Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*)

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Abstract: In the family Salmonidae, lake trout (*Salvelinus namaycush*) are considered the least tolerant of salt water. There are, however, sporadic reports of lake trout in coastal, brackish habitats in the Canadian Arctic. Otolith microchemistry analyses conducted on lake trout and Arctic char (*Salvelinus alpinus*) from four Arctic lakes in the West Kitikmeot region of Nunavut, Canada, revealed that 37 of 135 (27%) lake trout made annual marine migrations. Anadromous lake trout were in significantly better condition (K = 1.17) and had significantly higher C:N ratios (3.71) than resident lake trout (K = 1.05 and C:N = 3.34). Anadromous lake trout also had significantly higher δ^{15}N (mean = 16.4‰), δ^{13}C (mean = –22.3‰), and δ^{34}S (mean = 13.43‰) isotope ratios than resident lake trout (means = 12.84‰, –26.21‰, and 1.93‰ for δ^{15}N, δ^{13}C, and δ^{34}S, respectively); results were similar for Arctic char and agree with results from previous studies. Mean age of first migration for lake trout was 13 years, which was significantly older than that for Arctic char (5 years). This could be a reflection of size-dependent salinity tolerance in lake trout, but further research is required. These are the first detailed scientific data documenting anadromy in lake trout.

Résumé : Dans la famille des Salmonidae, ce sont les touladis (*Salvelinus namaycush*) qui sont considérés les moins tolérants à l'eau salée. On signale néanmoins de temps à autre la présence de touladis dans les habitats côtiers et saumâtres de l'Arctique canadien. Des analyses microchimiques des otolithes faites sur des touladis et des ombles chevaliers (*Salvelinus alpinus*) de quatre lacs arctiques dans la région du Kitikmeot occidental au Nunavut, Canada, montrent que 37 de 135 (27 %) touladis avaient fait des migrations annuelles en mer. Les touladis anadromes sont en significativement meilleure condition (K = 1,17) et possèdent un rapport C:N (3,71) relativement plus élevé que les touladis résidants (K = 1,05 et C:N = 3,34). Les touladis anadromes ont aussi des rapports d'isotopes δ^{15}N (moyenne = 16,4 ‰), δ^{13}C (moyenne = –22,3 ‰) et δ^{34}S (moyenne = 13,43 ‰) plus élevés que ceux des touladis résidants (moyennes de 12,84 ‰, –26,21 ‰ et 1,93 ‰ pour respectivement δ^{15}N, δ^{13}C et δ^{34}S); les résultats sont semblables chez les ombles chevaliers et concordent avec ceux des études antérieures. L'âge moyen de la première migration chez le touladi est de 13 ans, ce qui est significativement plus tard que chez l'omble chevalier (5 ans). Cela pourrait refléter une tolérance à la salinité reliée à la taille chez le touladi, mais il faut des recherches supplémentaires sur le sujet. Nos résultats représentent les premières données scientifiques détaillées sur l'anadromie chez le touladi.

[Traduit par la Rédaction]

Introduction

Although lake trout (*Salvelinus namaycush*) are commonly thought to be restricted to freshwater habitats, there are sporadic records of this species inhabiting brackish, coastal environments in the Canadian Arctic during summer months (reviewed in Martin and Olver 1980). Walters (1953) reported that members of the Canadian Arctic Expedition (1913–1918) found lake trout in river mouths around Coronation Gulf. Lake trout have also been caught in brackish coastal areas on Banks Island (Manning 1953), at the head of tidewater in the Nanek River, Bristol Bay, Alaska (Rounsefell 1958), and along the coast of Labrador (Weed 1934; Dunbar and Hildebrande 1952). In a review of zoogeography of lake trout, Lindsey (1964) points out that this species must have crossed seawater to reach lakes on King William Island, because it has risen since the last glaciation. They must have also crossed seawater (albeit likely low-

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salinity seawater) to reach Banks, Victoria, Southampton, and other islands in the Canadian Arctic archipelago. In a study of field observations, Boulva and Simard (1968) reported that lake trout were commonly found in Arctic waters between 6‰ and 9‰ salinity. Despite this history of field observations, virtually no research has been conducted on the ecology and life history of lake trout that may inhabit coastal and brackish waters in the Canadian Arctic.

In support of historical field observations, a recent physiological study showed that lake trout were capable of surviving direct and gradual transfers to full-strength seawater (30‰; Hiroi and McCormick 2007). Although concentrations of plasma ions and cortisol rose dramatically in lake trout that were transferred to full-strength seawater, Hiroi and McCormick (2007) concluded that lake trout retain some of the osmoregulatory capacity exhibited by anadromous or partially anadromous salmonid species such as the congeneric Arctic char (*Salvelinus alpinus*) and brook trout (*Salvelinus fontinalis*). Consistent with the observations of Boulva and Simard (1968), their results also indicate that lake trout should be able to survive for relatively long periods of time at salinities of 6‰–9‰.

Fishes with the capacity for anadromy will migrate if the benefits of marine migrations outweigh costs (Gross 1987; Jonsson and Jonsson 1993). In northern Canada, benefits of marine migrations likely include increased food availability, increased potential for growth, decreased intraspecific competition, and parasite shedding. Costs likely include increased risk of mortality, energy expenditure during migration, and osmoregulatory stress (Northcote 1978; Gross 1987; Radtke et al. 1996). Previous research has shown that anadromous Arctic char in the Canadian Arctic tend to be longer, heavier, and more fecund than their resident counterparts (Johnson 1980, 1989). With the new knowledge that lake trout have some ability to osmoregulate in seawater (Hiroi and McCormick 2007), it does seem possible that where freshwater productivity is very low (e.g., at the extreme northern end of their range), the benefits of anadromy may outweight costs, result in increased fitness for anadromous individuals, and facilitate the adoption of a partially anadromous life history strategy in lake trout.

Our ability to detect anadromy has advanced considerably in recent years. Stable isotope analyses and otolith microchemistry are now routinely used to differentiate between anadromous and resident fishes. Ratios of stable carbon (C; $\delta^{13}C$), nitrogen (N; $\delta^{15}N$), and sulfur (S; $\delta^{34}S$) isotopes are elevated in marine food sources relative to freshwater food sources and thus have been successfully used to differentiate between resident and anadromous Arctic char and brook trout (Doucett et al. 1999*a*, 1999*b*; Swanson and Kidd 2009). Otoliths from anadromous fishes typically show large annual oscillations in strontium (Sr) that reflect summer feeding migrations to marine environments, whereas otoliths from resident fishes show low, relatively flat Sr profiles (e.g., Radtke et al. 1996; Babaluk et al. 1997; Howland et al. 2001). A recent experiment conducted on several salmonid species (*Oncorhynchus* and *Salvelinus* spp.) validated the relationship between salinity and otolith Sr concentration; Zimmerman (2005) found that Sr concentrations in otoliths could be used to differentiate among fresh, brackish, and marine habitat use by salmonids.

