# An Investigation of Arctic Char *(Salvelinus alpinus)* and Lake Trout *(Salvelinus namaycush)* in Lake Clark National Park, Alaska

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# AUTHORIZATION TO SUBMIT THESIS

This thesis of Ryan Kreiner, submitted for the degree of Master of Science with a major in Fishery Resources and titled “An Investigation of Two Resident Fish Species in Lake Clark National Park, Alaska: Arctic Char *(Salvelinus alpinus)* and Lake Trout *(Salvelinus namaycush),”* has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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## ABSTRACT

Anadromous sockeye salmon *(Oncorhynchus nerka)* are a keystone species for freshwater ecosystems, and in Lake Clark National Park, Alaska (LCNP), declines in salmon runs over the past 25 years have raised concerns about the health of resident fish species. Data on resident arctic char *(Salvelinus alpinus)* and lake trout *(Salvelinus namaycush)* growth and condition from six lakes within LCNP were collected in 2004 and compared with an historical information collected by Russell (1980) during the summers of 1978-79. Four hypotheses were investigated: 1) arctic char and lake trout growth rates would be higher in lakes with sockeye salmon than in those without them; 2) arctic char and lake trout condition would be higher in lakes with sockeye salmon than in those without them; 3) arctic char and lake trout condition in 2004 would be lower than condition in 1978-79 in lakes with sockeye salmon coincident with declines in anadromous fish runs; 4) arctic char and lake trout diets would consist of sockeye salmon fry and eggs in those lakes with sockeye salmon. Growth of both resident species was not found to be faster in systems with anadromous sockeye salmon. It is more likely that a host of factors such as predation and available prey contributed to resident fish growth. Both species relied seasonally on sockeye salmon in the form of eggs and fry when available. This translated to a higher condition for lake trout but not for arctic char.

Because ages of fish captured were needed to estimate growth rates, reader precision and bias of age estimation using two calcified structures, otoliths and pectoral fin rays, were also investigated for both species. Otoliths provided more reliable results than fin rays for both species. In arctic char, fin rays produced higher estimates 81% of the time. In lake trout, fin rays did not produce interpretable results.

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# **Chapter 1**:  Growth and Condition of Arctic Char *(Salvelinus alpinus)* and Lake Trout *(Salvelinus namaycush)* in Lake Clark National Park, Alaska

## ABSTRACT

Anadromous sockeye salmon *(Oncorhynchus nerka)* are a keystone species for freshwater ecosystems, and in Lake Clark National Park, Alaska (LCNP), declines in salmon runs over the past 25 years have raised concerns about the health of resident fish species. Arctic char *(Salvelinus alpinus)* and lake trout *(Salvelinus namaycush)* growth rates and conditions were collected from six lakes within Lake Clark National Park, Alaska (LCNP), and compared among lakes and to historical information (Russell 1980). Four hypotheses were investigated: 1) arctic char and lake trout growth rates would be higher in lakes with sockeye salmon than in lakes without them; 2) arctic char and lake trout condition would be higher in lakes with sockeye salmon than in lakes without them; 3) arctic char and lake trout condition in 2004 would be lower than condition in 1978-79 in lakes with sockeye salmon coincident with declines in anadromous fish runs; 4) arctic char and lake trout diets would consist of sockeye salmon fry and eggs in those lakes with sockeye salmon. Growth and condition of arctic char populations in 2004 were not found to be higher in the presence of salmon, despite an observed seasonal food source of salmon eggs. Historically (1978-79) however, condition was higher in such lakes, coincident with higher salmon runs. As salmon runs have declined, other factors such as predation by lake trout and competition from various whitefish species *(Coregonus spp., Prosopium spp.)* may contribute more to the growth and condition of arctic char. Growth rates of lake trout were not found to be higher in the presence of salmon, but condition was higher in a lake in which lake trout fed exclusively on salmon fry. This higher condition did not result in larger fish, however. Instead, larger lake trout were associated more with larger lakes and more diverse prey species.

## INTRODUCTION

Anadromous Pacific salmon (*Oncorhynchus spp.)* are an important source of marine-derived nutrients for freshwater streams and lakes (Reed 1967; Kline et al. 1994). This nutrient enrichment is probably greatest in the case of high-density spawning species such as chum salmon (*Oncorhynchus keta)*, pink salmon (*Oncorhynchus gorbuscha)*, and sockeye salmon (*Oncorhynchus nerka)* (Bilby et al. 2003).

Nutrients from decomposing salmon have been found to result in measurable increases in the productivity of lakes and rivers, especially in oligotrophic lakes where few other significant nutrient sources are present. For example, trees and shrubs near spawning streams have been shown to derive 22-24% of their foliar nitrogen (N) from spawning salmon, and Sitka spruce *(Picea sitchensis)* have exhibited significantly higher growth rates near salmon spawning streams (Helfield and Naiman 2001). Aquatic insect abundances increased in systems artificially enhanced with nutrients similar to what would be deposited by decaying salmon (Quamme and Slaney 2003). In the Pacific Northwest, the effects of reduced salmon carcasses and derived nutrients on resident bull trout (*Salvelinus confluentus)* and westslope cutthroat trout (*Oncorhynchus clarki lewisi)* may be great, especially in nutrient-deficient high mountain streams (Peery et al. 2003).

Besides serving as an important nutrient source for non-fish species, salmon represent a significant direct food source to fish, particularly to other salmonids (Reed 1967; Ruggerone and Rogers 1984; Willson and Halupka 1995). For example, eggs from spawning Pacific salmon were an important seasonal food source for resident salmonids in a Lake Superior tributary, constituting more than 95% of the diet of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) in October (Johnson and Ringler

1979). Pink and chum salmon were a significant food source for arctic char (*Salvelinus alpinus)* in the Khaylyulya River in Russia (Tiller and Vvedenskaya 1988). During the fall spawning season, char fed almost exclusively on salmon eggs, whereas in spring they consumed an estimated 5.6 million juvenile pink salmon, about 15% of the total out-migration. Other studies documented lake trout *(Salvelinus namaycush)* predation on Atlantic salmon (*Salmo salar)* parr (Caron 1987), and arctic grayling (*Thymallus arcticus)*, rainbow trout *(Oncorhynchus mykiss*), and Dolly Varden (*Salvelinus malma)* predation on salmon eggs (Reed 1967; Willson and Halupka 1995).

By serving as a source of nutrients and food (prey), anadromous salmonids are thus identified as keystone species providing important ecological linkages in freshwater ecosystems (Willson and Halupka 1995). As such, variation in abundance of anadromous salmonids can affect productivity, phenology, and metapopulation dynamics of wildlife and hence affect regional biodiversity.

Lake Clark National Park (LCNP) (Figure 1), in southwest Alaska, contains numerous oligotrophic lakes and low productivity rivers. From 1979 to 1996, the size of the sockeye salmon run returning to LCNP declined from about nine million fish (1979) to a low of 36,000 (1996) (Alaska Department of Fish and Game 2003). Run size since 1996 has remained low; estimates from 2000 through 2005 ranged from 173,000 to 555,000 fish (National Park Service, Unpublished Data, 2006).

Because salmon are an important nutrient and food source to resident fish in LCNP, changes in salmon abundance may potentially affect the abundance and growth of resident fishes**.** Such linkages have been reported elsewhere. For example, Johnson and Ringler (1979) found that an increased contribution of salmon eggs in the diets of brown trout and brook trout resulted in significant increases in their mean condition factor ($P < 0.05$). Wilpfli et al. (2003) showed an increase in growth rates of Dolly Varden and cutthroat trout in streams enriched with pink salmon carcasses in contrast to fish in the non-enriched control stream. These increased growth rates may translate into higher fitness and survivorship of resident fish (Johnson and Ringler 1979; Wilpfli et al. 2003). Due to the seasonal timing of the sockeye salmon run in LCNP (August through November), resident fish may also depend on this late season food source for over-winter survival (Wilpfli et al. 2003).

A decline in anadromous LCNP fish runs and any corresponding decline in resident fish growth and abundance would impact subsistence fisheries. Because LCNP is remote and accessible only by air, residents of Port Alsworth and Nondalton, two villages inside or near the park boundaries, rely on sockeye salmon as a primary food source (Russell 1980). Both villages harvested an average of more than 30,000 sockeye salmon per year from 1963 to 1979 (Fall et al. 1996). Lake trout, Dolly Varden and arctic char are also harvested for subsistence (Fall et al. 1996). Since 1996, anadromous salmon runs have declined, and as of 2005 villagers have had to rely on resident fish populations to a greater extent to supplement their diets. Stock and harvest data from these resident fishes are needed in order to establish appropriate harvest guidelines.

If declines in anadromous fish abundance in LCNP have affected resident fish, the result should be apparent through analysis of historical trends in their condition, growth, and abundance. Historical data on resident fish abundance and growth are unavailable; however historical length and weight data for several important species exist, including for arctic char and lake trout (Russell 1980). Comparing historic and contemporary data may reveal whether the recent decline in sockeye salmon abundance has affected the growth and condition of resident fish.

Arctic char and lake trout are found throughout LCNP, and anadromous sockeye salmon are an important food source for both species (Russell 1980). Sampling in Kijik Lake (Figure 1) in 1978-79, revealed sockeye fry in 40% of sampled lake trout stomachs and arctic char feeding on salmon eggs (Russell 1980). The river draining Kijik Lake was observed to have an extremely high abundance of sockeye fry, such that the shoreline waters were darkened by their large schools. Kijik Lake is also where Russell (1980) found the largest arctic char among 27 lakes that he sampled, with some fish exceeding 600 mm in length and 2.4 kg in weight. Although lake-dwelling populations of arctic char are numerous in Alaska, they are often small in size (weight ≤ 0.9 kg). However, if forage fishes, such as juvenile sockeye salmon, are available, char may become piscivorous and grow to 4.5-5.5 kg (Behnke 2002).

The objective of this study assessed the system-level relationship between the perceived change in anadromous sockeye salmon abundance and the productivity of arctic char and lake trout populations among lakes in LCNP. Four hypotheses were tested: 1) arctic char and lake trout growth rates would be higher in lakes with sockeye salmon than in those without them; 2) arctic char and lake trout condition would be higher in lakes with sockeye salmon than in those without them; 3) arctic char and lake trout condition in 2004 would be lower than condition in 1978-79 in lakes with sockeye salmon coincident with declines in anadromous fish runs; 4) arctic char and lake trout diets would take advantage of sockeye salmon fry and eggs as a food source when available.

## STUDY SITE

Lake Clark National Park is a geologically young region located within the largest sockeye salmon producing system in the world, the Bristol Bay watershed in southwest Alaska (Figure 1) (Russell 1980; Kline et al. 1994). The park contains a combination of oligotrophic lakes and rivers as well as turbid glacial systems.

Seven lakes within LCNP were sampled: Lake Clark, Telequana Lake, Kijik Lake, Kontrashibuna Lake, Tazimina Lakes, and Portage Lake (Figure 1). Three lakes (Clark, Telequana, and Kijik) receive runs of anadromous sockeye salmon whereas the remaining four (Portage, Kontrashibuna, Upper Tazimina, Lower Tazimina), due to natural barriers, do not. Fish species composition differs among the seven lakes, and species diversity in most is low due to recent glacial events (Table 1).

Lake Clark is the sixth largest lake (area 267 km$^2$) in Alaska. The lake has a maximum recorded depth exceeding 300 m, and Secchi depth ranges from less than 1 m at its northeastern end to greater than 2 m at its southwestern end (Figure 1) (Russell 1980). Nineteen species of fish inhabit the lake (Table 1), although some, including arctic char, occur in low numbers. Lake trout, least cisco *(Coregonus sardinella),* humpback whitefish (*Coregonus pidschian*), and sockeye salmon have substantial populations in Lake Clark.

Telequana Lake is a large lake (area 41 km$^2$) in the northern section of LCNP, with a maximum depth exceeding 130 m and a Secchi depth of less than 4 m (Figure 1) (Russell 1980). The Telequana River exiting the lake drains into the Bering Sea via the Kuskokwim River. Telaquana Lake is the only lake in this study that lies outside the

Kvichak River drainage. It hosts a relatively diverse fish community including lake trout, least cisco, and sockeye salmon (Table 1).

Kijik Lake is a small (< 6 km²), deep (100 m), and clear (Secchi depth > 17 m) lake (Figure 1) that historically contained a large annual run of sockeye salmon (Russell 1980). Runs in 1978 and 1979 were estimated at 106,300 and 240,200 fish by aerial survey. Between 1994 and 2000 however, the highest run was only 8,750 fish (Alaska Department of Fish and Game 2003). Russell (1980) captured the largest arctic char in his study in Kijik Lake.

Three study lakes do not have anadromous sockeye salmon runs because of natural barriers. Portage Lake lies within the Kijik River drainage, and has similar physical characteristics to Kijik Lake (total area < 5 km², depth > 50 m, Secchi depth > 19 m), but a series of rapids at river kilometer (Rkm) 27 prevents upstream migration of sockeye salmon into the lake (Figure 1) (Russell 1980). Only arctic char, lake trout, and slimy sculpin *(Cottus cognatus)* inhabit the lake. Several large arctic char were caught in Portage Lake during Russell's (1980) study, but no salmon. The largest char exceeded 550 mm in length and 1.4 kg in weight.

Kontrashibuna Lake (area 25 km²) has a maximum depth of greater than 300m and ranges in Secchi depth from < 1m in its southeastern end to > 2 m in its north eastern end (Russell 1980). A large (> 9 m) waterfall on the Tanalian River at approximately Rkm 5 prevents upstream migration of fish, including anadromous salmon (Figure 1). Only arctic char, lake trout, pygmy whitefish, and slimy sculpin occupy this lake (Table 1).

Tazimina Lakes (Upper and Lower) are under 20 km$^2$ in total area with maximum depths of > 100 m, and range in Secchi depth from < 5 m to 12 m, (Russell 1980). The abundance of arctic char in Tazimina Lakes was historically higher than in any other lake in LCNP for which information is available (Russell 1980.) A large waterfall (>30 m) on the Tazimina River at Rkm 27.4 prevents upstream fish migration of sockeye salmon into the lake (Figure 1). Because migration between the upper and lower lakes is unobstructed, fish sampled from these two lakes were considered a single population in the present study.

