
Trout Population Parameters of Select Lakes within the Southern Tangier – Grand Lake Wilderness Area



Photo. E.A. Halfyard

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ABSTRACT

Brook trout population parameters were assessed in three lakes within the Tangier – Grand Lake Wilderness Area, Halifax County, Nova Scotia. Biological parameters assessed included population, density, biomass, size structure, relative weight, age, growth, mortality, and potential egg deposition. Additionally, angling activity and exploitation were estimated. The above parameters were also assessed against limnological and physical habitat parameters. The influence of competitor species was also evaluated.

Though these lakes were separated by only a few hundred meters and no impediments to fish passage were present, the population parameters of each lake were highly varied. Each of these three lakes could be considered productive to highly productive when compared to other Nova Scotia trout lakes with density estimated of between 6.1 and 37.6 trout per hectare and biomass estimates of between 1.8 and 5.3 kg per hectare. Increasing density and biomass correlated with decreasing mean length, mean weight, mean age and age-specific survival rate. Consequently, the size/age of trout providing the greatest contribution to total potential egg deposition varied greatly between lakes with 90% of eggs being deposited by trout smaller than between 25.0 cm to 31.0 cm. Management implications and research needs are discussed.

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BACKGROUND

Brook trout (*Salvelinus fontinalis*) are the most popular sport fish in the province, with anglers spending over 500 thousand days angling and catching an estimated 1.4 million trout in the year 2005 (Sport Fishing in Nova Scotia, 2005).

Brook trout are thought to be highly sensitive to habitat alteration, with increased temperatures (Lee and Rinne 1980, MacMillan et al. 2005, Wehrly et al. 2007), physical habitat destruction (Grant et al. 1986, Carline et al. 1992), inter-species competition (Faush and White 1986, Clark and Rose 1997, Rumsey et al. 2007) and over fishing (MacMillan and Madden 2007) all shown to adversely affect the number and size of brook trout. As climate change and land use patterns are anticipated to place continuing and increasing stress on the province's brook trout populations, a comprehensive understanding of the resource is essential to effective and sustainable management.

One approach to understanding the dynamics of brook trout in Nova Scotia is via modelling production. The formation of a model hinges on sufficient and biologically relevant data collected from Nova Scotia lakes and rivers. Several geophsicochemical grouping of both lake and river habitats exist in this province (Halfyard et al. 2008, MacMillan et al. 2008 *in press*) and while substantial data has been collected on the brook trout of Nova Scotia (Alexander and Merrill 1976, Leblanc 2000, MacMillan and Crandlemere 2005, MacMillan and Madden 2007) substantial additional information on population parameters is required to adequately describe brook trout across Nova Scotia.

The primary objectives of this study were to:

- 1) Estimate the population size of brook trout in selected lakes of the lower Tangier-Grand Lake Wilderness Area,
- 2) Estimate/assess population parameters for trout in the same systems to use in the formation of trout production models,
- 3) Describe typical angling activity in the area,
- 4) Test the morphoedaphic against trout population parameters, and
- 5) Assess exploitation in the study lakes and potential regulation

By achieving these four objectives, we aim to produce data-supported fisheries management options for the system. Furthermore, data obtained in this study can be used to compare trout populations from other ecologically/ limnologically similar lakes in an effort to understand provincially distributed trends in trout production.

STUDY AREA

Lakes sampled in this study lie in the lower (Southern) Tangier – Grand Lake Wilderness Area (TGLWA) (Figure 1). The TGLWA is a 16 000 hectare, provincially-designated wilderness protected area managed by the Nova Scotia Department of Environment. These areas are designed to protect portions of representative natural landscapes and ecosystems as well as to provide scientific, educational and recreational opportunities, including angling. Forestry, mining and hydroelectric operations are prohibited with wilderness areas.

The geology of the area is dominated by granite, shale and greywacke and thin or non-existent soils. Some glacially-derived till deposits are dispersed throughout the area, though they cover only a small proportion of the land surface. Forest type is generally coniferous, with various spruce species (*Picea* spp.), white pine (*Pinus strobus*) and balsam fir (*Abies balsamea*) the most prevalent. Sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are also present.

This area is relatively remote with no direct road access to the study lakes. These lakes are highly organic-stained systems, representative of the majority of Eastern Shore/ Southern Upland systems. Lake A is the smallest of all three lakes sampled, at approximately 11.8 ha. Lake C is slightly larger at approx. 13.6 ha while Lake B is the largest at approx. 63.0 ha.

Macrophyte growth in these lakes is limited. Of the species present, the family *Nymphaeaceae* (water lily) appears the most abundance. Also, in Lake C a submerged grass (potentially *Vallisneria* spp.) covers many shallow areas.

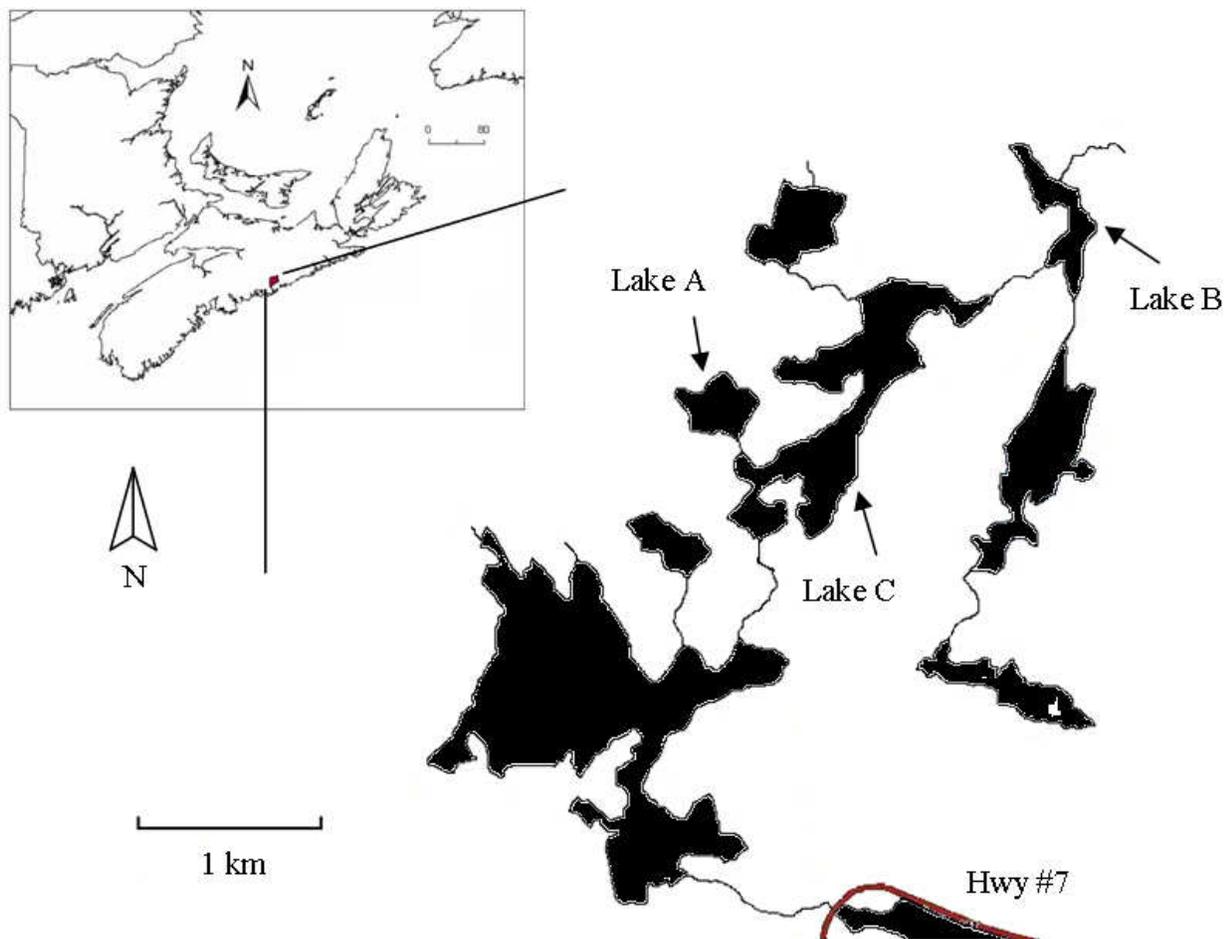


Figure 1 – Map of study lakes and surrounding watershed within the lower Tangier – Grand Lake Wilderness Area. The watershed includes additional lakes (not shown) but in general drains from Caribou Lake to Little River Lake and eventually empties into Ship Harbour (Atlantic Ocean). Lake A, Lake B and Lake C are approximately 11.8 ha, 63.0 ha and 13.6 ha, respectively.

METHODS

Sampling design

This project is unique as data collection was performed by four parties. The Nova Scotia Department of Fisheries and Aquaculture (NSDFA) was the primary investigator, and co-ordinated the sampling of the volunteer groups. Volunteer anglers include a group of camps owners from Lake B (NELCO) as well as anglers representing the conservation group of Trout Nova Scotia (TNS). Additionally, Anthony Heggelin, a student working at Dalhousie University (AH-Dal), was also sampling fish in the area and agreed to collect data useful for this project. Both volunteer groups captured fish via angling, measured fish to the nearest mm, marked the fish with an adipose clip and retained a sample of scales for age determination. Anthony Heggelin also captured fish with monofilament gill nets (mesh sizes 2.54cm, 3.81cm and 5.08cm), again measuring, clipping adipose fins and obtaining scale samples.

Finally, the NSDFA captured fish using a combination of angling, the aforementioned gill nets as well as trap net (1.5m opening). Fish were measured, weighed to the nearest gram, scale sampled, sexed based on phenotypic features (autumn only) and also marked. Marks consisted of Carlin tags applied to the anterior – posterior to the dorsal fin. Furthermore, a subsample of gravid females were retained for a separate fecundity study (Halfyard et al. 2008), and thusly sex determination was verified.

Sampling was conducted over two distinct periods, the spring/summer period (April-July) and the fall period (Sept.-Oct.). All parties conducted sampling during the spring/summer period, while only the NSDFA sampled in the autumn period.

Limnological data were collected on all lakes in late July, primarily to investigate the availability of thermal refugia provided by stratification, but also to give a general description of summer period water quality parameters. Variables measured included conductivity ($\mu\text{S}/\text{cm}$), dissolved oxygen (mg/L) and Secchi disk measurements of water clarity/ transparency.

Laboratory Processing

Scales were read by two NSDFA researchers and for scales where differing ages were estimated, a third researcher was asked to read the scale. Back-calculation was conducted using the Fraser-Lee method as described in Murphy and Willis (1996).

Water chemistry samples were sent to the Capital District Health Authority – Environmental Services Division. Analysis included major ions, nutrients, metals and standard limnological parameters.

Surface area and shoreline length estimates for this study were measured using ARCGIS software (ESRI ArcGIS v.9).

Statistical Analysis

Trout populations in each lake were estimated using two equations. The single census adjusted Petersen equation (Ricker 1975) is the most simplistic and used only one “marking” sample and one “recapture” sample for each lake. Where applicable (recaptures ≥ 3), a Schnabel maximum likelihood estimate (Ricker 1975) was also used. A major assumptions used for these

estimates was that each lake is a discrete population, and that no movement occurred between lakes (closed populations).

Because it is reasonable to assume that some mortality is associated capture and tag application, we made conservative estimates of mortality, with 5% mortality applied to all angled fish that were fin clipped, 10% mortality applied to all trout that were angled and tagged with a Carlin tag and 50% mortality for all trout that were net-caught and marked in any manor.

Density estimates were calculated by dividing the population estimate by the lakes surface area. Biomass was estimated by segregating the length-frequency data into 1 cm bins, and determining the proportion of the total sample that represents fish in any given length class. This proportion was then multiplied by the population estimate to give the estimated total number of trout of that length within the lake. This number was then multiplied by the expected weight for the mid-point of the length class, using the length-weight relationship. The sum total of the expected weights for all length categories represented the total biomass for the lake. This total biomass estimate divided by the lake's surface area to give the fall standing crop biomass per hectare estimate.

The relative weight equation, as described by (Wege and Anderson 1978) is $W_r = W / (W_s \cdot 100)$, where W_s is the length-specific standard weight equation, as determined via length-weight regression representing the species over its entire range (Murphy 1991). Standard weight equations have been derived for many species across their range (Murphy and Willis 1996, Murphy 1991) including the brook trout.

Only brook trout over 13.0 cm fork length were used in the relative weight calculations (Murphy et al. 1990, Murphy 1991) and parameters used in the standard weight equation were an intercept of -5.085 and a slope of 3.043.

Because the relative weight equation was developed to describe weight based on total length, and in this study we measured fork length, a conversions factor was applied to the length data. Using brook trout data from nearby Dollar Lake, Halifax Co. (NSDFA, unpublished data), a correction factor was calculated by dividing fork length by total length. This correction factor was then regressed on fork length to calculate a the correction factor based on length. The regression equation used was; total length (cm) = -0.0016 (fork length (cm)) + 1.0966, with $R^2 = 0.42$.

Fish lengths at past ages were back-calculated with the Fraser-Lee back-calculation equation as described by Murphy and Willis (1996). Annual growth was calculated as the mean difference of FL (age a+1) – FL (age a). Length-at-age and age specific growth was assessed using analysis of variance (ANOVA) with age as a factor.

