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Lake Productivity and Sustainable Fish Harvest Estimates

Methods Review

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Lake Productivity and Sustainable Fish Harvest Estimates: Methods Review

Government of Yukon
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Preface

Lake productivity characteristics are used to inform sustainable fish harvest estimates. This document recommends several initiatives to improve the methods used to predict sustainable estimates of lake trout harvest in Yukon. The Government of Yukon's fisheries program began implementing several of the recommendations included in this report in 2013.

Specifically, the fisheries program started to collect nutrient measurements and update bathymetry maps. To date, total dissolved solids and total phosphorus measurements have been updated for approximately 65 lakes. Data loggers were purchased and deployed in several lakes to examine annual variability in temperature and conductivity measurements. The fisheries program also began updating bathymetry maps of lakes from depth records collected during fish population assessments.

The fisheries program is in the process of developing a database of the variables that measure lake productivity. This database will improve data management and facilitate many of the initiatives recommended in this methods review.

Summary

In this paper, I review the methods used to estimate sustainable levels of fish harvest based on lake productivity characteristics. The goal of the review is to assess the existing model used by the Government of Yukon (in place since the 1980s) against other models and new information. I review the literature and practices from several neighbouring jurisdictions and examine how robust Yukon's existing model is to uncertainty in parameter estimates. The existing model has worked well in the past to identify sustainable levels of fish harvest; however, this approach was not intended for single-species management and could fail to identify the overexploitation of lake trout in a warming climate. Ontario and British Columbia are developing new methods to estimate sustainable fish yields that could be applied to Yukon lakes and may improve the management of lake trout.

Based on my review, I recommend the following initiatives:

1. Measure total dissolved solids and total phosphorus in Yukon lakes to update lake productivity estimates.
2. Develop a database of variables used to understand and model lake productivity, which include nutrient measurements, physical measurements, and lake morphology data.
3. Regularly update variables in the existing fish yield model with best available information.
4. Update maps of lake bathymetry opportunistically with sonar depth sounders when field workers are boating on lakes.
5. Investigate the application of thermal habitat volume model and lake trout population harvest model with data from Yukon lakes.
6. Calculate sustainable fish yield estimates from several models and adopt the model that applies the best to all Yukon lakes supporting lake trout.
7. Investigate the relationships among lake nutrients and fish production to better understand how nutrients affect primary productivity and fish production.

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Introduction

Sustainable levels of fish harvest in Yukon lakes are estimated from lake productivity predictions derived from morphological, physical, and chemical parameters. Using these parameters, the Government of Yukon estimates a lake-specific sustainable harvest level based on a model developed by Schlesinger and Regier in 1982 (for an example see Millar *et al.* 2011). When harvest exceeds the estimated sustainable level, the Government of Yukon works with partners to address conservation concerns and inform fisheries management decisions (Department of Environment 2010, 2014).

An evaluation of this approach is warranted because more novel and appropriate methods may be available. A review of data collection methods may also provide insight into how to improve the quality of information used to estimate lake productivity. In this review, I examine methods for estimating lake productivity and sustainable levels of fish harvest to improve Yukon's ability to manage fish harvest from lakes. I evaluate Yukon's existing approach and compare it to practices from neighbouring jurisdictions.

Review of Modeling Approaches of Lake Productivity and Sustainable Fish Harvest

Fish biomass and production (new biomass from growth and reproduction) are used to inform fish yields and sustainable harvest levels (Leach *et al.* 1987, Downing *et al.* 1990). Determining fish biomass and production involves intensive field work that can result in the unintentional mortality of fish. Collecting this information is also costly in terms of time and financial resources. It is not always feasible or desirable to collect this information for large regions. Instead, fisheries managers rely on habitat characteristics to estimate fish yield in lakes. Annual fish yield (kg/ha) is the amount of fish that can be taken annually without exhausting the ability of the fish community to compensate (Colby *et al.* 1982). One measure of yield is maximum sustainable yield, or the maximum number of fish that can be taken every year over an infinite period.

Fish yield is not a true measure of fish biomass and production; rather it estimates the potential harvest of a fishery. Most of the formulas predicting fish yield from habitat characteristics were developed from known fish catches taken from large lakes (Downing *et al.* 1990, Cote *et al.* 2011). These catches were assumed to be from lakes with moderate to intense fishing pressure near the maximum sustainable yield. Maximum sustainable yield underestimates total fish production in a population because yield is derived only from the larger fish selected by a fishery and it does not include natural mortality (Dickie *et al.* 1987, Hanson *et al.* 2010).

A wide variety of studies have linked fish yield to empirical measures of lake morphology, chemistry, physical features, and biological production. In the following text, I limit my discussion to those variables used to estimate yield of freshwater fishes found in lakes and reservoirs (Table 1). See Appendix 1 for a more detailed description of each variable and complete list of associated references.

Morphological Variables

Morphological variables of lakes influence fish biomass and productivity by affecting water temperature, sunlight, nutrient sources, and the amount of time required to replace the volume of water in a lake (Ryder 1965, Chow-Fraser 1991, Cote *et al.* 2011). The most common morphological feature used to predict fish yield is lake depth, which relates to lake stratification and nutrient cycling (Prepas 1983, Chow-Fraser 1991). Lake depth is a commonly used variable in a morphoedaphic index to predict fish yield (Ryder 1965). The morphoedaphic index is the ratio of total dissolved solids to mean lake depth (see page 2 for further description).

Lake surface area and volume are also used by some researchers as an index of habitat size (Ryder 1982). The Alaska Department of Fish and Game estimates lake trout yields from a lake area model (Burr 2006). Lake area is also applied to a morphoedaphic model and trophometric index (Rempel and Colby 1991, Lara *et al.* 2009; see page 4 for descriptions). Lake area is a parameter in lake trout population harvest models (Shuter *et al.* 1998, Shuter and Lester 2004). Lake area is also used to calculate yields for an entire lake from area-based estimates, such as the model currently used by the Government of Yukon (Schlesinger and Regier 1982).

An index of lake basin permanence, which is an index of shoreline, volume, and depth, was used in Newfoundland to predict salmonid biomass (Kerekes 1977, Cote *et al.* 2011). This index accounts for the productivity of the shallow littoral zone in lakes.

Physical Variables

Physical variables, such as climate and water temperature, affect the rate of photosynthesis and primary productivity (Christie and Regier 1988, Cote *et al.* 2011). They also affect fish growing degree days. Two approaches consider water temperature: a formula that uses mean annual air temperature as a surrogate for water temperature (existing Yukon model; Schlesinger and Regier 1982), and a formula that uses thermal habitat volume (Christie and Regier 1988).

Christie and Regier (1988) used thermal habitat volumes to estimate yields of lake trout in large lakes (8,000 to 19,000 ha). Thermal habitat volume measures the quantity of optimal thermal habitat for specific species (e.g., 8 °C to 12 °C for lake trout) when lakes are stratified from June to September. This approach was modified to apply to smaller lakes (100 to 4,000 ha) using temperature profiles from July (Payne *et al.* 1990, Burr 2006). The Ontario Ministry of Natural Resources preferred estimating lake trout yield with thermal habitat volume compared to the morphoedaphic index because thermal habitat volume models fit the data better, were more conservative, and the morphoedaphic index did not apply well to species-specific models (Payne *et al.* 1990). Mackenzie-Grieve and Post (2006a) applied thermal habitat volumes to predict the effects of climate change on lake trout yields in Yukon.

Chemical Variables

Nutrient levels of lakes are key regulators of primary productivity and are used to predict fish biomass and yields (Cote *et al.* 2011). The concentration of total dissolved solids is the most widely applied chemical variable and is used in the morphoedaphic index and lake trout population harvest models (Ryder *et al.* 1974, Jones and Hoyer 1982, Chow-Fraser 1991, Shuter *et al.* 1998, Shuter and Lester 2004). The concentration of total dissolved solids is considered a good predictor of fish yield because values are seasonally stable, relatively inexpensive to measure, and correlate to phosphorus and nitrogen (Ryder *et al.* 1974, Hanson *et al.* 2010). The concentration of total dissolved solids is often derived from a more easily measured and tightly correlated proxy, conductivity. In Yukon, total dissolved solids values are lowest in unglaciated lakes and highest in lakes situated in the upper Yukon River valley, where there is a thick layer of volcanic ash (Lindsey *et al.* 1981).

The concentration of total phosphorus is the next most commonly used chemical variable; however, it is less practical and more expensive to measure because it can fluctuate dramatically over space and time (Ryder 1982). Several researchers have been successful in measuring the spring loads of phosphorus as a surrogate for total phosphorus (Ryder 1982, Knösche and Barthelmes 1998). Total phosphorus is often a limiting nutrient in temperate lakes and a stronger predictor of primary productivity than total dissolved solids (Hanson and Leggett 1982, Dillon *et al.* 2004, Baigún *et al.* 2007).

