

Freshwater Form of Fourhorn Sculpin (*Myoxocephalus quadricornis*) from Lake Tuborg, Ellesmere Island, Nunavut, with Reference to other Canadian Lacustrine and Riverine Populations

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ABSTRACT. Fourhorn sculpin (*Myoxocephalus quadricornis*) is ubiquitous in Canadian Arctic waters with a more common marine and brackish form and a rarer freshwater form. There is a paucity of information available for the freshwater form from Canadian waters. In the summer of 2003, we serendipitously collected 28 of the freshwater form of fourhorn sculpin from Lake Tuborg, Ellesmere Island, Nunavut. The fish ranged in size from 62 mm to 171 mm total length and age from 1 to 12 years with females growing faster and to a larger theoretical maximum total length than males. The sculpin preyed mainly upon the crustacean, *Mysis segerstralei*, but were also opportunistic feeders (e.g., Arctic charr (*Salvelinus alpinus*) eggs) and cannibalistic. Although our sample of fourhorn sculpin is small, the data from these fish represent the only information from a fully freshwater form population of the species from Canadian waters. We also present an updated list of the known Canadian lacustrine and riverine populations of fourhorn sculpin.

Key words: fourhorn sculpin; *Myoxocephalus quadricornis*; freshwater form; age; growth; diet; *Mysis segerstralei*; habitat

RÉSUMÉ. Le chaboisseau à quatre cornes (*Myoxocephalus quadricornis*) est une espèce ubiquiste des eaux de l'Arctique canadien, se retrouvant sous une forme plus courante dans l'eau de mer et l'eau saumâtre, et sous une forme plus rare dans l'eau douce. Il n'y a pas beaucoup d'information au sujet de la forme d'eau douce de ce poisson au Canada. À l'été 2003, nous avons fait la collecte fortuite de 28 chaboisseaux à quatre cornes d'eau douce au lac Tuborg, sur l'île d'Ellesmere, au Nunavut. La longueur totale de ces poissons âgés d'un à douze ans variait de 62 mm à 171 mm. Les femelles grandissaient plus vite et atteignaient une longueur totale maximale théorique plus grande que celle des mâles. Le chaboisseau s'alimentait principalement du crustacé *Mysis segerstralei*, mais il était aussi opportuniste (œufs d'omble chevalier (*Salvelinus alpinus*), par exemple) et cannibale. Bien que notre échantillon de chaboisseaux à quatre cornes soit mince, les données prélevées grâce à ces poissons représentent les seules données d'une telle population évoluant entièrement en eau douce canadienne. Nous présentons également une liste à jour des populations lacustres et riveraines canadiennes connues de chaboisseaux à quatre cornes.

Mots clés : chaboisseau à quatre cornes; *Myoxocephalus quadricornis*; forme dans l'eau douce; âge; croissance; régime alimentaire; *Mysis segerstralei*; habitat

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INTRODUCTION

The fourhorn sculpin (*Myoxocephalus quadricornis*) (Fig. 1) has a global, Arctic circumpolar distribution (Kontula and Väinölä, 2003). The species mainly inhabits shallow, coastal, marine waters including brackish estuaries. It is ubiquitous in Canadian Arctic marine and estuarine waters from Yukon in the west to northern Labrador in the east and is present off the north coast of Ellesmere Island in the High Arctic and the southern portion of James Bay in the south (Coad, 2018). While the fourhorn sculpin is mainly a marine species, several freshwater

relict populations of the species have been found, including populations from Norway (Kraabøl et al., 2012), Sweden (Westin, 1968), Finland (Savolainen, 1975), and Russia (Bogutskaya et al., 2001). In Canada, it has been reported in several Arctic coastal lakes (e.g., Garrow Lake, Dickman, 1995; Romulus Lake, Davidge, 1994) and a glacial relict freshwater form of the species has been reported in several lakes on the Nunavut portion of Victoria Island (Johnson, 1964). Although current knowledge indicates that there is no overlap in distributions (Sheldon et al., 2008), there is potential to confuse the freshwater form of fourhorn sculpin with the deepwater sculpin (*Myoxocephalus*

