

Evidence for Non-Anadromous Behaviour of Arctic Charr (*Salvelinus alpinus*) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada, Based on Scanning Proton Microprobe Analysis of Otolith Strontium Distribution

JOHN A. BABALUK,¹ NORMAN M. HALDEN,² JAMES D. REIST,¹ ALLAN H. KRISTOFFERSON,¹ JOHN L. CAMPBELL³ and WILLIAM J. TEESDALE³

(Received 23 December 1996; accepted in revised form 20 May 1997)

ABSTRACT. Scanning proton microprobe analysis was used to determine the distribution of strontium (Sr) in otoliths from arctic charr (*Salvelinus alpinus*) of known non-anadromous, known anadromous, and unknown life histories. Strontium concentration patterns in otoliths of known non-anadromous charr were low and relatively flat (with little variation) from the core area to the outermost edge of the otolith, while patterns for known anadromous charr were characterized by a similar low, flat region for the first several years of life, followed by marked oscillatory increases and decreases in Sr content for the duration of the fish's life. Small and large forms of Lake Hazen charr of unknown life histories exhibited Sr profiles that were similar to those of the known non-anadromous charr, which strongly suggests that Lake Hazen charr are non-anadromous. These results indicate that Lake Hazen is a "closed" system with energy cycling primarily within the system; this conclusion suggests that a conservative approach would be appropriate for the management of the Lake Hazen charr population.

Key words: anadromy, arctic charr, *Salvelinus alpinus*, Ellesmere Island National Park Reserve, life history, otolith microchemistry, scanning proton microprobe, trace elements

RÉSUMÉ. À l'aide d'une sonde protonique à balayage, on a procédé à une analyse afin de déterminer la répartition du strontium (Sr) dans des otolithes prélevés sur des ombles chevaliers (*Salvelinus alpinus*) ayant eu soit un cycle biologique non anadrome connu, soit un cycle anadrome connu ou un cycle inconnu. Les courbes de concentration en strontium dans les otolithes d'ombles reconnus comme non anadromes étaient faibles et relativement uniformes (montrant peu de fluctuations) en allant du centre de l'otolithe vers la périphérie, tandis que les courbes relatives aux ombles reconnus comme anadromes se caractérisaient par une zone de concentrations faibles et uniformes pour plusieurs des premières années de vie, suivie par des oscillations à la hausse et à la baisse très nettes quant au contenu en Sr pour la durée de vie du poisson. De gros et de petits spécimens d'ombles au cycle biologique inconnu, trouvés dans le lac Hazen, affichaient des profils de Sr semblables à ceux des ombles reconnus comme non anadromes, ce qui suggère fortement que l'omble du lac Hazen est non anadrome. Ces résultats révèlent que le lac Hazen est un système où l'énergie circule surtout en circuit «fermé». Cette conclusion suggère qu'il faudrait adopter une approche prudente quant à la gestion de la population d'ombles du lac Hazen.

Mots clés: anadromie, omble chevalier, *Salvelinus alpinus*, réserve de parc national de l'île-d'Ellesmere, cycle biologique, microchimie otolithique, sonde protonique à balayage, éléments traces

Traduit pour la revue *Arctic* par Nésida Loyer.

INTRODUCTION

Lake Hazen is a large (542 km²), deep (280 m) lake located in Ellesmere Island National Park Reserve on Ellesmere Island in the Canadian High Arctic (Fig. 1). The only fish species present in Lake Hazen is arctic charr (*Salvelinus alpinus*). Despite the distant and isolated location of Lake Hazen, its charr are exploited by anglers to an unknown degree (Stewart, 1994). However, since the primary productivity of Lake Hazen is extremely low (Johnson, 1990), and since, in many respects, the lake may represent a closed

system, in which energy cycles primarily within the system, the ability of its charr population to withstand even limited human perturbation is unknown. Conservation and management of this charr population are primary goals of Parks Canada (Parks Canada, 1994). It is therefore essential to establish an understanding of the life history traits of the charr of Lake Hazen so an appropriate management approach may be developed.

Arctic charr exhibit a wide range of phenotypic diversity throughout their geographic range. Often, populations inhabiting areas with access to the sea exhibit the phenomenon of

¹ Canada Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada; Babalukj@dfo-mpo.gc.ca

² Department of Geological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

³ Department of Physics, University of Guelph, Guelph, Ontario N1G 2W1, Canada

© Department of Fisheries and Oceans, Government of Canada

“partial migration”: that is, migratory and resident individuals co-exist (Jonsson and Jonsson, 1993). These populations of charr are most often divided into a large-form component, which passes the first two to nine years in freshwater before migrating to the sea for the first time (anadromous), and a small form, which passes its entire life in freshwater (non-anadromous) (Johnson, 1980). Understanding the energetics of and the relationship between these forms is an important component of any conservation and management strategy.

Previous scientific investigations have described both large and small forms of arctic charr from Lake Hazen (Hunter, 1960; Johnson, 1983; Reist et al., 1995). The large form of Lake Hazen charr has a robust, rounded body form; light grey back and white belly; and orange or pale orange paired fins with white leading edges (Reist et al., 1995). These fish are similar in size, shape, and colouration to many anadromous charr from the Canadian Arctic described by Johnson (1980). The small form of Lake Hazen charr is characterized by its relatively small size and terete body form. It has a dark brownish to grey back, a rosy belly, and grey paired fins with dull white leading edges (Reist et al., 1995). These characteristics are similar to the generalized non-anadromous charr described by Johnson (1980). As Lake Hazen charr potentially have access to the sea via the Ruggles River (Fig. 2), and because of the morphological, colouration, and growth rate differences between the two forms, it was previously hypothesized that the larger of the two forms was anadromous while the smaller form was non-anadromous (Hunter, 1960; Johnson, 1983). This hypothesis was indirectly supported by the presence of numerous archaeological sites on the Ruggles River (Sutherland, 1989; Dick et al., 1994), which suggested utilization of a fishery resource in the distant past. However, no direct scientific investigations have previously been conducted to confirm this hypothesis regarding anadromous behaviour.

Distinguishing between anadromous and non-anadromous arctic charr in North America has generally been limited to monitoring fish migrating to and from the sea (e.g., Johnson, 1989), although in one case parasites were used as biological tags to distinguish the two forms (Dick and Belosevic, 1981). More recently, chemical analysis of otoliths has been used to describe the environmental histories, including anadromous behaviour, of individual fish of various species (e.g., Radtke, 1989; Coutant and Chen, 1993).

