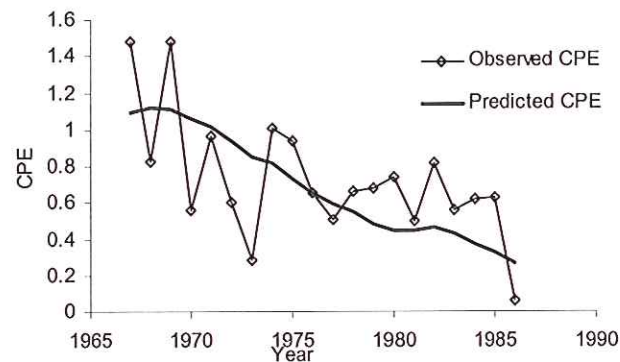


Figure 3.10. Best-fit model CPE trend plotted with observed CPE trend from 1967 to 1986 for the West Arm fishery.

The trend in harvest rate was evaluated at the best-fit model parameters (Fig. 3.12). There was a steady increase in harvest rate as effort increased through the late 60's. There was a dramatic increase in harvest rate as the recruitment failure began to impact the spawning stock. Yield per recruit analysis indicated that the optimum harvest rate, given the vulnerability schedule, for West Arm burbot was 19% and the maximum sustainable harvest rate was 43%. The reconstruction of the harvest rate pattern indicates that optimal harvest levels were passed a few years after the fishery started and maximum sustainable levels were passed in the late 1970's.

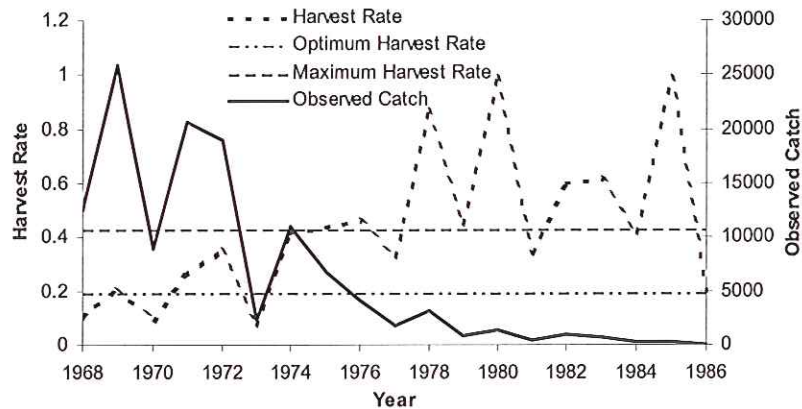


Figure 3.12. Yearly catch for the West Arm burbot fishery and the corresponding estimated harvest rates. Optimum and maximum harvest rates were calculated from yield per recruit analysis.

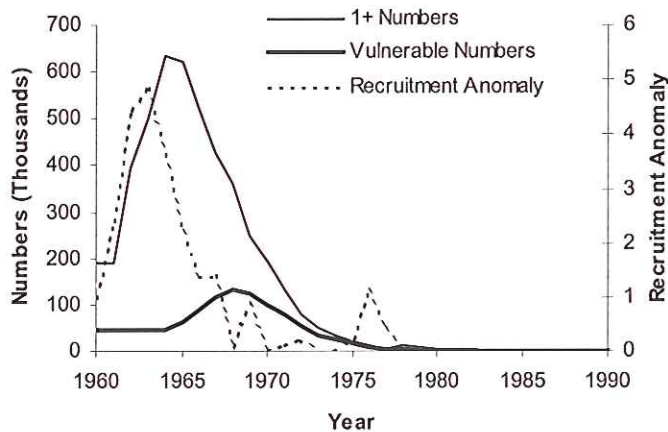


Figure 3.13. West Arm population size age 1+ numbers, vulnerable numbers and recruitment anomalies estimated from the model from 1960 to 1990.