The concentration of total nitrogen has been used successfully as a predictor of fish yields and chlorophyll *a* in a small group of studies (Chow-Fraser 1991, Ranta *et al.* 1992, Baigún *et al.* 2007).

Biological Variables

Biological variables of lakes measure the biomass of species at various levels in the food web, which can then be used to predict fish biomass and yield. Some researchers have succeeded in predicting potential fish yield from measures of chlorophyll *a*, a proxy for algal biomass (Jones and Hoyer 1982).

Primary productivity and fish biomass are strong predictors of fish production, a measure of new fish biomass not based on yield from known catches (Downing *et al.* 1990, Downing and Plante 1993). Fish biomass and primary productivity (measures of phytoplankton biomass in the water column) are better predictors of fish production than total phosphorus and the morphoedaphic index (Downing *et al.* 1990, Downing and Plante 1993).

Another approach is to use the total biomass of benthic macro-invertebrates to predict the yield of benthic-feeding fish, such as lake whitefish (Matuszek 1978, Hanson and Leggett 1982).

Multi-Category Indices and Models

Morphoedaphic Index

One of the most common methods to estimate fish yield is the morphoedaphic index, which was originally developed by Ryder (1965). This ratio includes total dissolved solids as the edaphic, or chemical, variable (numerator) and mean lake depth as a morphological variable (denominator). Other morphological and nutrient variables can be

Table 1. List of parameters used to estimate lake productivity and sustainable fish yields (see Appendix 1 for a detailed description).

Type	Parameter	Description
Morphological	Lake mean depth	Indicator of stratification and nutrient cycling
	Lake surface area	Indicator of habitat size and heat retention
	Lake volume	Indicator of habitat size and heat retention
	Lake basin permanence	Indicator of shoreline habitat size
Physical	Mean annual air temperature	Surrogate for water surface temperature
	Thermal habitat volume	Optimal thermal habitat quantity in summer
Chemical (Edaphic)	Total dissolved solids	Measurement of all dissolved nutrients
	Conductivity	Field measurement correlated to total dissolved solids
	Total phosphorus	Limiting nutrient in many temperate lakes
	Total nitrogen	Nutrient shown to predict lake productivity
Biological	Chlorophyll *a*	Surrogate for algal biomass
	Primary productivity	Measure of phytoplankton biomass
	Fish biomass	Measure of fish biomass
	Benthic invertebrate biomass	Measure of invertebrate biomass
Multi-Category Indices and Models	Morphoedaphic index	Ratio of total dissolved solids and lake depth
	Morphoedaphic model	Model includes total dissolved solids, lake area and volume
	Trophometric index	Model includes lake area, perimeter, volume, conductivity and chlorophyll *a*
	Lake trout population harvest model (Shuter model)	Model includes total dissolved solids, lake area, lake trout life-history parameters and angler harvest parameters
Harvest Effort	Fishing effort	Does not affect productivity of lakes but can affect estimate of fish yield when yield estimates come from lakes assumed to have moderate to intense fishing pressure near maximum sustainable yield

used in this index (including chlorophyll *a* which correlates with nutrients); however, Ryder (1982) argued that total dissolved solids and mean depth are the best indicators for their reliability and feasibility to measure. The model was originally developed for large temperate lakes in North America with similar climatic conditions and fishing pressures (Ryder 1965, Ryder *et al.* 1974). The index was then modified by various researchers and applied on a global scale (Ryder 1982). Schlesinger and Regier (1982) added a climatic variable (mean annual air temperature) to apply the morphoedaphic index to broader regions.

The morphoedaphic index was developed to estimate the maximum sustainable yield of all harvestable fish species within a lake. This multi-species yield estimate can be partitioned according to the percent composition of a species in the lake. For example, the Ontario Ministry of Natural Resources partitioned 25% of the maximum sustainable yield for lake trout (Colby *et al.* 1982). Ontario discontinued this approach several years later because the ministry found the morphoedaphic index did not partition well into species-specific models (Payne *et al.* 1990).

The morphoedaphic index is both favoured and criticized for its simplicity. The first criticism is the use of maximum sustainable yield as an estimate because most formulas did not consider the effects of fishing effort when they were developed (Colby *et al.* 1982). Researchers caution that maximum sustainable yield estimates should be treated conservatively (Schlesinger and Regier 1982). True fish productivity, which is not related to fish catches, was used to predict lake productivity in two studies (Downing *et al.* 1990, Downing and Plante 1993). In both studies the morphoedaphic index was not a good predictor of fish production; however, neither study controlled for climate when looking at morphoedaphic indices, which is necessary at a global scale (Schlesinger and Regier 1982).

A second criticism of the morphoedaphic index is the trophic linkages among total dissolved solids and fish productivity are much more complex than represented by the model. Although nutrients may accurately estimate zooplankton biomass in Canadian lakes, the predictive power of the morphoedaphic index became progressively weaker with increasing trophic level (Chow-Fraser 1991).

A third criticism of the morphoedaphic index is it does not predict yield well in small lakes (< 1,000 ha) where the littoral zone has more effect on productivity than in larger lakes (Cote *et al.* 2011).

A fourth criticism of the morphoedaphic index concerns the statistical shortcomings of using ratios. The morphoedaphic index was developed as a simple computation for managers prior to widespread access to computers and statistical software (Rempel and Colby 1991). Predictive models using the morphoedaphic ratio are biased by spurious correlations, thereby explaining more variance than it actually accounts for, because these ratios are not normally distributed (Schneider and Haedrick 1989, Jackson *et al.* 1990). Critics suggest using bivariate statistical approaches or other statistical distributions (Jackson *et al.* 1990).

Morphoedaphic Model

To account for the statistical shortcomings of the morphoedaphic index, Rempel and Colby (1991) developed a morphoedaphic model that avoids the use of ratio data. This model was developed from 20 lakes in Ontario and uses 3 variables (lake area, lake volume, and total dissolved solids) to describe lake thermodynamic and fertility properties. The use of this model should be restricted to lakes with similar physical environments because temperature variation is not considered as a variable in the model (Rempel and Colby 1991).

Trophometric Index

A trophometric index developed in Spain uses trophic and morphological variables to estimate fish production (Lara *et al.* 2009). The trophometric index includes lake area and perimeter, volume of water with sufficient oxygen to sustain fish life, conductivity, and chlorophyll *a* concentrations. Many aspects of this index are similar to the morphoedaphic index.

Lake Trout Population Harvest Model

In 1998, Shuter *et al.* developed a lake trout population harvest model (herein called the Shuter model) that incorporates a variety of parameters. Lake trout yields are estimated from total dissolved solids, lake area, and a series of life-history parameters derived from lake trout growth patterns and carrying capacities. In this model, lake trout growth rates early in life correlate to productive lakes with higher total dissolved solids values. Lake area correlates to maximum adult size because large lakes support more diverse prey for adult trout. Lake area also correlates to carrying capacity because larger lakes provide more thermally suitable habitat. This model also considers angler harvest parameters and allows fisheries managers to compare the effects of various regulatory options on sustainable harvest estimates. The Shuter model is being modified for application by fisheries managers in British Columbia and Ontario (see pages 7 and 8).

Harvest Effort

Fishing effort (often expressed as fishing hours) is a variable that does not affect fish production, yet several studies show it can affect estimates of fish yields. As fishing effort increases, observed yield increases until it approaches the maximum sustainable yield (Colby *et al.* 1982). Observed yield then tends to reach an asymptote with further fishing effort. When fishing effort is low, observed yields can underestimate the maximum sustainable yield. Many estimates of fish yield were developed from known catches assumed to have moderate to intense fishing pressure at or near maximum sustainable yield (Downing *et al.* 1990, Cote *et al.* 2011). Those studies that included fishing effort as a parameter found it to have a strong relationship with yield estimates

Table 2. Overview of models used to estimate lake trout productivity that are under development or currently in use in Yukon, Alaska, British Columbia and Ontario.