Otoliths, a part of a fish's inner ear, are composed mainly of calcium carbonate (aragonite) (Degens et al., 1969) that is deposited in layers as the fish grows (Mugiya, 1964). Because otoliths do not undergo resorption (Simkiss, 1974; Campana and Neilson, 1985), they are good indicators of age and have been shown to contain a permanent record of trace elements such as strontium (Sr) (Kalish, 1989; Radtke, 1989). The calcium (Ca) and trace elements are derived mainly from the waters in which the fish live (Simkiss, 1974; Ichii and Mugiya, 1983). Seawater contains, on average, 8.0 mg·l⁻¹ Sr, whereas freshwater contains only 0.1 mg·l⁻¹ Sr (Rosenthal et al., 1970). These differences in Sr concentrations have been shown to be reflected in otolith composition (Radtke et al.,

1990) and thus have great potential as indicators of anadromy; they may also provide details regarding the habitats occupied throughout a fish's life.

Using wavelength dispersive electron microprobe (EMP) analysis, Kalish (1990) found patterns in the Sr/Ca ratios of otoliths that distinguished anadromous and non-anadromous rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon (*Salmo salar*), and brown trout (*Salmo trutta*). Radtke (1995) and Radtke et al. (1996) suggested that otolith microchemistry could be used to look retroactively at arctic charr life histories. Coote et al. (1991) suggested that scanning proton microprobe (SPM) analysis of Sr distribution in otoliths could be used to detect anadromous behaviour in fishes, and in preliminary studies, we have demonstrated that SPM analysis of the Sr content of charr otolith annuli can be used to characterize anadromous behaviour (Halden et al., 1995, 1996).

In this study, we used SPM analysis to measure and determine the pattern of Sr distribution in the otoliths of known non-anadromous and anadromous arctic charr from various locations in the Canadian Arctic, and compared these patterns to those of the small and large forms of charr from Lake Hazen to determine whether either form is anadromous.

MATERIALS AND METHODS

Otolith Collection and Preparation

Otoliths were collected from Arctic charr from seven locations in the Canadian Arctic (Fig. 1): (1) four known non-anadromous charr were caught by gill net from an unnamed lake with no connection to the sea (69°26' N, 139°33' W; hereafter Lake 104) in September 1988 (Reist et al., 1997); (2) five known non-anadromous charr were caught by gill net from Capron Lake (71°50' N, 124°13' W) in August 1994 (Capron Lake has an impassable connection to the sea); (3) four known anadromous charr were caught by gill net while migrating from the sea to freshwater near the mouth of the Halovik River (69°09' N, 107°05' W) in August 1992; (4) three known anadromous charr were caught by gill net while migrating from the sea to freshwater near the mouth of the Jayco River (69°43' N, 103°16' W) in September 1990; (5) three known anadromous charr were caught by gill net while migrating from the sea to freshwater at the mouth of the Paliryuak River (69°27' N, 106°41' W) in September 1992; (6) seven known anadromous charr were caught by gill net while migrating from the sea to freshwater at the mouth of the Ekalluk River (69°23' N, 106°18' W) in September 1994; and (7) 13 small-form charr and 19 large-form charr of unknown life histories were collected by gill netting and angling from four sites in Lake Hazen (81°50' N, 70°25' W) (Fig. 2) during June 1992. The Lake Hazen charr chosen for analysis were all older than 19 years, well past the age at which smoltification and migratory behaviour to the sea should have been exhibited (Johnson, 1980; Dempson and Green, 1985).

One of each pair of otoliths was prepared for SPM analysis. The otoliths were embedded in epoxy resin, and a transverse

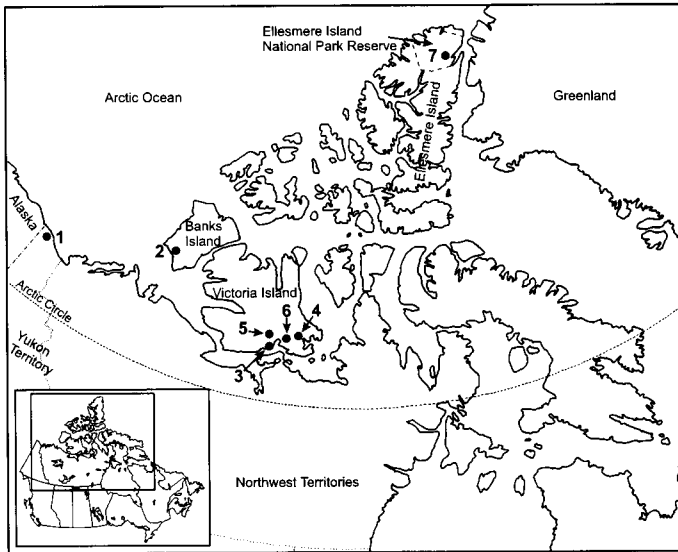


FIG. 1. Locations of Canadian arctic charr populations (dots) from which otoliths were collected for scanning proton microprobe analysis. 1) Lake 104, 2) Capron Lake, 3) Halovik River, 4) Jayco River, 5) Paliryuak River, 6) Ekalluk River, 7) Lake Hazen.

cut was made to create a dorso-ventral cross section through the core of the otolith, exposing all annuli (yearly growth increments). The posterior half of each otolith was re-embedded in a standard 25 mm diameter leucite probe mount. The exposed otolith surfaces were sequentially ground (240, 320, 400, and 600 grit silicon carbide), then polished (5, 3, 1, and 0.3 μm aluminum oxide), and finally coated with carbon. Videomicrographs of the otoliths were used to determine ages using criteria described by Kristoffersen and Klemetsen (1991) and as references for the proton microprobe. Annuli (age in years) marked on the x-axis in Figures 3–6 were correlated by determining the ratio between the total length in microns of the Sr profile (pattern) measured from the line-scan and the total length in microns of the line-scan transect measured on the videomicrograph. Ages at particular points along the Sr profile were then determined.