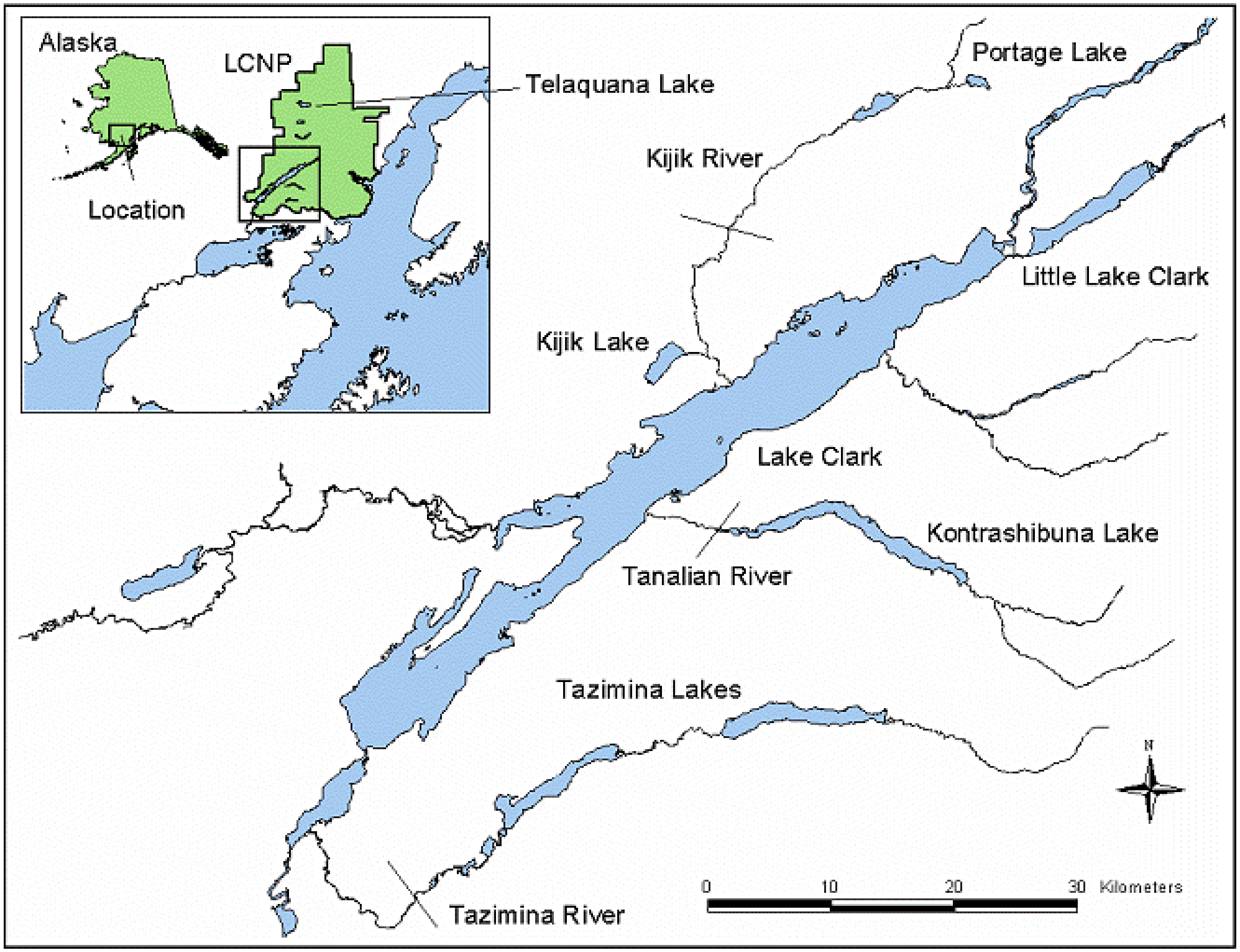

Figure 1 - Map of Lake Clark National Park, Alaska, including lakes investigated in this study. Barriers to anadromous sockeye salmon migration are indicated by lines across Kijik River, Tanalian River, and Tazimina River.

Table 1- Fish species present in the study lakes (X-present, ~-absent.)

| | Lake | | | | | |
|---|---|---|---|---|---|---|
| **Fish Species** | **Clark** | **Telaquana** | **Kijik** | **Portage** | **Kontrashibuna** | **Tazimina** |
| Sockeye Salmon<br>*(Oncorhynchus nerka)* | X | X | X | ~ | ~ | ~ |
| Arctic char<br>*(Salvelinus alpinus)* | X | ~ | X | X | X | X |
| Arctic grayling<br>*(Thymallus arcticus)* | X | X | X | ~ | ~ | X |
| Burbot<br>*(Lota lota)* | X | ~ | ~ | ~ | ~ | ~ |
| Humpback whitefish<br>*(Coregonus pidschian)* | X | ~ | ~ | ~ | ~ | ~ |
| Lake trout<br>*(Salvelinus namaycush)* | X | X | X | X | X | ~ |
| Least cisco<br>*(Coregonus sardinella)* | X | X | X | ~ | ~ | ~ |
| Longnose sucker<br>*(Catostomus catostomus)* | X | X | X | ~ | ~ | ~ |
| Ninespine stickleback<br>*(Pungitius pungitius)* | X | X | X | ~ | ~ | ~ |
| Northern pike<br>*(Esox lucius)* | X | X | ~ | ~ | ~ | ~ |
| Pygmy whitefish<br>*(Prosopium coulteri)* | X | ~ | ~ | ~ | X | ~ |
| Round whitefish<br>*(Prosopium cylindraceum)* | X | X | X | ~ | ~ | ~ |
| Slimy sculpin<br>*(Cottus cognatus)* | X | X | X | X | X | X |
| Threespine stickleback<br>*(Gasterosteus aculeatus)* | X | ~ | ~ | ~ | ~ | X |

## METHODS

Arctic char and lake trout were sampled during the period 1-Jul through 23-Sep 2004 (Table 2). For comparison with historical sampling, sampling dates and locations corresponded to those of Russell (1980) when feasible. At each site GPS coordinates were taken for future reference.

Table 2- Starting sample dates for both Russell's (1980) and the current study.

|  | **Dates Sampled** |  |
|---|---|---|
| **LAKE** | **1978-79** | **2003-04** |
| Little Lake Clark | 20-Jul | 5-Aug |
| Telaquana | 10-Jul | 10-Jul |
| Kijik | 25-Jun | 1-Jul & 22-Sep |
| Portage | 31-Aug | 9-Jul |
| Kontrashibuna | 22-Sep | 14-Sep |
| Tazimina | 8-Sep | 24-Aug |

Variable mesh gill-nets, both floating and sinking, were used for sampling fish in this study. Floating nets were identical to that of Russell (1980): monofilament mesh, 38.1 m long, 1.8 m deep, and consisting of five 7.62 m panels with mesh sizes 1.3, 1.9, 2.5, 3.8 and 5 cm respectively. The sinking nets had shorter lengths (30.5), the same depth (1.8 m), and larger mesh sizes (four 7.62 m monofilament panels with mesh sizes 1.27, 2.54, 5.08 and 10.16 cm respectively). Fishing time of nets was recorded, and hook and line sampling was also used to supplement netting effort. The sampling objective was fifty fish of each species (arctic char and lake trout). Up to thirty fish per lake were sacrificed for otoliths and other biological information. In cases of low catch rates, nets were placed in locations which differed from those sampled by Russell (1980). Areas of higher fish abundance, such as tributary inlets, steep drop-offs, or islands were chosen when new locations were needed. The target values for individual species were met in two of four lakes containing arctic char, and four of five lakes containing lake trout.

Length and weight data were measured for all captured fish of both species. Fish were released alive if possible.

Otoliths were removed from incidental mortalities for age determination. Other studies indicated that more accurate aging of both species was likely using otoliths, particularly with older fish (Nordeng 1961; Martin and Olver 1980; Barber and McFarlane 1987). Casselman (1990) reported that in slow-growing or old fish, otoliths grew more rapidly than other calcified structures used for aging and also continued to record cyclic seasonal variation in growth and age. Otoliths were mounted on transparent plastic microscope slides in a plastic casting resin. Each otolith was examined by a primary reader and if clearly defined annual rings and evidence of light transmission were observed from the edge of the otolith to the nucleus, the whole otolith was interpreted for age by two readers (Figure 2b). Most otoliths, especially those of arctic char, were too opaque near the nucleus to accurately interpret. In this case, the otolith was ground until transparent and annuli near the nucleus were detectable (Figure 2a), at which point age was independently interpreted by two readers.

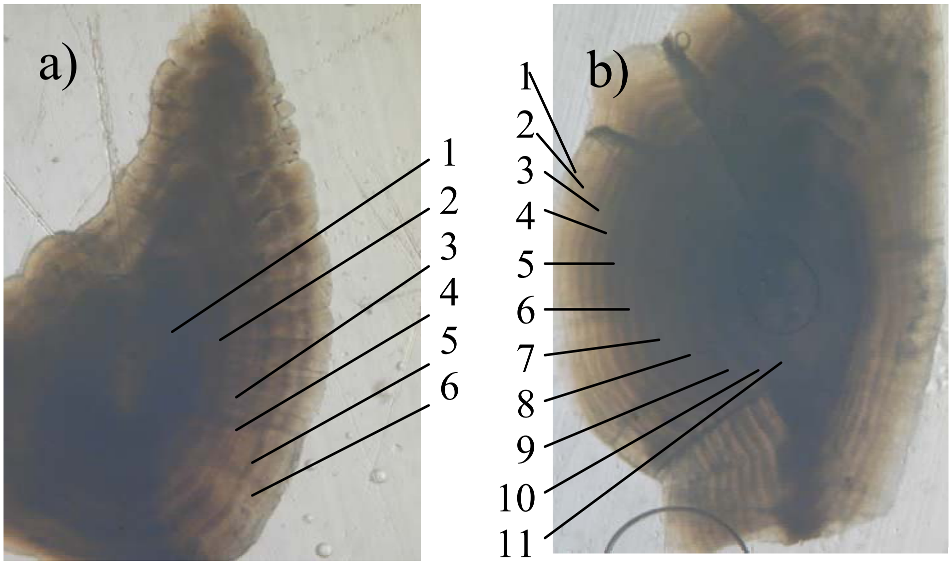

Figure 2– A ground arctic char otolith (a) and a whole lake trout otolith (b) displaying annuli. Each fish was interpreted similarly by both readers.

Ages were assigned using a double blind protocol with a tolerance for minor disagreement. Under this protocol, two readers were used. No age discrepancy between readers was tolerable for fish < age-10; a one year age difference was tolerable for fish age-10 to age-19; a two year difference was tolerable for fish age-20 to age-29; and a three year difference was acceptable for fish ≥ age-30. In cases where differences exceeded established guidelines, both readers independently re-aged samples with no knowledge of prior readings. If assigned ages still exceeded tolerable limits, readers aged the remaining samples together until an age was agreed upon. In all cases, fish age was assessed by the primary reader. Insufficient data were available to assess precision and bias of historic age estimates by Russell (1980), therefore growth curves were not constructed using these ages.

Length-at-age data was used to fit von Bertalanffy growth curves (Gallucci and Quinn 1979; Van Den Avyle and Hayward 1999) expressed as $L_\infty\ [1-e^{-k(t-t_o)}]$ where $L_\infty$ is the asymptotic or maximum length, k is the parameter expressing how fast a fish reaches $L_\infty$, and $t_o$ is the initial condition parameter. The parameters were estimated using a nonlinear least squares command (Kudo and Mizuguchi 2000). Parameter estimates were compared by constructing approximate 95% confidence intervals and assessing overlap. The null hypothesis ($H_o$) was that growth rates, as explained by the parameters $L_\infty$ and k, would not differ among lake populations. Van Belle (2002) stated that a statistically significant difference in the mean is suggested when confidence intervals overlap by 25% or less. All analyses and figures were generated in the data analysis environment R (Cran project) (Murrell 2006).

Condition of lake trout was characterized as relative weight, $W_r$ , expressed as ($W_r = (W/W_s)*100$), where $W_s$ (standard weight) is defined as $\log_{10}(W_s) = a' + b * \log_{10}(\text{Length})$, where W is the individual fish weight, and a' and b are the intercept and slope respectively, which are based on the genetically determined shape of the specific species (Anderson and Neuman 1996). Piccolo et al. (1993) established the $W_s$ equation for lake trout, and their guidelines were used here. Relative weight provides a convenient measure of the physiological status of fish populations (Hyatt and Hubert 2001), but avoids length-related bias of Fulton condition factors (Hubert et al. 1994).

Differences in $W_r$ values were evaluated using notched box-plots and a 1-way ANOVA plus Tukey's honest significant difference test for multiple comparisons. Box-plots provided a simple, visual way to present relative weight and condition data (McGill et al. 1978). Notches were added to visually assess differences in medians (i.e., non-overlapping notches) (McGill et al. 1978). Because a 1-way anova plus Tukey's honest significant difference test for multiple comparisons provided more conservative results than did the plots, significance was only concluded if Tukey's test was significant at $P < 0.05$.

As of 2006, a standard weight ($W_S$) equation for arctic char had not been developed, therefore length and weight data were used to compute Fulton's condition factor: (K), expressed as $K = (W/L^3) \times 10{,}000$ (Anderson and Neuman 1996). Condition was compared between lakes and between data collected in 1978-79 (Russell 1980) and 2004. Any bias between K and total length was checked graphically, and significant differences in condition data were tested and expressed using notched box-plots and a 1-way ANOVA plus Tukey's honest significant difference test for multiple comparisons in an identical manner as $W_r$ data for lake trout. For $W_r$ and K, the null hypothesis ($H_o$) was that condition would be the same among lake populations and years.

Stomach contents were evaluated in the field for presence or absence of prey items. Here, only general classifications were made; fish were broken down to genus and species, while all other prey items were identified to order. Tables displaying results were labeled with common names. These results, as well as the results of stomach analysis obtained by Russell (1980) were applied to the hypotheses tested. The null hypothesis ($H_o$) was that diet would not differ between lakes regardless of the presence of anadromous sockeye salmon.