Studies conducted as part of an environmental impact statement in a coastal region of Nunavut, Canada, reported both downstream and upstream movements of lake trout in association with movements of anadromous Arctic char (Miramar Hope Bay Ltd. 2005). Lake trout were also captured in nearby marine environments, and the stomach contents of some contained marine prey items such as capelin (*Mallotus villosus*) (Miramar Hope Bay Ltd. 2005). To further investigate the use of marine environments by lake trout and compare it with the well-known anadromous behaviour in Arctic char, we collected lake trout and Arctic char from several lakes and outflows located on the mainland central Canadian Arctic coast. All lakes were connected to the sea by passable streams. The objectives of this study were to (*i*) confirm the use of marine environments by lake trout using otolith microchemistry and stable isotope analysis, (*ii*) determine age and size of first migration and frequency of migrations in migratory lake trout and compare with anadromous Arctic char, and (*iii*) compare growth and condition between migratory and resident Arctic char and lake trout.

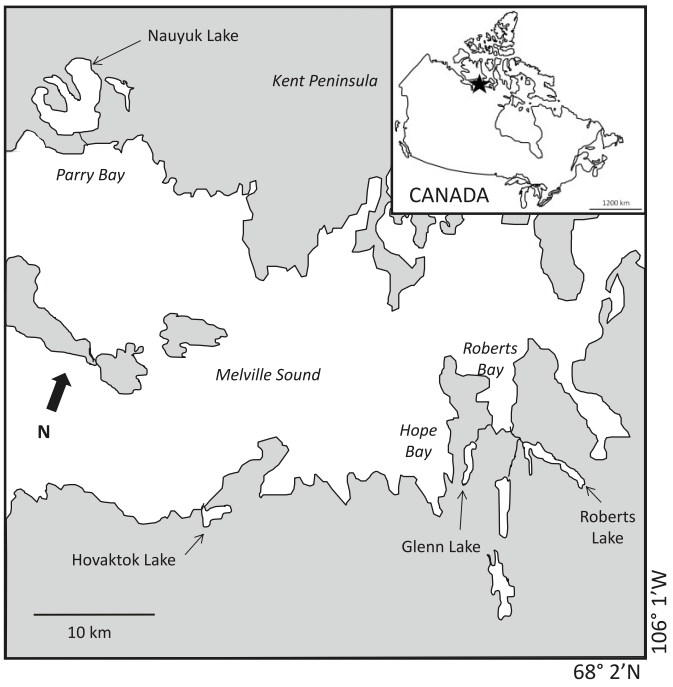
Although it is likely that lake trout are limited to brackish waters and that feeding forays into marine environments are relatively short, we henceforth refer to lake trout that make annual marine migrations as anadromous. Previous researchers have commented that anadromy in the subfamily Salmoninae represents a continuum from species that must leave freshwater to complete their life cycle to those, e.g., members of the genus *Salvelinus* (Arctic char, brook char, and Dolly Varden (*Salvelinus malma*)), that can complete their entire life cycle in freshwater. Rounsefell (1958) refers to these latter species as "optionally anadromous." Many optionally anadromous species (within and outside of the subfamily Salmoninae) have extensive freshwater rearing times, prefer brackish habitats, and overwinter in freshwater between sea migrations (Rounsefell 1958; Gross 1987; Quinn and Leggett 1987). Craig (1989) used the term "semi-anadromy" to describe iteroparous anadromous Arctic fish species that overwinter in freshwater and prefer brackish habitats to full-strength seawater during summer sea migrations. Using these two definitions, we view lake trout that make annual marine migrations as an example of optional, semi-anadromy within the subfamily Salmoninae.

Materials and methods

Field sampling methods

During the summers of 2006–2008, lake trout and Arctic char were captured in a series of lakes and lake outflows located near Hope Bay, Nunavut, Canada (68.1°N, 106.6°W; Fig. 1). Lake trout were captured in four lakes and lake outflows (Glenn, Roberts, Hovaktok, and Nauyuk), whereas Arctic char were captured in three (Roberts, Hovaktok, and Nauyuk). The lakes are located within 3 km of the Arctic coast and all have passable streams that flow to marine environments. Between 16 and 54 fish per species were captured in each lake and (or) lake outflow using a backpack electrofisher (Type 12, Smith-Root Inc., Vancouver, Washington), sinking gill nets (mesh sizes ranging from 1.9 cm to 8.9 cm stretched mesh), and angling. Sampling took place

Fig. 1. Map of the study area in the West Kitikmeot region of Nunavut, Canada. Lake trout (*Salvelinus namaycush*) were collected from Glenn, Roberts, Hovaktok, and Nauyuk lakes, and Arctic char (*Salvelinus alpinus*) were collected from Roberts, Hovaktok, and Nauyuk lakes. Roberts Bay, Hope Bay, Parry Bay, and Melville Sound are marine environments.



throughout the open-water seasons of 2006–2008, and a variety of habitats in each lake and outflow were targeted (i.e., sampling was not standardized among lakes). If fish were caught in or near estuaries of lake outflows, they were not included in the analysis unless a tag indicated the lake of origin (there were earlier tagging studies in the area; Miramar Hope Bay Ltd. 2005). Fish were measured (to the nearest millimetre) and weighed (to the nearest gram) in the field and dissected for dorsal muscle tissue and sagittal otoliths. Sex was determined for all mature fish. Muscle tissue was frozen immediately after processing, and otoliths were cleaned and dried.

Laboratory analyses

Stable isotopes

Muscle tissue from each fish was freeze-dried and ground into a fine powder with a mortar and pestle. All fish were analyzed for stable C and N isotope ratios, and a subset of 73 fish was analyzed for stable S isotope ratios. This subset was chosen to represent anadromous and resident Arctic char from Roberts Lake and anadromous and resident lake trout from both Roberts and Glenn lakes and was used to validate results from otolith microchemistry (see below) and stable C and N isotope analysis.

Analyses of stable C and N isotopes were performed on a continuous-flow isotope-ratio mass spectrometer (Finnigan Mat Delta Plus, Thermo Fisher Scientific Inc., Bremen, Germany) connected to an elemental analyzer (Carlo Erba NC2500, Thermo Fisher Scientific Inc.) (EA-CFIRMS) at the University of New Brunswick (Fredericton, New Brunswick). Carbon and nitrogen content were analyzed simultaneously with the elemental analyzer and converted to mole ratios (C:N). Analyses of stable S isotopes were performed at Northern Arizona University, Flagstaff, Arizona, with a continuous-flow elemental analyzer (model ESC4010, Costech Analytical Technologies Inc., Valencia, California) interfaced with a isotope ratio mass spectrometer (ThermoElectron Delta Plus Advantage, Thermo Fisher Scientific Inc.). Stable N, C, and S isotope ratios are expressed as parts per mil (‰) delta values (δ^{15}N, δ^{13}C, δ^{34}S, respectively) from an international standard. International standards used for C, N, and S were Pee-Dee Belemnite, N_2 gas, and Vienna Canyon Diablo Troilite, respectively. Delta values were calculated using the following formula:

$$(1)\qquad \delta^{15}\text{N or } \delta^{13}\text{C or } \delta^{34}\text{S} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{34}\text{S}/{}^{32}\text{S}$. At the University of New Brunswick laboratory, isotopic, elemental, and internal standards were analyzed between every 15–20 samples for a total of 74 samples and 22 standards per run. Replicate analyses of internal laboratory standards (e.g., NIST 1577b, bovine liver) typically yielded standard deviations of ±0.15‰ for δ^{15}N and δ^{13}C. The mean difference ± standard deviation (SD) between 59 duplicate subsamples was 0.12‰ ± 0.14‰ for δ^{15}N and 0.12‰ ± 0.23‰ for δ^{13}C. At the Northern Arizona University laboratory, a total of 20 isotopic, elemental, and internal standards were analyzed per run. Replicate analyses of internal laboratory standards typically yielded standard deviations of ±0.3‰ or better, and the mean difference ± SD between duplicate subsamples was 0.25‰ ± 0.55‰ ($n = 6$).