Scanning Proton Microprobe Analysis

In the University of Guelph proton microprobe, a 3 MeV proton beam entered the otolith surface at a 45° angle. The excitation volume was approximately a cylinder of 5–10 μm in diameter and 30 μm in depth. Ninety percent of the observed Sr X-rays from the aragonite matrix of the otolith originate within a depth of 31 μm (Halden et al., 1996). One-dimensional line-scans were obtained by rastering the proton beam along a transect from the core area to the dorsal edge of the otoliths, incorporating all annuli. With the Guelph SPM electrostatic scanning arrangement, the line-scan has a maximum length of 500 μm and contains 256 pixels. Line-scans from the core to the otolith edge were created by having the scanning software combine several of the 500 μm segments. Line-scanning of a typical arctic charr otolith took approximately 25 minutes at a proton beam current of 5–7 nA. Currents at this level caused no apparent damage to the

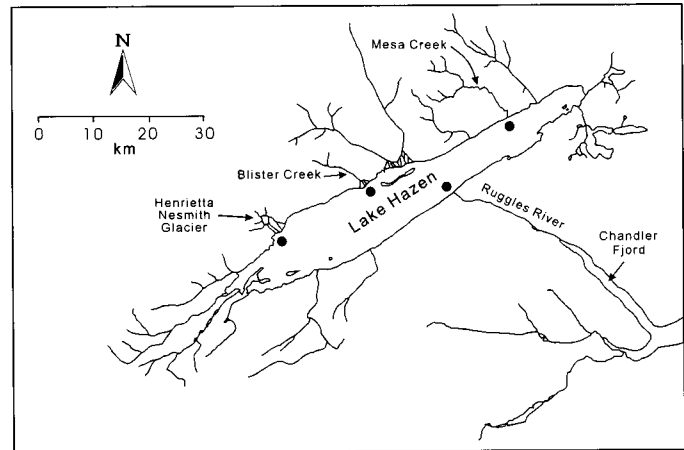


FIG. 2. The Lake Hazen area, showing collection sites (dots) for arctic charr from which otoliths were collected for scanning proton microprobe analysis.

otoliths. The X-ray detector is equipped with a compound filter of 125 μm Mylar and 106 μm aluminum to prevent low-energy X-rays from being recorded in the spectrum. Further details on proton microprobe procedures are given by Halden et al. (1995) and Halden et al. (1996). Calculations of Sr concentrations from X-ray intensities were done using procedures described by Campbell et al. (1995). For the purpose of correlating the Sr concentration in parts per million (ppm) with the line-scans, raw X-ray intensities were converted to ppm using a regression curve derived from point analyses. The limit of detection was 1–2 ppm.

Water Sample Analysis

Freshwater samples were collected from Lake Hazen in 1992 and 1995 and from the Ekalluk and Halovik Rivers in 1995. Seawater samples were collected from nearshore sites off Ellesmere Island in 1992 and off Victoria Island in 1995. Waters from these sources were analyzed for elemental Sr to describe the general relationship between the Sr of the otoliths and the Sr in the environment in which the otoliths developed. Strontium was analyzed by inductively coupled plasma-atomic emission spectrometry (ICP-AES) using commercial ICP standards and NRC standard reference materials (SLRS-1, SLRS-2). Detection limit for Sr in the water samples was 0.001 $\text{mg}\cdot\text{l}^{-1}$.

RESULTS

Known Non-anadromous Arctic Charr

Scanning proton microprobe transects across the otoliths of known non-anadromous arctic charr showed a pattern consistent with predicted results for a fish with a non-migratory life history. The Sr line-scans shown in Figure 3 were recorded from otoliths of two known non-anadromous charr, (a) from Lake 104 (14 years old) and (b) from Capron Lake (12 years old). These patterns show a relatively constant and

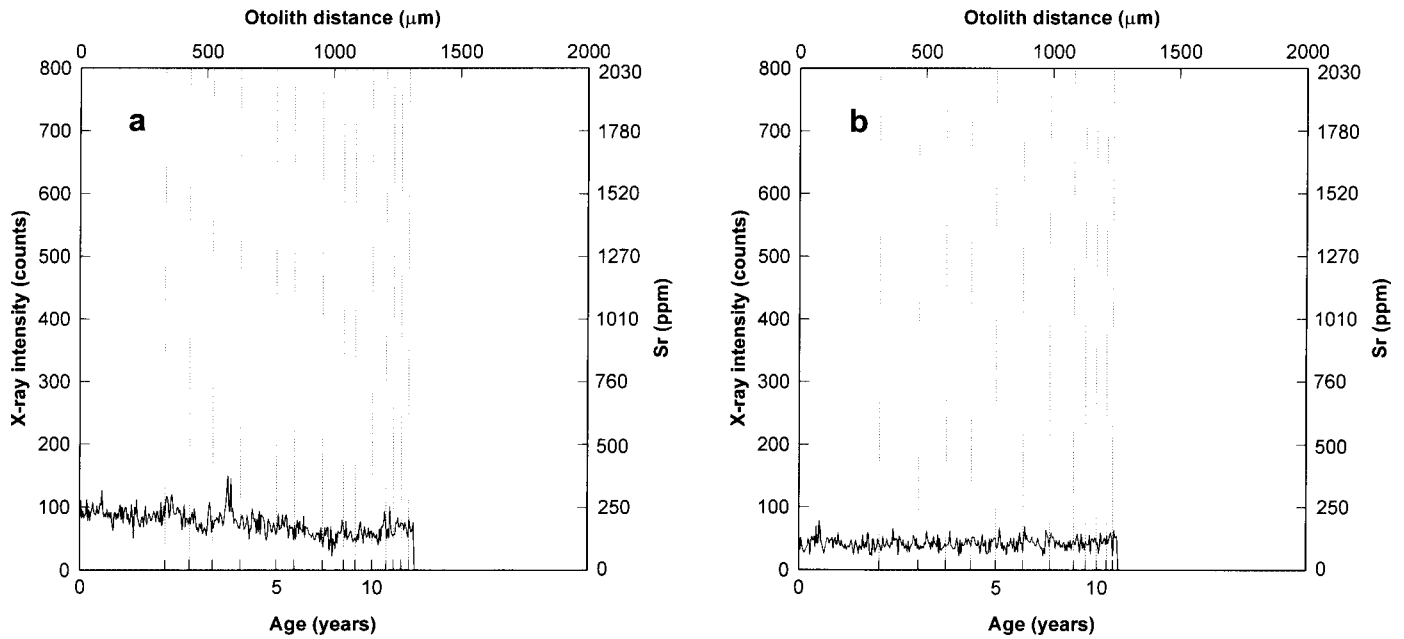


FIG. 3. Typical Sr profiles from scanning proton microprobe line-scans of otoliths collected from known non-anadromous arctic charr from (a) Lake 104 and (b) Capron Lake.

low Sr content (a “flat” Sr profile) from the core area (0 μm) to the outside edge of the otolith (ca. 1250 and 1300 μm , respectively), suggesting that the fish occupied an environment in which the Sr content was relatively constant and low (i.e., the fish did not migrate). All nine known non-anadromous charr analyzed from the two populations had similar Sr patterns. This pattern was also evident from the mean Sr X-ray intensities over the entire line-scans for Lake 104 and Capron Lake charr (Table 1).