The best estimate of the West Arm burbot population each year is shown in Figure 3.13. There is a substantial increase in population size starting in the early sixties, due to the high recruitment anomalies, reaching a maximum of 650,000 1+ individuals in 1965. The collapse of the population from these high levels began in 1965 and continued into the 1980's when the population is predicted to have reached a level of ~1000 1+ individuals.

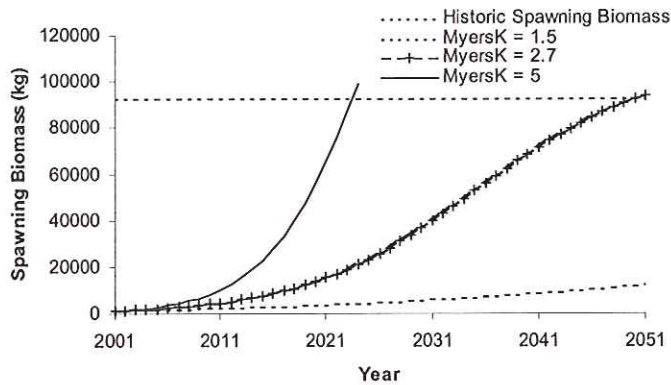


Figure 3.14. Estimated recovery time to historic spawning stock levels under various hypotheses about productivity (MyersK).

Population recovery was explored under different productivity hypotheses (Fig 3.14). If the juvenile environment returns to some “normal” condition and the West Arm is stocked with ~500 adults, the model, under the assumption that MyersK ~2.7, indicates a recovery time, to historical (pre-1950) levels of forty years.

Estimates of total consumption by the West Arm burbot population (Fig. 3.15) indicate that at the peak of the spawning population biomass (~1968) the burbot population was removing >1400 tonnes of prey. As the stock was depleted there would have been a substantial reduction in predation pressure by this species through the 70’s and 80’s.

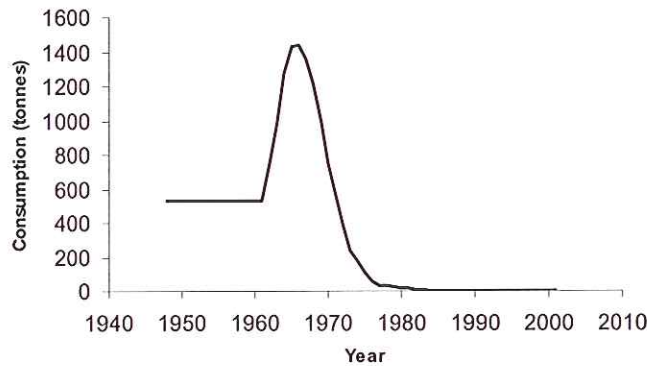


Figure 3.15. Potential total yearly biomass consumed (in tonnes) by the West Arm burbot population.

4.0 Discussion

4.1 Interpretation of Recruitment Trends

The goal of this modeling exercise was to explore potential explanations for the collapse of the burbot population in the West Arm of Kootenay Lake. One must keep in mind that there is considerable uncertainty in the model outputs due to the assumptions made about parameter values and the available data. However, the results from the modeling exercise do provide some insight as to the potential mechanisms for the decline in burbot. Recruitment anomalies (Fig. 3.7) indicate a substantial increase in recruitment in the mid 1960's followed by recruitment failure in the 1970's to 1980's. It is likely that overharvest (Fig. 3.12) was responsible for the erosion and extirpation of the substantial burbot biomass in the West Arm. However, the apparent recruitment failure beginning in the 70's certainly amplified the impact of harvesting and increased the rate of decline in the population.

A substantial increase in adult burbot biomass, resulting from up to a 5-fold increase in recruitment during the early sixties likely attracted substantial effort to the West Arm burbot fishery. This increase in effort was also seen in the kokanee fishery (Ashley et al. 1999). This rapid increase in effort in the late 1960's and early 1970's resulted in harvest levels above optimum of 19% as calculated from yield per recruit analysis. As recruitment returned to normal in the late sixties and early 1970's, the harvest from the fishery resulted in unsustainable harvest rates (>43%). It is more than likely that even while fishing effort was declining in the late 1970's the simultaneous reduction in the recruitment rate (anomalies <1) and the range collapse in the vulnerable population resulted in destructive harvest rates.