Otolith microchemistry

After drying, one otolith from each fish was embedded in ColdCure™ epoxy and sectioned transversely through its core with a low-speed saw (Buehler Isomet, Buehler Ltd., Lake Bluff, Illinois). Otoliths that were crystalline or had obvious vaterite inclusions were not used. Posterior ends of the thick sections (approximately 2.5 mm) were reembedded in epoxy in 25 mm acrylic ring probe mounts. After curing, the discs were ground on 30 μm and 3 μm lapping film to remove scratches. They were then polished at 400 rpm on a soft polishing cloth using a Buehler polishing machine with 0.05 μm diamond paste slurry. Each disc was ultrasonically cleaned and dried before analysis, and photographs of each otolith were taken before and after microchemical analyses.

Because of the large number of otoliths to be analyzed (i.e., time and cost) for microchemistry and the high sensitivity of laser ablation inductively coupled mass spectrometry (LA-ICP-MS), this method was used for the analysis of most otoliths. However, electron microprobe analysis was used on a small subset of otoliths where increased spatial resolution was required. For this small subset of samples, a thin carbon coating was applied to each disc before analysis. Only otoliths from fish that were greater than age 1 were analyzed for microchemistry.

LA-ICP-MS analyses were performed at the Department of Geological Sciences, University of Manitoba (Winnipeg,

Table 1. Typical operating conditions for the LA-ICP-MS system (the relatively small spot size and slow scan speed were used to increase spatial resolution).

Laser conditions		ICP-MS conditions		Data acquisition	
Repetition rate	20 Hz	Plasma power	1280 W	Protocol	Time-resolved analysis
Spot size	12 μm	Cooling gas	15.2 L·min^{-1}	Scanning mode	BScan and EScan
Laser scan speed	2 μm·s^{-1}	Auxiliary gas	1.00 L·min^{-1}	Detector mode	Analog and counting
Energy density on sample	~7.4 mJ·cm^{-2}	Sample gas (Ar)	0.74 L·min^{-1}	Magnet settling time	0.001–0.3 ms
Incident pulse energy	~0.01 mJ	Make-up gas (He)	0.67 L·min^{-1}		

Note: LA-ICP-MS, laser ablation inductively coupled plasma mass spectrometry.

Manitoba) with an ICP-MS (Thermo Finnigan Element 2, Thermo Fisher Scientific Inc.) coupled to a Nd:YAG laser (Merchantek LUV 213, New Wave Research/Merchantek, Fremont, California) (instrument parameters and typical running conditions are summarized in Table 1). Because the fish for this study were from slow-growing Arctic populations, a great deal of effort was put into optimizing the instrumentation for spatial resolution. We found that a 12 μm diameter spot size and 2 μm·s^{-1} scan speed optimized spatial resolution and sensitivity for the otoliths used in this study (H. Swanson and P. Yang, unpublished data). Continuous transects were ablated across the otoliths from the core to the outer edge. The dorsal lobe was used whenever possible, but when the dorsal lobe was damaged or had crystalline portions, the ventral lobe was analyzed. Calcium (Ca) was used as an internal standard and background-subtracted counts on Sr were adjusted to Ca and calibrated to glass standard reference material (SRM) 610 (National Institute of Standards and Testing). Scans of NIST 610 were performed after every 1–3 samples, depending on the time required for each sample.

Electron microprobe analyses were conducted at the Department of Geological Sciences, University of Manitoba, on a Cameca SX-100 electron microprobe (Cameca SAS, Gennevilliers Cedex, France). The accelerating voltage was 15 kV, the beam current was 200 nA, and the beam size and step size were both 3 μm. Strontium was acquired using three spectrometers simultaneously for 10 s each so that the effective counting time was 30 s. There was no sign of significant beam damage using these conditions. Background concentrations of Sr were measured at the first analysis point, and strontianite was used as a standard. Data were processed using the ZAF correction method (Scott et al. 1995).

When a second otolith was available, ages were determined for each fish using the "break and burn" technique (Chilton and Beamish 1982). Under reflected light, one year was defined as an opaque zone (summer growth) followed by a translucent hyaline zone (winter growth). When the second otolith was unavailable, ages were determined from the sectioned and polished otolith used for microchemistry. Ages were read from a subsample of otoliths using both methods. The mean difference (± standard error, SE) between ageing methods was 0.86 ± 0.087 years (n = 163) (R. Wastle, unpublished data).

Data analysis

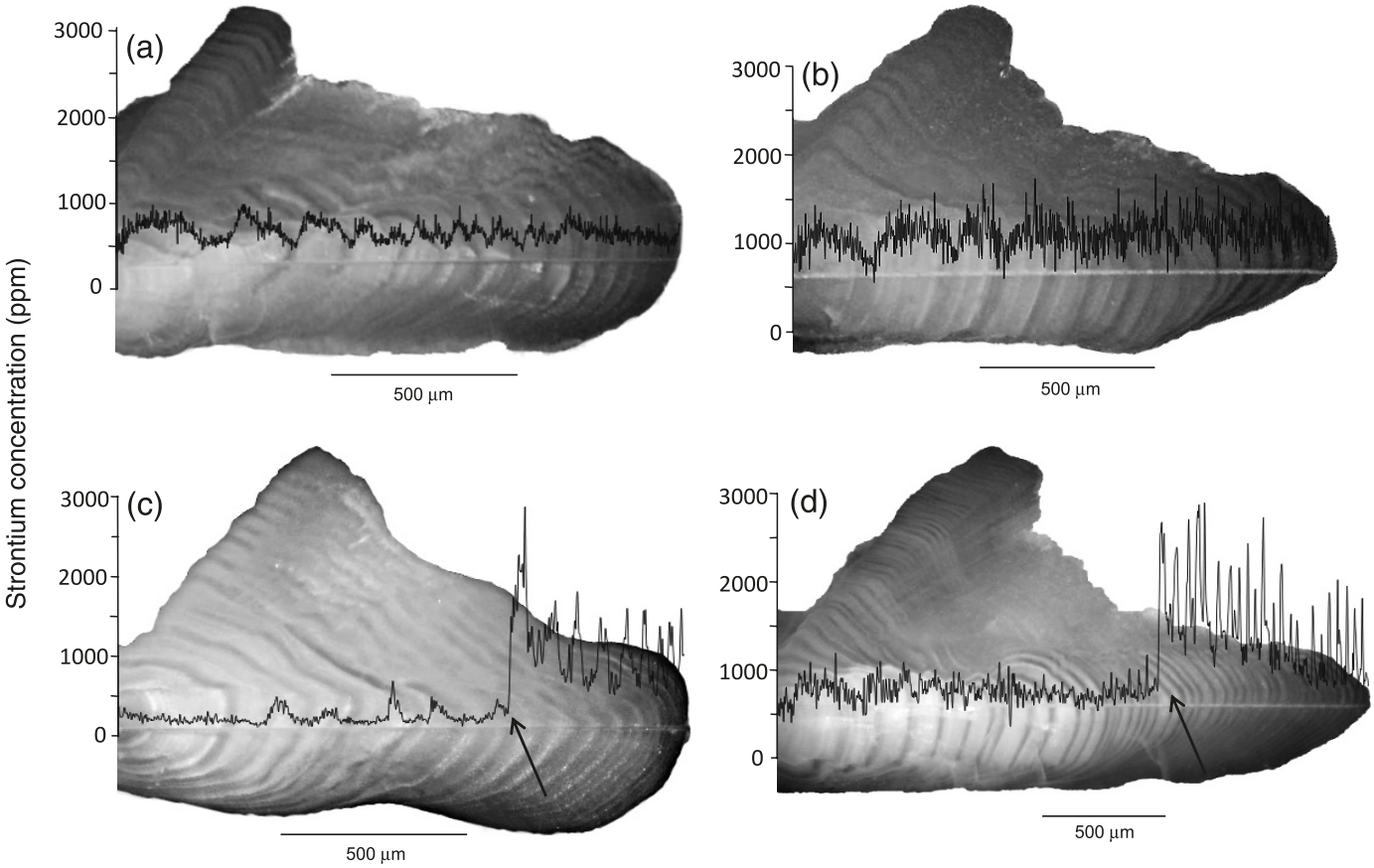
Each Sr concentration ([Sr]) profile was overlain on a digital photograph of the analyzed otolith to determine if the fish was anadromous or resident. When otolith [Sr] profiles were low and relatively flat from the otolith core to the outer edge, fish were classified as resident (Figs. 2*a*, 2*b*). When otolith [Sr] profiles were low and flat through early annuli but showed a marked increase after a number of years followed by oscillatory peaks and troughs, fish were classified as anadromous (Figs. 2*c*, 2*d*). This is consistent with previous otolith microchemistry analyses conducted on populations of landlocked (resident) and anadromous Arctic char (Babaluk et al. 1997), as well as several other species (e.g., Howland et al. 2001). The classifications were verified with available capture (e.g., caught at mouth of outflow) and stomach content (e.g., contained capelin (and caught in outflow or estuary)) data when available. Mean otolith [Sr] was calculated for each fish. Profiles from anadromous fishes (Figs. 2*c*, 2*d*) were then divided into two periods, "premigratory" and "migratory." Premigratory periods were characterized by relatively low [Sr] and dampened annual oscillations, whereas migratory periods were characterized by well-defined, high amplitude annual oscillations and an increase in mean [Sr] (Fig. 2). Mean [Sr] were calculated for premigratory and migratory periods. For each fish classified as anadromous, we checked to ensure that mean [Sr] in the migratory period was not within two standard deviations of mean [Sr] in the premigratory period. Age of first migration and frequency of migrations were visually assessed by overlaying [Sr] profiles on postablation photos of otoliths (Figs. 2*c*, 2*d*).