To further assess growth, von Bertalanffy growth parameters were calculated as discussed by Ricker (1975). As the von Bertalanffy equation frequently provides unrealistic estimates of L_∞ , the mean fork length of the ten largest trout for each sample was calculated to provide an empirical reference point (Adams and Hutchings 2004).

Mortality estimates were obtained via the Heincke estimate of age composition and the Chapman-Robson combined estimates of survival (Ricker 1975).

Estimated potential egg deposition for each lake was calculated by again segregating the length-frequency data into 1 cm bins, and determining the proportion of the total sample that represents fish in any given length class. This proportion was then multiplied by the population estimate to give the estimated total number of trout of that length within the lake. This number was then multiplied by the expected mean number of eggs for the mid-point of the length class, using the pooled fecundity data from Lake A, Lake B and Lake C (Halfyard et al. 2007). The sum total of all egg deposition for each length class was considered the potential total egg deposition.

For trout larger than 32.2 cm, fecundity may be underestimated as no fish larger than this were sampled and the fecundity curve estimation and the exponent of the fecundity regression is lower than those reported in other studies (Vladykov 1956, Van Zyll de Jong et al. 1999).

Angling activity was assessed using only the data reported by the Lake B camp owners as this group represent “normal” angling activity. Their data were reported as they angled under normal routines, that is, no angling effort was spent solely for the purpose of providing data for this study. Catch per unit effort (CPUE) was determined as the total number of trout caught by the total effort (in hours) spent angling.

Exploitation was estimated by estimating total potential catch of trout by estimated retention rates (as determined by angler log books) and an estimate of angling-induced catch-and-release mortality as determined in the literature.

Lake survey data from 1020 lakes across the province were compiled (NSDFA *unpublished data*) from which mean depth was regressed on maximum depth. A strong relationship was shown where mean depth increased at a rate of $0.3 * \text{maximum depth}$ ($R^2=0.75$). Mean depth was estimated by multiplying the slope (0.3) of the regression of mean depth on maximum depth by the measured maximum depth of each lake. From these data and the measured concentration of total dissolved solids, Ryder’s morphoedaphic index could be calculated where $M.E.I. = \text{TDS (mg/L)} / \text{mean depth (m)}$ (Ryder et al. 1964, Ryder 1974). Using the conversion factor provided by Ryder (1964), the square root of the M.E.I. was multiplied by 0.996 to give an estimate of yield (kg/ha/year).

RESULTS

It should be stated that very few small trout (<20cm) were sampled during this study, thus the data described below is only for catchable trout, not young-of-year (YOY). One year old trout and likely 2 year old trout are also thought to be underrepresented as a result of gear selectivity, as there numbers, relative to older trout, were less than expected.

Lake A

Population Estimates, Density and Biomass

A single census adjusted Petersen estimation of the Lake A brook trout population indicated a population of 703 trout (95% CI (408, 1317)). A similar Schnabel maximum likelihood estimation indicated a trout population of 613 trout (95% CI (380, 1043))(Table 1). Because a Schnabel estimate provides a mean estimate of a series of ratios as well the fact that the Schnabel equations confidence intervals are relatively tighter to the estimated mean, it is assumed that the Schnabel equation provides a better estimate of the actual trout population.

Assuming a population of 613 brook trout, Lake A has a fall standing crop biomass estimate of 7.3 kg / ha and a density estimate of 51.9 trout/ ha (Table 1). If shoreline length is used to standardize, density becomes 37.6 trout/ 100m shoreline and biomass becomes 5.3kg/ 100m shoreline (Table 1).

Population Size Structure

Mean fork length of 220 brook trout sampled from Lake A was 22.9cm, with a median value of 23.9cm and a range of 10.9cm to 28.2cm (Table 2). Our data suggests that in Lake A, the proportion of catchable trout greater than 30cm (the length preferred by anglers) is extremely low as none were captured in our sample (Figure 2). Mean fork length showed no obvious relationship with the time (month) of sampling (Figure 3).

Relative Weight

The condition, as expressed by relative weight, of trout in Lake A is in general low, well below the “species level” average value of 100. For the 129 trout which were weighed, the mean relative weight was 79.2 (sd=11.8) (Table 3, Figure 4). Relative weight of Lake A brook trout did increase slightly throughout the sampling year, however this increase was not significant as indicated by both an ANOVA ($P=0.76$) and simple regression of relative weight on date ($R^2=0.06$) (Figure 5). As a result, these relative weight values can be compared to other lakes without compensation for seasonal trends.

Age and Growth

Based on scale analysis and the sample’s length frequency distribution, the percent composition of the Lake A sample for 1, 2 and 3 year old trout is 12.7%, 75.0% and 12.3% (Table 4). Back-calculated length at age provided evidence of growth rates at each year (Table 5). The relative rate of growth during the first year (age 0) was 8.8 cm/year (sd=1.5, N=42), during the second year (age 1) was 8.6 cm /year (sd=1.5, N=140) and during the third year (age 2) was 6.4 cm/year (sd=1.5, N=10) (Table 6). A von Bertalanffy growth curve was estimated from which the Brody growth coefficient was estimated at 0.197, the asymptotic length (L_{∞}) was 48.0cm and the length at $t=0$ was estimated at $t_0 = -0.421$ (Table 7, Figure 6). The mean length of the ten largest trout sampled from Lake A was 27.3cm (SD= 0.4) (Table 7).

Mortality

Estimations of mortality were restricted to trout aged 3+ and older as the younger age classes were thought to be under sampled as a result of gear selectivity. Chi-square analysis of Chapman-Robson survival estimates reaffirmed gear bias for all study lakes, with χ^2 values for 1 year old trout equal to 245.1 and for 2 year old trout $\chi^2 = 4.2$ (Table 8).

In Lake A, no trout older than 3 year old were sampled, therefore mortality estimates were not obtainable for this lake.

Potential Egg Deposition

Estimates of potential maximum egg deposition in Lake A indicates that 157 880 eggs would be deposited given current fecundity rates and population structure. This equates to an estimate of 17 542 eggs/ha. Length of fish by which 50% 70% and 90% of cumulative total potential egg deposition occurs is approximately 23.5cm, 24.3cm and 26.5cm (Figure 7). Maximum potential egg deposition occurs at a length of approximately 25.0 cm (Figure 8, Table 9).

Angling Activity Estimates

Camp owners did not intensively angle in Lake A, capturing only 3 trout. Therefore angling effort could not be assessed. If trout angled by NSDFA is examined, a total of 129 trout

were angled. Based on the estimate of 613 trout in Lake A, NSDFA angled approximately 21% of the total population.

Lake B

Population Estimates, Density and Biomass

A single census adjusted Petersen estimation of the brook trout population in Lake B indicated a population of 1126 trout (95% CI (670, 1976)). A similar Schnabel maximum likelihood estimation indicated a trout population of 1038 trout (95% CI (629, 1771)) (Table 1). Again, because the Schnabel estimate provides a mean estimate of a series of ratios as well the fact that the Schnabel equations confidence intervals are relatively tighter to the estimated mean, it is assumed that the Schnabel equation provides a better estimate of the actual trout population.

Assuming a population of 1038 brook trout, Lake B has a fall standing crop biomass estimate of 4.8 kg/ ha and a density estimate of 16.5 trout/ ha (Table 1). When compared to shoreline length, biomass becomes 2.9 kg/ 100m shoreline with a trout density of 11.8 trout/ 100m shoreline and a (Table 1).

By segmenting the tagging data into age categories we were able to estimate the populations of 2 year old and 3 year old trout in Lake B via age-specific mark-recapture experiments. These indicated that there were 543 aged 2 trout (95% C.I. (243,1358)). Similarly, the estimated population of 3 year old trout was 249 trout (95% C.I. (130, 524)). No estimate could be made for age 1 trout as few were sampled.

Population Size Structure

Mean fork length of 468 brook trout sampled from Lake B was 27.6cm, with a median value of 28.0cm and a range of 12.5cm to 42.5cm (Table 2). Our data suggests that in Lake B, the proportion of catchable trout greater than 30cm (deemed preferred by anglers) is moderate to high relative to other TGLWA lakes, as 165 of the 467 trout (35%) captured in our sample were of this length or greater (Figure 2). Mean fork length showed a slight decrease with the time (month) of sampling, where fall-sampled fish were shorter (Figure 3).

Relative Weight

The condition, as expressed by relative weight, of trout in Lake B is generally lower than the “species level” average value of 100. For the 89 trout which were weighed, the mean relative weight was 85.5 (sd=11.0) (Table 3, Figure 4). Relative weight of Lake B brook trout did increase slightly throughout the sampling year, however this increase was not significant as indicated by both an ANOVA ($P=0.76$) and simple regression of relative weight on date ($R^2=0.09$) (Figure 5). As a result, these relative weight values can be compared to other lakes without compensation for seasonal trends.

Age and Growth

Based on scale analysis and the sample's length frequency distribution, the percent composition of the Lake B sample for 1, 2, 3, 4 and 5 year old trout is 6.4%, 27.2%, 56.5%, 9.0% and 0.9%, respectively (Table 4). Back-calculated length at age provided evidence of growth rates at each year (Table 5). Mean growth during the first year (age 0) was 8.7 cm/year (sd=1.6, N=52),

during the second year (age 1) was 10.3 cm/year (sd=1.8, N=36), during the third year (age 2) was 6.3 cm/year (sd=1.4, N=10) and during the fourth year (age 3) was 5.9 cm/year (N=1) (Table 6). No growth was estimated for age 4 trout. A von Bertalanffy growth curve was estimated from which the Brody growth coefficient was estimated at 0.349, the asymptotic length (L_{∞}) was 41.8cm and t_0 was estimated at -0.322 (Table 7, Figure 6). The mean length of the ten largest trout sampled from Lake B was 36.5cm (SD= 3.6) (Table 7).

Mortality

Estimates of mortality for Lake B were restricted to trout aged 3+ and older as the younger age classes were again thought to be under sampled as a result of gear selectivity. Chi-square analysis of Chapman-Robson survival estimates reaffirmed gear bias for all study lakes, with χ^2 values for 1 year old trout equal to 295.3 and for 2 year old trout $\chi^2 = 258.1$ (Table 8).

In Lake B, Chapman-Robson estimates of mortality indicated that 3 year old trout are subject to 86% mortality (95% C.I. = (82%, 90%), $\chi^2 = 1.6$) and that 4 year old trout are subject to 92% mortality (95% C.I. (85%,100%)) (Table 8). These estimates were similar to those obtained using Heinke's method, where 84% and 90% mortality was calculated for 3 year old and 4 year old trout respectively.

For comparative purposes, mortality was estimated from the mark-recapture estimates of age 2 and age 3 trout populations using the ratio method. Mortality from age 2 to age 3 is estimated at 54%. This is similar to the Chapman-Robson estimate (though invalid based on Chi-square values) of 55% (Table 8).

Potential Egg Deposition

Estimates of potential maximum egg deposition in Lake B indicates that 310 720 eggs would be deposited given current fecundity rates and population structure. This equates to an estimate of 5 650 eggs/ha. Length of fish by which 50% 70% and 90% of cumulative total potential egg deposition occurs is approximately 26.6 cm, 28.1 cm and 30.5 cm (Figure 7). Maximum potential egg deposition occurs at a length of approximately 28.5 cm (Figure 8, Table 9).

Angling Activity Estimates

Camp owners reported catching a total of 271 angled trout from Lake B. Based on the population estimate of 1038, this represents approximately 26.1% of the total population. Most trout are released following capture (85.2%) with only 40 of the 271 trout retained. The vast majority of trout capture occurred in May (86.3% of total captures), with only 7.4% and 6.3% being captured in April and June, respectively. Of the trout caught by the Lake B camp owners, 69% were 3 years old or older.

Anglers reported spending a total of 210.5 hours angling on Lake B giving mean annual effort of 3.3 hours/ha. Angler success, as measured by the number of trout caught per hour angling or catch-per-unit-effort (CPUE) was 1.27 trout per hour (1.27 +/- 0.13 [mean +/- 1 S.E.]).

In a meta-analysis of hooking mortality on non-anadromous trout, Taylor and White (1992) found that mean mortality of brook trout was 3.4% when caught on artificial fly or lure (4 studies). When caught on bait, they found that mortality was 30.3% (2 studies). Similarly, Nuhfer and Alexander (1992) found that brook trout caught on artificial lures was 4.3%. Though no formal survey of equipment was conducted, anglers in Lake B indicated that artificial fly and artificial lures were the preferred method. To be conservative, we assume an angling-induced mortality on released trout of 10%.

Mean length of all trout caught by Lake B camp owners was 28.1cm while the estimated mean weight is 275g, equating to fish primarily aged 3 years. If we assume that 85.2% of angled trout were released and of these and that angling-induced mortality of released trout was at a rate of 10%, then the exploitation rate is approximately 6.2% and the current yield of trout is $0.28 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$.

We assume total angling pressure to be greater than that of the camp owners exploitation, hence if we double the catch to 52.2% of the total estimated population and assume the same retention rates and angling-induced mortality for released trout, the yield estimate then becomes $0.55 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$. Effort would also be increased to 6.6 hours/ha.

When we combine all angled trout, those of NELCO, TNS and NSDFA, a total of 423 trout were captured, representing 41% of the catchable population.