Although our model suggests it was ultimately the fishery that caused the collapse of the burbot population, it was the improvement in recruitment in the 60's that likely attracted the fishing effort, and the recruitment failure in the 70's, that accelerated the stock collapse. The cause of the estimated recruitment variation will hopefully give insight into potential recovery scenarios.

The best correlation with the recruitment anomalies was related to the mean summer cladoceran density. It is possible that if cladocerans were a major component in the diet of juvenile burbot, their survival would be affected by significant changes in density. Ryder and Pesendorfer (1992) found that larval stages of burbot fed primarily on copepods and cladocerans. The 7-fold increase in cladoceran density from 1949 (~0.8 individuals/ liter) to 1964 (>6 individuals/ liter) (Zyblut 1967) would have resulted in improved juvenile survival and increased recruitment to the population. When cladoceran density declined after 1964 to levels below those in 1949 (~0.4 individuals / liter) it is possible that juvenile burbot survival declined enough to cause recruitment failure. The increase in the cladoceran community was a result of nutrient loading into Kootenay Lake from the Cominco fertilizer plant in Kimberley (Northcote 1972). However, at the same time the population of introduced mysid shrimp was also increasing (Northcote 1972). Nutrient levels did not peak in the reservoir until 1968 (Fig. 3.9 A) but cladoceran densities began to decline in 1964. Zyblut (1967) and Northcote (1972) hypothesized that this early decline resulted from either direct competition or predation by mysids that, by 1964, were being pumped over the sill into the West Arm in large numbers due to reduced vertical migration from eutrophication (shallower daytime depth

due to reduced light levels). An alternate explanation proposed was that selectively foraging for cladocerans by the large kokanee population that had developed due to high mysid densities reduced the cladoceran community (Northcote 1972). The increased competition/predation due to mysids on the cladoceran community was further complicated by the decline in nutrient loading in 1970's. The initial increase and then decline in cladoceran density match the recruitment anomaly pattern well and provide a reasonable explanation of the recruitment pattern predicted by the model.

There is no doubt that the West Arm fish community has undergone substantial changes since the 1960's. The collapse of the kokanee and burbot populations throughout the 1970's and 80's coupled with a trend toward hyper-oligotrophic conditions would have severely altered the community structure. Burbot alone were responsible for the consumption of a substantial biomass (Fig. 3.15). Recent underwater video surveys in the West Arm revealed a benthic community dominated by northern pikeminnow and largescale sucker (Baxter and Spence, 2001). The existing demersal community may complicate any attempt to reintroduce burbot in to the West Arm.

4.2 Management Options

Recent sampling has confirmed that burbot are largely absent from the mouth of the West Arm of Kootenay Lake (Baxter and Spence 2001). All participants at the workshops acknowledged that establishing a West Arm burbot population will require a stocking or transplant program. The Kootenai Tribe of Idaho has committed to initiating the development of conservation aquaculture techniques for burbot and will be utilizing individuals from the Duncan Lake population to develop these techniques (Baxter and Spence 2001). It may take a number of years before the hatchery techniques are developed to the point where sufficient numbers of juveniles can be produced. In the short term, a transplant program, where mature individuals are captured in Duncan Lake and/or Trout Lake and transplanted into the West Arm, appears to be the most viable option.