Type	Model	Region	Input Variables	Output Variables	Reference
Morphoedaphic Index	Schlesinger and Regier Model	Yukon	Total dissolved solids Mean lake depth Mean annual air temperature Lake surface area	Maximum sustainable yield (for all fish species)	Schlesinger and Regier (1982)
Lake Area	Lake Area Model	Alaska	Lake surface area	Annual lake trout harvest	Evans *et al.* (1991) & Burr (2006)
Lake Trout Population Harvest Model	Shuter Model	Ontario	Total dissolved solids Lake surface area Lake trout life-history parameters Angler harvest parameters	Sustainable lake trout yield	Shuter *et al.* (1998) & Shuter and Lester (2004)
	B. C. Model	British Columbia	Total dissolved solids Lake surface area Lake trout life-history parameters Angler harvest parameters	Sustainable lake trout yield	Shuter *et al.* (1998) & Shuter and Lester (2004)
	Ontario Model	Ontario	Total dissolved solids Lake surface area Lake trout life-history parameters Angler harvest parameters Climatic factors Thermal habitat volume Total phosphorus	Sustainable lake trout yield	Shuter *et al.* (1998) & Shuter and Lester (2004)
Thermal Habitat Volume	Thermal Habitat Volume Model	Ontario & British Columbia*	Optimal thermal habitat volume (8 – 12 °C)	Sustainable lake trout yield	Christie and Regier (1988) & Payne *et al.* (1990)

*The thermal habitat volume model was also applied to a subset of Alaska (Burr 2006) and Yukon lake trout populations (Mackenzie-Grieve and Post 2006a). See pages 6 and 7.

and sometimes environmental factors were not significant or useful additions to tested models (Schlesinger and Regier 1982, Ryan and Kerekes 1989, Evans *et al.* 1991, Laë *et al.* 1999, Gomes *et al.* 2002). Since few studies have used fish production to estimate fish yield, fisheries managers are cautioned to treat maximum sustainable yields conservatively (Schlesinger and Regier 1982).

Review of Approaches used by Yukon and Neighbouring Jurisdictions

I interviewed neighbouring jurisdictions to learn what methods they were using to estimate sustainable levels of lake trout harvest (Table 2). I chose jurisdictions with similar environments (see Appendix 2 for list of people interviewed). I discuss the perceived strengths and weaknesses of each approach described during our discussions.

Yukon

The Government of Yukon's Fish and Wildlife Branch uses the Schlesinger and Regier (1982) model that integrates the morphoedaphic index (TDS/Z) and climatic variability to estimate maximum sustainable yield. Specifically, the maximum sustainable yield is calculated as:

$$\log(MSY) = 0.05TEMP + 0.280 \cdot \log\left(\frac{TDS}{Z}\right) + 0.236$$

where MSY = maximum sustainable yield for *all fish species* (kg/ha*year), TEMP = mean annual air temperature (°C), TDS = total dissolved solids (mg/L), Z = mean lake depth (m).

Mean annual air temperature is modeled from existing climate data and represents the average from 1960 to 1990 (ClimateBC version 3.21; Wang *et al.* 2012). Total dissolved solids are measured from water samples or estimated from conductivity, a proxy measured in the field. Mean depth is a rudimentary calculation based on bathymetry mapping. For a description of methods used to measure each variable, see Appendix 3.

The Schlesinger and Regier equation was developed from known fish catches at 40 lakes situated between 62 degrees north and 15 degrees south. The model explained 81% of the variability in fish yields. A similar model that capped mean depth at 25 m explained slightly more variability in yields (Schlesinger and Regier 1982).

The model was based on fish catch yields from moderate to intensely fished lakes assumed to be near maximum sustainable yield. The authors considered fishing effort in the development of the model because fishing effort can affect fish yield estimates.

In Yukon, the maximum sustainable yield predicted from this equation is then partitioned by species (e.g., 30% for lake trout). Percentages other than 30% of maximum sustainable yield may be used for lake trout based on known species compositions from index netting surveys. This species-specific maximum sustainable yield is then converted to a species-specific optimal sustainable yield (OSY) which is 15% of maximum sustainable yield for lake trout (Department of Environment *et al.* 2010).

$$Lake\ Trout\ OSY = 0.15 \cdot 0.30MSY$$

When lake trout harvest estimates from angler harvest surveys exceed the optimal sustainable yield, the harvest is considered unsustainable.

Increases to the temperature variable in the Schlesinger and Regier formula result in higher estimates of fish yield, including lake trout; however, lake trout yields are predicted to decline with climate warming (Shuter and Lester 2004). This is likely a result of the Schlesinger and Regier model being developed to predict yield for all fish species. While productivity for many cool and warm water fish is expected to increase due to climate warming (Shuter and Post 1990, Dove-Thompson *et al.* 2011), lake trout, which are a cold water fish, are likely to experience reduced availability of their preferred thermal habitat and reduced production, although the effects vary depending on the physical characteristics of each lake (Shuter and Lester 2004, Dove-Thompson *et al.* 2011).

Mackenzie-Grieve and Post (2006a) estimated lake trout yields in 33 Yukon lakes with a thermal habitat volume model. The authors used this approach to predict the impacts of climate warming on lake trout yields in Yukon under 3 climate warming scenarios. For lakes in southern Yukon, a 2 °C, 4 °C, and 6 °C increase in mean annual air temperature led to shrinking of optimal thermal habitat in most lakes, and, as a result, an 8%, 19%, and 23% reduction in potential harvest, respectively.

Mackenzie-Grieve and Post (2006b) also measured thermal habitat preference. They found that lake trout in Kathleen Lake, situated in southwest Yukon, selected habitats that were slightly colder than the 8 °C lower limit of their literature-derived optimal thermal range.

Alaska

The Alaska Department of Fish and Game uses a lake area model to estimate potential lake trout harvest levels (Burr 2006). In this model, predicted annual harvest is calculated as:

$$\log(H) = 0.60 + 0.72 \cdot \log(A)$$

where H = annual harvest (kg/year) and A = lake surface area (ha). Annual sustainable harvest (in kg) is converted to an estimate of the number of fish per year using lake trout weight and length data.

This model was developed from a variety of Ontario lakes by Evans *et al.* (1991) and describes the relationship between lake area and observed annual yields of lake trout. Lake area was found to have a strong association with lake trout productivity. The size of lake trout and their age-at-maturity increase with lake size. Smaller lakes produce greater yields than large lakes on a per unit area basis, but because of their overall smaller populations, they are more vulnerable to overexploitation (Evans *et al.* 1991). The predicted annual harvest is treated as a threshold that should not be exceeded (Burr 2006).

The perceived strength of the lake area model is that it can be applied to very remote lakes since no site visit is required to collect morphological, chemical, or biological data. The model was developed on a large and diverse lake dataset (Evans *et al.* 1991). The lake area model also performed better than thermal habitat volume models (Christie and Regier 1988, Payne *et al.* 1990, Burr 2006). Thermal habitat volume models were applied to 2 Alaska lakes, but volume measurements varied by a factor of 3 among years (Szarzi and Bernard 1997, Burr 2006). This generated wide fluctuations in available habitat measurements and annual harvest estimates. Due to this variability and because many Alaska lakes are not temperature stratified during the summer, the Alaska Department of Fish and Game adopted the lake area model (Burr 2006).

One perceived weakness of the lake area model is that lake productivity estimates derived from lake area are imprecise and do not consider other lake variables that affect lake trout productivity. For example, the authors that developed the lake area model (Evans *et al.* 1991) found that harvest effort together with lake area were stronger predictors of annual harvest than lake area alone. They based harvest effort on creel surveys conducted throughout the year; this is not feasible in Alaska, due to remoteness and associated costs of implementing annual surveys. Since the lake area model was developed in Ontario lakes with different environmental and angling patterns, it is unknown how well this model applies to Alaska lakes; however, in the few Alaska lakes with lake trout assessments and harvest information, the lake area model provides a conservative estimate of annual harvest (Wuttig 2010).

Another weaknesses of the lake area model is the inability to compare predicted annual harvest with estimates of actual harvest. Lake trout weight and length composition data are needed to convert annual harvest predictions into an estimate of the number of fish per year (Burr 2006). Actual harvest is calculated from a state-wide mail survey of harvest, catch, and fishing effort data, which can be imprecise for lakes with only a few responses.

British Columbia

The Government of British Columbia's Fish Wildlife Branch is developing a lake trout management plan and a lake trout population harvest model (herein called the B. C. model) where sustainable harvest is measure by:

$$H = f(W\infty, \omega, t_m, f_{max}, \alpha_{max}, M; \beta, B_o; t_c, F, q)$$

where H = sustainable lake trout harvest (kg/year), $W\infty$ = maximum adult size, ω = rate of length growth in early life, t_m = age of maturation, f_{max} = fecundity and number of eggs per kg of mature female at low density, α_{max} = survival from egg to age 1 at low population density, M = instantaneous natural mortality rate/year for fish aged 1 year or older, β = constant, B_o = carrying capacity, t_c = age of first capture by fishery, F = fishing mortality/year, and q = catchability coefficient.

This B. C. model, which is under development, modifies the Shuter model (Shuter *et al.* 1998). The B. C. model estimates sustainable lake trout harvest levels using life-history parameters of lake trout growth and productivity, habitat, and angling effort derived from lakes in British Columbia. Life-history parameters such as growth early in life are associated with total dissolved solids and maximum adult length is associated with lake area. Both the Shuter model and B. C. model were built from a dataset of lake trout populations with a wide variety of life-history characteristics, lake morphology, and lake chemistry (Shuter and Lester 2004).

The B. C. model also takes into account the distribution of angling effort. Angling effort varies with lake area. The angling effort dynamics were derived from data of recreational fisheries for rainbow trout because sufficient lake trout angling information does not currently exist. The inclusion of angling effort in the lake trout population harvest model will allow fisheries managers to compare how various regulatory options will affect lake trout harvest, angling effort, and the status of lake trout populations.