Lake C

Population Estimates, Density and Biomass

A single census adjusted Petersen estimation of the brook trout population in Lake C indicated a population of 179 trout (95% CI (66, 448)). These estimates use a small sample size, namely a small number of recaptured trout ($R=2$), thusly the population estimate is likely not reliable. However, assuming a population of 195 brook trout, Lake C has a fall standing crop biomass estimate of 3.9 kg / ha and a density estimate of 13.2 trout/ ha. Again, if we use shoreline length to standardize these measurements, density becomes 6.1 trout/ 100m shoreline and biomass becomes 1.8kg/ 100m shoreline (Table 1).

Population Size Structure

Mean fork length of 78 brook trout sampled from Lake C was 29.7cm, with a median value of 31.0cm and a range of 11.4cm to 42.0cm (Table 2). Our data suggests that in Lake C, the proportion of catchable trout greater than 30cm (the length preferred by anglers) is extremely high as 46 out of 78 (59%) trout in our sample were of this size or larger (Figure 2). Mean fork length again showed a slight decrease with the time (month) of sampling, where fall-sampled fish were shorter (Figure 3). Sample sizes were low in the fall samples.

Relative Weight

The condition, as expressed by relative weight, of trout in Lake C is generally very near the “species level” average value of 100. For the 7 trout which were weighed, the median relative weight was 96.9 (sd=11.1) (Table 3, Figure 4). Seasonal changes in relative weight of Lake C brook trout could not be assessed as only fish captured in the autumn were sampled. If Lake C is similar to the other two study lakes, relative weight does not significantly change throughout the year. Comparison of relative weight measurements to other lakes should be done cautiously however as both low sample size and the uncertainty of seasonal trends in relative weight may influence the mean relative weight of this sample.

Age and Growth

Based on scale analysis and the sample's length frequency distribution, the percent composition of the Lake C sample for 1, 2, 3, 4 and 5 year old trout is 10.3%, 15.4%, 59.0%, 12.8% and 2.6% (Table 4). Back-calculated length at age provided evidence of growth rates at each

year (Table 5). Mean growth during the first year (age 0) was 8.6 cm/year (sd=2.4, N=19), during the second year (age 1) was 8.0 cm /year (sd=2.5, N=14), during the third year (age 2) was 6.8 cm/year (sd=1.5, N=10). During the fourth year (age 3) was 6.0 cm/year (sd=1.0, N=9) and during the fifth year (age 4) was 7.3 cm/year (N=1) (Table 6). A von Bertalanffy growth curve was estimated from which the Brody growth coefficient was estimated at 0.087 , the asymptotic length (L_{∞}) was 97.0cm and t_0 was estimated to be -0.094cm (Table 7, Figure 6). The mean length of the ten largest trout sampled from Lake C was 36.5 cm (SD= 2.1)(Table 7).

Mortality

As with the other two study lakes, estimates of mortality for Lake C were restricted to trout aged 3+ and older as the younger age classes were thought to be under sampled as a result of gear selectivity. Chi-square analysis of Chapman-Robson survival estimates reaffirmed gear bias for all study lakes, with χ^2 values for 1 year old trout equal to 32.8 and for 2 year old trout $\chi^2 = 55.8$ (Table 8).

In Lake C, Chapman-Robson estimates of mortality indicated that 3 year old trout are subject to 80% mortality (95% C.I. = (71%, 90%), $\chi^2 = 0.2$) and that 4 year old trout are subject to 85% mortality (95% C.I. (64%,100%)) (Table 8). These estimates were similar to those obtained using Weinke's method, where 78% and 80% mortality was calculated for 3 year old and 4 year old trout respectively.

Potential Egg Deposition

Estimates of potential maximum egg deposition in Lake C indicates that 61 833 eggs would be deposited given current fecundity rates and population structure. This equates to an estimate of 5 622 eggs/ha. Length of fish by which 50% 70% and 90% of cumulative total potential egg deposition occurs is approximately 31.0cm, 32.0cm and 34.0cm (Figure 7). Maximum potential egg deposition occurs at a length of approximately 31.5 cm (Figure 8, Table 9).

Angling Activity Estimates

Again, Lake B camp owners did not intensively angle in Lake C, capturing only 11 trout. Therefore angling effort could not be assessed. Also, only 5 trout were angled by the NSDFA, therefore exploitation rates based on angling could not be calculated.

Limnological data

Bathymetry of these lakes is largely unknown, however observations suggest that a large proportion of the lakes is <2m depth, though depressions of 7.5m, 6.2 and 11.0m were identified in Lakes A, B and C, respectively. Oxygen & temperature profiles conducted on July 30th, 2007 identified thermoclines in each lake (Figure 9). The hypolimnetic zone shows some evidence of providing suitable trout habitat as dissolved oxygen remained above 60% saturation for some depth within the hypolimnion (Figure 9).

Water clarity was as anticipated for the area, where high organic carbon (TOC 6.7 to 13.7 mg/L) (Table 9) contributed to a brown stain (Secchi disk readings showed water clarity to be 1.95m, 1.5m and 0.95m for Lakes A, B and C, respectively. Conductivity, acidity, total organic carbon (TOC), total phosphorous, color and total dissolved solids (TDS) was lowest in Lake A and highest in Lake C, with Lake B in the middle (Table 10).

Calculation of the morphoedaphic index (M.E.I.) revealed that Lake A is the least productive lake with a value of 3.33 and a calculated yield of $1.76 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and that Lake B had the highest M.E.I. at 10.75 leading to an estimated yield of $3.17 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Finally, calculation of the M.E.I. for Lake C showed a calculated M.E.I. of 7.58 and an estimated yield of $2.66 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, ranking Lake C as moderately productive relative to Lake A and Lake B. Based on mean weight of trout in each lake, total annual trout yield (ignoring resource use by American eels) was calculated as 148, 735 and 118 trout per year from Lakes A, B and C, respectively (Table 11).

Additional Information

In these lakes, we found very few additional fish species. American eel (*Anguilla rostrata*, Lesueur) were the only other species sampled and banded killifish (*Fundulus diaphanus*, Lesueur) were observed in the littoral zones of Lake A and Lake B. Presumably, killifish also reside in Lake C.

Summary of Results

As indicated by the population estimates, biomass per hectare was highest in Lake A and lowest in Lake C, however these estimates were not statistically significant (based on 95% C.I.'s). Density estimates followed the same trend however Lake A density was statistically significantly higher than either Lake B or Lake C (based on 95% C.I.'s).

Relative weight of brook trout was lowest in Lake A and highest in Lake C. The difference in the mean relative weight was significant in all cases (Tukey HSD, $P < 0.04$)

Unequal variances of length frequencies between lakes made statistical comparison of mean length of the population awkward therefore mean length at age was compared. Back-calculated length at age was not significantly different for 1 year old trout (ANOVA, $P = 0.92$) however age 2 trout from Lake B were significantly larger than trout in both Lake A (Tukey HSD, $P = 0.03$) and Lake C (Tukey HSD, $P = 0.00$). Length of age 2 trout from Lake A and Lake C were statistically similar (Tukey HSD, $P = 0.36$). This same trend continued for age 3 trout, where again Lake A and Lake C trout were not statistically different (Tukey HSD, $P = 0.84$) but Lake B was larger than both Lake A (Tukey HSD, $P = 0.00$) and Lake C (Tukey HSD, $P = 0.02$). By age 4, the sample size of trout from each lake was sufficiently small that statistical differences in the means could not be tested.

In a similar manor, growth was assessed between lakes. Age-specific growth is a better indicator of conditions than length-at-age because length-at-age is not independent of fork length at the start of each growing season. Absolute age-specific growth was statistically similar (ANOVA $P > 0.05$) for all year classes across all lakes with the exception of age 1+ trout, where Lake B fish grew faster than did trout from either Lake A or Lake C (Tukey HSD, $P = 0.00$ & $P = 0.00$, respectively). Insufficient sample size restricted comparison of growth for trout older than 3 years.

Mortality estimates are deemed unreliable for trout younger than age 3, therefore comparison between all lakes is not possible. However for age 3 and age 4 mortality, the differences between Lake B and Lake C were not significant (based on 95% C.I.'s) (Table 8).

In general, and without consideration of significance, calculated mean length, age and relative weight (condition) were negatively related with density and standardized biomass while mortality was positively related with density and standardized biomass (Table 11). Growth was also

positively related with density & biomass for young-of-year (YOY) trout, but no such relation occurred for growth in older trout (Table 12).

Additionally, density and standardized biomass was negatively related with conductivity, total organic carbon (TOC), color, total phosphorous, total dissolved solids (TDS) and hydrogen ion concentration (Table 12).

Unlike parameters for productivity described by water chemistry analysis, calculation of the morphoedaphic index revealed that density and standardized biomass did not show a relationship with density or biomass (Table 11). The highest densities and the highest biomass per hectare (Lake A) were related to the lowest M.E.I. values. Conversely, the lake with the lowest density and biomass per hectare (Lake C) ranked mid-way with relative M.E.I. values.

Using population parameter data reported in MacMillan and Crandlemere (2005) in addition to the data collected in these three study lakes, we regressed trout density and standardized biomass on the number of competitor species (Figures 10 & 11). Both were significantly negatively correlated ($R^2 = 0.60$ & 0.72 , respectively) with fewer competitor species correlating with higher trout density and high trout biomass. Competitor species used in this regression included American eel (*Anguilla rostrata* (Lesueur)), white perch (*Morone Americana* (Gmelin)), yellow perch (*Perca flavescens* (Mitchell)), white sucker (*Catostomus commersoni* (Lacepede)) and brown bullhead (*Ictalurus nebulosus* (Lesueur)).

DISCUSSION

Estimates of trout populations in the three study lakes were considered accurate with the exception of Lake C where the total number of captures and recaptures was insufficient. However, the Petersen estimate of 172 trout is used throughout the paper as this estimate is in line with anecdotal evidence of low catch rates by anglers and via netting.

Estimates of trout density were considerably higher for Lake A than in Lake B and Lake C. These estimates were not unlike density estimates from other Tangier Grand Lake Wilderness Area estimates, though Lake A was more similar (33% larger) to the estimate for Ingonish Lake in the Cape Breton Highlands. Also, in general, the Southern TGLWA lakes had higher density estimates than lakes from other parts of the province.

The ratio of shoreline length to total lake surface area may play a role in food resource availability (Fish 1968). Because many prey items preferred by trout associate with littoral zones, (increased invertebrate production) the amount of littoral zone habitat may provide an indication of prey availability. For example, two lakes of similar total surface size and similar mean depth but drastically different shoreline complexity, and consequently length, would offer more habitat preferred by prey – and thus a larger food source. Our trends suggest that in these lakes however, the trends of density and biomass are similar when standardized by either surface area or shoreline length.

Based on the length frequencies of these data, it is safe to assume that we underestimated the populations of smaller (younger) trout. This is surely a reflection of the selectivity of the sampling gear and is an important consideration in interpreting these data. Using the mark-recapture data to assess the populations of age 2 and age 3 trout did indeed indicate a larger 2 year old population than did length frequencies. On the contrary, M-R estimates showed the population of age 3 trout to be smaller than estimated by length frequencies. For the purposes of this study, both as an indication of trout availability to angling and as a comparative study between lake

(within study area and within the province), the population estimates obtained from the length frequency data has been used.

The negative slope of fork length plotted against capture date is perplexing. Presumably, mean length of trout would increase throughout the year as the fish grew. This was not the case. One could argue that the larger trout were captured and retained at the start of the year, however based on our estimates of exploitation few trout are retained from the lake. Additionally, as fish were removed from the system via angling, it is reasonable to expect that growth would increase with in the remaining individuals as a result of density-dependence.

The size of trout is one of the more important factors controlling anglers' perceptions on the quality of angling. The size structures of these lakes indicate that the trout in Lake B and Lake Cs are much more desirable than those of Lake A. In general, we assume trout over 30cm (12") to be trout preferred by most anglers. The fact that Lake A had no fish larger than 30cm while Lake B had 35 % and Lake C had 59% of the samples over this mark indicates that trout either had a) higher mortality resulting in few fish old enough to reach this size, b) slower growth resulting in few fish reaching this size by the end of their life, or c) a major emigration of out of Lake A prior to reaching the preferred size. Mortality and growth are discussed below and are likely controlling the size of trout in these lakes.

It is unlikely that emigration of any magnitude occurs as no tags we recovered from adjacent lakes in 2007, nor in the spring of 2008. Brook trout in Newfoundland lakes also showed high lake fidelity in the absence of physical barriers and consequently formed distinct and isolated spawning populations (Adams and Hutchings 2003).

Another proposed explanation of the size structure of fish in some lakes is related to decreased efficiency in distributing oxygen as fish grow. As objects increase in volume (exponent of 3), their surface area increases at a disproportionately slower rate (exponent 2). Similarly, fish experience a decreasing surface area to body volume ratio of fish as they grow. Smaller fish are therefore more efficient at respiration than larger fish (von Bertalanffy 1957, Pauly 1997) as gill surface area increases at a lower rate than total blood volume. Older trout may therefore be more affected by oxygen deficiencies. In lakes where periods of low oxygen infrequently occur for short durations, the larger individuals within a population may be more adversely affected. Fish (1968) suggested a similar circumstance for New Zealand rainbow trout. In Lake A few large trout were observed and periods of low oxygen may contribute to the selective mortality of larger trout. This however is not likely the case for two reasons; a) there was evidence of sufficient hypolimnetic habitat in Lake A, and b) summer conditions would have to consistently reach a state where only small fish could survive.