All statistical analyses were performed with SAS (version 9.1.3, SAS Institute Inc. 2002). Because the ecology of fishes is often related to body size, fork length was included as a covariate in many of the statistical analyses. We used 650 mm fork length as the covariate level of comparison whenever size-adjusted means (LSMEANS option, SAS Institute Inc. 2002) were calculated in an analysis of covariance (ANCOVA). This (650 mm) was within the range of sizes captured in each lake; no extrapolation was necessary. Homogeneity of variance was assessed by examination of residuals plots and variables were transformed as required. Alpha was set at 0.05.

Mean [Sr] in otoliths were compared between species and life history types (anadromous and resident) with a two-factor mixed model (lake was a random (block) variable). Estimates of age of first migration and [Sr] in the migration period were then compared between anadromous Arctic char and lake trout with a one-factor mixed model. Species-specific age of first migration was compared among lakes with an analysis of variance (ANOVA).

All statistical comparisons of $\delta^{15}N$ and $\delta^{13}C$ were done within lakes, thus a correction for among-lake differences in baseline $\delta^{15}N$ was not necessary. Because lipids are rela-

Fig. 2. Examples of [Sr] profiles overlain on postablation photos of otoliths from (*a*) resident Arctic char (*Salvelinus alpinus*), (*b*) resident lake trout (*Salvelinus namaycush*), (*c*) anadromous Arctic char, and (*d*) anadromous lake trout (all from different lakes). Strontium profiles from resident fishes (*a* and *b*) were relatively flat with low amplitude annual oscillations across the entire otolith. Profiles from anadromous fishes (*c* and *d*) had well-defined, high amplitude annual oscillations after a period of low amplitude oscillations. The LA-ICP-MS beam path is indicated by the resultant horizontal trough on each otolith. Age of first migration for these two anadromous fishes, as indicated by arrows, was estimated at 7 years (8th year of life) (*c*; Arctic char) and 17 years (18th year of life) (*d*; lake trout). Note that the *y* axes are consistent among overlays. The *x* axis represents distance.



tively depleted in the heavier isotope of carbon, there is often a negative relationship between fish $\delta^{13}C$ and carbon to nitrogen ratios (C:N, indicator of lipid content; Post et al. 2007). If this relationship is significant and negative, variation in lipid content among fishes may confound analyses of $\delta^{13}C$ (Post et al. 2007). A linear regression showed that $\delta^{13}C$ of lake trout and Arctic char was marginally and positively related to C:N (t = 1.97, P = 0.05, df = 1, 254); thus, $\delta^{13}C$ ratios were not adjusted for lipid content (Post et al. 2007).

Species-specific $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ were compared between life history types with ANCOVA, with fork length as a covariate. Residual plots were closely examined for outliers that could indicate mistakes made when fish were classified into life history types using otolith microchemistry results.

Absolute growth rates (mm·year^{-1}and g·year^{-1}) were calculated by dividing both length and mass by age. Log_e-transformed absolute growth rates were compared between species and life history types with a two-factor mixed model; lake was a random variable. Least-squares means (LS means) were then calculated for each species – life history type and compared with a post-hoc Tukey's test. Length-at-age plots were produced for each species – life history type, and length-frequency and age-frequency distributions were calculated and compared between species and life history types with a Kolmogorov–Smirnov test. To facilitate comparisons with previous studies (e.g., Johnson 1980, 1989), fish condition was estimated using Fulton's condition factor (K) (Ricker 1975) and was calculated for each fish as

$$(2) \qquad K = W \times 100/L^3$$

where W represents wet mass (g) and L represents fork length (cm). Species-specific condition factors and C:N were then compared between life history types using mixed models with fork length as a covariate.

Results

Otolith microchemistry

Otolith microchemistry analyses were conducted on 106 Arctic char and 135 lake trout. Nine fish could not be classified as anadromous or resident because of inconclusive [Sr] profiles. Anadromous Arctic char and lake trout were found in all study systems where residents of that species were present; however, only two anadromous lake trout were captured in Hovaktok Lake (Table 2). Of the 37 lake

trout that were classified as anadromous, eight had stomach contents that included marine prey items (all other stomachs were empty) such as capelin and saffron cod (*Eleginus gracilis*), and 10 were captured in or near estuary mouths where salinity varied from 8‰ to 12‰. Females accounted for 50% of anadromous Arctic char and 57% of anadromous lake trout.