The perceived strengths of the B. C. model are that the model requires very little data from individual lakes and simulates 50 years of population dynamics under various regulatory regimes. This landscape approach provides a range of scenarios and options for decision makers for all lakes in British Columbia with lake trout. The current level of staff resources and funds directed to lake trout management in British Columbia is unlikely to allow intensive stock assessment or fishery assessment activities on more than a small subset of lakes. Fisheries managers believe this approach is also beneficial because it shifts management focus away from productivity, and towards representing angler behaviour and the attributes of the lake trout fisheries that will attract or deter angling effort and harvest. The model parameters were developed from lake trout life-history data from 1975 to 2000.

The perceived weaknesses of the B. C. model are primarily the large levels of uncertainty in parameters and lack of methods for verification. Life-history parameters for lake trout populations sampled after 2000 do not fit the model. In addition, the researchers developing the B. C. model have not resolved how the model will acknowledge multiple lake trout growth trajectories associated with dietary specialization (fish-feeding versus invertebrate-feeding lake trout). The Shuter model focuses on the dominant growth trajectory.

Considerable uncertainty is also associated with angling effort. The angling effort distribution model is not an empirical model, rather it is a partial model derived from rainbow trout angling. Fisheries managers found it difficult to predict angling effort for scenarios that show a decline in harvest. This model also does not consider anglers switching species or lake trout as by-catch.

Another level of uncertainty is the variability associated with total dissolved solids measurements. The temporal and spatial variability of these measurements has not been examined. Most total dissolved solids measurements are calculated from conductivity, a proxy field measurement. Across the range of lake trout in British Columbia, the correlation between total dissolved solids and conductivity does not appear to be as tightly correlated as previously thought (De Gisi, personal communication).

In addition to developing the B. C. model, fisheries managers are beginning to explore thermal habitat volume methods to estimate lake productivity in specific lakes. Field crews are mapping bathymetry from depth sounders and recording temperature and oxygen profiles during summer profundal index netting surveys to gather the data required to quantify thermal habitat volume. The B. C. model does not account for climate and some method of predicting how climate warming affects the resilience of lake trout to exploitation will be necessary before regulatory scenarios can be simulated.

Ontario

The Ontario Ministry of Natural Resources is revising the Shuter *et al.* (1998) lake trout population harvest model. The revised Ontario model (herein called the Ontario model) continues to estimate sustainable levels of lake trout harvest from life-history, harvest effort, and habitat parameters. The revisions integrate thermal habitat volume, climatic concepts, and new habitat parameters into the model. Mean depth and the area or volume of the hypolimnion (the lower and colder layer of water in stratified lakes that has little circulation) will be added as habitat parameters. Total phosphorus will replace total dissolved solids, although total dissolved solids may still be considered as a substitute if total phosphorus measurements are not available for a given lake.

The perceived strength of the Ontario model is it integrates thermal habitat volume and climatic concepts. This modification helps overcome the primary criticism of the original Shuter model—that it does not consider physical or climatic variables. The Ontario model will include an index of the hypolimnetic habitat (either area or volume) available during the summer when lakes become stratified. Growth data of lake trout from colder climates (such as Yukon) will also be included in the model to further integrate climatic concepts from across the distribution of lake trout in Canada.

Another improvement to the Ontario model is the use of total phosphorus as a parameter.

Researchers found that total phosphorus was a better measure of lake trout productivity than total dissolved solids (Dillon *et al.* 2004). Total dissolved solids were originally chosen because in the 1960s they were easier to measure than other nutrients (Ryder 1965, Dillon *et al.* 2004). Advances in technology have made total phosphorus a more feasible option. Total phosphorus is measured during spring water chemistry sampling, before thermal stratification. Lake trout productivity increases with total phosphorus until a certain point, after which algal growth leads to oxygen depletion in the hypolimnion (Dillon *et al.* 2004).

To apply the Ontario model more broadly, differences in lake trout growth trajectories would need to be resolved. The Ontario model accounts for only the dominant growth trajectory. In Ontario, the large lake trout morph that feeds primarily on fish can be observed in lakes where cisco are absent as a food source and fishing pressures are light. In these lakes, the small-bodied lake trout become prey for larger lake trout. The small-bodied lake trout primarily support the recreational fishery in these lakes. In lakes with cisco, the growth curves show less variation. Therefore, the Ontario model uses two separate growth curves, one for small-bodied lake trout in lakes without cisco and another growth curve for lake trout existing in lakes with cisco.

In addition to the Ontario model, the ministry is undertaking a broad-scale ecosystem monitoring program that is designed to sample water chemistry for numerous lakes and be applied to the management of various species (Ecological Framework for Fisheries Management Monitoring and Reporting Project Team 2008). This program is coordinated with a broad-scale fish community monitoring program (Sandstrom *et al.* 2011). Researchers from University of Toronto are working with the ministry to develop ecosystem models that consider multiple fish species. The proposed multi-species model would use a biomass size spectrum from plankton to large fish to understand potential yields.

Ontario has a long history of leading the development of new methods to estimate fish yields. To recap, Ryder developed the morphoedaphic index (Ryder 1965) and the ministry applied this approach to partition maximum sustainable yields by species in several lakes (Colby *et al.* 1982). In 1988, Christie and Regier developed an empirical model based on thermal habitat volume, which was adopted by the ministry because yield estimates were more conservative and the morphoedaphic approaches did not partition well into species-specific models (Payne *et al.* 1990). In 1998, Shuter *et al.* developed the lake trout population harvest model which the ministry continues to use. In 2004, Lester *et al.* also developed an empirically-based thermal-optimal habitat model for walleye.

Analysis of Government of Yukon's Methodology

Scenario Analysis

I conducted an analysis to understand how inaccuracies or changes to the morphoedaphic index and climatic variables influence estimates of maximum sustainable yield in Yukon lakes. In this analysis, I looked at various scenarios where the values of the input variables in the Schlesinger and Regier model changed. The purpose was to determine how the model behaved for lakes of various size classes (Table 3) and how changes to the inputs to the model affected yield estimates.

Two concerns led to this analysis. First, Cote *et al.* (2011) criticized the application of the morphoedaphic index to small lakes (< 1,000 ha). The authors found that the index did not apply well to small lakes because it was developed for larger lakes and littoral zones may have more of an effect on productivity in smaller lakes. Second, the uncertainty or variability of these input measurements (mean depth, lake area, total dissolved solids, and mean annual air temperature) is unknown. To illustrate, Yukon lake depth profiles are rudimentary and few weather stations exist to build the climate model that estimate mean annual air temperatures (Appendix 3). More data are required to understand temporal and spatial variability in total dissolved solids in Yukon lakes. Preliminary data indicate that the average difference between repeated measurements of total dissolved solids is approximately 35 mg/L (range 0 mg/L to 175 mg/L; Government of Yukon, unpublished data).

To understand how each model input variable affects maximum sustainable yield estimates, I examined the following scenarios: a 2 °C increase in mean annual air temperature, a 10% increase of total dissolved solids values, an increase of 30 mg/L of total dissolved solids values, and a decrease of 5 m lake depth. I examined how changes to each variable increased estimates of yield per hectare (Figure 1) and yield for the entire lake (Figure 2). I chose to test these values because they represented practical scenarios of uncertainty or changes to each variable in the model based on existing information.

Yield estimates for very small lakes (< 100 ha) increased substantially per hectare due to changes to temperature and lake depth values in comparison to larger lakes (Figure 1). A 2 °C temperature increase also resulted in an increase of yield for a given lake by more than 1,500 kg/year (Figure 2). Similarly, yield estimates for small lakes (101 to 1,000 ha) increased substantially per hectare due to changes to temperature and depth values in comparison to larger lakes (Figure 1). Small lakes showed the least increase in lake-wide yield due to changes in input parameters relative to very small lakes and larger lakes (Figure 2).

Medium-sized lakes (from 101 ha to 2,500 ha) appeared robust to changes in the input variables per hectare and per lake. A 2 °C increase resulted in a moderate increase to annual yield estimates per hectare (0.5 kg/ha*year) and very low increase to annual yield estimates per lake (751 kg/year). Medium-large lakes (2,501 to 5,000 ha) showed a slightly higher increase to annual yield estimates per lake (1,725 kg/year).

Yield estimates for larger lakes (> 5,000 ha) were relatively robust to changes in input variables per hectare; however, lake-wide yield estimates were very responsive to changes in all variables. Yield increased substantially due to a 2 °C increase (up to 16,049 kg/year in lakes > 15,000 ha). Increasing total dissolved solids had a substantial effect on yield (increases of nearly 6,500 kg/year in lakes > 15,000 ha). Decreasing depth increased yield by nearly 1,000 kg/year in lakes larger than 5,000 ha.