Known Anadromous Arctic Charr

Figure 4 shows typical Sr line-scans obtained from otoliths of known anadromous arctic charr from the (a) Halovik, (b) Jayco, (c) Paliryuak, and (d) Ekalluk Rivers. The pattern of Sr distribution for the 16-year-old Halovik River fish has a low-Sr region corresponding to the core area (within the first annulus) and the first several optically defined annuli (Fig. 4a). This region was similar to that observed for the whole otolith transect in non-anadromous charr (Fig. 3). A marked increase in the Sr content (ca. 1050 μm) corresponds to the 7th annulus, indicating that in its 8th year the fish moved to an environment with a higher Sr content (i.e., the sea). The pattern of elevated Sr seen in the subsequent series of oscillatory peaks and troughs is easily distinguishable from the pattern before the 7th annulus and the “flat” patterns established for non-anadromous charr (Fig. 3). All 17 known anadromous charr analyzed from the four populations showed similar patterns, including an 18-year-old Jayco River fish (Fig. 4b), an 11-year-old Paliryuak River fish (Fig. 4c), and an 11-year-old Ekalluk River fish (Fig. 4d). These patterns were reflected by values for mean Sr X-ray intensities recorded for fish from the four locations (Table 1).

Strontium concentrations in water samples from two of the freshwater systems known to contain anadromous charr (the Ekalluk and Halovik Rivers) were at least an order of magnitude lower than the concentration of Sr measured in the marine environment near Victoria Island (Table 2). This difference in concentration in the water is reflected in the Sr content observed in the freshwater and saltwater growth regions of the otoliths of all charr from the Halovik and Ekalluk Rivers (Fig. 4a and d).

Lake Hazen Arctic Charr of Unknown Life Histories

Representative Sr line-scans from two small-form Lake Hazen arctic charr (Fig. 5a and b) have patterns similar to those of the known non-anadromous charr from Lake 104 and Capron Lake (Fig. 3) and are clearly distinguishable from the patterns evident in known anadromous charr (Fig. 4). The patterns for both 23-year-old Lake Hazen fish show a relatively constant, “flat” Sr profile from the core area to the outer edge of the otolith. All 13 small-form charr analyzed from Lake Hazen exhibited similar patterns; this uniformity was evident from mean Sr X-ray intensities from all line-scans from these fish (Table 1).

Figures 6a and b show typical Sr line-scans from otoliths of two large-form Lake Hazen charr of 23 and 27 years of age, respectively. These patterns, like those of the small-form Lake Hazen charr, lack significant structure in Sr distribution. They are similar to those of the known non-anadromous charr (Fig. 3) and are also distinguishable from the pattern evident in the known anadromous charr (Fig. 4). All 19 large-form charr analyzed from Lake Hazen exhibited similar patterns, as was evident from mean Sr X-ray intensities (Table 1).

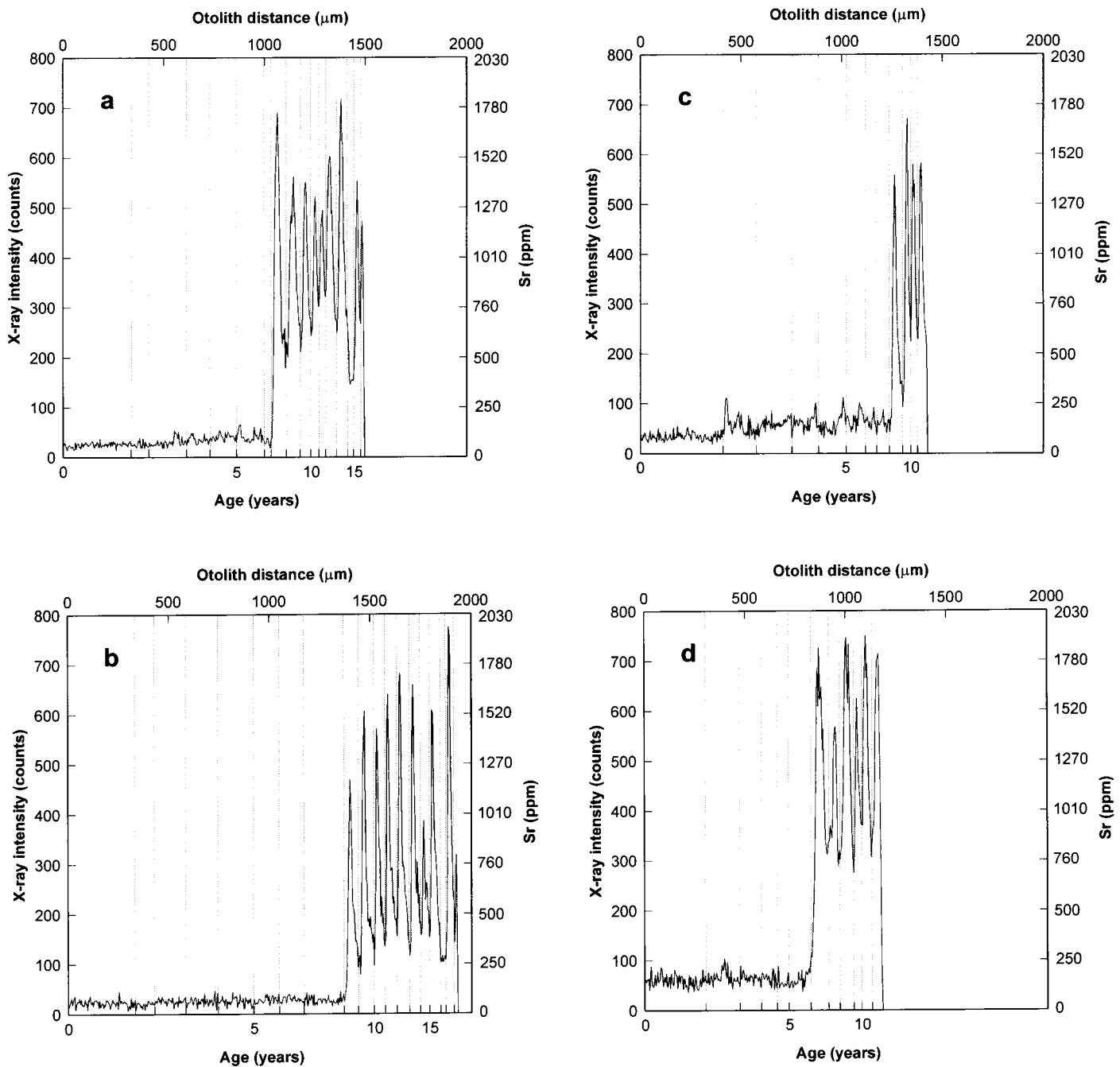


FIG. 4. Typical Sr profiles from scanning proton microprobe line-scans of otoliths collected from known anadromous arctic charr from (a) Halovik River, (b) Jayco River, (c) Paliryuak River, and (d) Ekalluk River.