Analyses of Sr profile overlays showed that mean age of first migration was five years (range 3–11) for Arctic char and 13 years (range 3–29) for lake trout (Table 3). This interspecies difference was significant (mixed model, $F = 227$, $P < 0.0001$, df = 1, 86). Age of first migration differed significantly among lakes for lake trout (ANOVA, $F = 6.94$, $P = 0.001$, df = 3, 31); it was highest in Hovaktok and Nauyuk lakes (mean age of first migration = 17 years), intermediate in Roberts Lake (mean age of first migration = 13 years), and lowest in Glenn Lake (mean age of first migration = 10 years). Age of first migration (mean = 5 years) was not significantly different among lakes for Arctic char (ANOVA, $F = 2.57$, $P = 0.09$, df = 2, 53). After the onset of migratory behaviour, Arctic char and lake trout migrated each year for an average of 6 and 7 years, respectively, before remaining in freshwater for a "rest" year. For the 35 fish that showed at least one break in their annual migration pattern, 31 began annual migrations again after 1 year in freshwater, three began migrating again after 2 years in freshwater, and one (lake trout) began migrating again after 5 years in freshwater. There was no interspecies difference in number of annual migrations before rest (mixed model, $F = 0.67$, $P = 0.42$, df = 1, 33).

In a two-factor mixed model, mean [Sr] in otoliths (encompassing the life of the fish) of lake trout and Arctic char was significantly higher in anadromous fishes (mean ± SE = 929 ± 141 ppm) than in resident fishes (mean ± SE = 782 ± 140 ppm) (mixed model, $F = 22.83$, $P < 0.0001$, df = 1, 218) but did not differ between species (mean ± SE = 835 ± 140 ppm for Arctic char and 877 ± 141 ppm for lake trout) (mixed model, $F = 1.73$, $P = 0.19$, df = 1, 218). However, when mean [Sr] was calculated for the migratory period only, Arctic char had significantly higher [Sr] (mean ± SE = 1479 ± 115 ppm) than lake trout (mean ± SE = 1214 ± 116 ppm) (mixed model, $F = 13.9$, $P = 0.0004$, df = 1, 83). Within life history types and species, mean [Sr] across the whole otolith differed significantly among lakes (ANCOVA, $F > 8.91$, $P < 0.0003$, df ≥ 2, 49). These differences likely reflect differences in water chemistry, but this could not be tested because water chemistry data were not available for all lakes.

Stable isotope analysis

Statistical comparisons of $\delta^{15}N$ and $\delta^{13}C$ between anadromous and resident life history types were possible for each lake–species combination except for lake trout in Hovaktok Lake, where the small sample size of anadromous lake trout precluded statistical analysis. In all cases, anadromous fishes had higher $\delta^{15}N$ than resident fishes (ANCOVA, $F > 10.4$, $P < 0.005$, df ≥ 1, 18; Fig. 3). Results for $\delta^{13}C$ were slightly more variable. $\delta^{13}C$ differed significantly between anadromous and resident individuals for all lake–species combinations (ANCOVA, $F > 12.54$, $P < 0.0023$, df ≥ 1, 18), except for Arctic char in Hovaktok Lake (ANCOVA, $F = 0.13$, $P = 0.722$, df = 1, 19) (Fig. 3). In most cases, $\delta^{13}C$ was more negative in resident fishes than in anadromous fishes, but in Arctic char from Nauyuk Lake, this trend was reversed (Fig. 3).

Anadromous Arctic char and lake trout had significantly higher muscle $\delta^{34}S$ than resident Arctic char and lake trout (ANCOVA, $F > 128$, $P < 0.0001$, df ≥ 1, 16) (Fig. 4), indicating their reliance on marine food sources. Within each life history type, lake trout from Roberts Lake had significantly higher $\delta^{34}S$ than lake trout from Glenn Lake (ANCOVA, $F > 22.17$, $P < 0.0033$, df > 1, 14) (Fig. 4). One lake trout from Glenn Lake that had been classified as anadromous using otolith microchemistry had a relatively low muscle $\delta^{34}S$. The otolith [Sr] profile from this fish revealed that it had not migrated in the previous 5 years. This highlights an important consideration in the use of isotopes to distinguish between anadromous and resident fishes; if fish have not migrated recently, isotopic turnover could lead to incorrect classification of life history types.

Age and growth

Comparisons of mean fork length (Table 4) and length- and age-frequency distributions illustrate that anadromous fishes were generally larger than resident fishes (Fig. 5) and that lake trout were generally older than Arctic char (Fig. 6). All pairwise comparisons between species – life history type pairs (e.g., anadromous Arctic char vs. resident Arctic char,

Table 2. Number of anadromous and resident fish captured in the four study lakes.

	Lake			
Life history	Glenn	Hovaktok	Nauyuk	Roberts
Arctic char				
No. anadromous	N/A	11	35	13
No. resident	N/A	13	5	23
Lake trout				
No. anadromous	14	2	10	11
No. resident	40	14	15	26

Note: Life history classification was based on results from otolith microchemistry. Arctic char, *Salvelinus alpinus*; lake trout, *Salvelinus namaycush*.

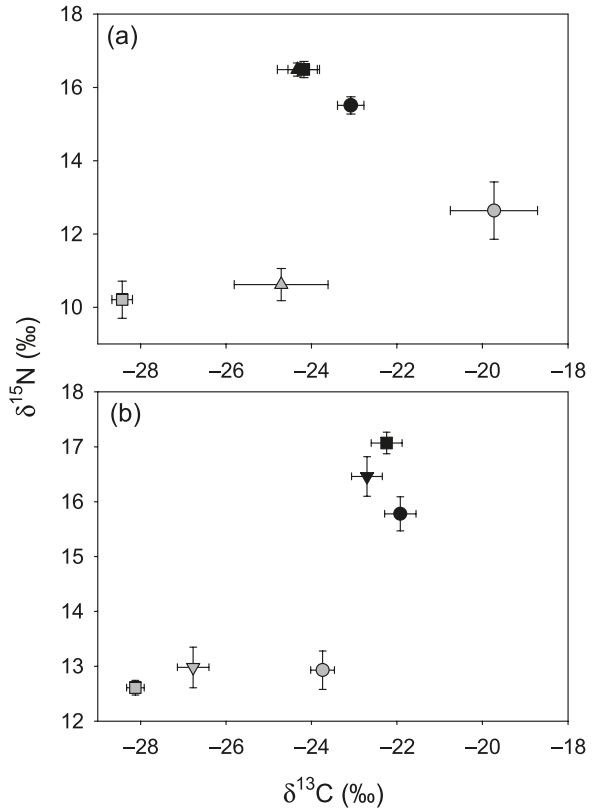
Table 3. Species-specific descriptive statistics for age of first migration.

Lake	*N*	Mean*	SD	Min.	Max.
Arctic char					
Hovaktok	9	5	0.87	4	6
Nauyuk	34	5	1.74	3	11
Roberts	13	4	0.93	3	6
Lake trout					
Glenn	14	10 (a)	4.05	3	18
Hovaktok	2	17 (ab)	5.66	13	21
Nauyuk	9	17 (b)	5.08	13	29
Roberts	10	13 (ab)	2.10	10	17

Note: *N*, number; SD, standard deviation; Min., minimum; Max., maximum; Arctic char, *Salvelinus alpinus*; lake trout, *Salvelinus namaycush*.

*Letters in parentheses after values indicate significant pairwise differences (Tukey's test, $P < 0.05$).