The scenario analysis shows that medium-sized lakes are more robust to uncertainty in parameters per hectare and per lake. Although Cote *et al.* (2011) caution the use of the morphoedaphic index in small lakes due to littoral effects, it is important to also recognize that yield estimates for larger lakes can be biased by multiplying the uncertainty of physical, morphological, and nutrient measurements by lake surface area.

Overall, when all 93 lakes were pooled together, a 2 °C increase in mean annual air temperature increased yield by 26% (1,802 kg/year on average) within a given lake (Figure 3). Increases of 30 mg/L total dissolved solids and a decrease of 5 m depth increased yield estimates by less than 9%.

This analysis suggests that fish yield estimates in Yukon lakes are very responsive to changes to mean annual air temperature. Yukon's existing model will result in higher estimates of optimal sustainable lake trout yield with warmer temperatures. These results contradict climate warming predictions that lake trout yields will decrease due to a reduction in optimal thermal habitat volume during the summer (Mackenzie-Grieve and Post 2006a). The Schlesinger Regier model predicts a 26% increase in lake trout yield with a 2 °C increase; however, Mackenzie-Grieve and Post predicted an 8% reduction in lake trout yield. As climate warms, Yukon's existing method becomes less conservative as a measure of sustainable lake trout yield.

Table 3. Yukon lake size categories.

Size Category	Size Range (ha)	Example Lake
XS	< 100	Chadden
S	101 - 1,000	Tarfu
M	1,001 - 2,500	Fox
M-L	2,501 - 5,000	Little Atlin
L	5,001 - 15,000	Kusawa
XL	15,001 - 65,000	Laberge

SWOT Analysis

A SWOT analysis was used to evaluate Yukon's existing method to estimate optimal sustainable lake trout yields. The SWOT analysis examines internal factors as strengths (S) and weaknesses (W) and external factors as opportunities (O) and threats (T). This analysis formed the basis for developing recommendations for the fisheries program.

Strengths

- Optimal sustainable yield estimates for lake trout are conservative and reduce the potential for over harvest (15% of 30% of the overall maximum sustainable yield for all fish species within a lake).
- The existing model was developed for temperate regions and is one of the few models to incorporate variability in yield associated with temperature.
- This method is simple to use and affordable.
- The model appears robust to uncertainty in parameters that estimate yield per hectare and per lake for medium-sized

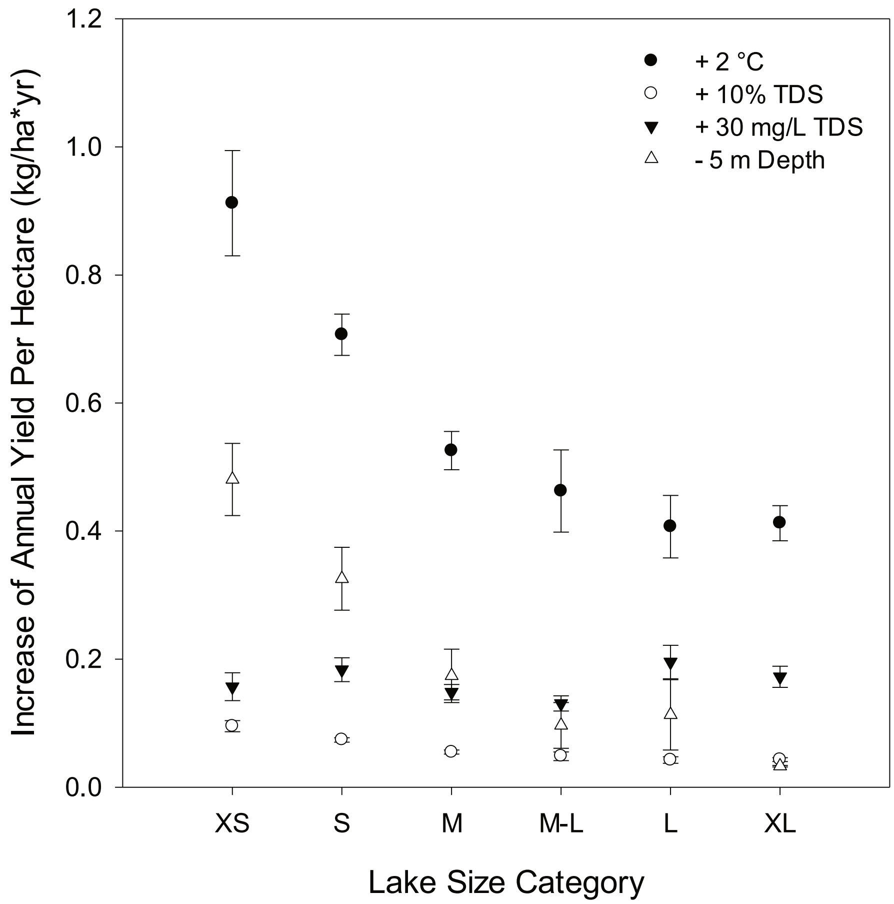

Figure 1. Mean (SE) increases to annual maximum sustainable yield estimates per hectare for Yukon lakes due to changes to variables in the Schlesinger and Regier model: an increase of the mean annual air temperature of 2 °C; a 10% increase of the total dissolved solids values; an increase of 30 mg/L of total dissolved solids values; and a decrease of 5 m depth. Lake size categories are described in Table 3.

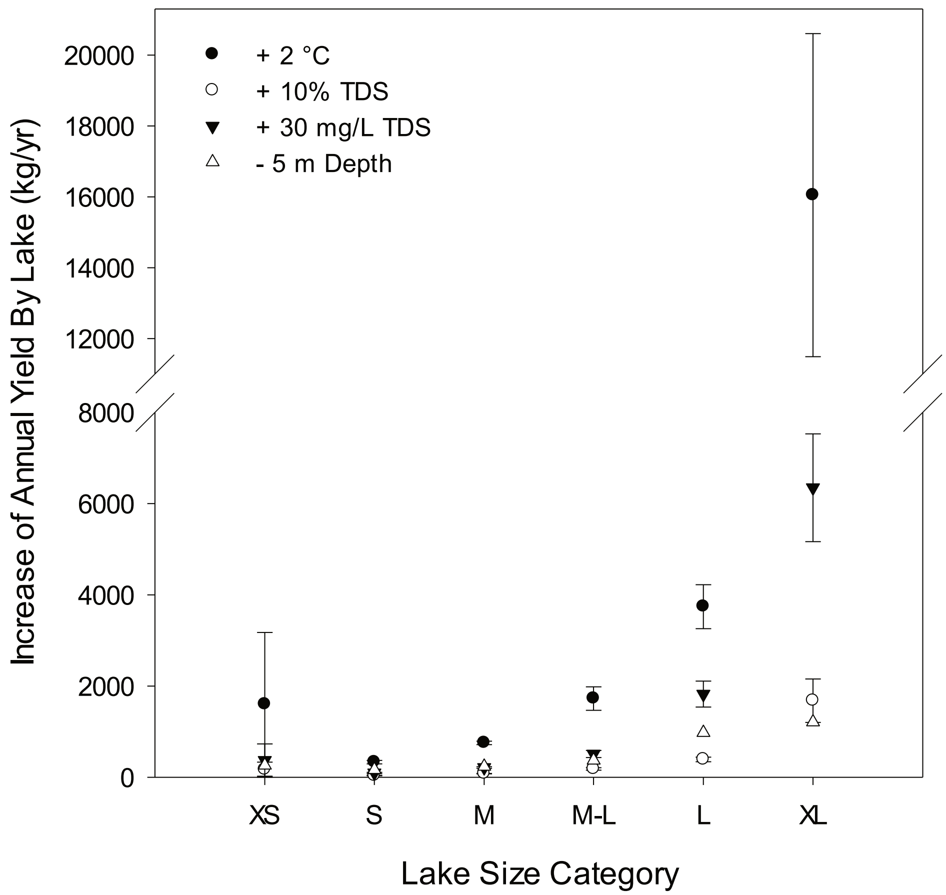

Figure 2. Mean (SE) increases to annual maximum sustainable yield estimates for entire Yukon lakes due to changes to variables of Schlesinger and Regier's model: an increase of the mean annual air temperature of 2 °C; a 10% increase of the total dissolved solids values; an increase of 30 mg/L of total dissolved solids values; and a decrease of 5 m depth. Lake size categories are described in Table 3.