Relative weight, as a measure of "plumpness" provides an indication of resource usage, where a relatively low mean relative weight (i.e. below the average relative weight value) indicates that resources may be limiting. Mean relative weights well below the species standard are often exhibited by stunted trout populations (Johnson et al. 1992). Conversely, if the mean relative weight of a population is above the mean of 100, then resources are in excess and there is potential for additional fish production.

Relative weight estimates for the three study lakes were such that trout condition was highest where densities were low and lowest where densities were high. This supports the theory that relative weight increases with increasing resource availability and decreased competition (Murphy and Willis 1996).

From an anglers perspective, fish of a higher relative weight or condition are preferred to those in poorer condition. The relative weight of Lake A would be considered poor by most anglers

while the condition of trout in Lake C would generally please most anglers. The trout in Lake B would likely be acceptable, however the show signs of a physiological trade off between individual mass and population density, therefore anglers would likely accept the weight of trout provided they had opportunity to catch more trout.

Length at age in the three study lakes showed considerable variation. In all lakes length at age 1+ was statistically similar, indicating that the quality of rearing habitats is similar. However, we do not know the overall availability (quantity) of spawning habitat in each lake nor how recruitment is affected as a result of spawning habitat availability. By the age of 2 years and carried through to age 3, brook trout in Lake B are larger than those of the other two lakes. This indicates that in Lake B density-dependant effects may better balance prey and habitat availability with trout population size. Presumably, density-dependence does not control growth in all lakes. Lake C brook trout experience lower densities than those in Lake B yet growth is higher in Lake B. Therefore it may be that growing conditions in Lake B are more favourable for growth of larger trout.

Length at age may not be an ideal indicator of growing conditions calculations are highly influenced by the length of trout as they enter the growing year. Therefore, the use of age-specific growth is a much better indicator. Age specific growth was statistically similar between all lakes, over all ages with the exception of age 1 (second year of growth) thus we can assume that growing conditions are similar between lakes. The significantly higher rate of growth for age 1 trout in Lake B may support our theory of prey shifts or angling mortality (and thus density) controlling growth. By age 3, growth was again similar among lakes, indicating that the discrepancies in length at age observed for age 2 trout was a function of substantial growth disparities in the previous year (age 1).

Because length-at-age showed significant larger trout at age 2 and age 3 in Lake B, but growth-at-age showed that only age 1+ trout have significantly greater growth, we can conclude that the age of 2 is where trout from Lake B either grow faster than the adjacent lakes or when Lake A and Lake B experience growth bottlenecks.

It is probable that substantial gear selectivity occurred and larger individuals were likely targeted. Evidence to support this is the length frequency plot where the number of 2+ trout was less than the number of 3+ trout. With the exception of massive immigration from adjacent areas, the number of trout in each successive cohort should decrease with age.

When estimating mortality, chi-square results indicated that sampling by our gears was incomplete for age 1 and age 2 trout. The age-specific mark-recapture estimates of age 2 and age 3 and the subsequent ratio-method mortality estimate is likely representative of actual mortality at that age. Incorporating all mortality estimates, it is obvious that mortality increased with age. This is likely primarily due to the increasing vulnerability to angling.

Mortality is generally expressed at $Z = F + M$, where Z = total mortality, F = fishing mortality and M = natural mortality (Ricker 1975). Because calculated rate of exploitation (Lake B only) was quite low, it stands to reason that total mortality (Z) is driven primarily by natural mortality (M). Sources of natural mortality in these systems are undefined however the absence of other large predators (with the exception of eels) may limit the impact of predators. Furthermore, piscivorous fish (Gregory and Levings 1998) and avian and terrestrial trout predators may experience reduced hunting success due to reduced visibility resulting from high dissolved organics concentrations.

Knowledge of potential egg deposition for a population is essential for assessment of early life-stage mortality (Serns 1982) and for modelling population dynamics. Unfortunately, in this

study estimation of 1 year old trout was not possible and thus early survival as YOY was not possible.

By examining total potential egg production we can also assess the importance of age classes and fish length on the overall reproductive dynamics of lakes. It is obvious that in populations with larger trout, the relative contribution of small fish is reduced. Thus, in Lake C the larger trout (> 30cm) which are most likely to be targeted by anglers contribute a major proportion of the total egg production. In Lake B, removal of large trout would have less of an impact on total egg deposition than in Lake C as their contributions are less than the more abundant 25cm to 30cm trout. In Lake A, the only trout likely to be taken by anglers are below the preferred size of 30cm. The vast majority of egg deposition in Lake A occurs by trout of 23cm to 27cm, therefore removal of the largest trout in the population (26cm to 29cm) would have only slight implications for total egg deposition.

Removal of large individuals based on reducing egg loss may not ideal however as there is some evidence that larger individuals are genetically predisposed to fast growth and removing these individuals can result in a population-level reduction in growth potential (Biro and Post 2008). This has yet to be observed in Nova Scotia trout, where naturally fast growth as a result of conditions may supersede genetic constraints on growth.

Anglers in Lake B catch primarily trout aged 3+ and mean length of their catch was 28.1cm. Looking at the plot of egg contribution by size we see that anglers target trout that contribute the largest proportion of eggs to total deposition. Thus, if exploitation increased a concomitant decrease in egg deposition would occur.

A limited number of larger specimens used to derive the fecundity curve expressed in Halfyard et al. (2008) may lead to underestimation of fecundity for trout longer than 32.2cm, thus their importance as egg contributors may also be underestimated. Similarly, estimates of total potential egg deposition are highly influenced by the length frequency distribution of our samples and any bias in length frequency associated with gear selectivity would influence this estimate. Because age 1 and age 2 trout were under-represented in the length frequency data, their contribution may also be underrepresented. Thus, cumulative egg deposition may potentially exhibit a faster initial increase and a slower increase for larger sized trout.

Angling activity reported by the Lake B Camp owners is likely a conservative estimate of exploitation. Over-land access to the study area is restricted to non-motorized vehicles and anglers accessing these lakes over-water are required to carry one (Lake B) or two (Lake A & Lake C) portages. It is therefore reasonable to assume that angling pressure in these lakes would be primarily (though not entirely) by camp owners and guests. Also, it is likely that these areas receive less angling pressure than more easily accessed lakes.

Our calculations of current yield are likely representative of actual current yield. Retention rates for angled trout and angling-induced mortality are not thought to significantly differ from the values used in this study. The one assumption that may alter estimates of current yield is the assumption that we sampled roughly half of the angling activity on the lake. Our estimate of catch (double the catch of the Lake B camp owners) may not represent actual angling pressure, however it is thought to be a fair estimate based on few observations of other anglers using these lakes during the study.

Survival of trout post-release from angling is affected by temperature, where higher temperatures correlated with decreased survival (Nuhfer and Alexander 1992). Because most trout are captured in the cool water period of April and May, with only a few in early June, water temperature is likely sufficiently low to promote high survival of released fish. The 10% angling-

induced mortality is double that suggested for artificial lure or fly but one third of that for natural bait (Taylor and White 1992, Nuhfer and Alexander 1992). In the last survey of Nova Scotia anglers, it was estimated that 20.6% of resident anglers prefer artificial lures, 23.0% prefer artificial fly, 17.2% prefer lure/bait combinations and the remainder prefer bait fishing (Sport Fishing in Nova Scotia, 2005). In this area however, the anglers whom frequent the area indicated that the majority of their angling is done with fly-fishing gear. We are therefore confident that a 10% angling-induced mortality following release is suitable for these purposes.

Based on camp owners' preferred lakes to fish, it would seem that Lake B attracts the majoring of angling pressure while Lakes A and C receive substantially less pressure. In Lake C the small population and lower trout density may reflect the impact of angling in terms of overall fishing mortality, F , where the current level of angling is sufficient to thin the population. On the contrary, angling pressure experienced in Lake A is obviously insufficient to thin the population as trout density and biomass is relatively high.

Estimated current yield in Lake B ($0.55 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) is well below the maximum sustainable yield as estimated by the M.E.I. of $3.17 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$. Current yield in Lake C is unknown, however assuming even low effort and consequently small catch and knowing that Lake C trout are the largest of all three lakes, the current yield is likely closer to the MSY. This would support our observations of low density and biomass considering MSY calculated by the M.E.I. ($2.66 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) was lower than in Lake B but substantially higher than Lake A. Other factors potentially controlling density in Lake C are lack of recruitment caused by inadequate spawning habitat, or additional sources of mortality associated with environmental conditions, though no such conditions were identified in this study.

Current yield in Lake A is also unknown, however angling effort is considered low relative to Lake B. Maximum sustainable yield was calculated as $1.76 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and knowing that mean weight is quite low, it is reasonable to assume that the removal of trout biomass is quite low and presumably well below MSY. The removal of trout in Lake A appears insufficient to offset density-dependant reductions in growth and survival.

The exclusion of American eel (and potentially banded killifish) when discussing maximum sustainable yield likely leads to substantial overestimation of trout MSY. Because no empirical data exist for the eel or killifish populations in these lakes, we cannot calculate exact trout MSY.

Brook trout prefer temperatures generally less than 20°C (Raleigh, R.F. 1982) and when summer temperatures exceed this threshold, brook trout will often seek areas of cool water refugia, primarily ground water seepages (Biro 1998, Baird and Krueger 2003) or hypolimnetic habitat provided it is well oxygenated. In Nova Scotia lakes it is therefore reasonable to assume a relationship between the minimum volume of suitable late summer hypolimnetic habitat and brook trout population size. In the study lakes, adequate mid-summer hypolimnetic habitat indicates that these lakes are not likely limited by lack of hypolimnetic habitat, however further investigation of the volume and quality of the habitat in late summer (end of August).

Discrepancies in standardized biomass, density and size structure between populations are likely driven by factors that can be placed into one of three categories. The first group are physical environment conditions such as habitat and temperature.

Differences in habitat and water chemistry between study lakes are thought to be non-significant. The exception may be in spawning habitat availability which we did not assess. Where suitable spawning habitat exists, "stunted" high density brook trout populations often occur (Donald and Alger 1989, Johnson et al. 1992) and where inadequate spawning habitat occurs, the

age/size structure of brook trout populations is often dominated by larger and older individuals at much lower densities (Rabe 1970, Johnson et al. 1992). Thus, it may be possible that spawning conditions are relatively superior in Lake A. Increased spawning habitat and thus increased recruitment in Lake B and Lake C may potentially lead to increased trout density. Curry et al. (2003) suggest that redd superimposition reduced survival of embryos in an Ontario brook trout population. In previous studies on the same population, it was suggested that limited spawning habitat lead to fixed recruitment such that typical Ricker stock-recruit relationships were not suitable and the “hockey stick” model of Barrowman and Myers (2000) would better describe the relationship (Curry and Noakes 1995). Similar conditions may exist in lakes of the TGLWA such that total available spawning habitat limits juvenile survival / recruitment independent of total population fecundity past a critical quantity of eggs. Trout population would then therefore be limited by available spawning habitat.

The second category of factors potentially driving differences in population parameters includes water chemistry and quality. The role of water chemistry on brook trout population parameters within these lakes is not entirely understood, however in general the trends were as anticipated. Lake A had the highest pH and the highest density, while Lake C was most acidic and exhibited the lowest density. The change in acidity among lakes may have biological significance and a pH change of 0.5 units may lead to differences in osmoregulatory stress, efficiency of oxygen uptake and ultimately survival.

It is essential to note that the trends expressed in the data (as summarized in Table 11), represent the trends of the data and not indication of statistical significance is given. Biologically, the differences in water chemistry parameters between lakes are likely insignificant (with the aforementioned exemption of pH). For example, conductivity was lowest in Lake A and highest in Lake C, however conductivity values were only 27.5 and 32.4, respectively. This change is likely not sufficiently large to affect trout population parameters. There is insufficient data to suggest that differences in water chemistry control brook trout population parameters in these lakes.

The final group of factors potentially driving population parameter discrepancies are the mortality-related influences such as predation and perhaps more importantly density-dependant mortality and angling pressure (exploitation). Total mortality (Z) is equal to the sum of natural mortality (M) and fishing mortality (F). Assuming density-dependant mortality drives current population structure, Lake A must be exposed to high density-dependant M , and the rate of F is presumably low, allowing densities to reach their current state. Conversely, rates of F in Lake B and Lake C are presumably at levels that sufficiently thin population density, resulting in reduced natural mortality M , reduced total mortality Z , increased condition, larger size and an older age structure.

When trout population parameters were assessed against the morphoedaphic index, the relationship between trout density and biomass was not clear. Factors affecting total potential fish production in lakes is generally associated with abiotic influences (primarily nutrient concentration or some proxy thereof), the morphometry of the lake and the local climate. Often the chemical (or edaphic) characteristics of a lake are the primary focus when determining the potential fish production. This is largely because the limiting nutrient in freshwaters is phosphorous, which is the principal control of primary productivity and consequently fish production. In an effort to simplify estimations of total potential fish production, several indices have been proposed, the most popular of which is the morphoedaphic index (Ryder 1965).

The morphoedaphic index appears best suited for lakes where nutrients are the limiting factor (thus the inclusion of total dissolved solids as a proxy for nutrients). In dark, organic stained

Nova Scotia lakes where light may limit nutrient cycling, the morphoedaphic index may not accurately predict maximum sustainable fish yield without compensation for light attenuation and the depth of the photic zone. At this point, it should be stated that water clarity in Lake A, Lake B and Lake C, as measured by secchi disk, showed a positive relationship with density and biomass. This supports our theory that photic zone depth plays a role in the production of fish in Nova Scotia lakes. A larger data set should be analyzed to further assess the relationship of dystrophy and the morphoedaphic index.