Fig. 3. Muscle $\delta^{15}N$ and $\delta^{13}C$ for (*a*) Arctic char (*Salvelinus alpinus*) and (*b*) lake trout (*Salvelinus namaycush*) classified as anadromous (solid symbols) or resident (shaded symbols) in the study lakes (Glenn Lake, inverted triangle; Hovaktok Lake, upright triangle; Nauyuk Lake, circle; Roberts Lake, square). Symbols are adjusted means (to 650 mm FL) ± standard error (SE) and are coincident for Arctic char in Hovaktok Lake and Roberts Lake (*a*). With the exception of $\delta^{13}C$ for Arctic char in Hovaktok Lake (*a*, upright triangle), there were significant differences in $\delta^{15}N$ and $\delta^{13}C$ between anadromous and resident fishes in each lake (analysis of covariance (ANCOVA), $F > 12.54$, $P < 0.002$, df $\geq 1, 18$).

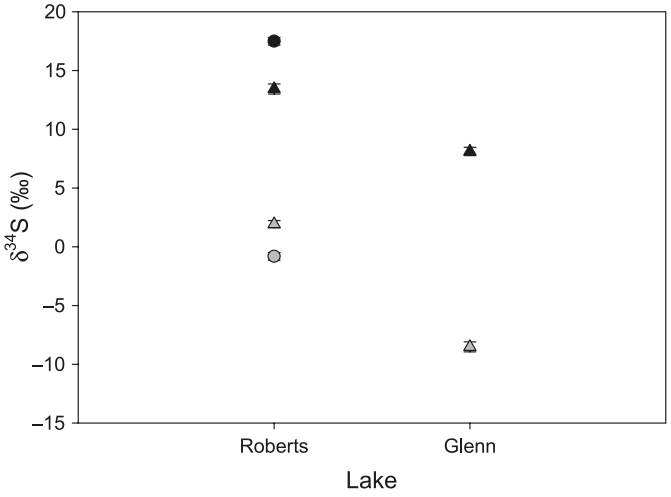


anadromous Arctic char vs. anadromous lake trout) for length- and age-frequency distributions were significantly different (Kolmogorov–Smirnov test, $D \geq 0.368$, $P \leq 0.001$, $N \geq 95$).

Consistent with the finding that lake trout started migrating at an older age than Arctic char, the youngest captured anadromous lake trout was 13 years old, whereas the youngest captured anadromous Arctic char was 6 years old (Fig. 6). The size and age range of anadromous lake trout represented a larger, older subset of the size and age range of resident lake trout (Figs. 5, 6). Anadromous Arctic char were larger and older than resident Arctic char (Figs. 5, 6).

In terms of both mass and length, Arctic char grew significantly faster than lake trout (mixed models, $F \geq 5.59$, $P < 0.019$, df $\geq 1, 23$; Table 4). Absolute growth rates for mass also differed significantly between life history types (mixed model, $F = 305.0$, $P < 0.0001$, df $= 1, 233$; Table 4) and were significantly higher in anadromous fishes than in resident fishes (Tukey's test, $P < 0.05$; Table 4). Absolute growth rates for length did not differ significantly between life history types (mixed models, $F = 0.24$, $P = 0.62$, df $= 1, 235$; Tukey's test, $P < 0.05$) and were highest in anadromous Arctic char and lowest in anadromous lake trout (Table 4). Length-at-age plots (Fig. 7) further illustrate that anadromous fishes did not have higher length at age than resident fishes. This is particularly obvious for lake trout.

Fig. 4. Muscle $\delta^{34}S$ of anadromous (solid symbols) and resident (shaded symbols) Arctic char (*Salvelinus alpinus*) (circle) and lake trout (*Salvelinus namaycush*) (triangle). Symbols are least-squares means (at 650 mm FL) ± standard error (SE) generated with an analysis of covariance (ANCOVA). Within each lake and species, anadromous fish had higher $\delta^{34}S$ than resident fish (analysis of covariance (ANCOVA), $F > 128$, $P < 0.0001$, df $\geq 1, 16$). Within life history types, lake trout from Roberts Lake had significantly higher $\delta^{34}S$ than lake trout from Glenn Lake (ANCOVA, $F > 22.17$, $P < 0.0033$, df $>1, 14$).



Condition and C:N were generally higher in anadromous fishes than in resident fishes, but these differences were not always significant. Differences in condition were only significant for lake trout (mixed model, $F = 17.33$, $P < 0.0001$, df $= 1, 131$), whereas differences in C:N were only significant for Arctic char (mixed model, $F = 47.72$, $P < 0.0001$, df $= 1, 126$) (Table 4).

Discussion

In 1958, Rounsefell evaluated a number of North American Salmonidae species for degree of anadromy. Lake trout were assigned to the category "wholly freshwater." He went on to say that, "lake charr so rarely leave fresh water that the only instances recorded are not established beyond a reasonable doubt" (Rounsefell 1958, p. 172). In the intervening 51 years, there have been sporadic reports of lake trout inhabiting coastal marine waters and a single report of capelin in the stomach of a lake trout caught at the mouth of the Coppermine River (Ellis 1962; see Martin and Olver 1980). This is the first study to present multiple lines of evidence for directed marine migrations in lake trout and show, beyond a reasonable doubt, that this species inhabits and feeds in marine coastal areas in the Canadian Arctic. Otolith microchemistry and stable C, N, and S isotope ratios, as well as limited stomach content and capture data, revealed the occurrence of annual marine migrations and marine feeding in the studied populations of lake trout.

Table 4. Indicators of growth and body condition in anadromous and resident Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*).

		Fork length (mm)		Growth rate (length; mm·year^{-1})*		Growth rate (mass; g·year^{-1})*		Condition†	C:N‡
	N	Mean	SE	LS mean	SE	LS mean	SE	LS mean	LS mean
Arctic char									
Anadromous	60	694	16	61 (a)	1.05	296 (a)	1.16	1.11 (a)	3.67 (a)
Resident	71	261	14	53 (a)	1.06	24 (b)	1.17	1.06 (a)	3.36 (b)
Lake trout									
Anadromous	37	604	19	23 (b)	1.06	97 (c)	1.18	1.17 (1)	3.71 (1)
Resident	99	439	19	25 (b)	1.05	45 (d)	1.15	1.05 (2)	3.34 (1)

Note: LS mean, least-squares mean; SE, standard error.

*LS means were calculated in a mixed model, with lake as a random variable. Letters in parentheses after values indicate pairwise differences.

†LS means were calculated in a mixed model, with lake as a random variable. Letters and numbers in parentheses after values indicate pairwise differences in LS mean condition and LS mean C:N between life history types for each species.

‡LS means were calculated at a standardized size of 650 mm in a mixed model with lake as a random variable. Letters and numbers in parentheses after values indicate pairwise differences in LS mean condition and LS mean C:N between life history types for each species.

Compared with residents, anadromous lake trout had higher $\delta^{15}N$ and $\delta^{34}S$ ratios and less negative $\delta^{13}C$ ratios. This is consistent with previous results and indicates that anadromous lake trout were feeding on marine food sources (Doucett et al. 1999*a*, 1999*b*; Swanson and Kidd 2009). Stable isotope ratios differed similarly between resident and anadromous Arctic char in Hovaktok and Roberts lakes, but in Nauyuk Lake, resident Arctic char had less negative $\delta^{13}C$ than anadromous Arctic char. Many resident Arctic char were caught in the outflow of Nauyuk Lake, and we observed that Arctic char often moved downstream to the mouth of the estuary during high tide. Stomachs of these resident Arctic char primarily contained *Mysis relicta*, and we suspect that these fish, though they did not make marine migrations, fed primarily on marine mysids. This may explain the relatively enriched $\delta^{13}C$ signal.