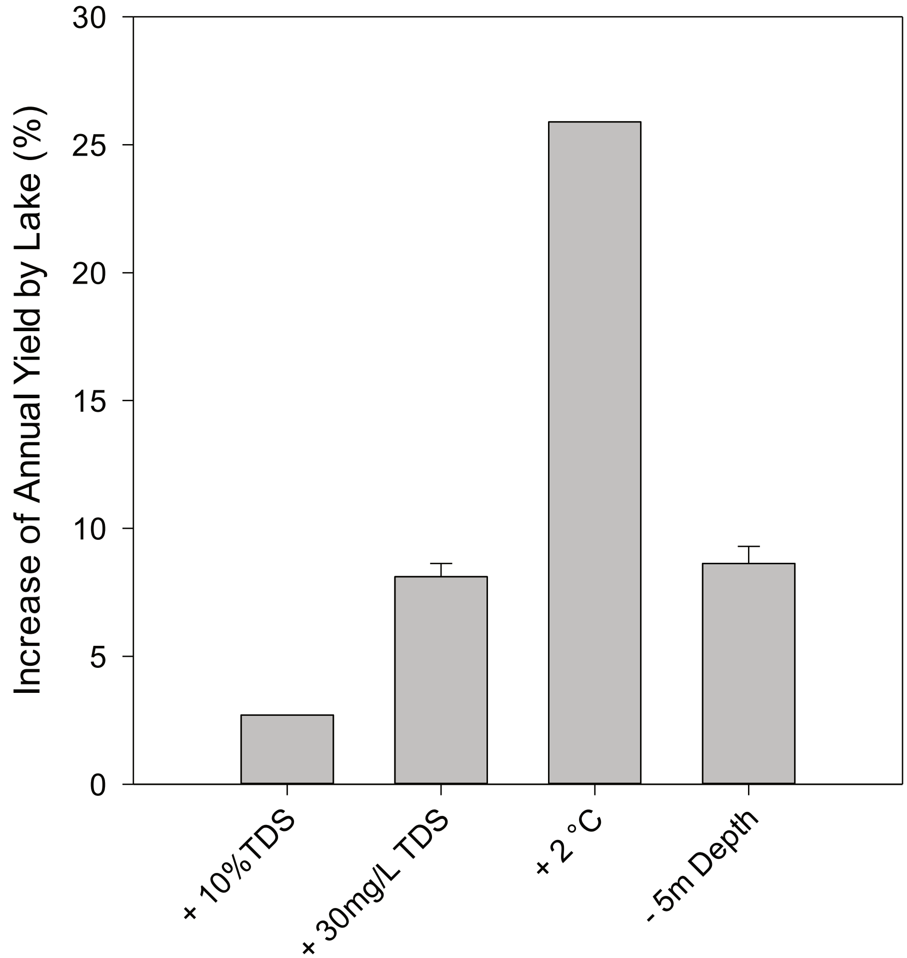

Figure 3. Overall mean percent increase (SE) to maximum sustainable yield estimates for Yukon lakes due to changes to variables of Schlesinger and Regier's formula: a 10% increase of the total dissolved solids values; an increase of 30 mg/L of total dissolved solids values; an increase of the mean annual air temperature of 2 °C; and a decrease of 5 m depth. Lakes of all sizes are included in overall change.

lakes with surface areas between 1,001 and 2,500 ha.

- The Government of Yukon has over 20 years of experience using this approach as a management tool and the model successfully results in the identification of lakes with harvest concerns (Department of Environment 2010).

Weaknesses

- Yukon applies the morphoedaphic index to estimate optimal sustainable lake trout yields; however, the index was developed as a multi-species model and other jurisdictions found maximum sustainable yield estimates did not partition well into species-specific yields.
- The model results in higher estimates of optimal sustainable lake trout yield with warmer annual air temperatures (which are a surrogate for water temperature); however, studies predict Yukon lake trout yields will decrease with climate warming due to a reduction in optimal thermal habitat volume during the summer.
- The model is very responsive to changes in mean annual air temperature and that parameter has not been updated with the most recent annual air temperature model that can calculate average temperatures up to 2015 (ClimateWNA version 5.21; Wang *et al.* 2012).
- The model is responsive to variability in total dissolved solids. The measurement uncertainty and spatial and temporal variability associated with that parameter are unknown.
- The model was developed from fish harvest data and not a true measure of fish production. It was also developed from large lakes with heavy to moderate harvest. It is unknown how well the model applies to small lakes with very little fishing effort.
- The model appears to be less robust to uncertainty in parameters used to estimate yield per hectare and per lake for small (< 1,000 ha) and large lakes (> 2,500 ha).
- Several input parameters in the model have not been updated in many years and may be inaccurate. For example mean depth estimates are rudimentary and lake surface area measurements predate digital mapping methods.

Opportunities

- Neighbouring jurisdictions are applying new methods to estimate sustainable lake trout harvests and these methods could be adopted in Yukon, including a modified Shuter lake trout population harvest model and thermal habitat volume model.
- Technical advances offer the ability to refine lake morphology, nutrient, and physical measurements, such as new methods to model lake bathymetry and loggers that continuously measure lake conductivity.
- Agencies and organizations that boat frequently on Yukon lakes with sonar depth sounders could collect depth data. These data could be used to refine bathymetry maps using geographic information system (G. I. S.) software.

Threats

- The existing model could over-estimate optimal sustainable lake trout yield as climate warms. This could lead to failing to identify overexploitation of Yukon lake trout. Climate change is predicted to decrease the potential yield of lake trout in Yukon because of a reduction in optimal thermal habitat volume; however, the Schlesinger and Regier model would estimate an increase in optimal sustainable yield.

Conclusion and Recommendations

In this paper I reviewed the methods used by fisheries managers to estimate lake productivity and sustainable angler harvests. The existing method used by the Government of Yukon to estimate lake productivity and sustainable lake trout harvests has worked well in identifying lakes of conservation concern; however, the model was not intended for single-species management and could lead to failing to identify overexploitation of lake trout as climate warms. Ontario and British Columbia are developing new methods to estimate sustainable harvests that could be applied to Yukon lakes and may improve the management of lake trout. Based on my review, I recommend exploring the following initiatives:

1. Measure total dissolved solids and total phosphorus

I recommend updating nutrient measurements for various Yukon lakes, including total dissolved solids and total phosphorus. Sampling protocols for both nutrients include single visits to the main lake basin to collect water samples near the surface after ice-off (before a lake has stratified). The concentration of total dissolved solids is a critical parameter for the Schlesinger and Regier model and is also included as a parameter in the Shuter lake trout population harvest model. I recommend collecting total phosphorus samples because phosphorus was shown to be a better predictor of lake trout productivity and could be a useful parameter in a lake trout population harvest model.

I also recommend examining the spatial and temporal variability of total dissolved solids measurements by deploying conductivity data loggers. Conductivity and total dissolved solids are highly correlated and these data loggers provide a better understanding of how a single point measurement does or does not represent the spatial and temporal variability in a lake.

2. Develop a database of variables that model lake productivity

I recommend developing a Yukon database for measurements of lake morphological, chemical, biological, and physical parameters from existing data files and literature (Lindsey *et al.* 1981, Horler 1982, Kirkland and Gray 1986, Shortreed and Stockner 1986, Stockner and Shortreed 1991, Wilson and Gajewski 2002, Wilson and Gajewski 2004, Bunbury and Gajewski 2005). This database should also include estimates of lake productivity and sustainable yield. A database will facilitate updates and archive past values, improve data management, and support spatial models of lake productivity yields in Yukon lakes.

3. Regularly update existing fish yield model for Yukon with best available information

I recommend regularly updating the input parameters with the best available information. This includes using G. I. S. derived measurements of lake area and mean depth and using the most up-to-date mean annual air temperatures (e.g., ClimateWNA version 5.21; Wang *et al.* 2012). For example, mean annual air temperatures are now available up to 2015 (rather than 1960 to 1990 which is used in the existing Yukon model). Incorporating the mean annual air temperature from the last century or 50 years would provide a more consistent and up-to-date measure of mean annual air temperature.

4. Update lake bathymetry maps

I recommend updating bathymetry maps for lakes, with priority given to lakes with complex littoral structures and potentially less accurate bathymetry maps. I recommend that field workers continue to use a combination of global positioning sytems (G. P. S.) and sonar depth sounders to record depth in Yukon lakes during fish population assessments. These data should be provided to the geomatics administrator with the Government of Yukon on a regular basis to update bathymetry maps using G. I. S. software.

I also recommend working with other agencies and organizations with boats fitted with sonar depth sounders to opportunistically map Yukon lakes. To facilitate this initiative, I recommend working with the geomatics administrator to develop guidelines for the collection and analysis of bathymetry data.

Updated bathymetry maps provide more refined and accurate bathymetric information to measure lake volume and mean depth. These data are particularly valuable for the Schlesinger and Regier model, as well as the application of alternative methods to estimate lake trout productivity, including the thermal habitat volume model or a lake trout harvest population model (e.g., the B. C. or Ontario models).

5. Investigate thermal habitat volume and lake trout population harvest models

I recommend investigating the applicability of yield models specific to lake trout in Yukon waters. To investigate thermal habitat volume models, I recommend that field workers continue to collect oxygen and temperature profiles, as well as depth, when conducting fish population assessments during the summer. This information provides updated and refined information to pilot a model for a candidate set of lakes and builds on the work of Mackenzie-Grieve and Post (2006a and b).