The concentration of Sr in Lake Hazen water was substantially greater than that found in the other freshwaters sampled, but still much lower than that measured in seawater sampled from near Ellesmere Island (Table 2). These lower levels are reflected in the low Sr content of Lake Hazen charr otoliths (Fig. 5 and 6, Table 1). The otoliths of Lake Hazen charr exhibit Sr levels higher than those of Victoria Island charr in their freshwater phase (although still substantially lower than anadromous-phase levels; see Table 1). This higher level is most likely due to the higher levels of Sr in Lake Hazen (Table 2).

DISCUSSION

Arctic Charr of Known Life Histories

The results of our study with SPM analysis of otoliths of known non-anadromous and anadromous arctic charr clearly demonstrated two distinct patterns of Sr distribution, each associated with a particular life history. The Sr patterns for all known non-anadromous charr analyzed typically showed a relatively low and flat profile from the core area to the outermost edge of the otolith. These levels were consistent

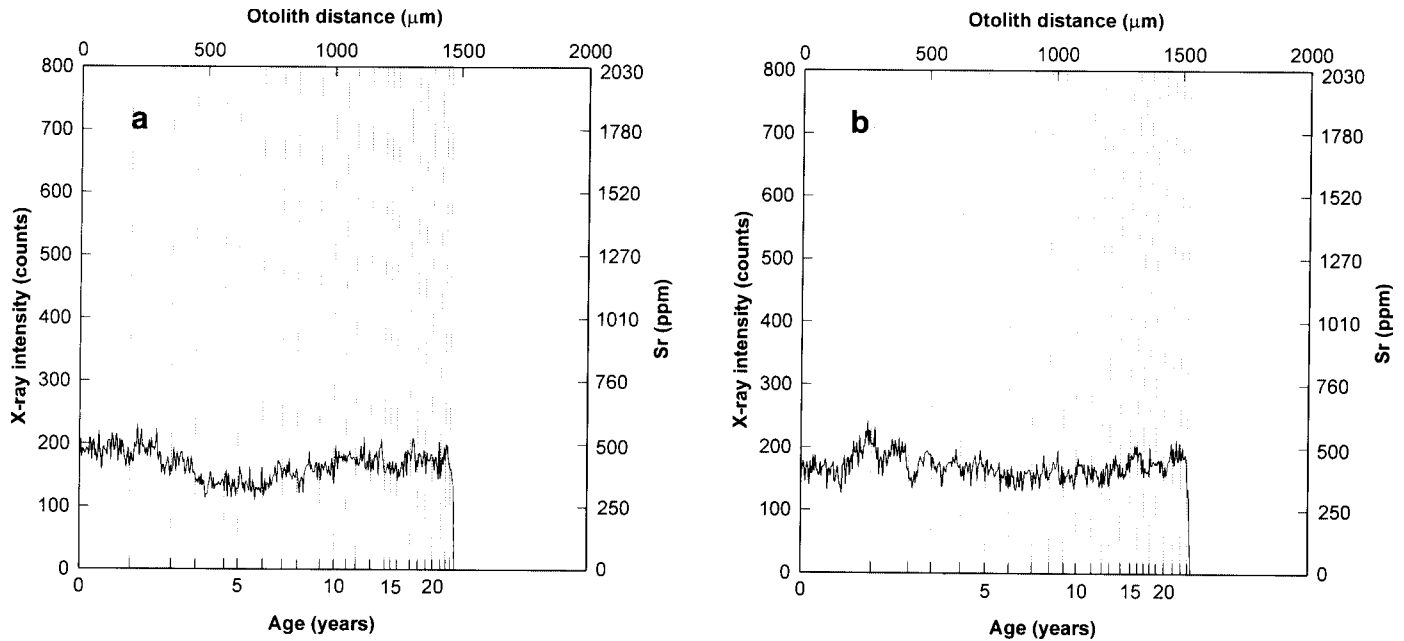


FIG. 5. Typical Sr profiles from scanning proton microprobe line-scans of otoliths collected from small-form arctic charr found in Lake Hazen (a, b).

with low Sr concentration values associated with freshwater: because the concentration of Sr in freshwater is relatively low, only small amounts are available for incorporation into the otolith. Rieman et al. (1994) also reported similar results for otoliths from sockeye salmon (*Oncorhynchus nerka*). The flat pattern indicated minimal change in the Sr content of the fish's environment. The small variations in Sr that were apparent in the profiles may be due to seasonal variations in water temperature (Radtke and Targett, 1984) and growth rate (Sadovy and Severin, 1994), hence incorporation into the otolith. The Sr patterns obtained by our SPM analysis for non-anadromous charr were similar in profile to the Sr/Ca ratio patterns obtained with EPM analysis by Kalish (1990) from known non-anadromous rainbow trout and Radtke et al. (1996) from resident (non-anadromous) arctic charr from Spitsbergen, Norway.

The Sr pattern common to all known anadromous charr was characterized by a low Sr region corresponding to the first several annuli, followed by a marked increase in Sr content, consistent with migration to a high Sr environment (i.e., the sea) for the first time. This is followed by oscillatory peaks and troughs that are easily distinguishable from the "background" or "flat" levels typical of the freshwater phase of the life history. In the absence of any external evidence of a change in the Sr content of the fish's freshwater environment, such as an influx of Sr from the weathering of surrounding rock, the most reasonable interpretation of the sudden increase in Sr and its oscillatory character was that the fish moved regularly between freshwater and marine environments in the later part of its life. Anadromous charr, after having reached a length of 15–20 cm and an age of 2–9 years, annually migrate to the sea in summer to feed, but because of winter water temperatures below 0°C and hypersaline conditions in the marine environment, are obliged to

return to freshwater in the fall to overwinter (Johnson, 1980). The observed peaks are consistent with such annual feeding forays to a marine environment. These patterns were similar to the previously described patterns obtained by SPM for known anadromous charr (Halden et al., 1995, 1996). Using EPM analysis, Radtke (1995) and Radtke et al. (1996) observed similar Sr/Ca ratio patterns for anadromous charr from Spitsbergen. Similarly, using a scanning proton microprobe on an otolith from a New Zealand quinnat (chinook) salmon (*Oncorhynchus tshawytscha*), Coote et al. (1991) observed low levels of Sr that corresponded to the initial freshwater phase of the fish's life followed by a region of high Sr content consonant with a number of years at sea and then a return to low Sr content when the fish returned to freshwater to spawn.