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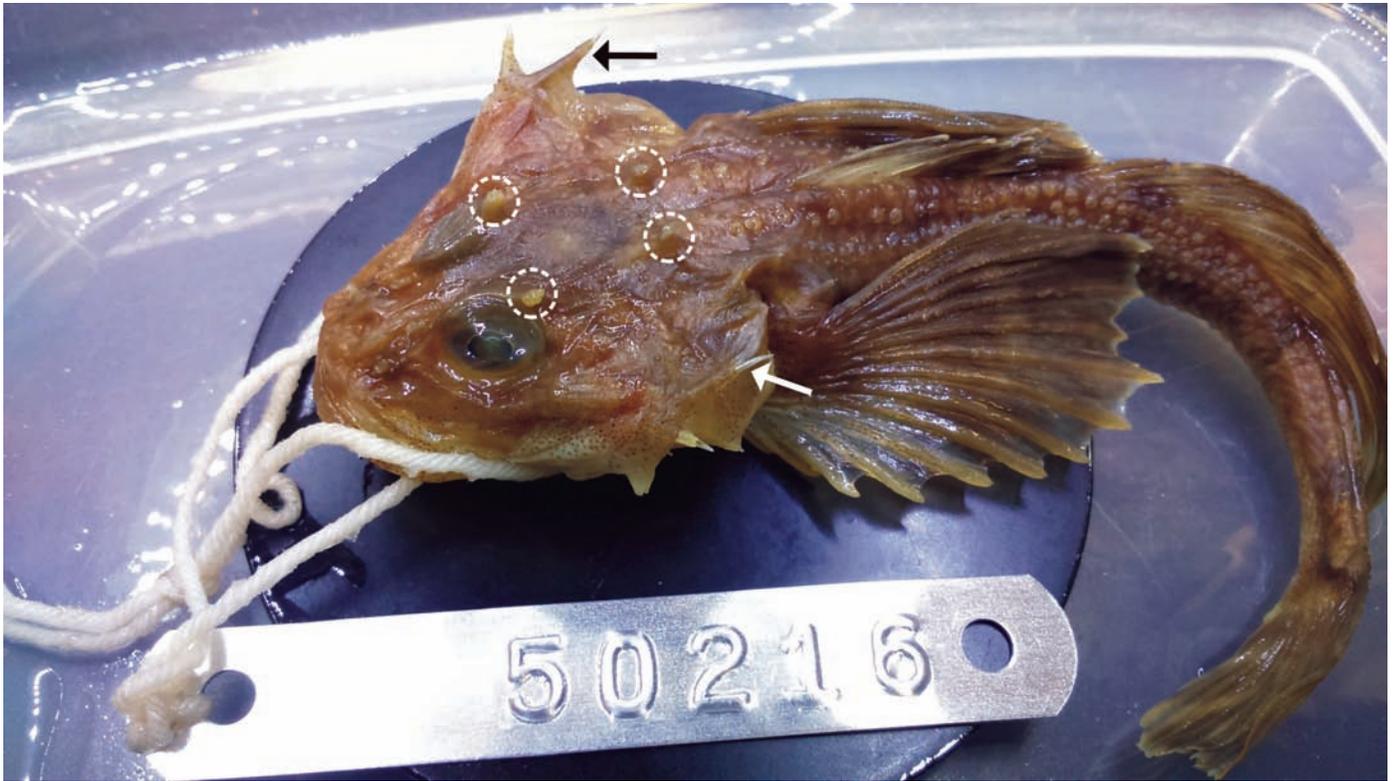


FIG. 1. Freshwater form of fourhorn sculpin from Lake Tuborg (total length = 154 mm). Preopercular spines indicated by arrows. Reduced cephalic spines (“horns”) indicated by broken-line circles.

thompsonii), another relict freshwater, lake-dwelling species that is closely related phylogenetically (Kontula and Väinölä, 2003; Goto et al., 2015) and similar phenotypically (McAllister, 1961; McAllister and Aniskowicz, 1976).