I recommend investigating the development of a lake trout population harvest model derived from Yukon parameters based on the Ontario model. This model would include lake nutrients, morphology, thermal habitat and lake trout life-history parameters. The thermal habitat volume data will also inform this model.

6. Calculate sustainable fish yield estimates from several models

I recommend that sustainable lake trout yield estimates be calculated for Yukon lakes using several different models and that the fisheries program adopt the best model (or models). The most suitable candidate models for comparison are the thermal habitat volume model, lake trout population harvest model, and currently used Schlesinger and Regier model. The yield estimates would then be examined for consistency with our understanding of lake trout life history, lake ecology and morphology, and history of exploitation by angling. The merits of each model should also be compared with the costs and constraints involved when applying each model to all Yukon lakes supporting lake trout.

7. Investigate relationships among lake nutrients and fish production

I recommend investigating food web relationships in various Yukon lakes to understand how nutrient availability affects primary productivity and fish production. Nutrients are good predictors of primary productivity; however, that relationship was shown to become progressively weaker with increased trophic level. (Chow-Fraser 1991). By examining how nutrients affect primary productivity and plankton assemblages, we will gain a broader ecosystem perspective of how lake nutrients affect primary productivity and fish production.

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Appendix 1 Parameters Used to Estimate Fish Yield in Lakes

Table 4. Detailed description of parameters used to estimate lake productivity and fish yields. A = lake surface area; Benthic = benthic macro invertebrate biomass; BPI = index of lake basin permanence; Chl *a* = Chlorophyll *a*; MEI = morphoedaphic index (TDS/Z); MEM = morphoedaphic model; PP = primary productivity; TDS = total dissolved solids; TEMP = mean annual air temperature; THV = thermal habitat volume; TN = total nitrogen; TP = total phosphorus; V = lake volume; Z = lake mean depth.

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Morphological			
Lake Mean Depth (Z)	• Yield decreases with increased Z because deeper lakes are less productive • Z used as an indicator of stratification and nutrient cycling • Denominator of MEI (see MEI) • Better indicator of lake morphology than A (Chow-Fraser 1991) • Maximum depth correlated to Z and could be used as denominator of MEI (Chow-Fraser 1991) • A superior predictor than MEI and TDS in a study (Prepas 1983) • Not a useful predictor in some studies compared to Benthic Macro Invertebrate Biomass, TP, Fishing Effort, A, and BPI	Prepas 1983, Chow-Fraser 1991 (See MEI)	Matuszek 1978, Hanson and Leggett 1982, Quiros 1990, Plante and Downing 1993, Laë *et al.* 1999, Cote *et al.* 2011
Lake Surface Area (A)	• Yield increases with larger A, although yield starts to decrease with very large lakes because they are less productive and oligotrophic • Z is positively correlated to A • An important predictor on a global scale and less important on a regional scale because nutrient inputs and Z vary more in lakes as a useful predictor (Ryder 1982) • Related to habitat size and heat retention • A superior predictor than Z, TDS and MEI in some studies • A proxy calculation for THV • Parameter in the Morphoedaphic Model (MEM) and Trophometric Index • Applied to multi-species, lake trout and whitefish and not useful in a salmonid study • Not a useful predictor in some studies compared to Z and Fishing Effort • Parameter in Lake Trout Population Harvest Model	Ryder 1982, Youngs and Heimbuch 1982, Christie and Regier 1988, Payne *et al.*1990, Evans *et al.* 1991, Rempel and Colby 1991, Marshall 1996, Shuter *et al.*1998, Shuter and Lester 2004, Burr 2006, Lara *et al.* 2009, Cote *et al.* 2011	Chow-Fraser 1991, Plante and Downing 1993, Laë *et al.*1999

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Lake Volume (V)	• Yield increases with V • Parameter in the MEM and Trophometric Index and used with optimal thermal habitat volume (See THV) • Related to optimal thermal habitat volume and used to predict lake whitefish yield • Better predictor than MEI (Payne *et al.* 1990)	Christie and Regier 1988, Payne *et al.* 1990, Rempel and Colby 1991, Lara *et al.* 2009	
Index of Lake Basin Permanence (BPI) = (littoral length/A)/Z	• Yield decreases with BPI (less shoreline per volume of lake) • Morphological index that considers the productive littoral zone, A, and Z • Useful in small lakes < 10 km2 because MEI developed for larger lakes and yield decreases slightly with A in larger lakes • BPI a superior predictor than Z and edaphic measurements	Kerekes 1977, Cote *et al.* 2011	
Physical			
Mean Annual Air Temperature (TEMP)	• Yield increases with increased TEMP • Climatic predictor useful for broad scale studies • Surrogate for water surface temperature • Useful predictor with MEI and fish production models built from actual production calculations	Schlesinger and Regier 1982, Downing and Plante 1993	
Thermal Habitat Volume (THV)	• Yield increases with increased THV • Measures optimal thermal habitat quantity when lakes are stratified and based on summer lake temperature profiles • Species-specific and applied to lake trout (8 °C to 12 °C; MacKenzie-Grieve and Post 2006b) • In Yukon, THV from July and early August improved precision and a single profile represented July average • Better predictor than partitioned yields based on MEI because data fit model better and yield estimates were more conservative (Payne *et al.* 1990) • Use cautioned for small lakes (<10 ha) because factors other than temperature may be limiting	Christie and Regier 1988, Payne *et al.* 1990, Marshall 1996, Mackenzie-Grieve and Post 2006b	

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Chemical			
Total Dissolved Solids (TDS)	• Yield increases with increased TDS • A surrogate for lake nutrients which control primary productivity (such as phosphorus and nitrogen) • Numerator of MEI (see MEI) • TDS stronger predictor of nutrients than TP because TDS stays constant over the year and is cheaper to measure. For example, TDS is 10,000 times more common and generally unaffected by TP fluctuations (Ryder *et al.* 1974) • Correlated to conductivity and alkalinity. TDS can be calibrated from conductivity measurements • A strong predictor of Chl *a* (Jones and Hoyer 1982) and PP; however, that relationship is thought to weaken up the food chain (Chow-Fraser 1991) • Not as useful a predictor in some studies compared to A, Z, Benthos, TP, and BPI • Parameter in Lake Trout Population Harvest Model	Ryder *et al.* 1974, Jones and Hoyer 1982, Ryder 1982, Chow-Fraser 1991, Rempel and Colby 1991, Shuter *et al.* 1998, Shuter and Lester 2004, Lubinski *et al.* 2008	Matuszek 1978, Hanson and Leggett 1982, Youngs and Heimbuch 1982, Prepas 1983, Dillon *et al.* 2004, Cote *et al.* 2011
Total Phosphorus (TP)	• Yield increases with increased TP • Phosphorus is a nutrient that predicts primary productivity and potential fish production • TP could substitute TDS in an MEI and may be more appropriate when TP is the limiting nutrient; however, TP varies more spatially and seasonally and is often not practical to measure (Ryder 1982) • TP spring load measured as a proxy TP to account for seasonal variation (Ryder 1982, Knösche and Barthelmes 1998) • TP used to predict chlorophyll and zooplankton (Shortreed and Stockner 1986, Chow-Fraser 1991, Stocker and Shortreed 1991, Hanson *et al.* 2010) • MEI was used to calculate TP (Cardoso *et al.* 2007) • Better predictor than TDS, Z, and MEI (Hanson and Leggett 1982, Baigún *et al.* 2007) • MEI was a better predictor than TP (Leach *et al.* 1987) • A and BPI performed better as predictors than TP (Cote *et al.* 2011)	Hanson and Leggett 1982, Shortreed and Stockner 1986, Downing *et al.* 1990, Chow-Fraser 1991, Stocker and Shortreed 1991, Ranta *et al.* 1992, Plante and Downing 1993, Knösche and Barthelmes 1998, Brämick and Lemcke 2003, Dillon *et al.* 2004, Baigún *et al.* 2007, Cardoso *et al.* 2007, Hanson *et al.* 2010	Ryder *et al.* 1974, Jones and Hoyer 1982, Ryder 1982, Leach *et al.* 1987, Cote *et al.* 2011