# RESULTS

## Growth

### *Arctic Char*

Arctic char growth rates were not found to differ significantly between lakes with and without anadromous sockeye salmon. Neither asymptotic length ($L_\infty$), nor the curvature parameter k differed significantly among Kijik ($L_\infty$; 495 mm), Portage ($L_\infty$; 552 mm), Kontrashibuna ($L_\infty$; 501 mm) (Figure 3), or Tazimina ($L_\infty$; N/A) lake populations (Figure 4). Variability of data points was high in the first three lakes, but parameters were able to be estimated. However, an overlap of greater than 50% in all confidence intervals resulted in the test for statistical significance being very insensitive. In Tazimina Lakes, arctic char did not have a single, population-wide growth rate. For example, ten Tazimina char were estimated as age-10, but ranged in size from 243 mm and 45 g, to 529 mm and 1724 g. As a result, stable von Bertalanffy parameters were not able to be estimated for this lake (Figure 4).

Although the insensitivity of the statistical tests did not permit an adequate evaluation of the hypotheses, the length frequency histograms indicated that in 2004, more large fish were captured in Portage Lake (without sockeye salmon) than all others (Figure 5). Nineteen of 50 (37%) char caught were >500 mm; a higher proportion in this population than in other lakes (Kontrashibuna: 14%, Kijik: 12%, Tazimina: 7%). Using a 2-sample test for equality of proportions, the proportion of large arctic char in Portage Lake was significantly higher than all others ($\chi^2 = 6.29$; $P = 0.006$). However, Kijik Lake (with sockeye salmon) produced more large arctic char than the other lakes in Russell's study (1980).

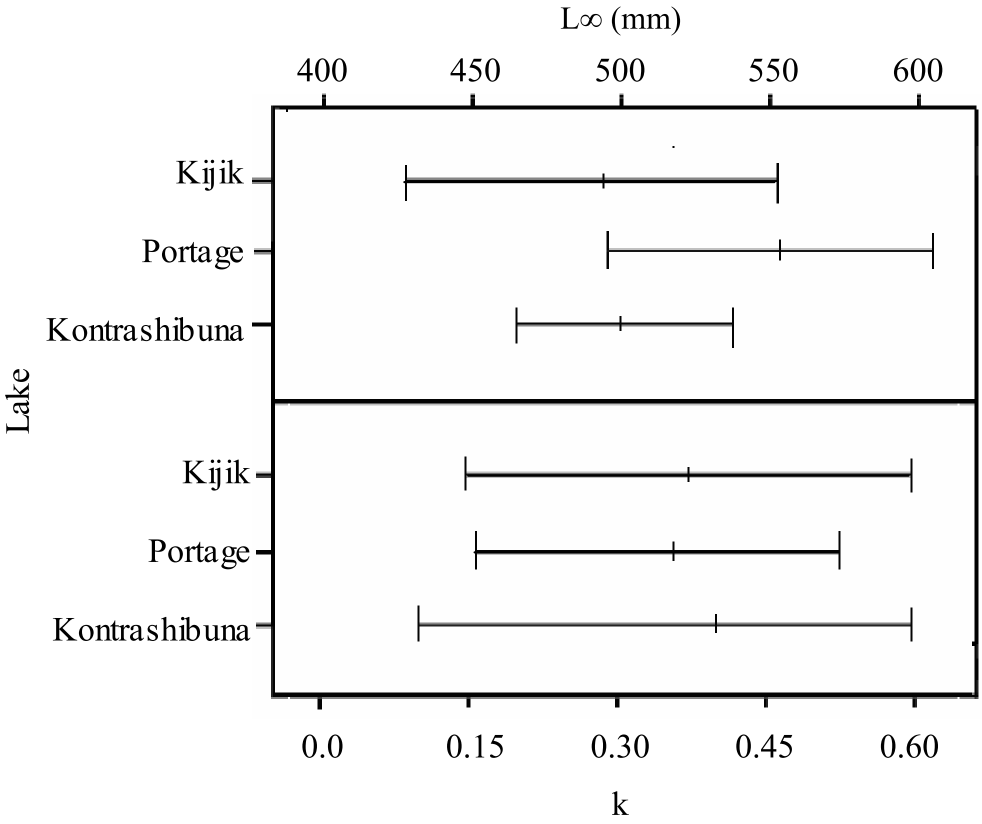

Figure 3 - Von Bertalanffy parameters ($L_\infty$ and k) for arctic char in Lake Clark National Park, Alaska.

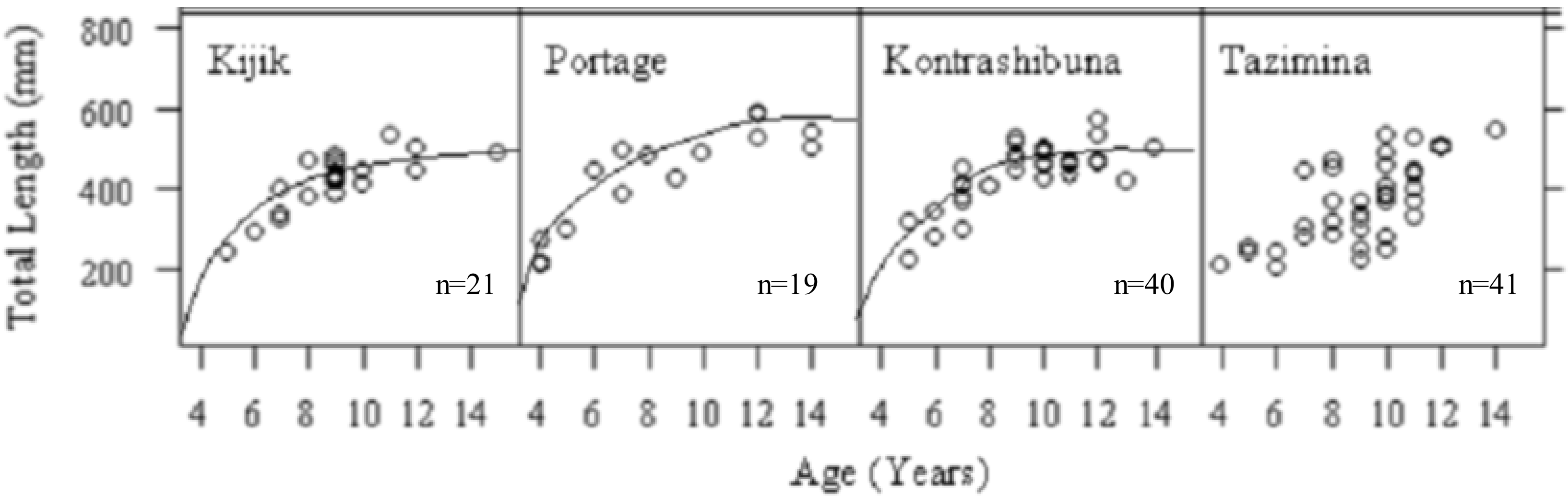

Figure 4—Von Bertalanffy growth curves in 2004 of arctic char in Lake Clark National Park, Alaska.

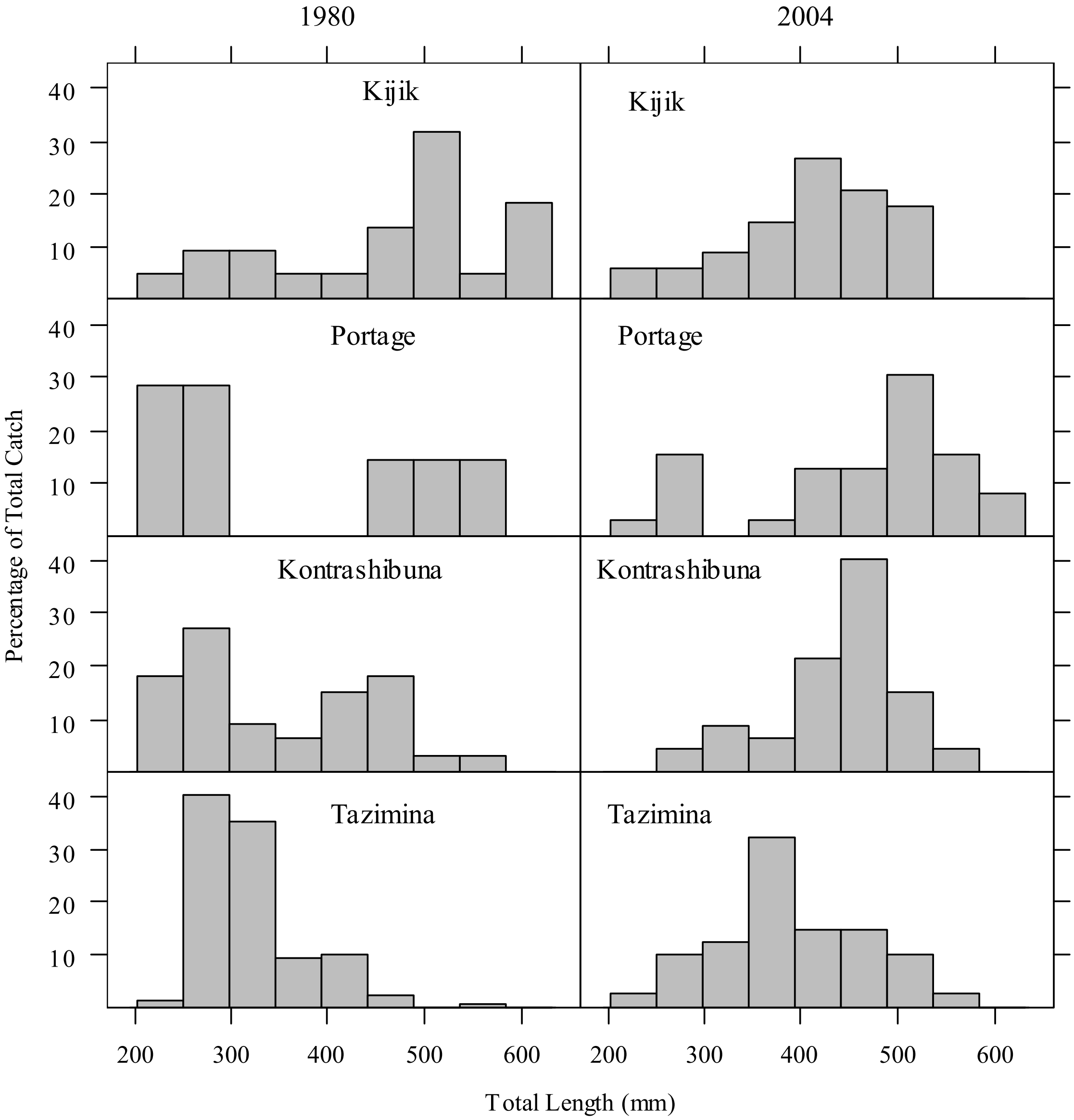

Figure 5 - Length frequency histogram of arctic char captured from four lakes in Lake Clark National Park, Alaska in 1978-79 (Russell 1980) and 2004.

### *Lake Trout*

As with arctic char, lake trout von Bertalanffy growth rates were not greater in systems with anadromous sockeye salmon runs than in lakes without runs. Also, as with char, data for lake trout were variable and von Bertalanffy parameters had wide confidence intervals (Table 3, Figure 6). For example, Telaquana Lake had the highest estimated asymptotic length ($L_{\infty}$, 1239 mm), with a 95% confidence interval of ± 135% of the mean. All confidence intervals of lake trout parameters overlapped greatly and therefore no significant differences among von Bertalanffy population growth rates were detected (Table 3).

Considerably more large lake trout were captured in certain lakes than others, however. Little Lake Clark and Telaquana Lake, the two largest lakes sampled, had the highest proportion of large lake trout captured (> 550 mm TL): 41% and 39%, respectively. In all other lakes this percentage was less than 10%, in Kijik it was 0%. Using a 2-sample test for equality of proportions, the proportion of large lake trout in Little Lake Clark and Telaquana was significantly higher than all others ($\chi^2 = 20.46$; $P < 0.0001$).

Table 3 - Von Bertalanffy parameters for lake trout in Lake Clark National Park, Alaska.

| | Lake | | | | |
|---|---|---|---|---|---|
| Parameter | Little Lake Clark | Telaquana | Kijik | Portage | Kontrashibuna |
| $L_{\infty}$ | 537 | 1238 | 581 | 502 | 659 |
| 95% CI | (466,608) | (0,3333) | (456,707) | (463,540) | (0,2379) |
| k | 0.39 | 0.34 | 0.36 | 0.34 | 0.39 |
| 95% CI | (0.10,0.46) | (0,0.61) | (0.04,0.22) | (0.10,0.46) | (0,0.28) |
| Sockeye Present- | x | x | x | ~ | ~ |

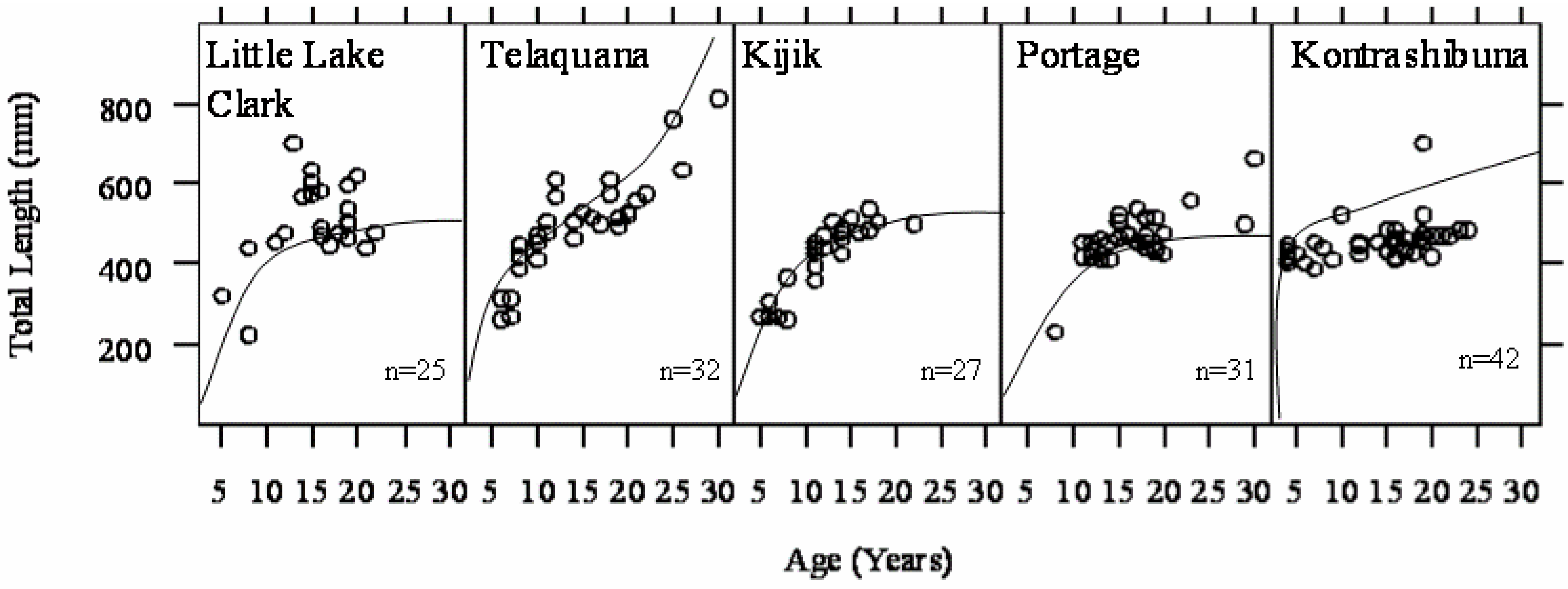

Figure 6— Von Bertalanffy growth curves in 2004 of lake trout in Lake Clark National Park, Alaska.