While there has been some incidental research conducted on the marine form of fourhorn sculpin in Canada (e.g., Lawrence et al., 1984; Roux et al., 2014) and some directed research in Scandinavia and other areas of its distribution (e.g., Goldberg et al., 1987; Bengtsson, 1993), there is a general lack of biological and ecological information available for the freshwater form. While some studies have been conducted on the geographic distribution, ecology, and feeding of the freshwater form in the Scandinavian countries (e.g., Savolainen, 1975; Hammar et al., 1996), the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) noted that there was a paucity of information on the freshwater form of fourhorn sculpin in Canada and designated the freshwater form a species of “special concern” in 1989 (Houston, 1990). A wildlife species of special concern is defined as one “that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats” (COSEWIC, 2008:19). COSEWIC (2003) formally declared that the freshwater form of fourhorn sculpin was “data deficient,” defined as “a category that applies when the available information is insufficient (a) to resolve a wildlife species’ eligibility for assessment or (b) to permit an assessment of the wildlife species’ risk of extinction” (COSEWIC, 2019:1). Currently, the freshwater form of

fourhorn sculpin in Canada is still considered data deficient (COSEWIC, 2020). Although there is little biological, morphometric, and meristic data available on the freshwater form, specimens of several lake-dwelling populations in the Canadian Arctic are in the permanent collection of the Canadian Museum of Nature (<https://nature.ca/en/research-collections/collections>) and are referred to and listed as the glacial, relict, freshwater form of the species by COSEWIC (2003).

Here, we present the first insights into the biology and ecology of the freshwater form of fourhorn sculpin from Lake Tuborg, Ellesmere Island, Nunavut, and where possible, compare this information to other populations of the freshwater form. We also comment on the current status of the freshwater form of the species in Canada.

MATERIALS AND METHODS

Study Area

Lake Tuborg, Ellesmere Island, Nunavut (80°58'N, 75°37'W) (Fig. 2) has a surface area of ~42 km², a maximum length of 29.4 km, and a maximum width of 3.4 km (Lewis et al., 2007). It was formed approximately 3000 years ago when the Antoinette Glacier advanced and pinched off Greely Fiord “trapping” sea water and creating a fiord-type lake (Hattersley-Smith and Serson, 1964; Bowman and Long, 1968). The lake is comprised of two basins: a