Although differences between anadromous and resident fishes were significant for all three isotopes, stable C and S are likely to have more consistent applicability in differentiating between life history types because there is very little fractionation with trophic transfer (Peterson and Fry 1987). It is interesting that $\delta^{34}S$ values in resident and anadromous lake trout differed significantly between Roberts and Glenn lakes. Further investigation revealed that this did not reflect feeding differences between lakes, but between-lake differences in $\delta^{34}S$ values of baseline organisms (e.g., mysids, H. Swanson, unpublished data). Thus, similar to $\delta^{15}N$, we suggest that in some systems, it may be necessary to correct for among-lake differences in baseline $\delta^{34}S$.

Previous studies in this region (Nauyuk Lake) have shown that the first sea migration in Arctic char usually occurs at 180–240 mm fork length and 3–8 years of age (Johnson 1980). Thus, many of the Arctic char captured in this study that were classified as resident could have become migratory later in life. The presence of resident Arctic char larger than 300 mm and older than 10 years, however, suggests that there are true residents. This is in agreement with Johnson's (1980) assertion that anadromous and resident Arctic char often occur in sympatry in the study region.

Although differences were not always significant, anadromous lake trout and Arctic char were generally in better condition and had higher C:N than residents of the same species. This is consistent with previous findings for Arctic char (Johnson 1980; Doucett et al. 1999*a*; Swanson and Kidd 2009). Absolute growth rates for mass were significantly higher in anadromous fishes than resident fishes, but there was no significant difference between life history types in absolute growth rates for length. Thus, it seems that the main growth advantage for these anadromous fishes is increased mass rather than length. This likely allows access to better spawning sites and mates, as well as increased fecundity (McCart 1980; Gross 1987). It has also been shown that females are more likely to be anadromous than males (e.g., Northcote 1978; Doucett et al. 1999*a*; Howland et al. 2001). This is because female fecundity often increases with size, and thus individual fitness is more size-dependent in females than in males (reviewed in Jonsson and Jonsson 1993). We found, however, that 50% of anadromous Arctic char were female and 57% of anadromous lake trout were female. Previous research conducted at Nauyuk Lake showed that anadromous females outnumbered anadromous males in migration runs by two- to nine-fold (Johnson 1989). In another study in Quebec, 82% of anadromous Arctic char were female (Doucett et al. 1999*a*). It is likely that sample sizes in this study were too low to detect a significant skew in the sex ratio, but further research is needed to confirm this, particularly for lake trout.

Anadromous lake trout started migrating at a significantly older age (mean = 13 years) than anadromous Arctic char. Our estimates of mean age of first migration for anadromous Arctic char (mean = 5 years) were similar to previous estimates from Nauyuk Lake (mean = 6 years; Johnson 1989, based on smolt sampling) and the Norwegian Arctic (mean = 6.7 years; Radtke et al. 1996, based on otolith microchemistry). Mean size of 5-year-old Arctic char in this study was 275 mm and was similar to or within the range of sizes reported for first-time migrants at Nauyuk Lake (180–240 mm; Johnson 1989) and Roberts Lake (180–300 mm; Golder Associates Ltd. 2008, based on smolt sampling). In contrast to Arctic char, mean age of first migration for lake trout was 13 years (range 3–29 years); this corresponds to a size of approximately 400 mm.

Fishes of the genus *Salvelinus* (chars) are not as tolerant of seawater as other members of the subfamily Salmoninae

Fig. 5. Length-frequency distributions of (*a*) anadromous Arctic char (*Salvelinus alpinus*) (n = 60), (*b*) resident Arctic char (n = 71), (*c*) anadromous lake trout (*Salvelinus namaycush*) (n = 37), and (*d*) resident lake trout (n = 100). Data were pooled for all four lakes. Bin size is 25 mm. Modal size of anadromous fishes was larger than that of resident fishes, and anadromous Arctic char were slightly larger than anadromous lake trout.

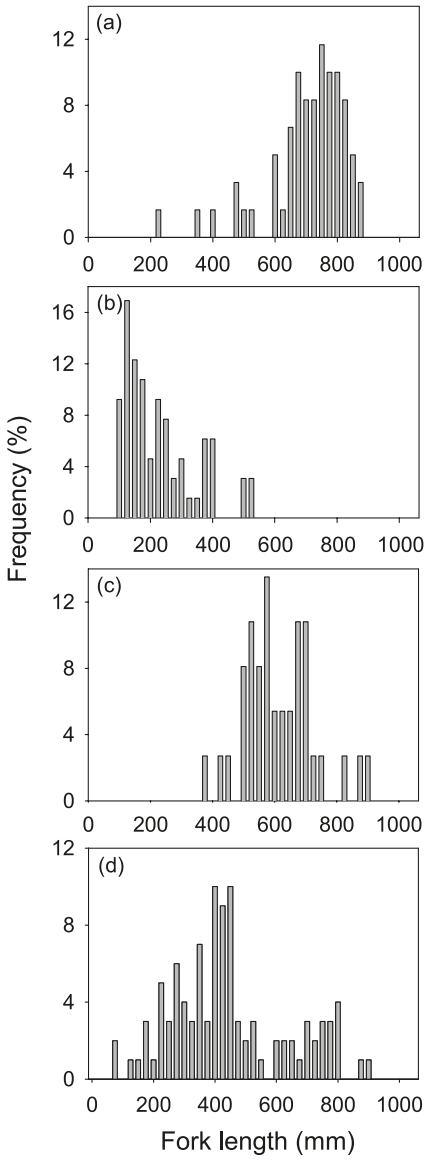
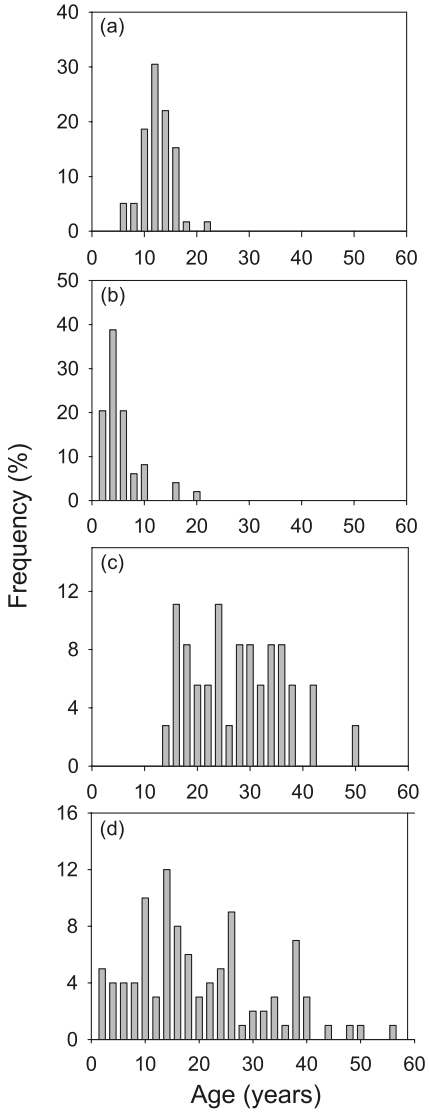
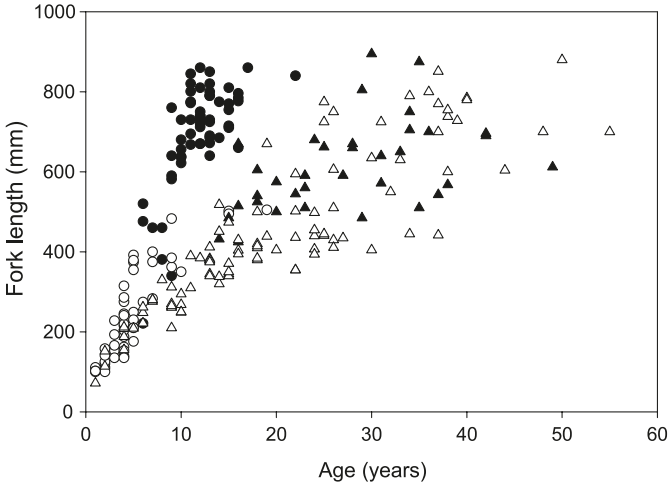