Workshop participants discussed a number of uncertainties associated with stocking or transplanting burbot into the West Arm. First, there was considerable uncertainty as to whether stocked juveniles can survive there given the large biomass of northern pikeminnow and largescale sucker that have been observed in recent surveys (Baxter and Spence 2001). Second, there was a reasonable amount of scepticism about whether stocking or transplanting would result in a viable, self-sustaining West Arm stock. It was hypothesized that the original stock had unique local adaptations cuing it to spawn on shoals near Balfour and rear in West Arm habitats downstream of the spawning area, and that it may be wishful thinking to assume that individuals from a hatchery or transplanted from another system will adopt the necessary life history characteristics to do this. Finally, there was concern that stocking of juveniles or transplanting mature burbot into the West Arm could have negative impacts on West Arm kokanee stocks or remaining burbot populations in the North Arm of Kootenay Lake.

All participants acknowledged that any reintroduction program for burbot in the West Arm would be very experimental in nature, with no guarantee of success. The timing of the recruitment failure generated by the model supports the hypothesis that reduced cladoceran

densities, due to changes at the Cominco fertilizer plant and mysid abundance, was the most likely initial cause for recruitment declines. Fertilization of the West Arm, either by direct application of fertilizer in the arm or by enhancing the current fertilization program in the North Arm, was therefore considered to be the best option for improving the chances of success for burbot introductions. The question that was not resolved was whether introductions and fertilization should be conducted at the same time to maximize the probability of success, or whether introductions should initially occur before fertilization to evaluate the possibility of developing a self-sustaining population in the absence of additional enhancement. The latter approach was recognized as yielding potentially more information in the long term, but at the possible cost of increasing the time required to develop a self-sustaining population in the West Arm.

The review of model results at the workshop stimulated discussion on harvest management and stock assessment for other burbot populations in B.C. The most likely instantaneous mortality estimate for the West Arm stock was reasonably well defined (Fig. 3.4) at ~ 0.3 . Assuming this mortality rate is representative of other stocks in B.C., yield per recruit analysis suggests that optimal harvest rates for burbot be around 20%. As $h = \text{Catch}/N$, a sustainable catch of $0.2N$ could be used as a guideline to manage fisheries in other systems if the population size is known. Workshop participants discussed the difficulties of estimating population size for burbot. Tagging studies to date have not yielded much information on population sizes in other lakes because the process of bringing fish up to the surface to tag them can result in considerable mortality. Tag recaptures have been extremely low, even in Columbia Lake where the majority of the spawning run has been tagged. It is suspected that the cause of the low recaptures is non-representative marking, that is, the marked fish tagged during spawning are not representative of the population as a whole. Estimating N by depletion through repeat trapping, or through video surveys were suggested as alternate, albeit unproven, techniques.

In the absence of direct estimates of population size, length-frequency and catch and effort statistics could be used to estimate N or recruitment trends based on the modeling approach described in this report. Our analysis has demonstrated that there is likely extreme hyperstability in the CPE- N relationship for burbot and CPE information only becomes informative about stock size when the stock is virtually gone. Length-frequency data can be used to detect changes in recruitment rates, but the approach is relatively insensitive and generally only useful for detect trends in recruitment for long-lived fish or for populations that have undergone catastrophic recruitment failures. In addition, because burbot become vulnerable to fishing at about the same size as they mature, detecting a recruitment failure by length-frequency sampling occurs too late to effectively manage the population.

It appears that there are no easy solutions for burbot management. Our analysis has demonstrated that standard fisheries statistics are unreliable for detecting anything short of complete recruitment failures. Reliable estimates of population size, and hence sustainable harvest rates, are not possible with existing tagging approaches. Alternative techniques such as depletion estimates through trapping or video transects have not been evaluated, but would require a level of effort that is probably not realistic given current levels of funding. In the absence of reliable stock assessment data, fisheries management will either have to err on the

side of caution and sometimes impose restrictive harvest policies in situations where they are not necessary, or adopt a laissez-faire attitude and risk collapse of other burbot populations.