## Condition

### *Arctic Char*

Arctic char condition was not found to be higher in lakes with anadromous sockeye salmon than in those without them. Despite being the only char population in this study sympatric with sockeye salmon, Kijik Lake char had the lowest mean and median condition factor of contemporary populations (Figure 7); though it only differed significantly from Tazimina (Tukey; $P < 0.05$). Arctic char from Tazimina Lakes had the highest mean and median condition among the populations, although the range was extremely wide (0.32 - 1.45). Condition of char in this lake was dependent on body size, with small fish exhibiting low condition, and large fish exhibiting high condition (Figure 8); this relationship was higher in Tazimina Lakes than in all other lakes sampled.

Mean condition factor of arctic char differed between 1980 and 2004 in three of four lakes sampled. A significantly higher condition was found in the 1980 Kijik Lake population than in the current Kijik population, as well as in all other lakes sampled in 1980. This result was consistent with hypotheses. However, condition declined significantly (Tukey; $P < 0.05$) in Kontrashibuna Lake and increased in Tazimina Lakes (both allopatric from sockeye salmon). Because of the lack of salmon in these lakes, the latter changes cannot be attributed to declines in salmon runs.

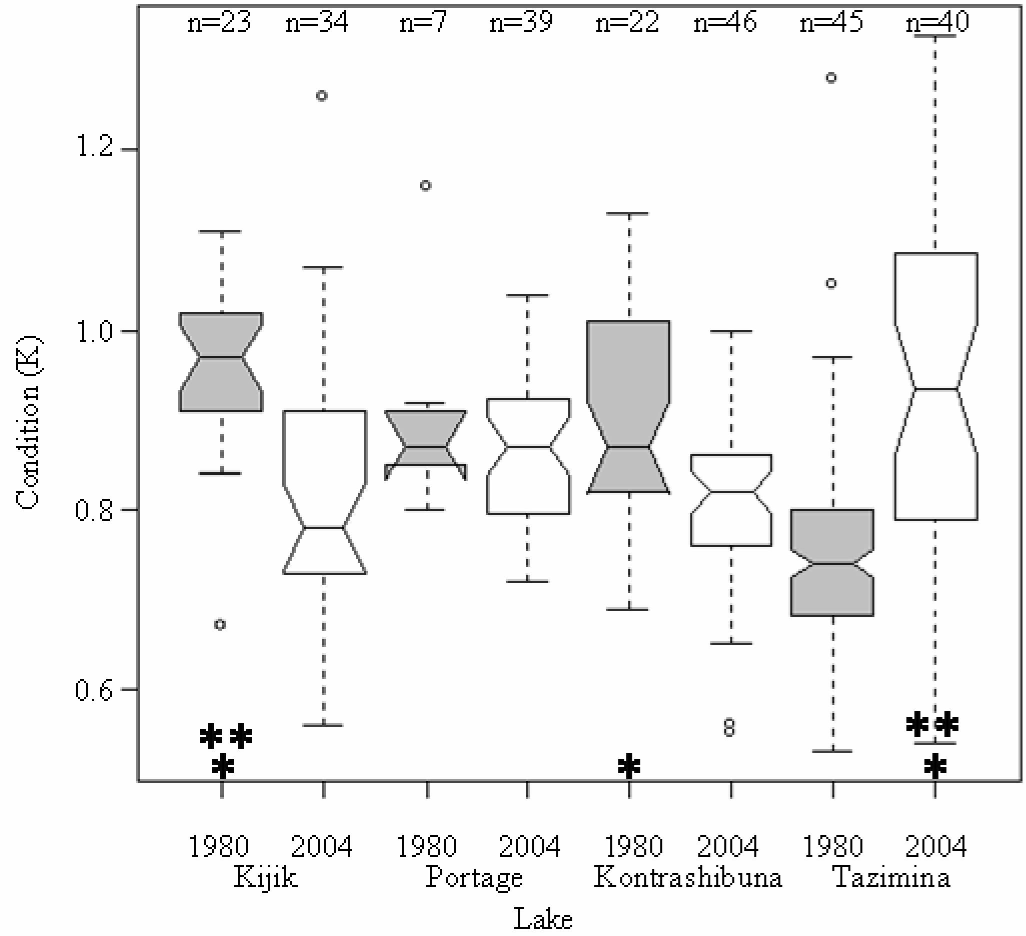

Figure 7 - Arctic char condition by lake and year within Lake Clark National Park, Alaska (gray= 1980, white = 2004). A single asterisk indicates a significantly higher condition in a lake between years based on Tukey's test ($P < 0.05$); a double asterisk indicates the significantly highest condition of all populations sampled that year based on Tukey's test ($P > 0.05$).

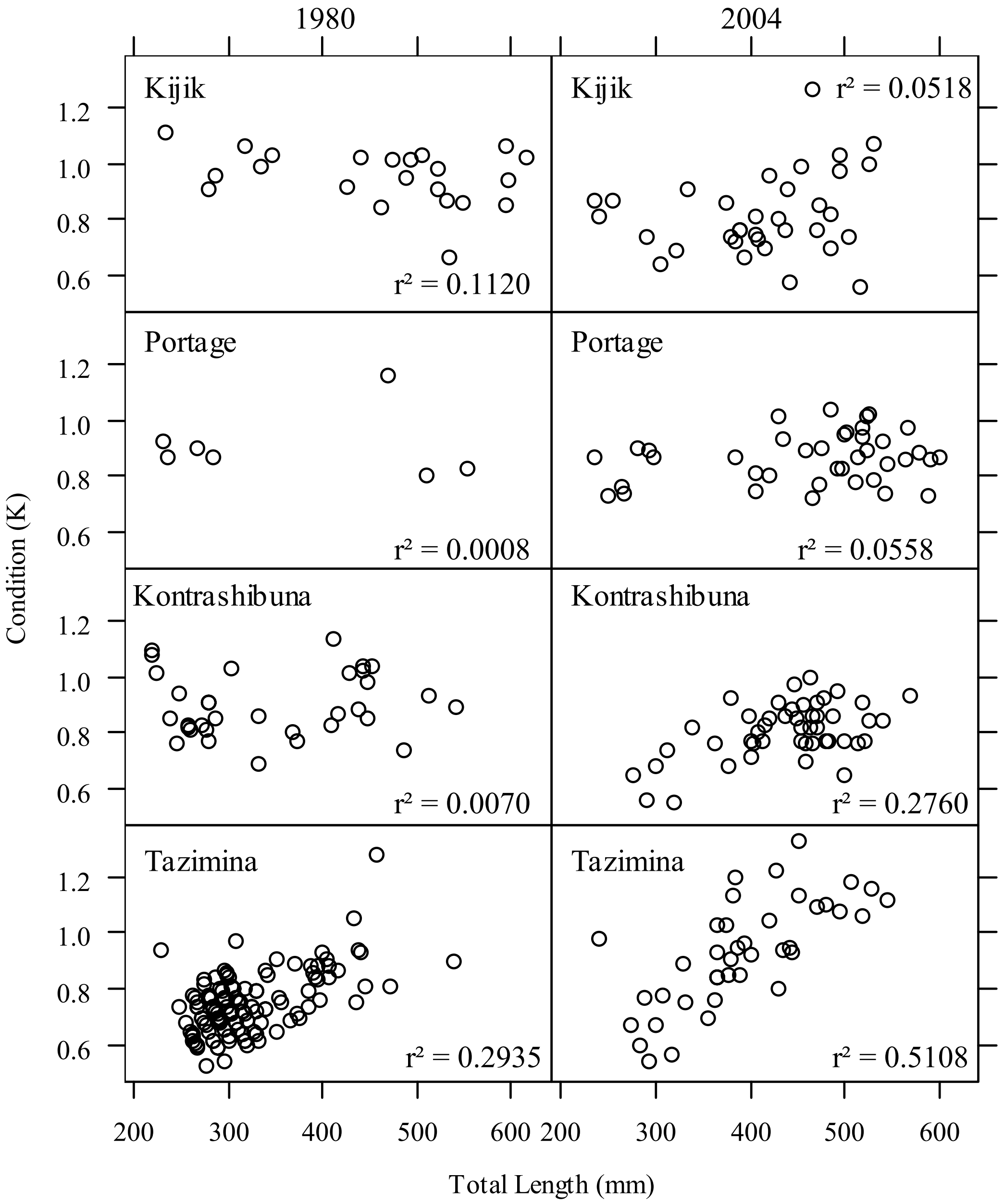

Figure 8 - Condition (K) of arctic char plotted against total length of the fish in Lake Clark National Park, Alaska 2004.

### *Lake Trout*

Mean $W_r$ of lake trout was not found to be consistently higher in lakes with anadromous salmon runs than in lakes without them. Of the three lake trout populations sampled in 2004 which provided access to salmon runs (Little Lake Clark, Telaquana, Kijik), Kijik had the significantly highest overall mean $W_r$ (Tukey; $P < 0.05$), whereas Little Lake Clark and Telaquana had the lowest (Figure 9). Lake trout from Portage Lake and Kontrashibuna Lake, which lacked anadromous salmon runs, had intermediate $W_r$ values.

In comparison of lake trout $W_r$ within lakes between 1980 and 2004, values were significantly lower only in Portage and Kontrashibuna lakes, both of which lacked salmon runs (Figure 9). This result did not support the third hypothesis of lower condition in contemporary populations based on current declines in salmon runs. In Little Lake Clark and Telaquana Lake, $W_r$ values were not significantly lower in 2004 than in 1980, and $W_r$ values in Kijik Lake in 2004 could not be compared to those in 1978-79 because of the small sample size (n=5) collected by Russell (1980).

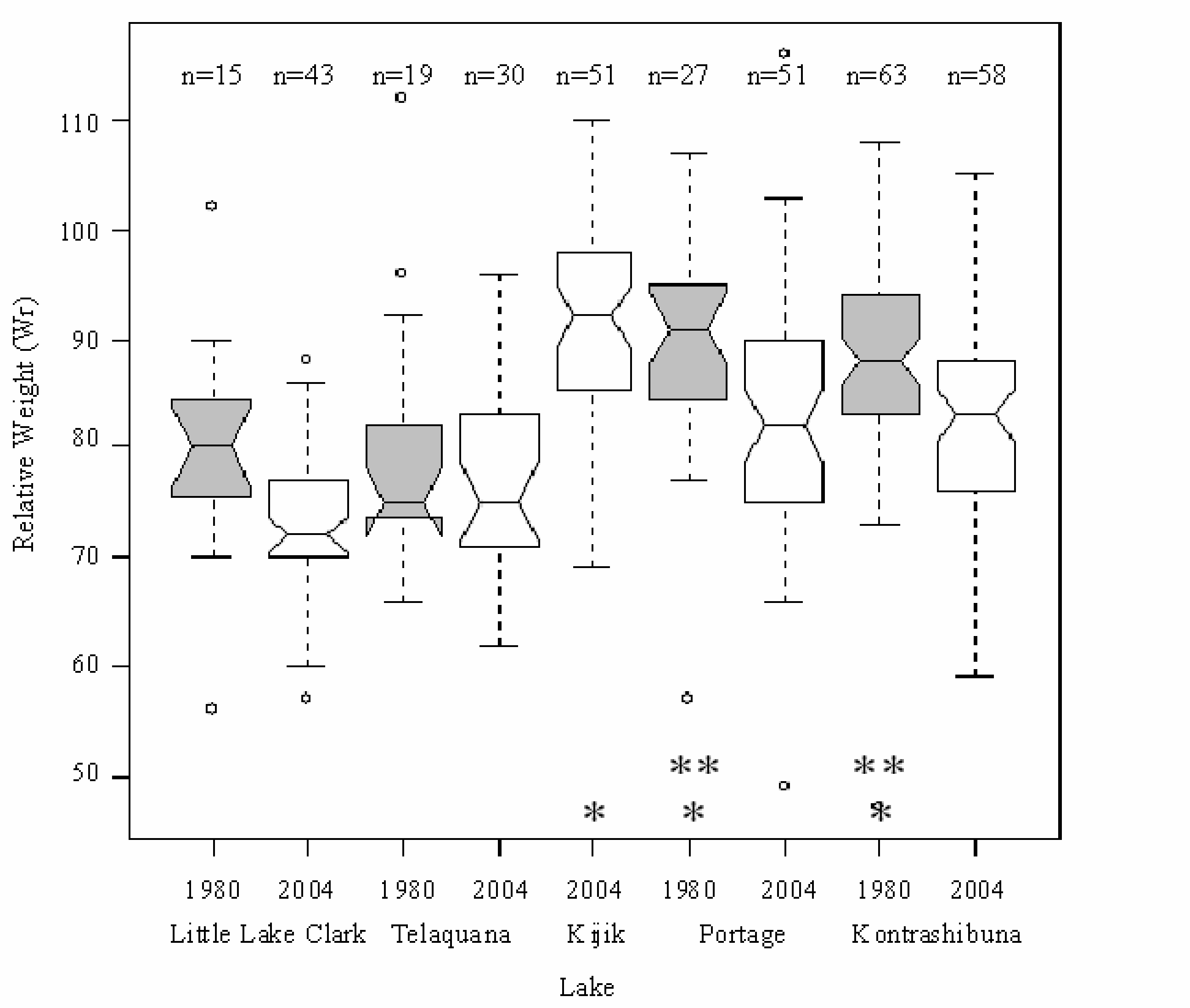

Figure 9 – Lake trout relative weights by lake and year within Lake Clark National Park, Alaska (gray = 1980, white = 2004). A single asterisk indicates a significantly higher relative weight in a lake between years based on Tukey's test ($P < 0.05$); a double asterisk indicates the significantly highest relative weight of all populations sampled that year based on Tukey's test ($P < 0.05$). In the case of two double asterisks for one year, there was no significant difference between the two highest lakes.