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Total Nitrogen (TN)	• Yield increases with increased TN • Better predictor of Chl *a* than MEI and TP • TN and TP good predictor of yield in Finnish lakes • Best predictor in a study in Patagonia	Chow-Fraser 1991, Ranta *et al.* 1992, Baigún *et al.* 2007	
Biological			
Benthic Macro Invertebrate Biomass (Benthic)	• Yield increases with increased Benthic • Measures of biomass of benthic macro invertebrates, which correlate to fish production • Incorporates the importance of allochthonous materials which are a major source of energy for invertebrates in small lake food chains (Hanson and Leggett 1982) • Better predictor than TDS and Z in studies where fish yields were based primarily on benthic-feeding lake whitefish (Matuszek 1978, Hanson and Leggett 1982) • An invertebrate production model (Borgmann method) was also used (Leach *et al.* 1987) • Considered a poor predictor because of trophic distance from TDS, macrobenthos, and fish (Knösche and Barthelmes 1998)	Matuszek 1978, Hanson and Leggett 1982, Leach *et al.* 1987	Knösche and Barthelmes 1998
Chlorophyll *a* (Chl *a*)	• Yield increases with increased Chl *a* • Measures Chlorophyll *a* concentration in the water column which correlates to algal biomass • Best predictor in study where Z too small and uniform to apply into an MEI and where Chl *a* was highly correlated to TDS (Jones and Hoyer 1982) • Parameter in Trophometric Index • Fishing Effort was a better predictor than Chl *a* (Gomes *et al.* 2002)	Oglesby 1977 (in Downing *et al.* 1990), Shortreed and Stocker 1986, Jones and Hoyer 1982, Stocker and Shortreed 1991, Lara *et al.* 2009, Hanson *et al.* 2010	Gomes *et al.* 2002
Primary Productivity (PP)	• Yield increases with increased PP • Measures phytoplankton biomass in water column • PP stronger predictor than Fish Biomass and TP in a study not influenced by Fishing Effort and catch data (Downing *et al.* 1990) • PP estimated from TP (Brämick and Lemcke 2003)	Oglesby 1977 (in Downing *et al.* 1990) Downing *et al.* 1990. Brämick and Lemcke 2003	

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Fish Biomass	• Yield increases with increased Fish Biomass • There is a strong relationship between fish biomass and annual fish production based on studies not influenced by Fishing Effort and catch data	Downing *et al.* 1990. Downing and Plante 1993	
Multi-Category Indices and Models			
Morphoedaphic Index (MEI) = TDS/Z	• Yield increases with increased MEI • Index that combines nutrient status and morphology and was originally applied to north temperate lakes and then to lakes around the world • TEMP added to model to account for climatic conditions (Schlesinger and Regier 1982) • TDS and Z measurements are relatively inexpensive and consistent to measure • MEI has been applied successfully on a global scale • Fish yield, which was used to develop models, is highly influenced by Fishing Effort and is not a true estimate of fish production • Predictive models using ratios may not be statistically valid due to lack of normal distribution, confidence limits, and spurious correlations • Too much trophic distance from TDS and fish production to use as model (Chow-Fraser 1991) • THV was a better fit to yield data and slightly more conservative (Payne *et al.* 1990)	Ryder 1965, Ryder *et al.* 1974, Colby *et al.* 1982, Ryder 1982, Schlesinger and Regier 1982, Schneider and Haedrick 1989, Chow-Fraser 1991, Nissanka *et al.* 2000, Baigún *et al.* 2007, Cardoso *et al.* 2007, Lubinski *et al.* 2008, Minns 2009, Mustapha 2009	Hanson and Leggett 1982, Prepas 1983, Downing *et al.* 1990, Jackson *et al.* 1990, Payne *et al.* 1990, Bajdik and Schneider 1991, Rempel and Colby 1991, Downing and Plante 1993, Knösche and Barthelmes 1998, Cote *et al.* 2011
Morphoedaphic Model (MEM) =A, V, TDS parameters	• Yield increases with increased MEM • A, V, and TDS in model capture lake thermodynamics and fertility • Model does not consider latitudinal or altitudinal temperature variation and it’s use should be restricted to lakes with similar physical environments • An analogue to MEI because MEI is a ratio with unknown distribution of errors and no confidence estimates	Rempel and Colby 1991	

Parameter	Relationship to Fish Yield	References in Support of Parameter	References Criticizing Parameter
Trophometric Index = A, V, O_2, Conductivity, Chl *a*, perimeter parameters	• Yield increases with increased Trophometric Index • Index developed from principle components analysis of 20 variables where fish productivity was based on hydro-acoustic and catch sampling	Lara *et al.* 2009	
Lake Trout Population Harvest Model = A,TDS, lake trout life-history parameters, angler harvest parameters	• Yield estimated from A, TDS, and parameters derived from lake trout growth, asymptotic length, and carrying capacity • Lake trout growth in early life correlates to productivity and TDS • A is correlated to asymptotic length because large lakes support more diverse prey for adult trout • A is correlated to carrying capacity because larger lakes provide more thermally suitable habitat • Angler harvest parameters allow managers to compare effects of regulations on potential yields	Shuter *et al.* 1998, Shuter and Lester 2004	
Harvest Effort			
Fishing Effort	• As Fishing Effort increases, observed yield increases until it approaches the potential or maximum sustainable yield (Colby *et al.* 1982) • Those studies that examined Fishing Effort found it to be a strong predictor of potential yield estimates and sometimes environmental variables were not significant • Parameter in Lake Trout Population Harvest Model • Fishing Effort often expressed as fishing hours	McCombie 1981 (in Colby *et al.* 1982, Schlesinger and Regier 1982, Ryan and Kerekes 1989, Evans *et al.* 1991, Ranta *et al.* 1992, Shuter *et al.* 1998, Laë *et al.* 1999, Gomes *et al.* 2002, Parkinson *et al.* 2004, Shuter and Lester 2004	

Appendix 2 People Interviewed for Jurisdictional Review

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Appendix 3 Methods Used to Measure Lake Productivity Variables

The following text describes the common methods that Yukon used to measure lake physical, morphological, and nutrient parameters.

Mean Annual Air Temperature

Mean annual air temperature is modeled from existing climate data and represents the average from 1960 to 1990 (ClimateBC version 3.21; Wang *et al.* 2012). The model was recently updated for western North America (ClimateWNA version 5.21) to include climatic variables from 1901 to 2015. The model estimates a series of monthly, seasonal, and yearly climatic variables for a specific point using latitude, longitude, and elevation. This modelling approach incorporates weather station data, a digital elevation model, and expert knowledge of climate patterns. Growing degree days above 5°C are also available, which may be more relevant for lake productivity. Mean annual air temperatures are directly calculated from monthly data; however, degree days are calculated from formulas.

Although this modelling approach provides a refined ability to understand how climatic variables affect physical parameters in lakes, the model has several limitations. First, error in mean annual air temperature increases for shorter time periods (less than 30 year norms) due to a lack of weather station data in historical records and annual climatic variability. Also, Yukon has sparse weather station coverage and stations are primarily located in open areas. As a result they may not accurately consider microclimates of lakes (Wang *et al.* 2012).

Mean Lake Depth

Depth profiles in Yukon lakes are rudimentary and accuracy is widely variable, as the source data was collected using multiple methods and technologies. Horler (1982) describes mapping bathymetry contour lines in many Yukon lakes. The author used a fish finder and ran transects across lakes by boat or float plane to record depth. Transect number and location varied by lake due to lake size, shape, and time restrictions. Transect lines were superimposed on 1:50,000 scale maps or aerial photos. Depth contour profiles were hand-drawn from depth readings at 2, 5, 10 or 20 m intervals (Horler 1981). In another set of lakes, a grid pattern was used to record depth readings from weighted lines during ice-covered months (Aaron Foos, personal communication).

Mean lake depth was calculated by dividing lake volume with surface area (Horler 1982). Lake volume was calculated by adding the volume of each depth interval in the lake bathymetry map (Horler 1982). Lake area was also calculated by computer, although the method used was not described (Horler 1981).

This rudimentary approach to bathymetry mapping is least accurate for lakes with complex littoral zones. In recognition on the limitations of existing bathymetry maps, Government of Yukon field crews began using a combination of G. P. S. and sonar chart plotters to log latitude, longitude, and depth while conducting fish population assessments. G. I. S. software was used to model new bathymetry maps for several lakes. The modelled bathymetry maps appear to work well and accurately map the shallow zone visible in aerial photos. The fisheries program continues to record depth along with location to refine bathymetry maps in the future.

Total Dissolved Solids

Total dissolved solids measurements in Yukon lakes were collected from a variety of methods. Horler (1982) describes collecting measurements during the last week of July and collecting a litre of water 1 m below the surface with a Kemmerer water sampler. Sites were chosen to represent the average lake depth. Samples were then stored at 4°C and sent to be analysed within 7 days at a laboratory.

In recent years, conductivity, a proxy for total dissolved solids measurements, was used to opportunistically update lake measurements during lake trout population assessments. Conductivity can be measured in the field from hand-held water quality units because conductivity correlates tightly with total dissolved solids. The following formula was used to calculate total dissolved solids from field conductivity measurements:

$$TDS = Conductivity_{25°C} \cdot 0.67$$

$$Conductivity_{25°C} = Conductivity / (1 + 0.02 \cdot (TEMP - 25))$$

Where TDS = total dissolved solids,
$Conductivity_{25°C}$ = specific conductivity at 25°C,
Conductivity = Conductivity measured in field,
TEMP = water temperature measured in field.