5.0 References

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Figure 3.1 – Length-Frequency Data for Kootenai Lake West Arm Burbot 1968-1978

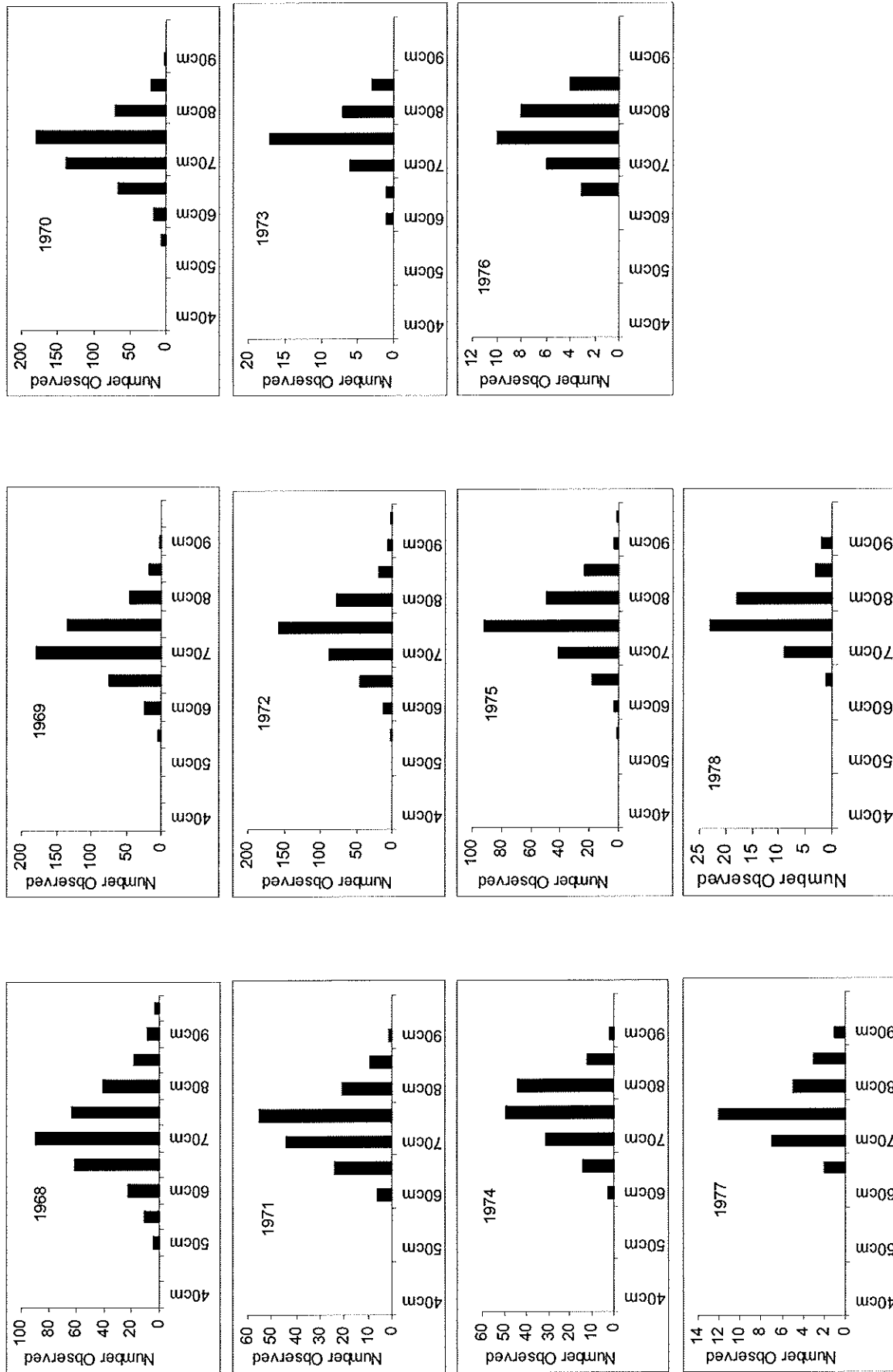


Figure 3.11 –Best Model Fit to Length-Frequency Data for Kootenai Lake West Arm Burbot 1968-1978 Using Recruitment Anomalies