Our interpretation of these results regarding the anadromous behaviour of charr is straightforward. However, variations in individual Sr profiles also suggest that a finer scale analysis of the data might identify and elucidate other behavioural traits (e.g., age at smoltification; periodicity of migrations; duration of migrations; residency in different environments). These questions will be explored in subsequent studies.

Lake Hazen Arctic Charr of Unknown Life Histories

The existence of anadromy in arctic charr populations depends on access to the sea by the fish. The Ruggles River, over its course of 29 km from Lake Hazen to the sea (Chandler Fjord), drops approximately 158 m in elevation. It is shallow (less than 2 m) and fast-flowing but has no waterfalls, and thus provides a readily available passageway for charr between Lake Hazen and the sea (Stewart, 1994). Johnson (1980) stated that there is no northern limit to the existence of anadromous populations of charr (i.e., charr with access to the

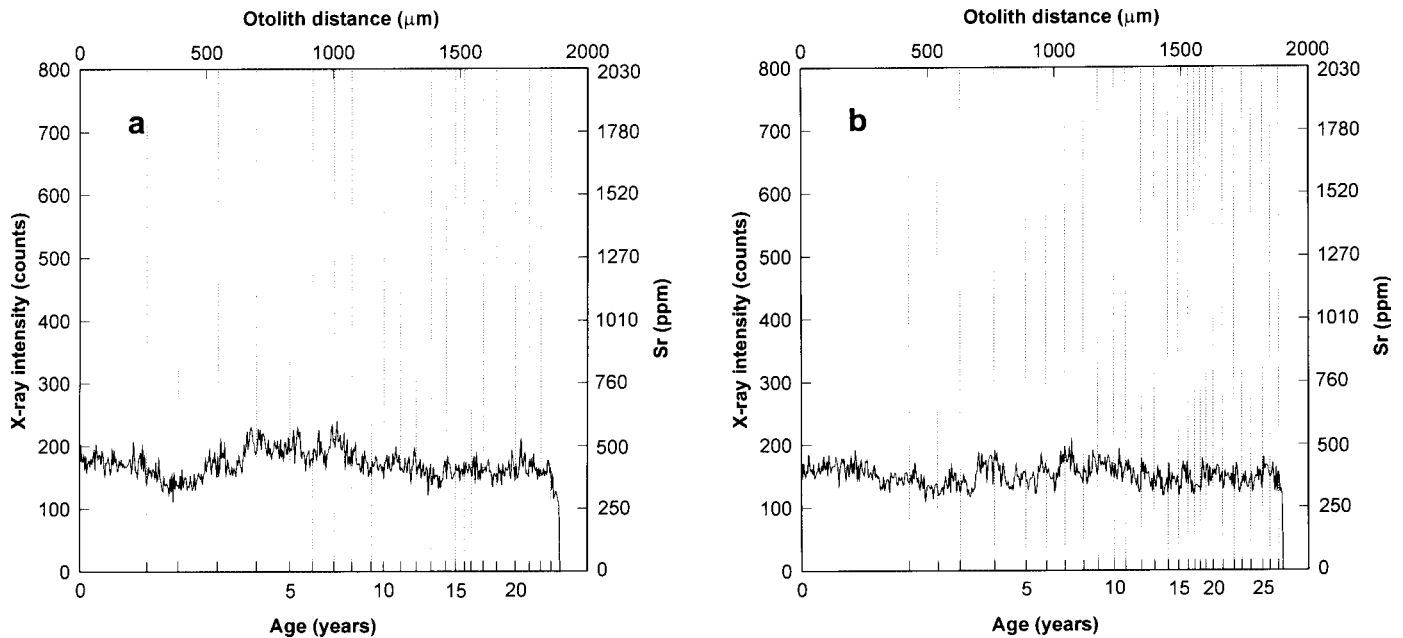


FIG. 6. Typical Sr profiles from scanning proton microprobe line-scans of otoliths collected from large-form arctic charr found in Lake Hazen (a, b).

sea on northern Ellesmere Island). He based this hypothesis on a report of silver-coloured charr caught in a lake with an outlet to the sea on the north coast of Ellesmere Island (Gunther, 1877) and Hunter's assumption (1960) that the large form of Lake Hazen charr was anadromous. While there may be no northern limit for anadromous behaviour by charr, the Sr patterns of the Lake Hazen charr that we analyzed, when compared to those of known non-anadromous and anadromous charr, provided strong evidence that the Lake Hazen charr, irrespective of form and even though they had access to the sea, were not anadromous. The Sr patterns from all Lake Hazen charr (13 small-form, 19 large-form) were similar to those of the known non-anadromous charr. There was no evidence of even isolated increases in Sr content great enough to indicate opportunistic forays to the sea or even to brackish water environments, as might have been expected if environmental conditions in the lake occasionally favoured migration.

The small and large forms of Lake Hazen charr are characterized by distinct growth trajectories in the adult phase of their life. Growth rates are similar until approximately age nine, after which a rapid divergence occurs (Hunter 1960; Reist et al., 1995). These differences in growth likely occur as a result of differences in life histories between the two forms. Two possible explanations for the difference are anadromy and cannibalism.

A major factor determining the existence of anadromy in a fish population is whether the benefits are greater than the costs of migration (Jonsson and Jonsson, 1993). Anadromy is hypothesized to evolve when, given access, fish migrate to the sea to find more abundant food resources, which provide increased growth sufficient to improve reproductive potential and outweigh the costs of migration (Northcote, 1978; Gross, 1987). However, if conditions for feeding (and there-

fore growth) in freshwater are good, any advantage gained by migrating to the sea is diminished (Svenning et al., 1992); therefore, given that migration uses energy which could be used otherwise, migration would likely be avoided. Under experimental conditions, Nordeng (1983) demonstrated that the proportion of non-anadromous charr increased at the expense of anadromous charr if sufficient levels of food were available. In the case of Lake Hazen, we suggest that the large form has a readily available food source within the lake in the form of juvenile and small-form charr. Preliminary analysis of stomach contents tends to support cannibalism and not anadromy as the more plausible explanation for the difference in growth. Thirty-eight of 53 stomachs examined from large-form charr contained charr remains. In the case of the small-form charr, 16 of 16 stomachs examined contained only benthic invertebrates (J. Babaluk, unpubl. data).