Discrepancies between the calculated mean depth and the true mean depth would alter the M.E.I. values and may potentially explain the unexpected relationship between trout density/biomass and the morphoedaphic index.

An additional potential cause of the disparity between the M.E.I. and observed density/biomass is the current exploitation rates of the study lakes, in particular Lake A. Maximum sustainable fish yield as an estimate derived from the M.E.I. is ideally used in lakes where exploitation by fishing is sufficiently large so that density-dependant compensation effects are experienced by the fish (Ryder 1964). The balance of density and growth is dramatically different between Lake A and the other two study lakes, potentially reflecting exploitation, intra-lake comparison of M.E.I. predicted MSY may not be valid.

To relate M.E.I. and maximum sustainable fish yield we used data for lakes in Algonquin national park, Ontario (Ryder 1964). Alexander and Merrill (1976) also used this data to describe fish production in Big Indian Lake, Halifax Co. N.S. Climatic conditions of Algonquin Park are not drastically different than Nova Scotia thus the relationship of morphoedaphic and climatic factors is likely similar and these values are suitable for use in Nova Scotia. Unlike Alexander and Merrill, we could not estimate maximum sustainable yield of trout using the Algonquin data because fish species diversity of Lake A, Lake B and Lake C is significantly lower than in the Ontario lakes as well as most mainland lakes of Nova Scotia and this impact of this has yet to be elucidated.

In waters with marginal brook trout habitat, it appears probable that factors limiting trout production may also be related to habitat suitability such as adequate hypolimnetic habitat, the availability of other thermal refugia and sufficient spawning habitat. These parameters could be loosely grouped as climatic factors controlling production, with some influence of localized hydrology. To streamline calculations, Ryder's morphoedaphic index did not incorporate climatic influences though he discussed its potential importance.

Finally, the apparent trend of standardized trout biomass estimates negatively correlating the number of fish species competing with trout for resources is of interest. In Nova Scotia lakes, our limited productivity is divided among all fish species leading to relatively poor production of each species. It has been suggested that inter-specific competition can negatively affect trout populations (Fraser 1972, Alexander and Merrill 1976, Alexander et al. 1986, Tremblay and Magnan 1991) as species with a competitive advantage over trout are likely to be more successful and thus sequester a larger portion of the food resources. This is likely exasperated in marginal trout habitat, leading to poor trout production as exemplified by Smith (1938). It has been shown that removal of competitor species can increase trout production and yield (Hayes and Livingstone 1955, Flick and Webster 1992). In Nova Scotia, very few lakes have species assemblages similar to the lakes in this study. Using the lake survey database (FINS), it was determined that of the 395 NS mainland lakes where brook trout were sampled, only approx. 18% of these had similar species assemblages (i.e. no spiny-rayed fishes or major competitors). If we examine all 1283 surveyed lakes on the mainland (with or without brook trout), only 10% are of similar species assemblages. This suggests that the lakes in this study are representative of a small proportion of all brook trout

lakes on the mainland and that there are very few additional lakes where the species assemblage is favourable for brook trout production and brook trout are absent.

MANAGEMENT IMPLICATIONS

In an experiment using the closely related arctic charr (*Salvelinus alpinus*), Amundsen et al. (1993) found that a stunted population showed a shift to older and larger individuals and increased growth following large-scale artificial exploitation. Regulations encouraging increased harvest in Lake A could be used to increase the size and age structure of this apparently stunted population. However, similar regulations in nearby Lake B and Lake C, separated by only 100m and without barriers for trout migration, would most probably lead to over-exploitation and a reduction in the overall quality of angling. Thus a single set of regulations may not provide the desired resulting trout populations for this area. There is a need for lake-by-lake assessment of trout populations and likely lake-by-lake regulations. Given the sheer number of lakes in Nova Scotia (~3500) this of course is grossly cost-prohibitive and largely impossible to enforce regulation. Therefore, the grouping of lakes based on surficial geology, trophic state and the presence of competitor species tempered with the most common issue facing brook trout populations in these groupings (i.e. water quality, physical habitat or exploitation) is the best approach for regulating trout exploitation in this province. Additionally, it may be reasonable to expect that exploitation does not currently limit some trout populations as seen in recent historical creel survey comparisons (MacMillan and Madden, *in press*) and thus regulation may not lead to the desired increase in trout population abundance and size.

To create a model for trout production in Nova Scotia lakes additional data must be collected and various parameters require evaluation. Such parameters include:

- 1) Assessment of typical recruitment (i.e. egg to YOY survival, egg to age 1+) and the factors that influence early survival in Nova Scotia,
- 2) Assessment of inter-relationship between the Morphoedaphic index, the role of dystrophy and fish yield in Nova Scotia Lakes, and
- 3) The collection and interpretation of a larger data on the set on the relationship between trout production and the number of competitor species in Nova Scotia lakes.

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TABLES

Table 1 – Population, biomass and density estimates for study lakes. 95% C.I. = 95% confidence intervals. * Includes shoreline of islands. ** lake surface was re-calculated using ArcGIS as outlined in methods section. *** As determined by Copper Sulfate poisoning

<i>Lake</i>	<i>Area (ha)</i>	<i>Shoreline Length (km)</i>	<i>Petersen Estimate</i>	<i>Schnabel Estimate</i>	<i>Biomass (kg/ha)</i>	<i>Density (# trout/ha)</i>	<i>Biomass (kg / 100m shoreline)</i>	<i>Density (# trout / 100m shoreline)</i>	Number of Competitor Species
Lake A (95% C.I.)	11.8	1.63	703 (408, 1317)	613 (380, 1043)	7.3 (4.5, 12.4)	51.9 (32.2, 88.4)	5.3 (3.3, 9.0)	37.6 (23.3, 64.0)	1
Lake B (95% C.I.)	63.0	8.78*	1115 (670, 1976)	1038 (629, 1771)	4.1 (2.5, 7.1)	16.5 (10.0, 28.1)	2.9 (1.8, 5.1)	11.8 (7.2, 20.2)	1
Lake C (95% C.I.)	13.6	2.94	179 (66, 448)	n/a (n/a)	3.9 (1.6, 10.8)	13.2 (4.6, 32.9)	1.8 (0.7, 5.0)	6.1 (2.2, 15.2)	1
<u>Comparative Lake – MacMillan and Crandlemere (2005)</u>									
Ingonish	32		1262		3.7	39			1
Fourth	12.3**	2.45	212		2.2	17.2	1.08	8.7	2
Bluewoods	24.8**	4.65*	102		0.7	4.1	0.37	2.2	3
Croucher	13.6**	2.44	172		1.8	12.6	1.02	7.0	3
Big Indian	106		2346	N/A	2.3	22			1
L. Jesse	18		29		0.4	2			4
Trefry	21		0***		0.0	0			4
Boarsback	23		23***		0.1	1			4
Tedford	21		0***		0.0	0			4

Table 2 – Description of length frequencies for Lake A, Lake B and Lake C. Data represents trout sampled by all researchers.

	<i>Lake A</i>	<i>Lake B</i>	<i>Lake C</i>
Minimum (cm)	10.9	12.5	11.4
Mean (cm)	22.9	27.6	29.7
Median (cm)	23.9	28.0	31.0
Maximum (cm)	28.2	42.5	42.0
% > 30cm	0	35	59
Sample Size (N)	220	468	78

Table 3 – Description of relative weight for Lake A, Lake B and Lake C. Data represents trout sampled by NSDFA only.

	<i>Lake A</i>	<i>Lake B</i>	<i>Lake C</i>
Minimum	46	58	79
Mean	79	86	97
Median	78	86	97
Maximum	131	114	112
Sample Size (N)	129	89	7

Table 4 - Age proportions of trout in total sample for each of three study lakes. Length classes for each age determined as the midpoint between the length of the longest fish aged a-1 from the length of the shortest fish aged a.

	<i>% Age 1+</i>	<i>% Age 2+</i>	<i>% Age 3+</i>	<i>% Age 4+</i>	<i>% Age 5+</i>	<i>Total Sample Size</i>
Lake A	12.7	75.0	12.3	0.0	0.0	N=220
Lake B	6.4	27.2	56.5	9.0	0.9	N=468
Lake C	10.3	15.4	59.0	12.8	2.6	N=78

Table 5 – Description of back-calculated length at age data for Lake A, Lake B and Lake C. No age 4 (or older) trout were sampled from Lake A. Sample size indicates only the number of trout for which back-calculated length at age was assessed. For example, only one aged 4+ trout from Lake B was processed, though 42 were sampled for the whole project. Additionally, there were 4 trout estimated to be aged 5+ captured from Lake B and 2 additional 5 year old trout captured from Lake C. n/s = none sampled. ¹From MacMillan and Crandlemere (2005), ²From Alexander and Merrill (1975), ³From MacMillan and Crandlemere (2004), ⁴From MacMillan and Leblanc (2002).

<u>Lake A</u>				
	Age 1	Age 2	Age 3	Age 4
Mean	8.77	17.38	21.96	n/a
Std. Deviation	1.54	2.05	1.99	n/a
Sample Size (N)	42	40	10	n/a
<u>Lake B</u>				
	Age 1	Age 2	Age 3	Age 4
Mean	8.65	18.64	25.30	29.18
Std. Deviation	1.59	1.84	1.56	n/a
Sample Size (N)	52	36	10	1
<u>Lake C</u>				
	Age 1	Age 2	Age 3	Age 4
Mean	8.59	16.49	22.50	28.43
Std. Deviation	2.42	2.84	2.73	2.51
Sample Size (N)	19	14	10	9
	Age 1 (mean)	Age 2 (mean)	Age 3 (mean)	Age 4 (mean)
Fourth¹	10.4	17.3	24.4	34.9
Bluewoods¹	17.4	21.8	25.7	30.3
Long¹	12.6	18.9	26.1	n/s
Croucher¹	10.9	17.9	26.4	n/s
Big Indian²	10.8	17.9	25.5	n/s
East Taylor³	7.6	15.4	23.8	n/s
CB Highlands³	8.4	13.9	19.0	23.2
Other Halifax – Guysborough Co. Lakes⁴	10.2	17.6	23.5	n/s

Table 6 – Brook trout growth for all three study lakes. N/S – None sampled. Note A – Trout assumed to be age 5+ trout were captured in Lake B, though no scale samples were obtained.

Lake A					
	Age 0+	Age 1+	Age 2+	Age 3+	Age 4+
Mean	8.8cm	8.6cm	6.4cm	N/S	N/S
Standard Deviation	1.5cm	1.5cm	1.5cm		
Sample Size	42	40	10		
Lake B					
Mean	8.7cm	10.3cm	6.3cm	5.9cm	
Standard Deviation	1.6cm	1.8cm	1.4cm	n/a	Note A
Sample Size	52	36	10	1	
Lake C					
Mean	8.6cm	8.0cm	6.8cm	6.0cm	7.3cm
Standard Deviation	2.4cm	2.5cm	1.5cm	1.0cm	n/a
Sample Size	19	14	10	9	1

Table 7 – Growth parameters derived from the von Bertalanffy growth curve and mean length and standard deviation of the ten largest trout for Lake A, Lake B and Lake C.

	L_{∞} * (cm)	Brody Growth Coefficient K^*	Hypothetical size at time 0 t_0	Mean FL of ten largest trout (cm)	Standard Deviation ten largest trout (cm)
Lake A	48.0	0.197	-0.421	27.3	0.4
Lake B	41.8	0.349	-0.322	36.4	3.6
Lake C	97.0	0.087	-0.094	36.5	2.1

Table 8 – Estimates of annual mortality for the three study lakes. # – Heincke’s estimate of survival (and consequent mortality) not calculated as the proportion of trout aged 1+ and 2+ were not thought to be truly representative of the population.

* Chi-square test indicates that the cohort was not fully recruited by capture gear and that the survival (and thus mortality) estimate is likely inaccurate. n/a = not applicable. Presumably, mortality of 5 year old trout in Lake B and Lake C is 100%, as no 6 year old trout were captured.

	Age	Lake A			Lake B			Lake C		
		Estimated Mortality	95% CI	χ^2	Estimated Mortality	95% CI	χ^2	Estimated Mortality	95% CI	χ^2
Heincke’s Method	1+	#	n/a	n/a	#	n/a	n/a	#	n/a	n/a
	2+	#	n/a	n/a	#	n/a	n/a	#	n/a	n/a
	3+	n/a	n/a	n/a	0.84	n/a	n/a	0.78	n/a	n/a
	4+	n/a	n/a	n/a	0.90	n/a	n/a	0.80	n/a	n/a
Chapman-Robson Method	1+	0.50*	(0.45,0.55)	245.1	0.37*	(0.34,0.40)	295.3	0.35*	(0.29,0.42)	32.8
	2+	0.87*	(0.83,0.92)	4.2	0.55*	(0.51,0.58)	258.1	0.49*	(0.41,0.51)	55.8
	3+	n/a	n/a		0.86	(0.82,0.90)	1.6	0.80	(0.71,0.90)	0.2
	4+	n/a	n/a		0.92	(0.85,1.0)	n/a	0.85	(0.64,1.0)	n/a

Table 9 - Summary of potential egg deposition parameters for all study lakes. Length @ x% TPED is the point where x% of the TPED is potentially deposited by fish smaller than that length. Length @ Maximum egg contribution is the theoretical length which contribute the largest proportion of eggs to the TPED (Fecundity x Abundance).