Fig. 6. Age-frequency distributions of (*a*) anadromous Arctic char (*Salvelinus alpinus*) (n = 59), (*b*) resident Arctic char (n = 53), (*c*) anadromous lake trout (*Salvelinus namaycush*) (n = 36), and (*d*) resident lake trout (n = 100). Data were pooled for all four lakes. Bin size is 2 years. No age classes younger than 13 to 14 years are represented by captured anadromous lake trout.



(*Oncorhynchus* and *Salmo*) and show the lowest degree of anadromy (i.e., they are optionally anadromous) (Rounsefell 1958). Salinity tolerance is size-dependent in salmonids (McCormick 1994), and perhaps because they are less saltwater-tolerant, anadromous *Salvelinus* species begin migrating at a larger size and older age than anadromous *Oncorhynchus* and *Salmo* species (McCormick 1994). Previous studies have stated that brook trout (char) have the lowest salinity tolerance of any anadromous salmonid species (lake trout were not viewed as an anadromous species and were thus not included in the comparison; Rounsefell 1958). Accordingly, brook char have been reported to have the largest minimum size and oldest age at first migration of any anadromous salmonid species studied to date (McCormick 1994). Physiological studies have shown that brook trout survival in seawater increases with size until a maximum is reached at approximately 200 mm, but that osmoregulatory capacity increases between the sizes of 60 mm and 320 mm (McCormick and Naiman 1984). Lake trout have less osmoregulatory capacity than brook trout (Hiroi and McCormick 2007). It is therefore not surprising that we found lake trout to have greater size and age of first migration than Arctic char and, indeed, a greater mean size and age of first migration than any reported anadromous salmonid. We found that mean [Sr] in the migratory period was higher in otoliths from anadromous Arctic char than in otoliths from anadromous lake trout. This could indicate that anadromous Arctic char use higher-salinity habitats or

Fig. 7. Scatterplots of fork length vs. age for anadromous Arctic char (*Salvelinus alpinus*) (solid circles), resident Arctic char (open circles), anadromous lake trout (*Salvelinus namaycush*) (solid triangles), and resident lake trout (open triangles). Data from all lakes were pooled.



stay at sea longer than anadromous lake trout, but further research is required.

The occurrence of sympatric anadromous and resident lake trout in the study area indicates that these populations display partial anadromy (one example of partial migration); some individuals are freshwater residents, whereas others are anadromous. Many salmonid species, including the congeneric Arctic char and brook char, exhibit partial anadromy (e.g., Johnson 1980; Jonsson and Jonsson 1993; Radtke et al. 1996). In some species and populations, it has been shown that this variation in life history (anadromy vs. residency) between individuals may result from phenotypic plasticity rather than a genetic polymorphism (e.g., Nordeng 1983). Partial anadromy may function as a form of "bet hedging" that allows populations to persist in extreme and variable environments (Jonsson and Jonsson 1993; Secor 1999) and is likely selected for when fish that produce both resident and anadromous progeny have greater reproductive fitness than fish that produce progeny of only one life history type (Jonsson and Jonsson 1993). Some researchers have proposed that partial anadromy in salmonid populations is maintained by a conditional strategy in which all individuals share a genetically based life history strategy and an interaction between physiological condition (i.e., state (Gross and Repka 1998)) and environment determines the life history tactic adopted by individual fish (i.e., anadromous or resident) (e.g., Gross 1996; Gross and Repka 1998; Kerr et al. 2009). In many of these species, anadromous and resident individuals differ in early growth rate and (or) energetic state (e.g., Nordeng 1983; Jonsson and Jonsson 1993), and these are thought to "cue" either anadromy or residency, but effects are not consistent among species (Jonsson and Jonsson 1993).

If partial anadromy is maintained by a conditional life history strategy in lake trout, further research is required to elucidate what factors (e.g., early growth, lipid content, etc.) determine whether an individual fish becomes migratory or resident. Because we found that mean age and size of first migration was 13 years and 400 mm, respectively, in lake trout, it seems unlikely that early (i.e., first 1–2 years) growth rate differs between anadromous and resident individuals. It is possible, however, that early growth rate does have an effect and that the reason that anadromous behaviour is not observed until many years later is because the fish must grow to a relatively large size to tolerate seawater. Alternatively, the physiological cue for anadromy vs. residency could occur later in life. Partial anadromy in lake trout may also be maintained by behavioural entrainment (McQuinn 1997), or a combination of a conditional strategy and behavioural entrainment (Secor and Kerr 2009). It is also possible that partial anadromy in lake trout is maintained by a genetic polymorphism or frequency-dependent selection, but these explanations are less likely (e.g., Gross and Repka 1998; Kerr et al. 2009).

Rounsefell (1958) postulated that the incidence of anadromy increases with latitude in salmonid species, and this appears to be true for lake trout. Anadromy in lake trout may be limited to northern latitudes because temperatures in migratory streams and (or) at the sea surface exceed upper lethal limits in the southern part of the species' range (Rounsefell 1958), or because the difference in productivity between lakes and the sea is greatest at more northerly latitudes (productivity is higher in the sea; Gross 1987). Whatever the cause, the incidence of partial anadromy in northern lake trout populations has likely (*i*) increased their productivity in Arctic lakes, similar to Arctic char (Campbell et al. 1999), (*ii*) enhanced their ability to colonize new habitats (Wilson and Hebert 1998; Secor 1999), and (*iii*) allowed them to persist in extreme and highly variable environments (Secor 1999).

As pointed out by previous investigators, understanding the diversity of life history tactics within a species is extremely important for conservation and stock management (e.g., Babaluk et al. 1997). Anadromous fishes may be especially vulnerable to anthropogenically induced changes in habitat or climate because they rely on more than one habitat (Gross 1987). We have determined that lake trout display anadromy in lakes along the mainland coast of the Canadian Arctic. Obviously, much further research is required to elucidate the mechanisms that maintain partial anadromy in lake trout populations, the life history characteristics of anadromous lake trout, and the extent and duration of their marine migrations. Field evidence suggests that anadromous lake trout may range from Bristol Bay, Alaska, to the coast of Labrador, and that anadromous lake trout may be present in Coronation Gulf, Hudson Bay, and Ungava Bay (reviewed in Martin and Olver 1980). Additional research is needed, however, to determine the geographic extent of anadromy in lake trout populations.

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