Further evidence to support non-anadromous behaviour of Lake Hazen charr is available from the archaeological records for the area. Twenty-four prehistoric campsites have been found along the Ruggles River (Dick et al., 1994), but the few fishing artifacts (e.g., a three-pronged leister) that have been found were from a site on Lake Hazen at the Ruggles River outflow, and these were associated with a winter fishery (Sutherland, 1989; P. Sutherland, Canadian Museum of Civilization, Hull, Quebec, pers. comm. 1997). A very important Inuit fishing technique was the stone weir (*saputit*) method that was used during the autumn upstream migration of charr (Balikci, 1980). As there are no remnants of *saputits* along the Ruggles River (G. Adams, Parks Canada, Winnipeg, pers. comm. 1996), it appears that the river and Chandler Fjord were used by prehistoric Inuit as a travel corridor between Lake Hazen and the east coast of Ellesmere Island (Dick et al., 1994) rather than as a destination for fishing upstream runs of returning anadromous charr.

TABLE 1. Summary of Sr X-ray intensities from SPM line-scans of otoliths from arctic charr populations in the Canadian Arctic.

Life history	Location	No. of fish	Mean Sr X-ray intensity \pm s.e. (counts)		
			Pre-peak or entire ¹	Peaks ²	Troughs ³
non-anadromous	Lake 104	4	70 \pm 2	—	—
	Capron Lake	5	44 \pm 1	—	—
anadromous	Halovik River	4	36 \pm 1	438 \pm 8	277 \pm 10
	Jayco River	3	39 \pm 8	402 \pm 23	179 \pm 22
	Paliryuak River	3	52 \pm 1	476 \pm 37	277 \pm 46
	Ekalluk River	7	47 \pm 4	571 \pm 27	324 \pm 15
unknown	Lake Hazen (small form)	13	178 \pm 4	—	—
	Lake Hazen (large form)	19	169 \pm 4	—	—

¹ Sr X-ray intensities averaged over line-scan to first peak for anadromous fish or over entire line-scan for non-anadromous fish.

² Sr X-ray intensities averaged for all oscillatory peaks for all fish from a location.

³ Sr X-ray intensities averaged for all troughs between peaks for all fish from a location.

TABLE 2. Concentration of Sr in water samples from selected water bodies in the study area.

Water type	Location	Elemental Sr (mg l ⁻¹)
freshwater	Ekalluk River	0.009
	Halovik River	0.008
	Lake Hazen	0.122
seawater	off Victoria Island	3.226
	off Ellesmere Island	4.220

Our SPM study provides strong evidence that Lake Hazen charr do not exhibit anadromous behaviour. However, our sample of the large-form charr was small ($n = 19$), and the possibility that some Lake Hazen charr do exhibit anadromous behaviour still exists. In known anadromous charr populations from the Canadian Arctic, peak upstream migrations occur in August (Johnson, 1980). Future SPM studies will be conducted on charr collected from Lake Hazen near the Ruggles River during August, when upstream migration might be expected to occur. Also, our study does not rule out the possibility that Lake Hazen charr may have been anadromous originally, during postglacial colonization of the lake or during periods when environmental conditions were more favourable (e.g., postglacial warm periods). Thus, a facultative strategy for anadromy may be present in the Lake Hazen and other High Arctic populations of charr. In such a situation, given sufficient environmental diversity to maintain size polymorphism in charr, when environmental conditions are appropriate, individuals or a subcomponent of the population may possibly become anadromous during their life histories. When conditions are not favourable, these fish may then revert to non-anadromy.

Conservation Implications of Non-anadromous Behaviour

Populations (or individuals) of arctic charr that exhibit anadromous behaviour have greater access to larger food

reserves in marine environments. Theoretically, this increases their opportunities for growth and reproductive output (quality and quantity of young). Sustainable harvest levels for such populations are higher than they would be for parallel populations that do not have an anadromous component in their life history. Anadromous fish provide an energy linkage between the sea and freshwater. For freshwater forms, this linkage does not exist; energy cycles primarily within the freshwater system. This is especially true for High Arctic lakes such as Lake Hazen, where climatic restrictions and nutrient cycling limit overall productivity. The finding that both forms of charr present in Lake Hazen are non-anadromous raises significant questions regarding the productivity of these fish and hence the exploitation levels that can be maintained. The productivity of freshwater systems at this latitude is much less than that of similar systems in lower latitudes and systems in the marine environment. Thus the sustainable exploitation rate for this population of charr is likewise very low. Despite its extreme northern location, this population of charr—the large form, in particular—is already being exploited by anglers to an unknown degree. In order to adequately conserve the population, very conservative harvest levels must be maintained.

ACKNOWLEDGEMENTS

This work was done in part with the support of the Department of Canadian Heritage (Parks Canada). We thank E. Gyselman, K. Kiguktak, and R. Wissink for field support while at Lake Hazen. The Department of Energy, Mines and Resources (Polar Continental Shelf Project) and the staff at Resolute provided logistical support. The Tungavik Federation of Nunavut and NSERC also provided support. We thank K. Mathers, S. Mejia, and R. Wastle for preparation of otoliths for SPM analysis; J. Maxwell for computer programming; and B. Hunt and C. Ranson for water sample analysis. F. DeCicco, E. Gyselman, L. Johnson, R. Wagemann, and an anonymous reviewer provided constructive comments on earlier versions of the manuscript.