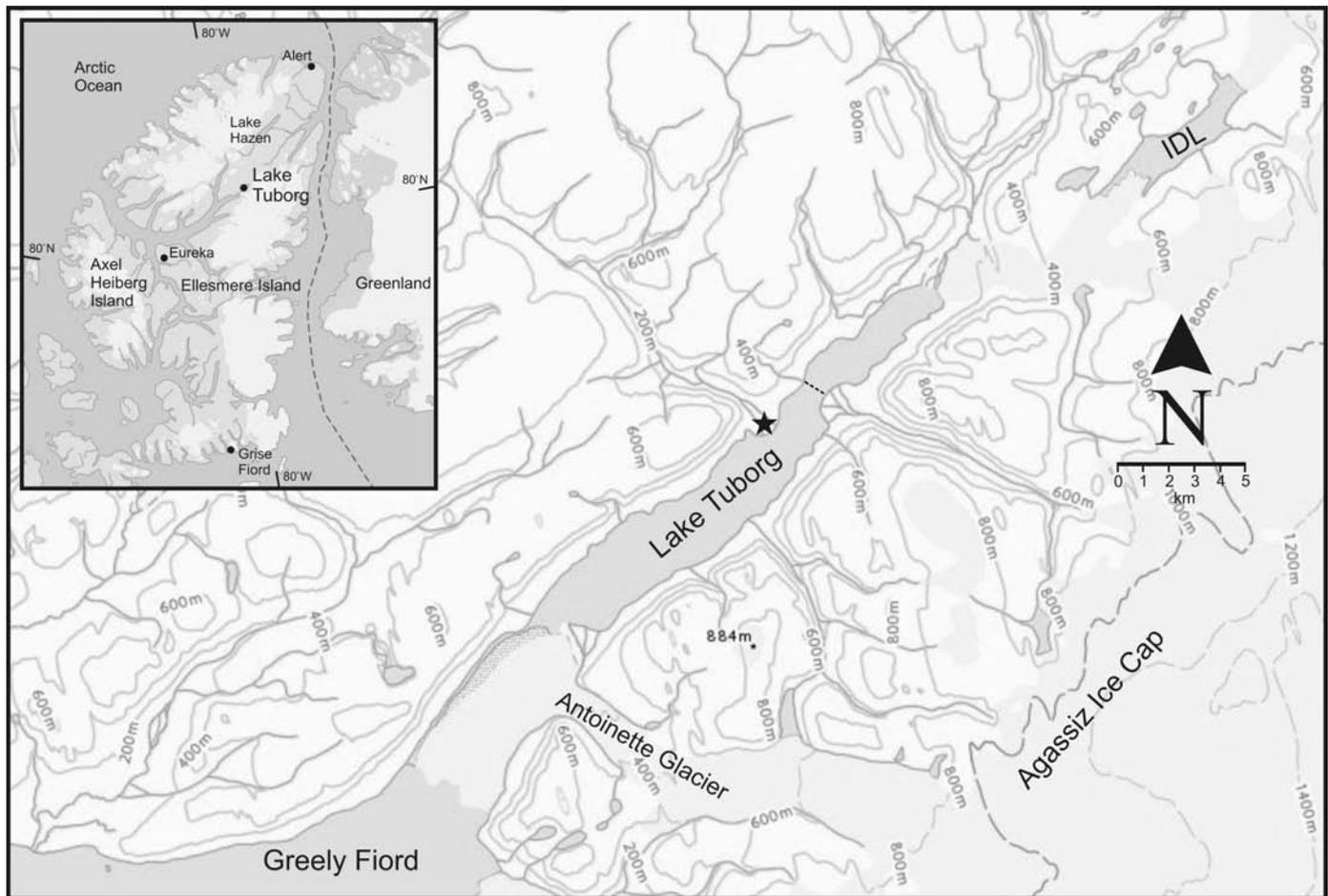


FIG. 2. Lake Tuborg area, Ellesmere Island, Nunavut showing the collection site (star) for fourhorn sculpin. Dashed line indicates separation of lake basins. IDL = ice-dammed lake.

larger, deeper (maximum depth = ~145 m) meromictic basin at its southwest end, which is made up of a 50–60 m layer of freshwater overlying anoxic, marine water, and a smaller, shallower (maximum depth = ~74 m) totally freshwater basin at its northeast end (Lewis et al., 2007) (Fig. 2). Lake Tuborg is fed by snow and glacial meltwaters. The lake is ~10–12 m above sea level (Hattersley-Smith and Serson, 1964), drains via a short stream (~6 km) into Antoinette Bay (Greely Fiord) (Bowman and Long, 1968), and it retains partial ice cover in most summers (Lewis et al., 2007). The limnology, sedimentology, and hydrology of Lake Tuborg are further described by Smith et al. (2004) and Lewis et al. (2007). The only biota previously reported from Lake Tuborg are three copepods: *Drepanopus bungei*, *Limnocalanus macrurus grimaldii*, and *Oncaea borealis* (now *Triconia borealis*) (Bowman and Long, 1968). Anadromous and resident Arctic charr (*Salvelinus alpinus*) (Babaluk and Reist, unpublished data) and fourhorn sculpin (this study) are the only known fish species in Lake Tuborg.

Fish Collection

Commencing on 25 July 2003, and lasting for approximately 3.5 days, a large ice-dammed lake (IDL) to

the northeast of Lake Tuborg (Fig. 2) drained catastrophically and completely (a jökulhlaup, Icelandic term meaning glacial outburst flood) into Lake Tuborg. During this time the water level in Lake Tuborg rose by 7.6 m (Lewis et al., 2007). By 4 August 2003 the level of Lake Tuborg had dropped, leaving large pools on previous flooded flat areas near the lake shore. Presumptive fourhorn sculpin were stranded in these pools. A sample of sculpin ($n = 28$) representing the size range available in the pools was collected by hand from residual pools adjacent to a large delta (Fig. 2). The sculpin were fixed in the field in 10% formalin and then transported to the laboratory in Winnipeg, Manitoba, where they were flushed with water, placed in 70% alcohol, and subsequently identified after being processed for morphologic, meristic, and biological information.

The IDL occupies a small valley (between 300 m and 460 m asl) above Lake Tuborg (~11 m asl), is in contact with glacier ice at both ends, and is fed by supraglacial meltwater from the Agassiz Ice Cap (Lewis et al., 2007). The IDL also drained in 1993 and 1960 (Lewis et al. 2009). Similar ice-dammed lakes in western Canada contain no fish populations (J. Claque, Simon Fraser University, Burnaby, British Columbia, pers. comm. 2022). The topography around the IDL above Lake Tuborg coupled with the

sporadic draining of this ephemeral lake strongly suggested that the provenance of the sculpin was Lake Tuborg rather than the IDL.