Lake	Total Potential Egg Deposition	Eggs / ha	Length @ 50% TPED	Length @ 70% TPED	Length @ 90% TPED	Length @ Max. Egg Contribution
A	157 880	17 542	23.5	24.3	26.5	25.0
B	310 720	5 650	26.6	28.1	30.5	28.5
C	61 833	5 622	31.0	32.0	34.0	31.5

Table 10 – Summary of water chemistry parameters for Lake A, Lake B and Lake C.

TCU = True color units. Level of detection for total alkalinity is 3.0 mg/L and 5.0 mg/L for total calcium.

<i>Parameter</i>	<i>Statistic</i>	<i>Lake A</i>	<i>Lake B</i>	<i>Lake C</i>
Conductivity µS/cm	Mean	27.5	30.7	32.4
	SD	2.2	1.6	3.3
	N	4	4	4
Total Organic Carbon (TOC) mg/L	Mean	6.70	9.00	13.73
	SD	0.36	0.61	1.59
	N	3	3	3
Acidity pH units	Mean	5.2	4.9	4.7
	SD	0	0	0.2
	N	3	3	3
Total Alkalinity mg/L	Mean	<3.0	<3.0	<3.0
	SD			
	N	3	3	3
Total Calcium mg/L	Mean	<5.0	<5.0	<5.0
	SD			
	N	3	3	3
Total Phosphorous mg/L	Mean	0.005	0.009	0.015
	SD	0.001	0.004	0.009
	N	3	3	3
Total Dissolved Solids (TDS) mg/L	Mean	7.5	20.0	25.0
	SD			
	N	1	1	1
Color TCU	Mean	62.5	86.3	135.3
	SD	4.3	6.8	15.5
	N	3	3	3
Clarity (Secchi Disk) (m)	Mean			
	SD	1.95	1.50	0.95
	N			

Table 11 - Morphoedaphic parameters for the three study lakes. TDS = total dissolved solids, M.E.I. = morphoedaphic index, Yield is the potential yield of all fish based on the M.E.I., TPAY = total potential annual yield.

<i>Parameter</i>	<i>Lake A</i>	<i>Lake B</i>	<i>Lake C</i>
Maximum Depth (m)	7.50	6.2	11.0
Est. Mean Depth (m)	2.25	1.86	3.3
TDS (mg/L)	7.5	20.0	25.0
M.E.I.	3.3	10.8	7.6
Yield (kg/ha/year)	1.8	3.2	2.7
Total Potential Annual Yield (kg/year)	20.8	199.7	36.2
Number of Trout Harvested @ TPAY	148 (mean = 141g)	735 (mean = 272g)	118 (mean = 308g)

Table 12 – Comparative summary of various population and limnological parameters for all study lakes. Age N Growth is a ranking, with 1 being the fastest growth and 3 being the slowest growth. No age 4 growth was available for Lake A because no trout older than 3 years were sampled. TDS = Total Dissolved Solids, TOC = Total Organic Carbon.

	<u>Lake A</u>	<u>Lake B</u>	<u>Lake C</u>
Density			
Biomass / unit			
Mean Length			
Relative Weight			
Mean Age of Trout			
Mortality			
YOY Growth	1	2	3
Age 1 Growth	2	1	3
Age 2 Growth	3	1	2
Age 3 Growth	n/a	1	2
pH			
Conductivity – TDS Phosphorus			
TOC – Color			
Morphoedaphic Index	3	1	2

FIGURES

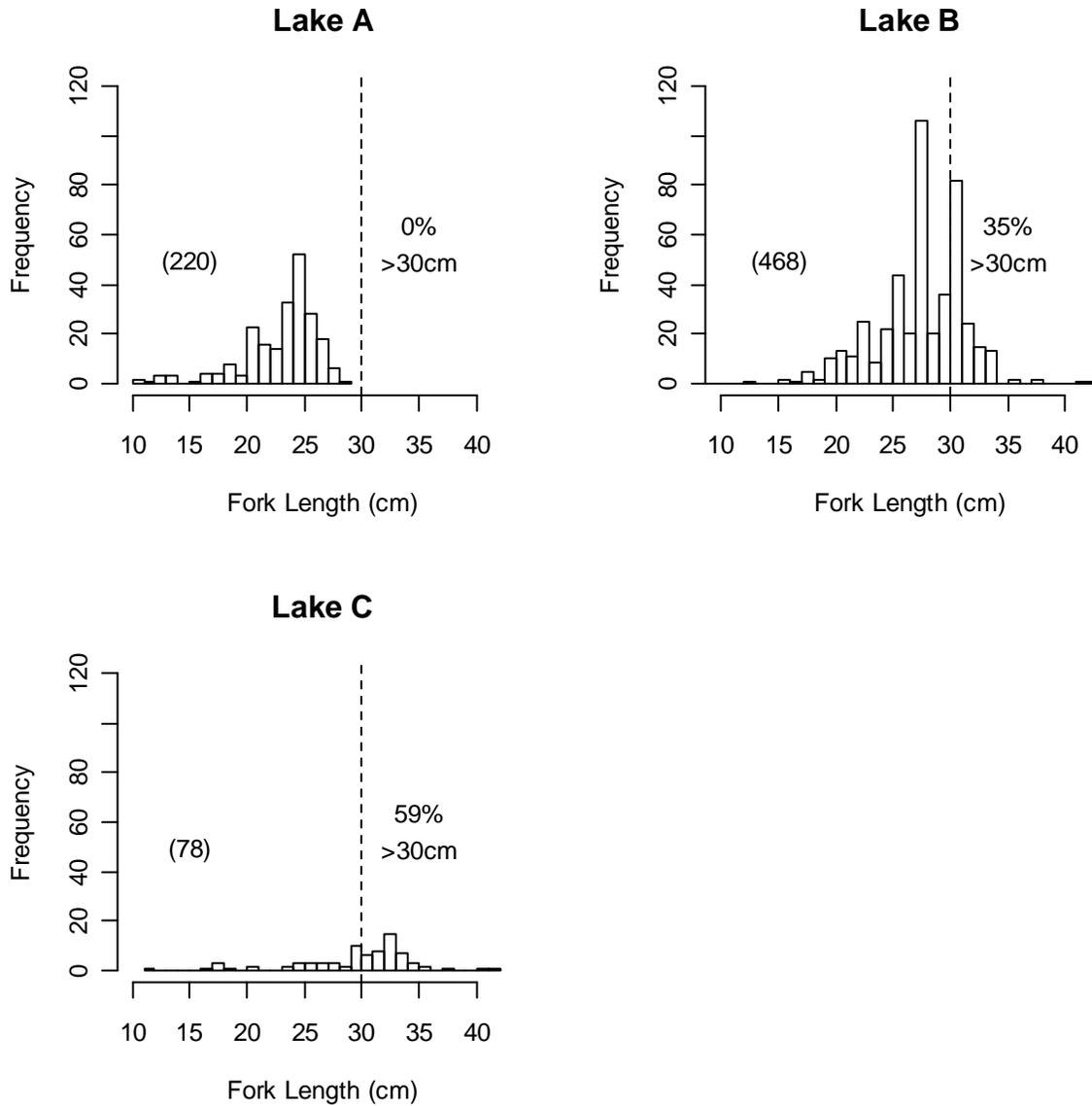


Figure 2 – Length frequency histograms for Lake A, Lake B and Lake Cs. Fork length bins represent 1.0 cm increments. Sample size represented in parentheses (N). Data represents brook trout captured by all researchers.

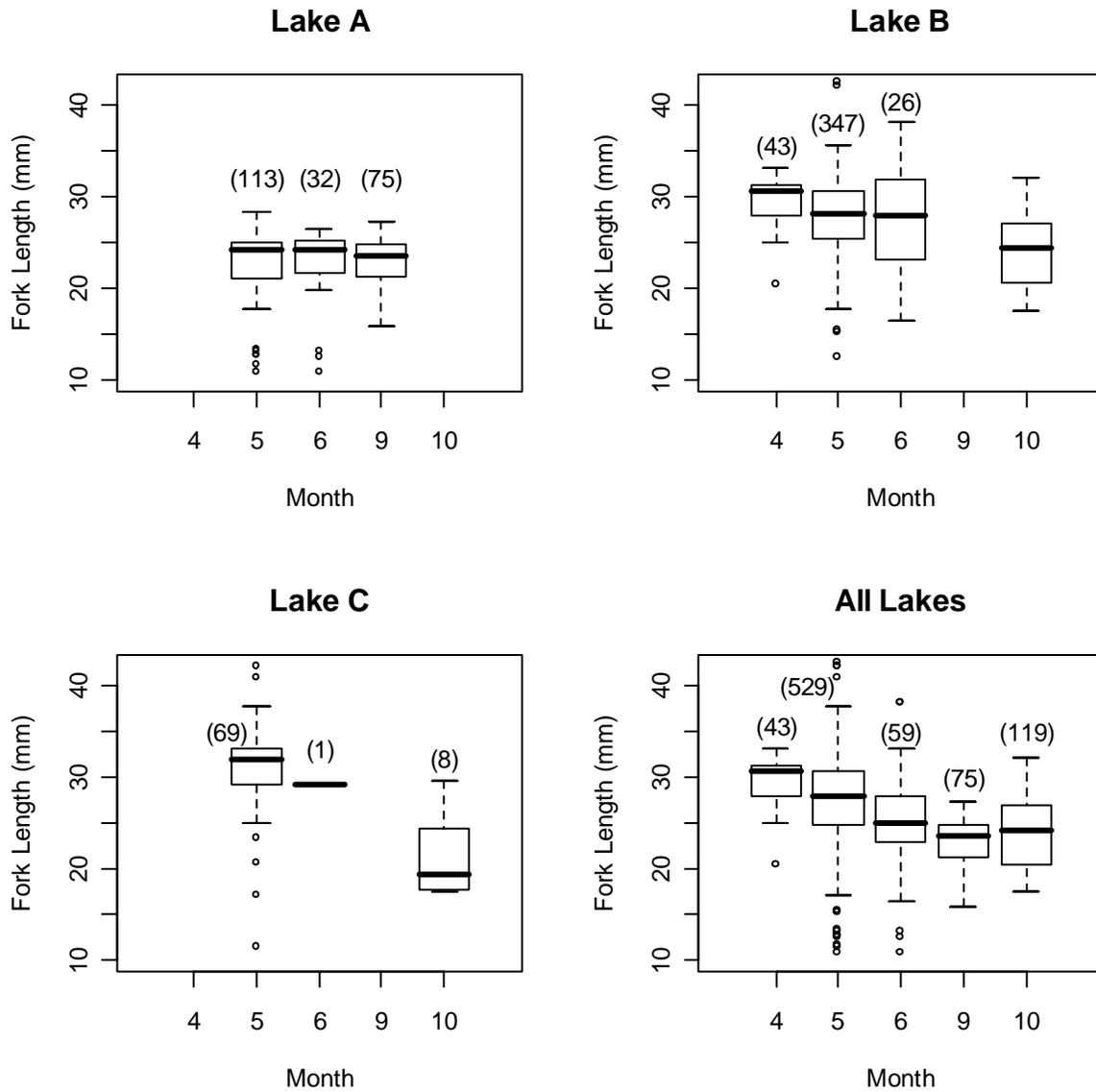


Figure 3 – Boxplots of fork length (cm) of brook trout sampled during each month from each lake. Sample size represented in parentheses (N). Data represents brook trout captured by all researchers.