Diet

*Arctic char*

In Kijik Lake, the only lake with both arctic char and anadromous salmon, sockeye salmon eggs were an important food source for resident char in 2004 (Table 4). In June, snails were the main food item, but by September, stomach samples of 12 of 13 char contained only salmon eggs. In the other three lakes which contained arctic char (Portage, Kontrashibuna, and Tazimina) diet was dominated by snails and insects. Piscivory was documented in less than 1% (1 of 139) of all char sampled, and occurred only in a population without access to anadromous salmon (Tazimina). Food habits were similar to those reported by Russell (1980)

Table 4 - Percentages of arctic char stomachs containing specific prey items for lakes within Lake Clark National Park, Alaska.

| | | | Lake | | | | |
|---|---|---|---|---|---|---|---|
| Lake | n | Date | Salmon Eggs | Insects | Clams | Snails | Fish |
| Kijik | 27 | Jun-78 | | 48 | 44 | 92 | |
| | 11 | Jul-04 | | | 27 | 82 | |
| | 13 | Sep-04 | 92 | | 18 | | |
| Portage | 15 | Aug-78 | | 80 | | 20 | |
| | 21 | Jul-04 | | 10 | 52 | 57 | |
| Kontrash | 38 | Aug-78 | | 76 | 18 | 71 | |
| | 45 | Sep-04 | | 33 | 7 | 73 | |
| Tazimina | 35 | Sep-78 | | 34 | 17 | 20 | 8 |
| | 52 | Jul-04 | | 31 | | 63 | 2 |

### *Lake Trout*

Sockeye salmon fry were a food source for resident lake trout in varying degrees among the three populations sympatric with salmon (Table 5). In Kijik Lake, salmon fry were the only food item found in lake trout stomachs, with 11 of 12 (92%) of stomachs containing salmon fry. In Telaquana and Lake Clark, salmon fry were not as dominant of a food source. Only 27% of lake trout stomachs from Telaquana Lake contained salmon, and none of 21 from Little Lake Clark contained them. Contemporary food habits of lake trout varied slightly from those collected by Russell (1980) in degree of importance in some lakes, but historical data from Little Lake Clark and Telaquana were unavailable.

Table 5 - Percentages of lake trout stomachs containing specific prey items for lakes within Lake Clark National Park, Alaska.

| | | | Prey Item | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lake | n | Date | Sockeye Fry | Insects | Sculpin | Snails | Rodents | *Salvelinus spp.* | Least Cisco | Round Whitefish | Unidentified fish | Empty |
| Little Lake Clark | 25 | Aug-04 | | | 10 | | 10 | | | | 10 | 67 |
| Telaquana | 15 | Jul-04 | 27 | | | | | | 20 | 13 | 13 | |
| Kijik | 5 | Jun-78 | 40 | 60 | | | | | | | | |
| | 12 | Jul-04 | 92 | | | | | | | | | 8 |
| Portage | 23 | Aug-78 | | 34 | 26 | | | 4 | | | 26 | |
| | 32 | Jul-04 | | 25 | 28 | | | 35 | | | | |
| Kontrashibuna | 46 | Aug-78 | | 76 | 3 | | | | | | 39 | |
| | 47 | Sep-04 | | 47 | 45 | 17 | | | | | | |

# DISCUSSION

## Growth

### *Arctic char*

The failure to reject the null hypothesis that growth rates of char were the same in lakes without anadromous sockeye salmon as in lakes with them may indicate that (1) factors other than the presence of anadromous salmon exert stronger influences on char growth in lakes of LCNP, or (2) the data were inadequate to evaluate the hypotheses with an appropriate level of sensitivity. Although I was unable to assess which other factors may have influenced growth, one possible factor that deserves more inspection is predation by lake trout. In LCNP, some evidence was found that growth of arctic char was affected by the predation threat associated with lake trout. In Tazimina Lakes, where lake trout were absent, a dwarf population of arctic char exhibited slow growth rates, small maximum sizes, and low condition (Russell 1980). Dwarf fish were not found elsewhere. The slower growth of these char may enable them to reproduce earlier and more often (Klemetsen and Grotnes 1980). However, when lake trout are present, the benefit of early maturity may be outweighed by the risk of predation. In Portage Lake, which was the only lake in this, or Russell's (1980) study with documented cases of lake trout predation on arctic char, resident char had the highest asymptotic length and the largest fish captured. A length frequency histogram also showed a bimodal distribution of Portage Lake arctic char in both 1978-79 (Russell 1980) and 2004, indicating a shortage of intermediate sized (300-400 mm) arctic char from both time periods, possibly due to predation by lake trout (Figure 5). In this lake, selection may favor that char delay maturity in order to grow quickly and reach a size at which they are less susceptible to predation by lake trout.

The influence of predation on the growth of prey species has been documented elsewhere (Chase 1999). Reznick and Endler (1982) found that guppies *(Poecilia reticulata)* in the presence of the predator *(Rivulus hartii)* had higher growth rates than guppies allopatric from this predator. In the presence of *Rivulus*, which predominately fed on small, immature size classes, guppies delayed maturity and allocated more of their energy into growth. The benefit of this action was greater than the reproductive benefit associated with maturing earlier and remaining susceptible to predation. A similar phenomenon occurred in crucian carp *(Carassius carassius)* (Bronmark and Miner 1992). When sympatric with the predator, northern pike, crucian carp grew larger in body depth than when allopatric from pike. This increased growth enabled carp to reach a size at which they were no longer susceptible to predation. In this case, the increased survival was a trade-off for decreased swimming efficiency, as the deeper body increased drag. In addition, Fraser and Power (1989) recommend the stocking of lake trout into waters in which an increase of arctic char growth is desirable. The fact that arctic char have the most variable life history of all North American salmonids (Behnke 2002) increases the likelihood that a predator species could affect and alter growth rates. More investigations are needed on possible influences of predation on arctic char growth rate.

A second possibility for the failure to reject the null hypothesis on growth rates of arctic char was that the data collected in this study may have been inadequate to evaluate the hypotheses with an appropriate level of sensitivity. Cerrato (1990) stated that when comparing von Bertalanffy growth equations of different populations, sample sizes in excess of 300 measurements are sometimes necessary to produce adequate statistical sensitivity. The suggestion of Kritzer et al. (2001) was that samples consist of 7-10 fish per age-class, or about 100 fish. In order to accurately age arctic char, otoliths were needed, and in this study otolith sample sizes ranged from 19 to 42 per lake. Although it was impractical to collect 300 otoliths per lake; a larger sample size may have resulted narrower confidence intervals around estimated parameters.

The failure to reject the null hypothesis of no measurable differences in char condition between lakes containing anadromous salmon and lakes lacking them is inconsistent with several past studies which documented significant increases in weight and condition of resident salmonids as a result of consumption of anadromous Pacific salmon eggs and carcasses (Johnson and Ringler 1979; Wipfli et al. 2003). However, because resident char populations in LCNP historically had higher conditions when sympatric with anadromous sockeye salmon than when not sympatric, the decline of returning salmon may be exposing other factors which can influence resident char condition (Russell 1980). For example, a possibility not explored in this study is that when runs were higher in the past, competition with other species such as whitefish *(Coregonus spp, Prosopium spp.)* was masked due to the abundance of food provided by those salmon. As runs decline, competition would then increase. Bettoli et al. (1991) documented a similar phenomenon in Lake Conroe, Texas, between brook silversides (*Labidesthus sicculus)* and inland silversides *(Menidia beryllina)*. In many locations, inland silversides rapidly displace brook silversides, but in Lake Conroe the two species were able to co-exist because of extensive aquatic vegetation and the resulting high abundance in macroinvertebrate populations. When this abundant food source was removed however, inland silversides increased and brook silversides became rare.

Competition between whitefishes and char has been documented elsewhere. Dean (2004) presented a small niche size for arctic char in the presence of whitefish, while Johnson (1980) reviewed several studies in which whitefish populations harmed char populations. In Europe, when species of whitefish *(Coregonus spp.)* were introduced, char populations suffered greatly and were often eliminated from lakes (Nilsson and Pejler 1973; Svärdson 1976; Nilsson 1985).

In LCNP, distribution data collected by Russell (1980), suggests the possibility of competitive exclusion of arctic char by whitefish. Of the 25 lakes sampled in his study, char did not occur in any lakes containing humpback whitefish *(Coregonus pidschian)* or least cisco *(Coregonus sardinella)*. Additionally, char occurred in varying degrees in only five lakes with round whitefish (*Prosopium cylindraceum)*, but all of these lakes also received runs of anadromous salmon.

### *Lake trout*

The fact that growth rates of lake trout did not differ consistently between lakes with and without anadromous sockeye salmon was consistent with several other studies on lake trout growth. Trippel and Beamish (1989) found that lake trout reached larger sizes more quickly in lakes of high cisco *(Coregonus artedii)* abundance. Similarly, Scott and Crossman (1973) reported that ciscoes were the preferred natural food of adult lake trout in most populations and Matuszek et al. (1990) found that lake trout growth rates in Ontario increased after an introduction of ciscoes into a lake system. In LCNP, least ciscoes occur in large numbers in Telaquana and Lake Clark and have been documented as food items for resident lake trout in those lakes (Russell 1980). The larger size of many lake trout in those lakes may be related to the presence of least cisco. Additionally, lake size has been shown to influence lake trout growth potential in other studies. Shuter et al. (1998) found that lake trout populations from large lakes exhibit greater maximum sizes and greater ages than fish from smaller lakes. They attributed this larger growth to the greater species richness found in larger lakes, which provided a wider range of prey size. In LCNP, both species diversity and lake area were greatest in Lake Clark (19 species) and Telaquana (ten species). This, along with the abundance of the least cisco, may account for the higher numbers of large lake trout captured there.

The null hypothesis was rejected that condition of lake trout would be the same in all populations, regardless of the presence of sockeye salmon (Hypothesis 2). Kijik Lake, which had the highest conditioned lake trout, was the only lake sampled in which salmon fry were the sole food item. When lakes sampled in this study were compared with 58 other North American lake trout populations (Hubert et al. 1994), only Kijik Lake had a median $W_r$ above the 50th percentile (Figure 10). In the other two lakes which contained lake trout and received anadromous salmon runs (Little Lake Clark and Telaquana), sockeye salmon fry were not as significant a food source to resident lake trout, and median $W_r$ values were well below the fifth percentile of other North American populations. The higher density of sockeye salmon found in Kijik Lake seemed to provide intermediate-size lake trout with a higher condition. This could be critical within the oligotrophic lakes of LCNP, however it did not necessarily translate into larger fish, as no large lake trout were found in Kijik Lake. It has been shown elsewhere that large pelagic predators which continue to feed on smaller prey, no matter how abundant, significantly decrease their growth efficiency (Kerr 1971). Additionally, as lake trout grow larger, they require larger prey (Pazzia et al. 2002). After reaching a certain size, lake trout in Kijik Lake may migrate to Lake Clark in order to take advantage of the more diverse prey items found there.

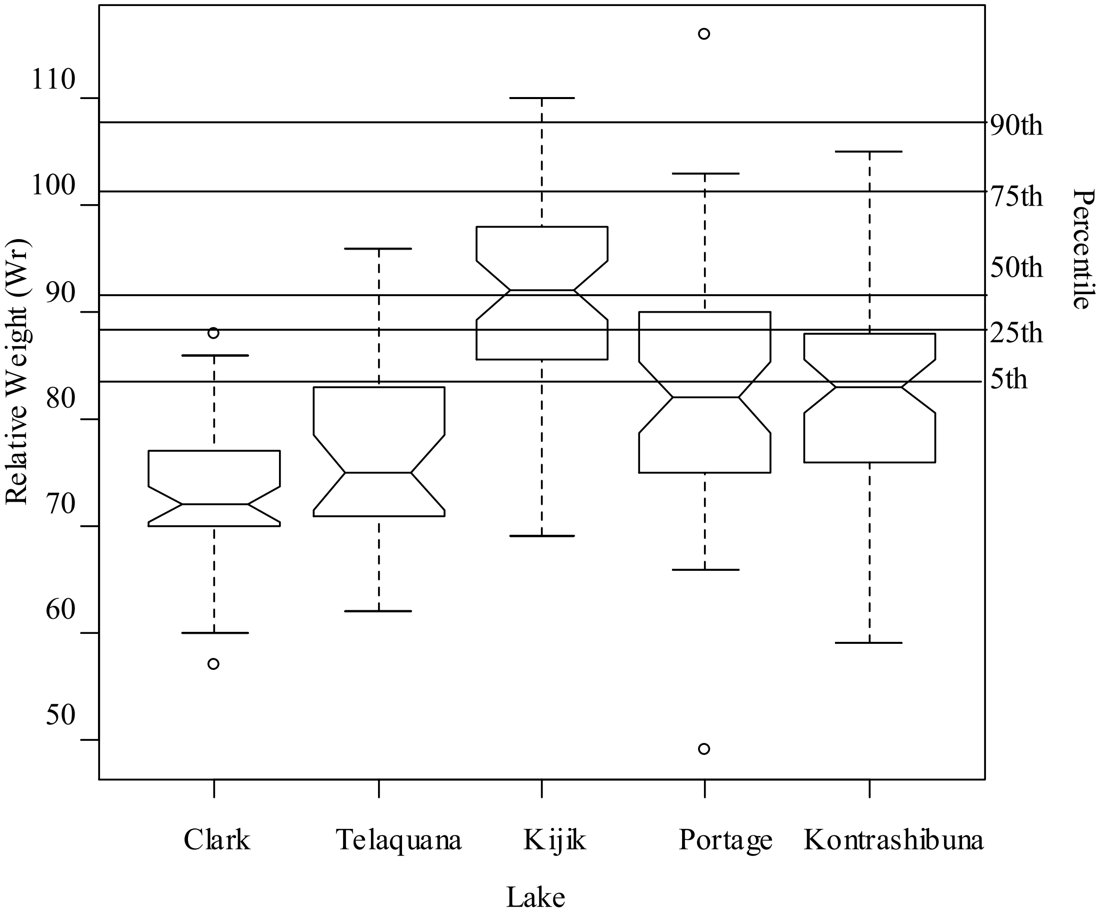

Figure 10 - Relative weight of lake trout in 2004 from LCNP showing percentiles from 58 North American populations of lake trout (Hubert et al. 1994).