Morphological and Meristic Data

Ideally, morphological data (e.g., total length [TL]) should be collected from fresh specimens as preservation methods of any kind will alter body shape and size (e.g., Sotola et al., 2019). In our study, formalin fixation and alcohol preservation would have resulted in shrinkage in lengths (e.g., Shields and Carlson, 1996; Kristoffersen and Salvanes, 1998). However, Kristoffersen and Salvanes (1998) noted that shrinkage in length was small when a formalin/alcohol preservation regimen was used (0.8–3.0%). With this in mind, we present data collected from preserved specimens.

To confirm the field identification of the sculpin, a suite of morphometric measurements (e.g., total and standard length in mm) and meristic counts (e.g., fin ray counts) following Reist et al. (1995) was collected from all 28 fish. Included in the morphometric measurements for each fish was preoperculum spine length. According to McAllister (1961), the ratio of the preopercular spine length to standard length is a key identifier of the species (i.e., to separate fourhorn sculpin from deepwater sculpin). Meristic counts also included vertebral counts (including the urostyle) for seven specimens. McAllister and Aniskowicz (1976) demonstrated that vertebral number could also be used to separate fourhorn from deepwater sculpins. Another meristic count for all Lake Tuborg sculpin was that of cephalic “horns”. Fourhorn sculpin, as its common name implies, possess four prominent cephalic horns (modified spines) atop their heads that are more prominent on marine-dwelling than on lake-dwelling individuals (Leim and Scott, 1966; Dickman, 1995, respectively). These spines are absent in deepwater sculpin (Stewart and Watkinson, 2004). One specimen, collected from Lake Tuborg in 2002 as by-catch of an Arctic charr collection project, was sent to the Canadian Museum of Nature, Ottawa, for confirmation of identification.

Biological Data

Sex was determined from gross observation of the gonads. Sagittal otoliths were collected for age estimation using a break and burn technique as described in Reist et al. (1995) and age estimation criteria described in Chilton and Beamish (1982). Although the sculpin, including the otoliths were stored for a short period in formalin and then alcohol, there would be no impact on clarity of otolith annual growth increments (i.e., age estimation) (Kristoffersen and Salvanes, 1998). The stomach contents of seven of the sculpin were examined under a microscope and identified to the lowest taxonomic level possible and enumerated. Length-at-age growth analysis (von Bertalanffy growth curves) was conducted for each sex using the FiSAT II

computer software program (Gayanilo et al., 2005). Small (< 80 mm TL), immature specimens, where sex was uncertain, were used in both male and female estimation calculations so male $n = 18$ (12 known male, six uncertain sex) and female $n = 16$ (10 known female, six uncertain sex). The von Bertalanffy growth curve equation is:

$$TL_t = TL_\infty [1 - \exp^{-K(t-t_0)}]$$

where TL_t = total length at age t ; TL_∞ = asymptotic (maximum) length; K = rate at which the growth curve approaches the asymptote; and t_0 = theoretical age at which length is zero. The male and female growth curves were tested for differences with an F -test (Snedecor and Cochran, 1983).

Habitat Type

On 30 July 2002, we collected water samples from the freshwater layer (3.0 m) and the anoxic, relict, marine layer (70.0 m) of Lake Tuborg through a hole in the ice using a Van Dorn sampler. Samples were preserved in the field for subsequent analyses at Fisheries and Oceans Canada's Freshwater Institute Analytical Water Chemistry Laboratory in Winnipeg following the procedures of Stainton et al. (1977). Most of the referenced articles for this study reported salinities as parts per thousand (‰) (e.g., Hattersley-Smith and Serson, 1964 for Lake Tuborg). We report those values, but in keeping with current limnological studies convention (Wetzel, 2001), we have converted salinity values to conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) according to the procedures in Wagner et al. (2006) and have noted the converted data in the text. Freshwaters generally have conductivities < 1000 $\mu\text{S}\cdot\text{cm}^{-1}$ (Wetzel, 2001), brackish waters have conductivities that can range from 1000 $\mu\text{S}\cdot\text{cm}^{-1}$ to 3000 $\mu\text{S}\cdot\text{cm}^{-1}$ (Hillel, 2000), and Tyler et al. (2017) reported 33,100 $\mu\text{S}\cdot\text{cm}^{-1}$ as an average for the global ocean.