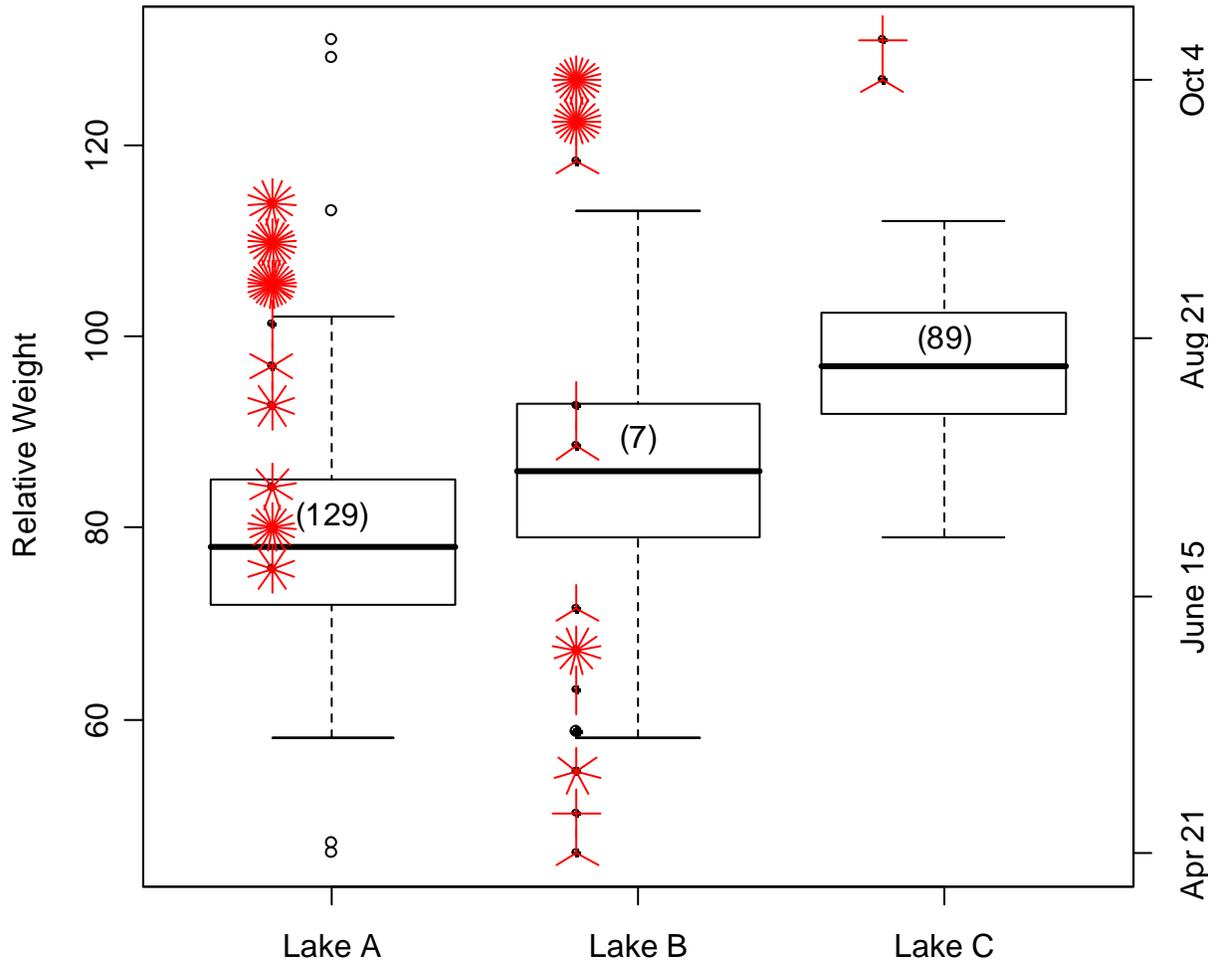


Figure 4 – Boxplots of relative weight for Lake A, Lake B and Lake C brook trout. Also, the sunflower plot represents the sampling distribution for each respective lake. Each dot of the sunflower plot represents a single sample, and each additional “petal” attached to the dot represents an additional sample. Thus, on April 21st at Lake B, 4 samples were collected. Data represents brook trout captured by NSDFA only.

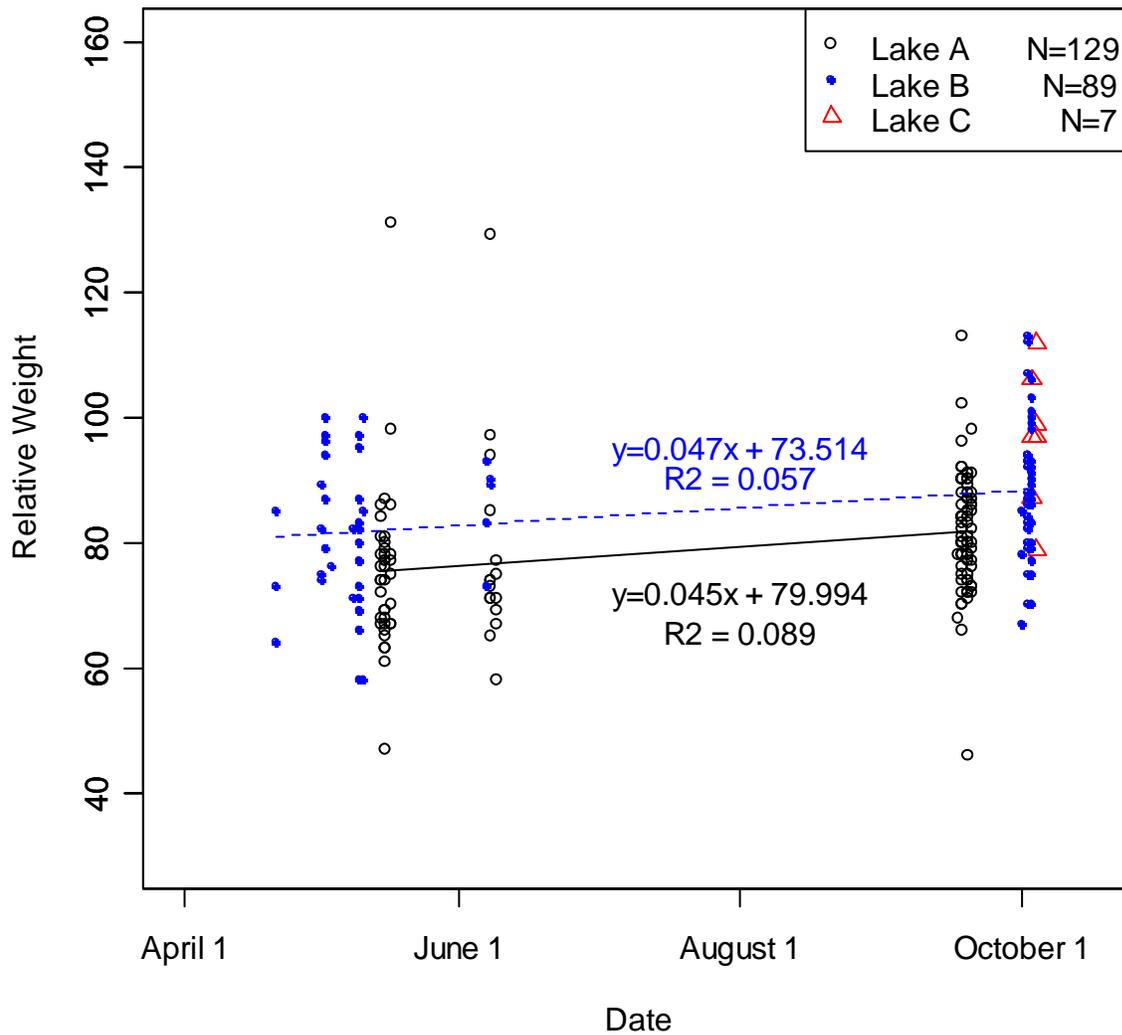


Figure 5 –Regression plot of relative weight for Lake A, Lake B and Lake Cs against sampling date. No regression line was constructed for brook trout from Lake C as weight measurements were recorded from October only. The solid (black) regression line represents trout from Lake A while the dashed (blue) line represents trout from Lake B. Data represents brook trout captured by NSDFA only.

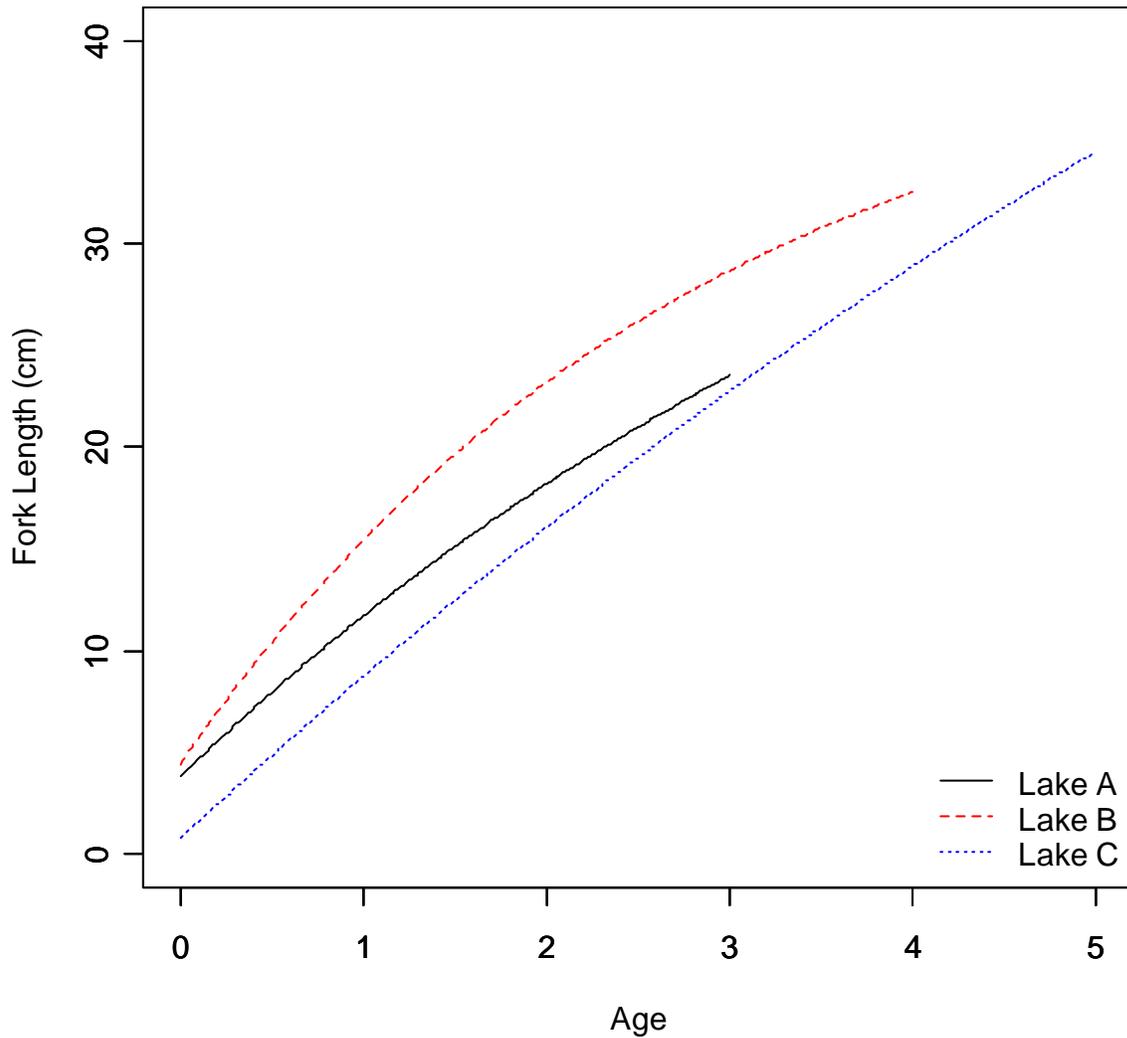


Figure 6 – von Bertalanffy growth curves for Lake A, Lake B and Lake C brook trout. The Lake A sample contained no trout older than 3 years and the Lake B back-calculated sample contained no trout older than 4 years (though there were trout assumed to be age 5+ trout captured).

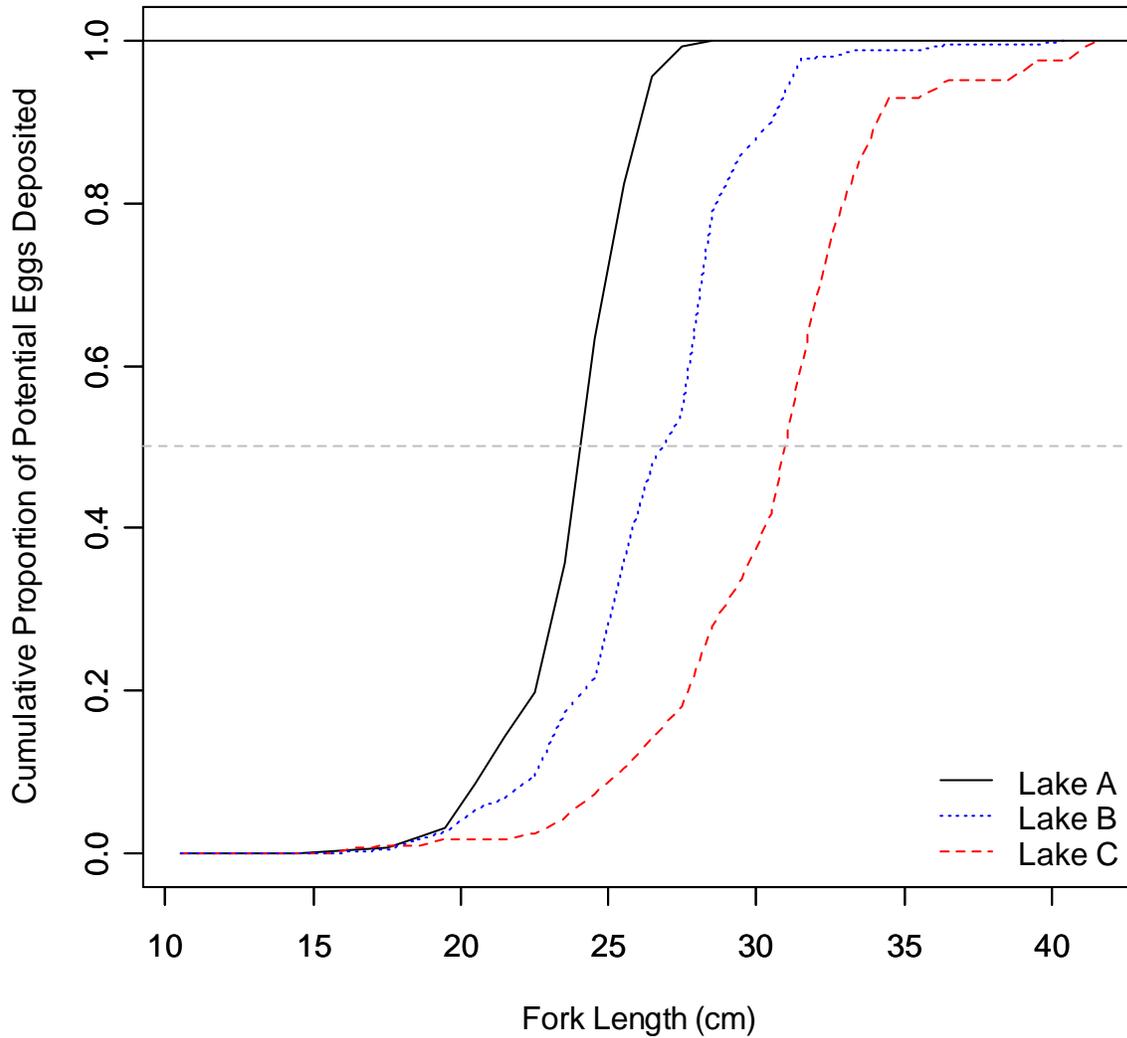


Figure 7 – Cumulative proportion of the total potential eggs deposited based on fork length. For example, in Lake C, approximately 0.2 of total potential egg deposition is contributed by fish less than 27.7cm, and 0.5 of total potential egg deposition is contributed by fish less than 30.9cm. Data represents brook trout captured by NSDFA only.