REFERENCES

- BALIKCI, A. 1980. Charr fishing among the Arviligjuarmiut. In: Balon, E.K., ed. Charrs: Salmonid fishes of the genus *Salvelinus*. The Hague: Dr. W. Junk Publishers. 7–9.
- CAMPANA, S.E., and NEILSON, J.D. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014–1032.
- CAMPBELL, J.L., TEESDALE, W.J., and HALDEN, N.M. 1995. Theory, practice and application of micro-PIXE analysis and element-distribution maps. The Canadian Mineralogist 33:279–292.
- COOTE, G.E., GAULDIE, R.W., and WEST, I.F. 1991. Application of a nuclear microprobe to the study of fish otoliths and scales. Nuclear Instruments and Methods in Physics Research B54:144–150.
- COUTANT, C.C., and CHEN, C.H. 1993. Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. Canadian Journal of Fisheries and Aquatic Sciences 50:1318–1323.
- DEGENS, E.T., DEUSER, W.G., and HAEDRICH, R.L. 1969. Molecular structure and composition of fish otoliths. Marine Biology 2:105–113.
- DEMPSON, J.B., and GREEN, J.M. 1985. Life history of anadromous arctic charr, *Salvelinus alpinus*, in the Fraser River, northern Labrador. Canadian Journal of Zoology 63:315–324.
- DICK, L., ADAMS, G., and SUTHERLAND, P. 1994. Archaeology and history. In: Ellesmere Island National Park Reserve resource description and analysis. Winnipeg: Department of Canadian Heritage.
- DICK, T.A., and BELOSEVIC, M. 1981. Parasites of arctic charr *Salvelinus alpinus* (Linnaeus) and their use in separating sea-run and non-migrating charr. Journal of Fish Biology 18:339–347.
- GROSS, M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14–25.
- GUNTHER, A. 1877. Account of the fishes collected by Capt. Fielden between 78° and 83°N lat., during the Arctic Expedition of 1875–6. Zoological Society of London Proceedings 1877:293–297.
- HALDEN, N.M., BABALUK, J.A., CAMPBELL, J.L., and TEESDALE, W.J. 1995. Scanning proton microprobe analysis of strontium in an arctic charr, *Salvelinus alpinus*, otolith: Implications for the interpretation of anadromy. Environmental Biology of Fishes 43:333–339.
- HALDEN, N.M., BABALUK, J.A., KRISTOFFERSON, A.H., CAMPBELL, J.L., TEESDALE, W.J., MAXWELL, J.A., and REIST, J.D. 1996. Micro-PIXE studies of Sr zoning in Arctic charr otoliths: Migratory behaviour and stock discrimination. Nuclear Instruments and Methods in Physics Research B109/110:592–597.
- HUNTER, J.G. 1960. Hazen Lake. In: Fisheries Research Board of Canada, Arctic Unit. Annual Report and Investigators Summaries (April 1, 1959 to March 31, 1960). Ottawa. 18–20.
- ICHII, T., and MUGIYA, Y. 1983. Effects of dietary deficiency in calcium on growth and calcium uptake from the aquatic environment in the goldfish, *Carassius auratus*. Comparative Biochemistry and Physiology 74(A):259–262.
- JOHNSON, L. 1980. The arctic charr, *Salvelinus alpinus*. In: Balon, E.K., ed. Charrs: Salmonid fishes of the genus *Salvelinus*. The Hague: Dr. W. Junk Publishers. 15–98.
- . 1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 40:987–1024.
- . 1989. The anadromous arctic charr, *Salvelinus alpinus*, of Nauyuk Lake, N.W.T., Canada. In: Kawanabe, H., Yamazaki, F., and Noakes, D.L.G., eds. Biology of charrs and masu salmon: Proceedings of the International Symposium on Charrs and Masu Salmon. Physiology and Ecology Japan. Special Vol. 1. 201–227.
- . 1990. Hazen Lake. In: Lake Biwa Research Institute and International Lake Environment Committee, eds. Data book of world lake environments. Otsu, Japan: United Nations Environment Programme. 1–9.
- JONSSON, B., and JONSSON, N. 1993. Partial migration: Niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348–365.
- KALISH, J.M. 1989. Otolith microchemistry: Validation of the effects of physiology, age and environment on otolith composition. Journal of Experimental Marine Biology and Ecology 132:151–178.
- . 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fishery Bulletin 88:657–666.
- KRISTOFFERSEN, K., and KLEMETSEN, A. 1991. Age determination of arctic charr (*Salvelinus alpinus*) from surface and cross section of otoliths related to otolith growth. Nordic Journal of Freshwater Research 66:98–107.
- MUGIYA, Y. 1964. Calcification in fish and shell-fish-III. Seasonal occurrence of a prealbumin fraction in the otolith fluid of some fish, corresponding to the period of opaque zone formation in the otolith. Bulletin of the Japanese Society of Scientific Fisheries 30:955–967.
- NORDENG, H. 1983. Solution of the “charr problem” based on char, *Salvelinus alpinus*, in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40:1372–1387.
- NORTHCOTE, T.G. 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S.D., ed. Ecology of freshwater fish populations. New York: John Wiley and Sons. 326–359.
- PARKS CANADA. 1994. Ellesmere Island National Park Reserve resource description and analysis. Winnipeg, Manitoba: Department of Canadian Heritage.
- RADTKE, R.L. 1989. Strontium-calcium concentration ratios in fish otoliths as environmental indicators. Comparative Biochemistry and Physiology 92(A):189–193.
- . 1995. Otolith microchemistry of charr—use in life history studies. Nordic Journal of Freshwater Research 71:392–395.
- RADTKE, R.L., and TARGETT, T.E. 1984. Rhythmic structure and chemical patterns in otoliths of the Antarctic fish *Notothenia larseni*: Their application to age determination. Polar Biology 3:203–210.
- RADTKE, R.L., SVENNING, M., MALONE, D., KLEMETSEN, A., RUZICKA, J., and FEY, D. 1996. Migrations in an extreme northern population of arctic charr *Salvelinus alpinus*: Insights from otolith microchemistry. Marine Ecology Progress Series 136:13–23.

- RADTKE, R.L., TOWNSEND, D.W., FOLSOM, S.D., and MORRISON, M.A. 1990. Strontium:calcium concentration ratios in larval herring otoliths as indicators of environmental histories. *Environmental Biology of Fishes* 27:51–61.
- REIST, J.D., GYSELMAN, E., BABALUK, J.A., JOHNSON, J.D., and WISSINK, R. 1995. Evidence for two morphotypes of arctic char (*Salvelinus alpinus*) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. *Nordic Journal of Freshwater Research* 71:396–410.
- REIST, J.D., JOHNSON, J.D., and CARMICHAEL, T.J. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. *American Fisheries Society Symposium* 19:250–261.
- RIEMAN, B.E., MYERS, D.L., and NIELSEN, R.L. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. *Canadian Journal of Fisheries and Aquatic Sciences* 51:68–77.
- ROSENTHAL, H.L., EVES, M.M., and COCHRAN, O.A. 1970. Common strontium concentration of mineralized tissues from marine and sweet water animals. *Comparative Biochemistry and Physiology* 32:445–450.
- SADOVY, Y., and SEVERIN, K.P. 1994. Elemental patterns in red hind (*Epinephelus guttatus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. *Canadian Journal of Fisheries and Aquatic Sciences* 51:133–141.
- SIMKISS, K. 1974. Calcium metabolism of fish in relation to ageing. In: Bagenal, T.B., ed. *Ageing of fish*. London: Unwin Brothers. 1–12.
- STEWART, D.B. 1994. Limnology and marine biology. In: *Ellesmere Island National Park Reserve resource description and analysis*. Winnipeg, Manitoba: Department of Canadian Heritage.
- SUTHERLAND, P.D. 1989. An inventory and assessment of the prehistoric archaeological resources of the Ellesmere Island National Park Reserve. Microfiche Report Series 431. Winnipeg, Manitoba: Department of Canadian Heritage.
- SVENNING, M.-A., SMITH-NILSEN, A., and JOBLING, M. 1992. Sea water migration of arctic charr (*Salvelinus alpinus* L.)—correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. *Nordic Journal of Freshwater Research* 67:18–26.