One final aspect not thoroughly considered in this study is the effect of salmon declines on other resident fish species. More than fifteen species of fish inhabit Lake Clark, and most species are likely affected by the presence, absence, and abundance of anadromous salmon (Willson and Halupka 1995). In this study, a negative effect on another resident species, such as whitefish, could greatly influence both lake trout, which feed on whitefish (Russell 1980; Scott and Crossman 1974; Trippell and Beamish 1989), and arctic char, which compete with whitefish (Johnson 1980; Nilsson 1985; Dean 2004). This effect on a species may not only occur directly, as whitefish feed on salmon, but indirectly as well, as when whitefish feed on macroinvertebrates which feed on salmon carcasses (Chaloner and Wipfli 2002). Additionally, as the amount of salmon-borne nutrients continues to decline in systems with lower returns, plankton populations and quality habitat may decline for juvenile salmon which rear in these same lakes (Budy et al. 1998; Schmitt et al. 1998; Helfield and Naimen 2001). The result could be less fry surviving their first years, thus further decreasing the amount of salmon returning to the system and adding to the degradation of the cycle.

### *Recommendations*

This was the first study conducted on the arctic char and lake trout of LCNP in 25 years, and it raises many new questions regarding future research in the park. Specifically related to the importance of spawning sockeye salmon, several investigations would be useful. A more thorough dietary analysis involving stable isotope analysis (SIA) would compliment the results from this study, which provided a limited point-in-time "snapshot" of gut contents (Grey et al. 2002). An SIA would more accurately evaluate a resident species' diet over time and could also indicate the importance of sockeye salmon as a food item by determining concentrations of marine-derived nutrients in resident fish tissue. Other questions such as overlapping dietary niches of arctic char and whitefish, lake trout predation on arctic char, and the dwarf char of Tazimina Lakes could also be examined using SIA (Grey et al. 2002, McCarthy et al. 2004).

Resident fish migration is another aspect worth investigating. Because all bodies of water open to anadromous sockeye salmon migration are also open to resident fish migration, it is possible that resident arctic char and lake trout migrate to follow spawning salmon into different systems. Furthermore, the spawning dates of specific stocks of sockeye salmon within the park vary by greater than two months (Young 2004), and it is possible that resident fish may migrate between the spawning grounds of early and late spawners in order to take advantage of salmon eggs for an extended period of time.

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# **Chapter 2**:  Precision and Bias for Two Methods of Aging Arctic Char *(Salvelinus alpinus)* and Lake Trout *(Salvelinus namaycush)*

## ABSTRACT

The feasibility of aging arctic char (*Salvelinus alpinus*) and lake trout (S*alvelinus namaycush*) using otoliths and fin rays was investigated for six lake populations within Lake Clark National Park, Alaska (LCNP) in 2004. Precision and bias of age estimation were determined for the two species using both structures. For arctic char, fin rays produced a lower coefficient of variation (CV) and lower bias than otoliths, but resulted in lower age estimates 81% of the time. A significant difference in arctic char otolith readability was documented in one of four lakes, emphasizing the importance of assessing each technique prior to use. Otoliths from lake trout provided the lowest CV and bias of all structures analyzed, and fin rays did not produce interpretable results for lake trout. It is recommended that otoliths be used to age both species when possible; however, fin rays and other non-lethal methods should still be explored in particular situations where lethal sampling is not feasible.

## INTRODUCTION

Accurate and precise estimates of age are vital for reliable estimates of growth, mortality, and production of fish populations (Campana 2001). Age estimates in fish are obtained from a variety of anatomical structures including spines, vertebrae, scales, otoliths, fin rays, and cleithra (Jearld 1983). In the family Salmonidae, scales and otoliths are typically used to age fish (Nordeng 1961, Shuter et al. 1998); however, several other structures have also been used, including fin rays (Howland et al. 2004, Mills and Chalanchuck 2004), vertebrae (Sharp and Bernard 1988), branchiostegal rays (Bulkley 1960), and cleithra (Baker and Timmons 1991).

Otoliths have often been found to be more useful than scales in accurately determining ages of longer lived salmonids. Nordeng (1961) determined that in nearly half of his samples from northern Norway, scales underestimated arctic char ages, and he deemed them unsuitable. Casselman (1990) concluded that in slow-growing or old fish, otoliths grew more rapidly than the other calcified structures used for aging and continued to record cyclic seasonal growth and age. Studies on lake trout (*Salvelinus namaycush*), the longest lived salmonid (maximum age > 60 years), and arctic char (*Salvelinus alpinus*) (maximum recorded age, 33 years; Behnke 2002), have shown that more accurate estimation of both species is possible using otoliths rather than scales, particularly with older fish (Nordeng 1961, Martin and Olver 1980). Removal of otoliths is lethal however, whereas other sampling methods, such as scales and fin rays, are not. In situations where age information is required, but fish cannot be killed, effective alternatives to otoliths are needed.

Fin rays have been found to be useful for age determination in a variety of situations. Shirvell (1981) showed agreement between ages of brown trout (*Salmo trutta*) estimated from fin rays and length-frequencies, but cautioned against underestimating ages of older fish. He recommended that aging by fin ray be assessed in each situation prior to use. Chilton and Bilton (1986) found that fin rays provided accurate ages of adult Chinook salmon (*Oncorhynchus tshawytscha*), a short-lived fish (typically ≤ 6 years). Barber and McFarlane (1987) compared ages of arctic char estimated from otoliths and sectioned fin rays. They concluded that otoliths were more reliable, and recommended against using fin rays for age estimation North American arctic char. Campana (2001) however, showed that in studies spanning many species, the median coefficient of variation (CV) of fin ray estimates was lower (5%) than otolith estimates (7.6%). The range of CV among stocks was much wider with fin rays however, suggesting inconsistency among situations (i.e., species, location, etc.). Beamish and McFarlane (1995) found that for the long-lived species walleye pollock (*Theragra chalcogramma)*, the most appropriate method for age determination varied among stocks between otoliths and fin rays. Beamish and Chilton (1977) found well-defined annuli in lingcod fin rays up to 16 years old, and Howland et al. (2004) found no significant difference between fin ray and otolith age estimates of inconnu (*Stenodus leucichthys)* up to 33 years old.

Lake trout scales have also been deemed unsuitable for aging older fish (Sharp and Bernard 1988). Bulkley (1960) used branchiostegal rays as a non-lethal way to age lake trout, but only verified this method for fish less than five years old, while Shuter et al. (1998) referenced several studies which used fin rays for the aging of lake trout.

In this study, age estimates were needed from arctic char and lake trout in Lake Clark National Park, Alaska (LCNP). An evaluation was conducted to determine the feasibility of using a non-lethal aging method for these two long-lived salmonids. A lack of known age fish made assessment of accuracy (validation) impossible, however it was possible to assess the precision (reproducibility of given measurements) of the different methods, as well as bias (Campana 2001). Without a known-age reference collection, aging consistency is the best that can be achieved (Campana et al. 1995). Fin rays were chosen as the non-lethal method and age estimates from them were compared to the estimates obtained from otoliths, the more commonly used structure. The objective of this study was to determine the precision and bias of age estimates based on otoliths and fin rays for arctic char and lake trout.

## METHODS

Sampling was conducted in six lakes within LCNP during the summer of 2004. Four of these lakes (Kijik, Kontrashibuna, Portage, and Tazimina) contained arctic char and five lakes contained lake trout (Kijik, Kontrashibuna, Little Lake Clark, Portage, and Telaquana). Primary sampling gears were floating and sinking variable mesh gill nets. Hook and line sampling was also used. Total length (TL) and weight, as well as pectoral fin rays were collected from all lake trout and arctic char captured. On fish which were killed during the collection process, otoliths were removed. In all, 193 arctic char were captured and sampled for fin rays, with 121 sacrificed for otoliths; and 278 lake trout were captured and sampled for fin rays, with 157 sacrificed for otoliths. Total sample sizes are broken down by lake in Table 1.

Table 1- Sample sizes by lakes of arctic char and lake trout captured in Lake Clark National Park, Alaska.

| | Arctic Char | | Lake Trout | |
|---|---|---|---|---|
| Lake | Fin Rays | Otoliths | Fin Rays | Otoliths |
| Little Lake Clark | 2 | 0 | 46 | 25 |
| Telaquana | 0 | 0 | 51 | 32 |
| Kijik | 34 | 21 | 60 | 27 |
| Portage | 51 | 19 | 53 | 31 |
| Kontrashibuna | 50 | 40 | 68 | 42 |
| Tazimina | 56 | 41 | 0 | 0 |

Otoliths were mounted on microscope slide-sized transparent plastic with a plastic casting resin. Each otolith was examined by the primary reader and if clearly defined annual rings and evidence of light transmission were observed from the edge of the otolith to the nucleus, the intact otolith was interpreted for age. Most otoliths, especially those of arctic char, were too opaque near the nucleus to accurately interpret. In these cases, otoliths were ground on a rock grinding/polishing machine until annuli near the nucleus were easily detectable. Two readers independently interpreted the age of each whole or ground otolith.

Pectoral fin rays were collected and stored dry. Fins were mounted length-wise on labeled wooden craft sticks with epoxy and allowed to dry for 24 hours. After drying, the fins were sectioned using a Buehler Isomet low-speed saw with diamond-edged blades, at thicknesses of 1.0, 1.02, 1.04 and 1.06 mm and mounted on slides with clear nail polish. Two readers independently interpreted the age of each fin ray.

Because we had no fish of known age in this study, we were unable to verify the accuracy of our age estimates; however verifying reader bias and precision were possible. Bias and precision were exhibited in age frequency tables, and via the coefficient of variation (CV) (Campana et al. 1995). Because stock-specific differences in readability can occur (Beamish and McFarlane 1995), bias and variation were compared between lakes as well. An age frequency table plots one reader's estimated ages against the other reader's estimates using numbers to depict the number of fish estimated to be a specific age. They were used to visually inspect reader bias. The coefficient of variation equation was expressed as a ratio of the standard deviation to the mean for an individual fish and is averaged across a population to produce a mean CV (Campana 2001). A higher CV represents a greater difference in estimates by the two readers. A 5% CV is a typical target value; Campana (2001) showed a median value of 7.6% in a review of 117 aging studies. Overall CV, as well as stock-specific CV was compared between methods and between the two readers using Mann-Whitney test (Conover 1980).

# RESULTS

## Otoliths

### *Arctic Char*

Overall estimates of arctic char ages using otoliths ranged from three to fourteen years with a mean age of 8.7 for reader one, and from four to sixteen years with an average of 9.6 for reader 2. The mean difference of 0.818 years between readers was significant (t-test; $P < 0.01$) however, and CV between readers was relatively high (12%). Some bias between readers was evident; reader one generally estimated lower ages across all fish sizes (Table 2).

When analyzed as separate populations, a significant difference in bias was detected in Portage Lake, compared with the other lakes (Table 3). The CV of this population (17%) was also significantly higher (Mann-Whitney test) than two other populations, Kijik: 12%; $P = 0.04$, and Kontrashibuna: 10%; $P = 0.05$, but not Tazimina: 12%; $P = 0.06$. Because excluding the Portage Lake population from the total pooled population resulted in only a non-significant reduction in overall CV from 12% to 11% (Mann-Whitney test; $P = 0.47$), it was retained in the analysis.

Table 2 - Age frequency table of otolith readings from four populations of arctic char in Lake Clark National Park, Alaska.

| | Reader 2 Age | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Reader 1 Age | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| 3 | | 1 | | | | | | | | | | | | |
| 4 | | 1 | 3 | 3 | | | | | | | | | | |
| 5 | | | 3 | 3 | 1 | 1 | | | | | | | | |
| 6 | | | | 2 | 2 | 3 | 1 | | | | | | | |
| 7 | | | 1 | 3 | 1 | 4 | 3 | 1 | 2 | | | | | |
| 8 | | | | | | 5 | 9 | 4 | 2 | 1 | | | | |
| 9 | | | | | 2 | 3 | 2 | 1 | 3 | 5 | | | | |
| 10 | | | | | 1 | 2 | 3 | 8 | 7 | 3 | 2 | | 1 | |
| 11 | | | | | | | 3 | 3 | 2 | 3 | | | 2 | 1 |
| 12 | | | | | | | | 1 | 4 | 1 | | | 1 | |
| 13 | | | | | | | | 1 | | | | 1 | 1 | |
| 14 | | | | | | | | | 2 | | | 1 | | |
| 15 | | | | | | | | | | | | | | |

Table 3 - Stock-specific age frequency table of otolith estimates from four populations of arctic char in LCNP.