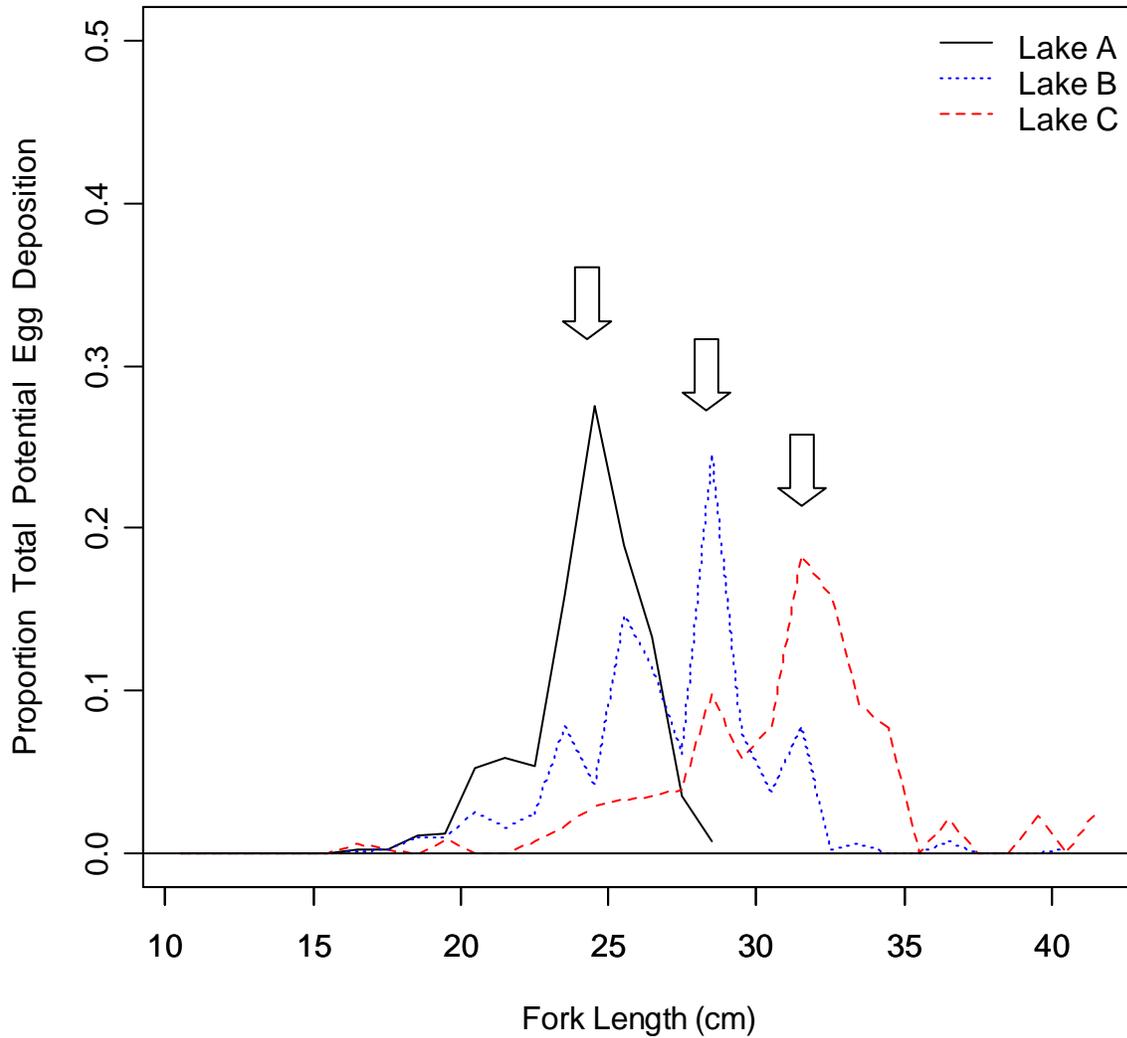


Figure 8 – Percent of total potential egg deposition contributed by each length class for Lake A, Lake B and Lake C. For example, in Lake C, trout approximately 31.5cm of fork length provide the largest percentage of total potential egg deposition (18%), relative to other lengths, as indicated by the arrow. Data represents brook trout captured by NSDFA only.

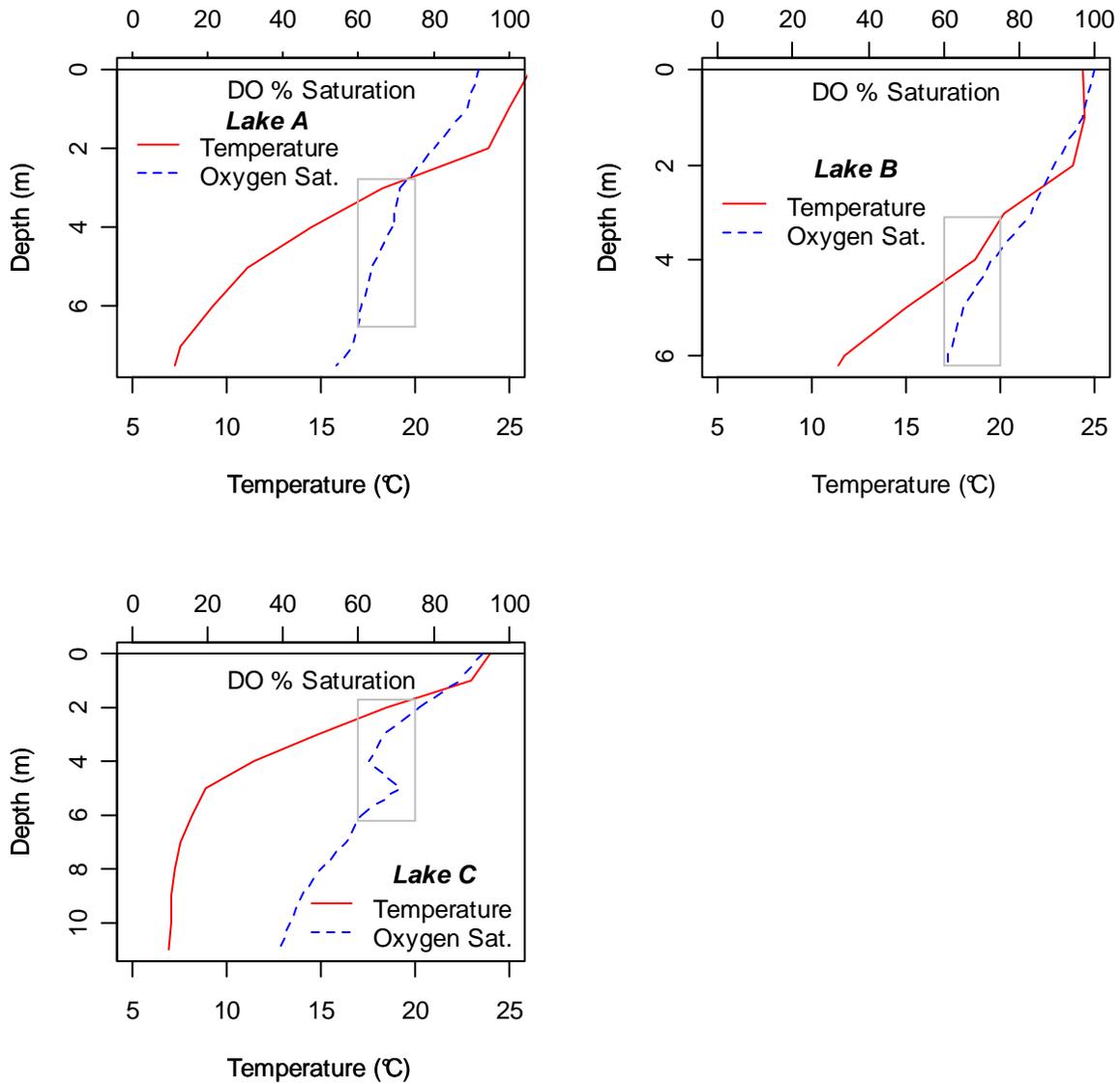


Figure 9 – Temperature (°C) and dissolved oxygen (% saturation) depth profiles for Lake A, Lake B and Lake C. The area in the box (grey) represents the depths at which trout may find suitable habitat (>60% DO saturation and < 20°C. Note – Not all x-axes are of equal scale.

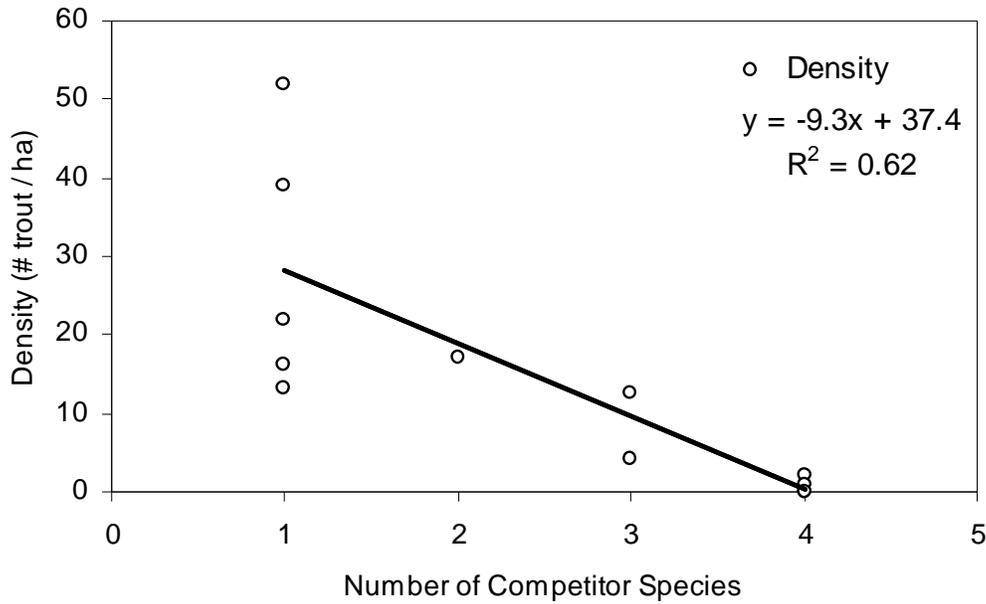


Figure 10 – A plot of correlation between the number of competitor species and the density of brook trout in Nova Scotia lakes. Data include Lake A, Lake B and Lake C (this study) in addition to lakes outlined in MacMillan and Crandlemere (2005).

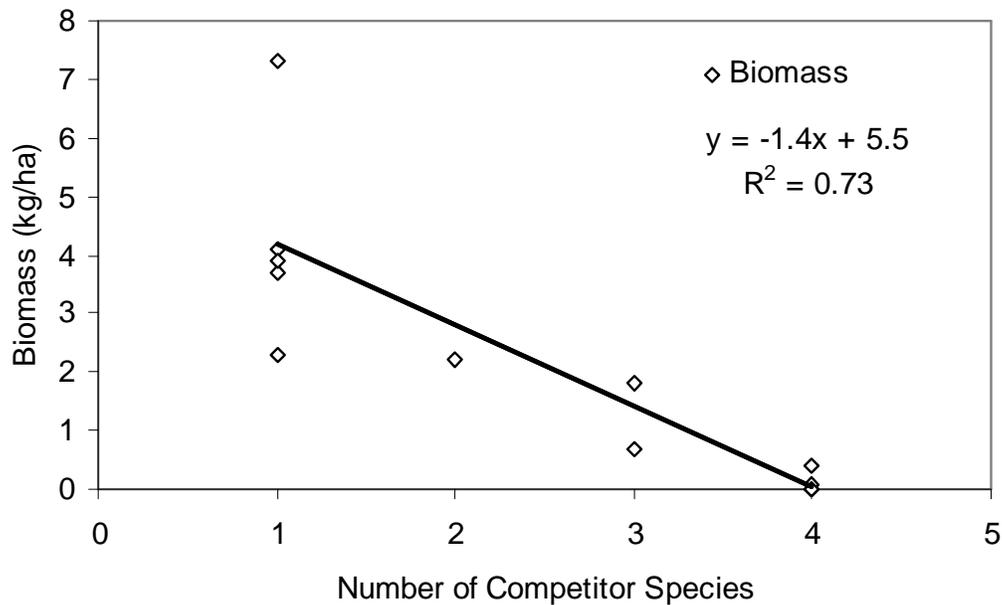


Figure 11 – A plot of correlation between the number of competitor species and the standardized biomass of brook trout in Nova Scotia lakes. Data include Lake A, Lake B and Lake C (this study) in addition to lakes outlined in MacMillan and Crandlemere (2005).