Reader 1 Age (rows) × Reader 2 Age (columns)

| Kijik | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | | | | | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | |
| 13 | | | | | | | | | | | | | | 1 |
| 12 | | | | | | | | | | 1 | | | | |
| 11 | | | | | | | | | 1 | | | | | |
| 10 | | | | | | | | 1 | | 2 | | 1 | | |
| 9 | | | | | | 1 | 1 | | | 1 | 2 | | | |
| 8 | | | | | | | 2 | 1 | | | 1 | | | |
| 7 | | | | | 1 | | 1 | 1 | | | | | | |
| 6 | | | | | 1 | | 2 | | | | | | | |
| 5 | | | | | | | | | | | | | | |
| 4 | | | | | | | | | | | | | | |
| 3 | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | |

| Portage | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | | | | | | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | | |
| 13 | | | | | | | | | | | | | 1 | | |
| 12 | | | | | | | | | | | | | | 1 | |
| 11 | | | | | | | | | | | 2 | | | 2 | 1 |
| 10 | | | | | | | | | | 1 | | | | | |
| 9 | | | | | | | | | | | | | | | |
| 8 | | | | | | | | | | | | | | | |
| 7 | | | | | | | | 1 | 1 | 1 | | | | | |
| 6 | | | | | | 1 | | | | | | | | | |
| 5 | | | | | | 1 | | | | | | | | | |
| 4 | | | 1 | 2 | 2 | | | | | | | | | | |
| 3 | | | 1 | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | | |

| Kontrashibuna | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | | | | | | | | | | | | | | |
| 14 | | | | | | | | | 1 | 2 | | | 1 | |
| 13 | | | | | | | | | | | | | | |
| 12 | | | | | | | | | | 3 | | | | |
| 11 | | | | | | | | 2 | 2 | 1 | 1 | | | |
| 10 | | | | | | 1 | 1 | 1 | 6 | 2 | 2 | | | |
| 9 | | | | | | | 1 | 1 | | 1 | 1 | | | |
| 8 | | | | | | | | 2 | | | | | | |
| 7 | | | | | 1 | 1 | 2 | 1 | | 1 | | | | |
| 6 | | | | | 1 | | | | | | | | | |
| 5 | | | | | 2 | | | | | | | | | |
| 4 | | | | 1 | | | | | | | | | | |
| 3 | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | |

| Tazimina | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 | | | | | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | |
| 13 | | | | | | | | | | | | | | |
| 12 | | | | | | | | | 1 | | 1 | | | |
| 11 | | | | | | | | 1 | | 1 | | | | |
| 10 | | | | | | | 1 | 1 | 2 | 2 | 1 | 1 | | 1 |
| 9 | | | | | | | 1 | 1 | 1 | 1 | 2 | | | |
| 8 | | | | | | | 3 | 6 | 4 | 2 | | | | |
| 7 | | | | 1 | | | 1 | | | | | | | |
| 6 | | | | | 1 | 1 | 1 | 1 | | | | | | |
| 5 | | | | | 1 | | 1 | | | | | | | |
| 4 | | | | | 1 | | | | | | | | | |
| 3 | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | |

Reader 2 Age

### *Lake Trout*

For lake trout, age estimates from otoliths ranged from five to thirty-one years old with an average of 14.7 for reader one, and six to thirty years old with an average of 15.1 for reader two. The mean difference of 0.325 years between readers was not significant (t-test; $P > 0.25$). Bias was low across size classes, but generally showed a lower age estimate from reader one (Table 4).

Stock-specific differences in bias were not detected across populations of lake trout in LCNP (Table 5). Coefficient of variation values were as follows: Portage: 5.6%; Little Lake Clark: 5.8%; Kijik: 6.3%; Telaquana: 8.1%; Kontrashibuna: 9.1%, with a mean of 7.3%. These differences in CV between populations were not significant (Mann-Whitney test; $P > 0.17$).

Table 4 - Age frequency table of otolith readings from five populations of lake trout in Lake Clark National Park, Alaska.

| | Reader 2 Age | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Reader 1 Age | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5 | | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | |
| 6 | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | |
| 7 | | | | 1 | 2 | 1 | 1 | | 1 | | 1 | | | | | | | | | | | | | | | | | |
| 8 | | | | | | 5 | 1 | 2 | 1 | | | | | | | | | | | | | | | | | | | |
| 9 | | | | | | | | | 3 | | | | | 1 | | | | | | | | | | | | | | |
| 10 | | | | | | | | 2 | 2 | 1 | 2 | 1 | 1 | | | | | | | | | | | | | | | |
| 11 | | | | | | | | | 5 | 2 | 2 | | | | | | | | | | | | | | | | | |
| 12 | | | | | | | | 1 | | 3 | 5 | 1 | 3 | | | | | | | | | | | | | | | |
| 13 | | | | | | | | | | 2 | 1 | | | | 1 | | | | | | | | | | | | | |
| 14 | | | | | | | 1 | | | 1 | 2 | 5 | 4 | 3 | 1 | | | | | | | | | | | | | |
| 15 | | | | | | | | | | | 3 | 1 | 2 | 1 | 3 | | | | | | | | | | | | | |
| 16 | | | | | | | | | | | 1 | 1 | 3 | 2 | 4 | 2 | | | | | | | | | | | | |
| 17 | | | | | | | | | | | | | 1 | 2 | 4 | 2 | | 1 | | | | | | | | | | |
| 18 | | | | | | | | | | | | | | 1 | 1 | 4 | 1 | 1 | | | | | | | | | | |
| 19 | | | | | | | | | | | 1 | | 1 | | 1 | 1 | 7 | 1 | | 1 | | | | | | | | |
| 20 | | | | | | | | | | | | | | | 2 | 1 | 3 | 2 | | | 1 | 1 | | | | | | |
| 21 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 22 | | | | | | | | | | | | | | | | | | | 2 | | | | | | | | | |
| 23 | | | | | | | | | | | | | | | | 1 | 1 | | | | | | | | | | | |
| 24 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| 25 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| 26 | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | 1 | | | |
| 27 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 28 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 29 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 30 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| 31 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |

Table 5 – Stock-specific age bias plots of estimates obtained from lake trout otoliths in LCNP (continued onto next page).

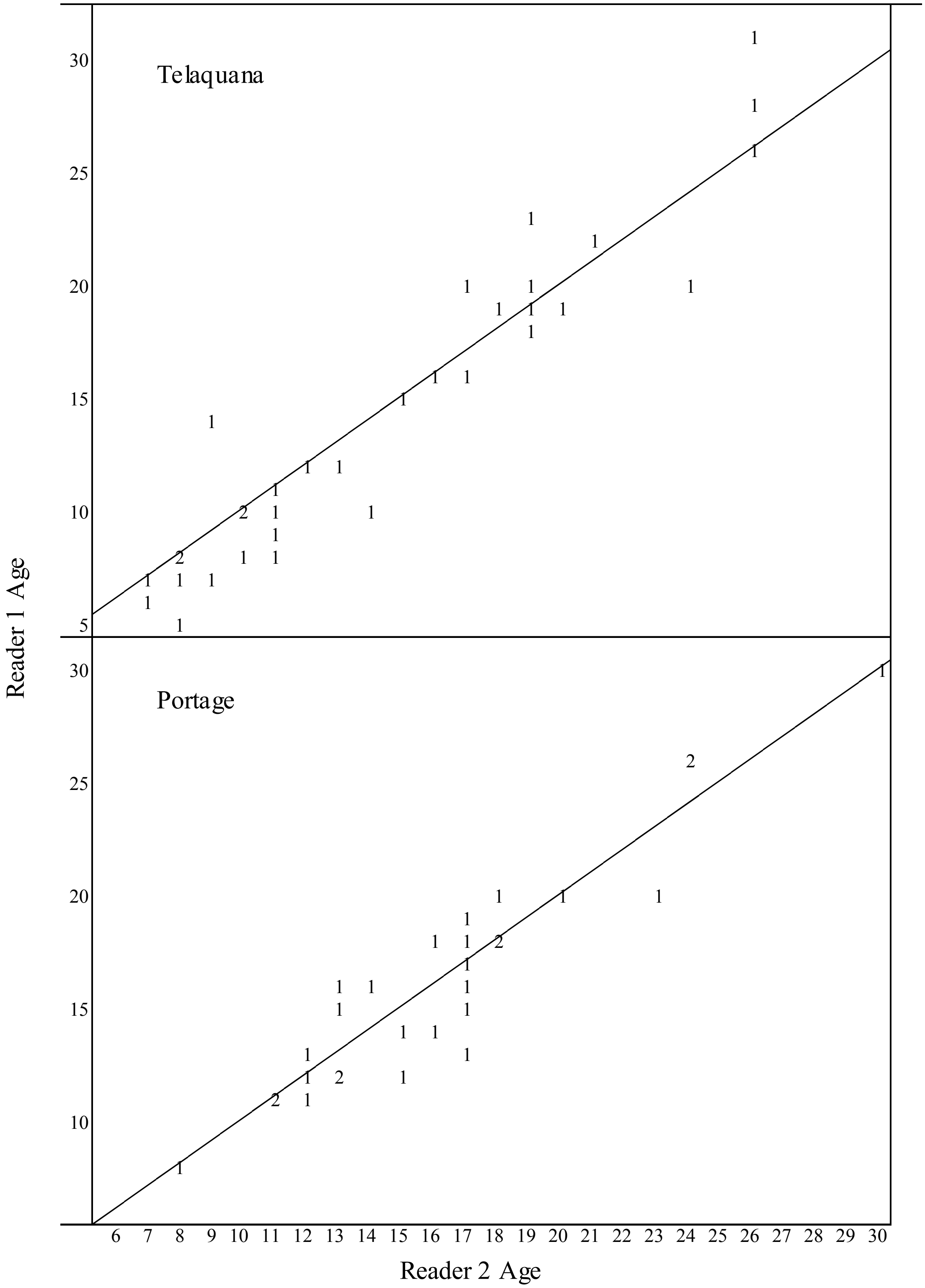
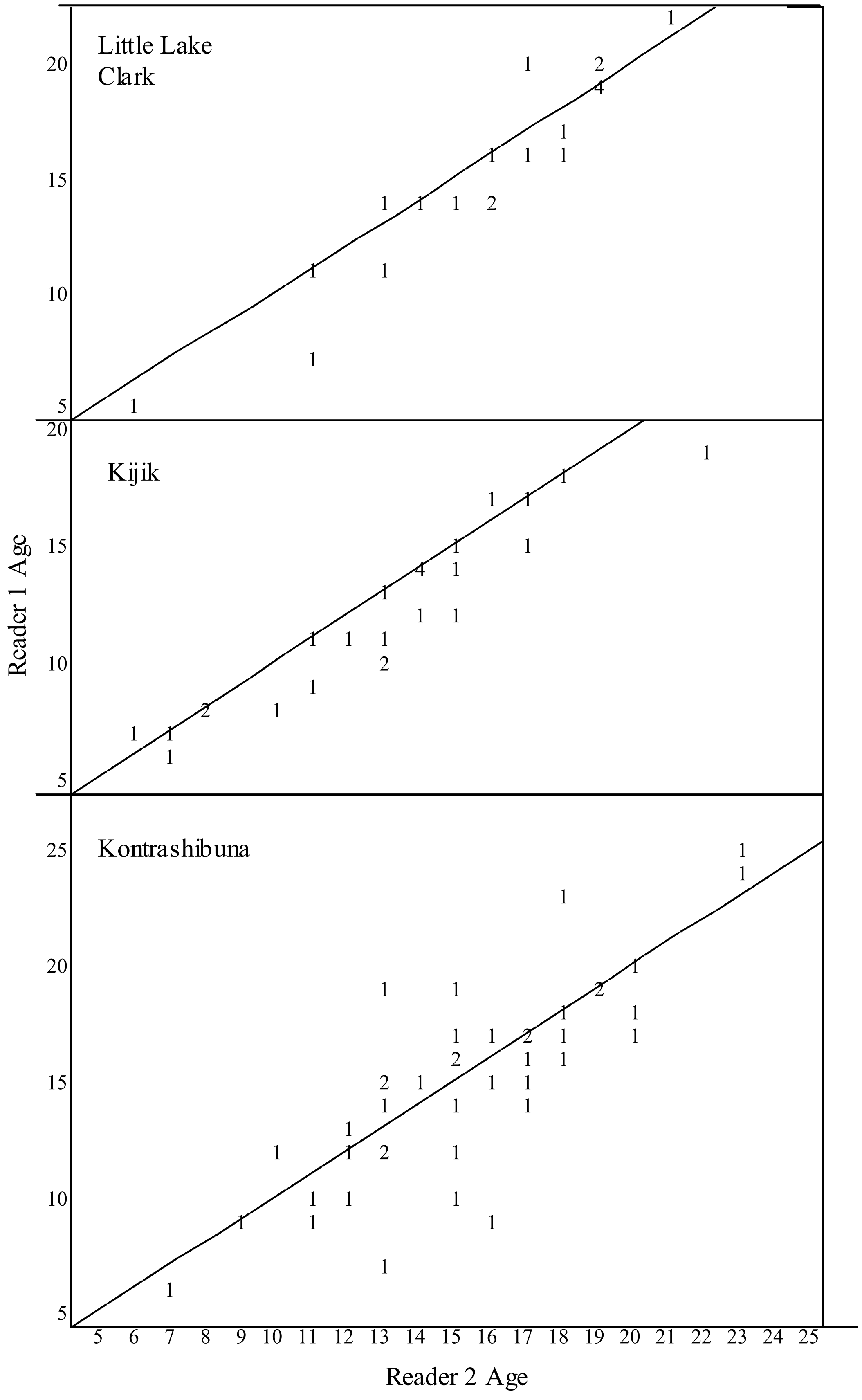


Table 5 (cont.)


Little Lake Clark
Kijik
Kontrashibuna
Reader 1 Age
Reader 2 Age
5
10
15
20
25
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

## Fin Rays

### *Arctic Char*

For arctic char, age estimates from fin rays ranged from three to twelve years old with an average of 6.7 for reader one, and two to eleven years old with an average of 6.2 for reader two. The mean difference of 0.48 years between readers was not significant (t-test; P > 0.10). Overall CV between readers using fin rays was 10%. Bias was low between readers; with reader one generally estimating lower than reader two (Table 6).

Stock-specific differences in the readability of arctic char fin rays were not apparent. Bias was similar in the three lakes, and individual population CV values did not differ significantly from the overall CV (Kontrashibuna: 9%; Tazimina: 10%; Kijik: 11%) (Mann-Whitney Test; P > 0.60) (Table 7).

Table 6 - Age frequency table of pectoral fin ray readings of arctic char in LCNP.

| | Reader 2 Age | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Reader 1 Age | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| 1 | | | | | | | | | | | |
| 2 | | 1 | | | | | | | | | |
| 3 | | | 8 | 1 | | | | | | | |
| 4 | | 1 | 5 | 5 | 1 | 1 | | | | | |
| 5 | | | | 6 | 2 | 2 | | | | | |
| 6 | | | | 2 | 7 | 6 | 5 | 1 | | | |
| 7 | | | | | 1 | 4 | 4 | 2 | | 1 | |
| 8 | | | | | | 4 | 10 | 5 | 3 | | |
| 9 | | | | | | | 3 | 4 | 5 | 1 | |
| 10 | | | | | 1 | | 2 | | | 3 | 1 |
| 11 | | | | | | | 1 | | | | 1 |
| 12 | | | | | | | | | | 1 | 1 |

Table 7- Stock-specific age frequency table for estimates obtained from arctic char fin rays.

| Reader 1 Age | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kijik | 12 | | | | | | | | | | 1 | |
| | 11 | | | | | | 1 | | | | 1 | |
| | 10 | | | | | | 1 | | | | | |
| | 9 | | | | | | 1 | 1 | 4 | 1 | | |
| | 8 | | | | | 1 | 4 | 2 | | | | |
| | 7 | | | | | 1 | | 1 | | | | |
| | 6 | | | 2 | 1 | | 2 | | | | | |
| | 5 | | | 1 | | | | | | | | |
| | 4 | 1 | 1 | 1 | | 1 | | | | | | |
| | 3 | | 3 | | | | | | | | | |
| | 2 | | | | | | | | | | | |
| Kontrashibuna | 12 | | | | | | | | | 1 | | |
| | 11 | | | | | | | | | | | |
| | 10 | | | | | | 1 | | | 2 | 1 | |
| | 9 | | | | | | 2 | 3 | 1 | | | |
| | 8 | | | | | 3 | 2 | 1 | | | | |
| | 7 | | | | | 2 | 3 | | | 1 | | |
| | 6 | | | | 6 | 4 | 1 | 1 | | | | |
| | 5 | | | 4 | | | | | | | | |
| | 4 | | 2 | 4 | | | | | | | | |
| | 3 | | 4 | | | | | | | | | |
| | 2 | 1 | | | | | | | | | | |
| Tazimina | 12 | | | | | | | | | | | |
| | 11 | | | | | | | | | | | |
| | 10 | | | | 1 | | | | | 1 | | |
| | 9 | | | | | | | | | | | |
| | 8 | | | | | | 4 | 2 | 2 | | | |
| | 7 | | | | 1 | 1 | 1 | 1 | | | | |
| | 6 | | | | 1 | 2 | 2 | | | | | |
| | 5 | | | | 1 | 2 | | | | | | |
| | 4 | | 2 | | 1 | | | | | | | |
| | 3 | | 1 | 1 | | | | | | | | |
| | 2 | | | | | | | | | | | |

Reader 2 Age

### *Lake Trout*

Lake trout fin rays did not show clearly defined annuli or produce interpretable results. In most instances, annuli were tightly and irregularly spaced, and difficult to distinguish (Figure 1). Apparent annuli were typically much more numerous in corresponding otoliths than in fin rays.

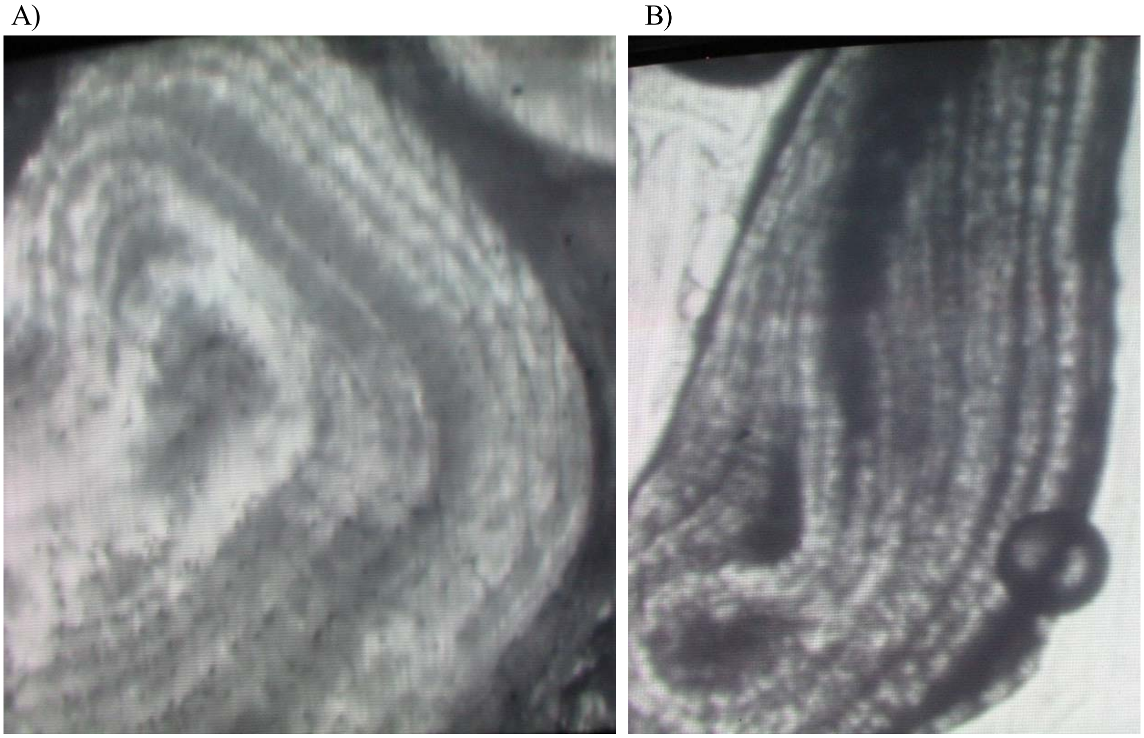


Figure 1 - Sectioned pectoral fin rays from two lake trout in LCNP. Age estimates for the same fish using otoliths were: A) Age-18, and B) Age-30.

## Fin Rays vs. Otoliths

### *Arctic Char*

In char, fin ray age estimates had a CV of 10%, and otoliths had a CV of 12%, a difference that was not statistically significant (Mann-Whitney test; P = 0.83). Otoliths typically showed more apparent annuli than fin rays (Figure 2). Age estimates from otoliths averaged 2.05 years higher than fin rays for reader one and 3.04 years higher for reader two. Both differences were highly significant (t-test; P < 0.0001). Because of these significant differences in estimates, the CV between otolith and fin ray estimates from the same fish was high: 22% for reader one and 30% for reader two.

Variation was high in both bias and CV for both fin rays and otolith estimates among populations. Otoliths provided consistently higher estimates of ages than did fin rays in all populations regardless of the reader (Table 8). The CV of reader two's estimates were not significantly different among the three populations compared (Kijik: 26%; Tazimina: 28%; Kontrashibuna: 33%) (Mann-Whitney test; P > 0.08). However, the CV of reader one's estimates showed significantly more variability (Tazimina: 14%; Kijik: 19%; Kontrashibuna: 28%), with a significant difference occurring between Kontrashibuna and both of the other lakes (Mann-Whitney test; Kijik: P = 0.015, Tazimina: P < 0.001). The difference between Tazimina and Kijik was not significant (Mann-Whitney test; P = 0.33).

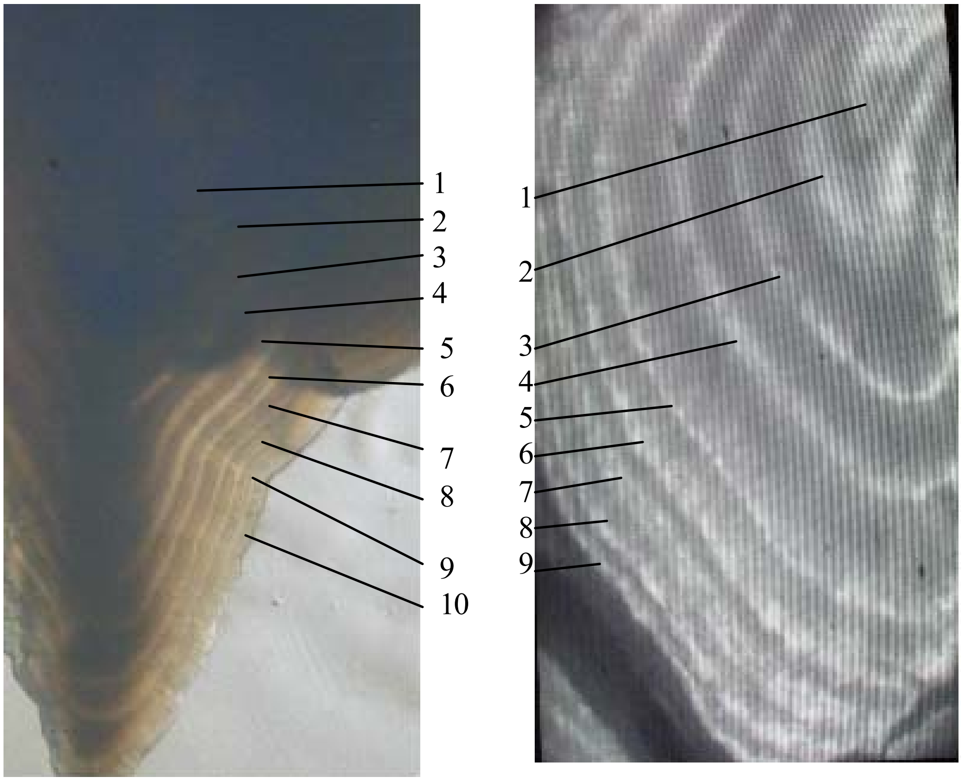


Figure 2 - An otolith and a pectoral fin ray from the same arctic char showing an estimated ten annuli in the otolith, and nine in the fin ray.

Table 8 - Stock-specific age frequency table comparing both reader estimates between corresponding otoliths and fin rays from arctic char in LCNP.

| Otolith Age | Reader 1 | | | | | | | | | | | Reader 2 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fin Ray Age | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | Kijik | | | | | | | | | | | Kijik | | | | | | | | | | |
| 15 | | | | | | | | | | | | | | | | | 1 | | | | | |
| 14 | | | | | | | | | | | | | | | | | | | | | | |
| 13 | | | | | | | 1 | | | | | | | | | | 1 | | | | | |
| 12 | | | | | | | | 1 | | | | | | | | | | 1 | 2 | | | |
| 11 | | | | | | | 1 | | | | | | | | | | 1 | 1 | 1 | | 1 | |
| 10 | | | | | | 1 | 1 | 1 | | | 1 | | | | | | | | 1 | | | |
| 9 | | | | | | | 2 | 2 | | 1 | | | | 1 | | 1 | | 1 | | | 1 | |
| 8 | | | 1 | 1 | | 1 | | 1 | | | | | 1 | 1 | | 1 | 2 | | 1 | | | |
| 7 | | | 1 | | | | 1 | | | | | | | | | | | 1 | | | | |
| 6 | | 1 | 1 | | | | 1 | | | | | 1 | | | | 1 | | | | | | |
| 5 | | | | | | | | | | | | | | | | | | | | | | |
| 4 | | | | | | | | | | | | | | | | | | | | | | |
| 3 | | | | | | | | | | | | | | | | | | | | | | |
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## DISCUSSION

### *Arctic Char*

The lower CV of fin rays versus otoliths, as well as the more consistent mean age between readers demonstrated more precise results using this method. However, it was not possible to verify the accuracy of our estimates, and arctic char otoliths in this study showed more apparent annuli 81% of the time. Other studies have shown that in slow-growing or old fish, while the growth of scales and other structures may virtually cease, otoliths continue to grow at a steady rate and record cyclic seasonal growth and age (Nordeng 1961, Casselman 1990). Because fin rays produced lower estimates consistently, it is likely that this is occurring here. It is possible that fin rays in this study produced ‘precisely wrong’, or more easily duplicated but inaccurate age estimates (Campana 2001). Otoliths have been previously recommended for use in arctic char of other systems (Nordeng 1961, Barber and McFarlane 1987). Based on these results, it is not recommended that fin rays be used to age arctic char of any age in LCNP.

In this study, one of four (25%) arctic char populations sampled had a significantly higher CV and visual bias using otoliths, suggesting a stock-specific difference in readability. Arctic char have some of the most variable life histories of all North American salmonids (Behnke 2002), and it should not be assumed that all populations will be aged similarly. Because of this variability, fin rays should remain a consideration for situations in which lethal sampling is not possible. While fin rays in this study may not have provided accurate results, they may in some other situations, as has been the case for several other species (Beamish and McFarlane 1995, Howland et al. 2004).

### *Lake Trout*

Based on this study, otoliths were a suitable method for use in the estimation of lake trout ages. Two readers were able to achieve a similar mean age and consistently low bias over 155 samples. In addition, the CV between readers was lower than Campana's (2001) median value of 7.3%, with two individual populations displaying a CV of less than 6%. These characteristics demonstrate a high precision with this method; and with the lack of known age fish, high precision is the best that can be obtained.

Although fin rays did not provide interpretable results for lake trout in this study, they should not necessarily be deemed unacceptable for all studies. Beamish and McFarlane (1995), for example, found that for the long-lived species walleye pollock (*Theragra chalcogramma)* (> 30 years), the most appropriate method of age determination varied among stocks between otoliths and fin rays. Lake trout in LCNP are slow-growing relative to many North American populations. It is possible that fin rays from a faster-growing population may produce annuli which are more widely spaced and easier to distinguish. In situations where known age fish exist, more rapid growth occurs, and/or lethal sampling is not desirable, a similar study could be conducted and a more definitive conclusion drawn regarding the usefulness of lake trout fin rays for age determination.

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