RESULTS

Identification

According to McAllister (1961), the relationship between preopercular spine length and standard length (as a percentage) is a key identifying characteristic between the fourhorn (marine/freshwater) and deepwater (freshwater) sculpins. If the value is $\geq 4.6\%$, the fish is a fourhorn sculpin and if it is $\leq 4.5\%$, it is a deepwater sculpin. All 28 of the Lake Tuborg sculpin had values $\geq 4.6\%$ (range = 5.1–7.3%). When standard length was plotted against preopercular spine length for Lake Tuborg sculpin, all fell into McAllister's (1961) range for fourhorn sculpin (Fig. 3). McAllister and Aniskowicz (1976) noted that the mean vertebral count for brackish- and marine-dwelling fourhorn sculpin was 41.8, freshwater relict fourhorn sculpin from Victoria Island lakes was 41.1, and for deepwater sculpin,

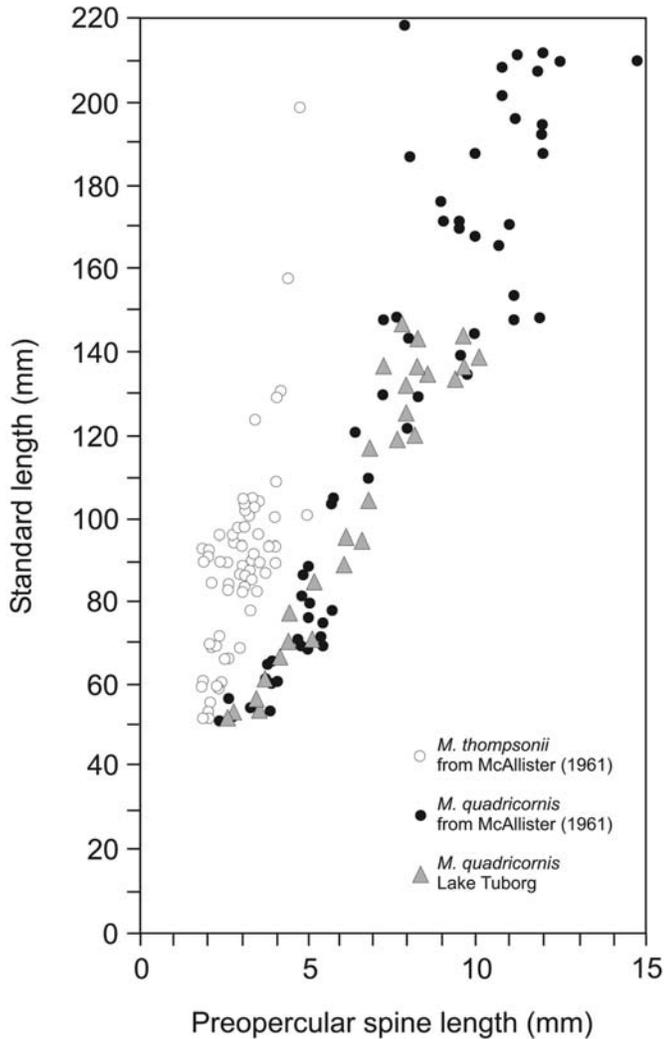


FIG. 3. Relationship between preopercular spine length and standard length for selected Canadian fourhorn (*M. quadricornis*) and deepwater (*M. thompsonii*) sculpin (modified from McAllister, 1961) and Lake Tuborg fourhorn sculpin (this study).

the mean count was 38.4. For Lake Tuborg sculpin, the mean vertebral count was 41.6, placing them in the fourhorn sculpin range. Twenty-three of 28 Lake Tuborg sculpin had four countable cephalic horns (see Fig. 1), while the remaining five specimens had only two countable horns. The sculpin specimen collected in 2002 and sent to the Canadian Museum of Nature for identification was also identified as fourhorn sculpin. It was deposited in the museum's collections and assigned the collection number CMNFI 2002-0013.1. Hardcopies of the biological, morphometric, and meristic data for the sculpin from the 2003 Lake Tuborg collection have also been deposited in the fish collection documentation room at the museum.

Age and Growth

The 28 fourhorn sculpin captured from Lake Tuborg in 2003 ranged in total length from 62 mm to 171 mm and age from 1 to 12 years old. Using the fish where sex was known,

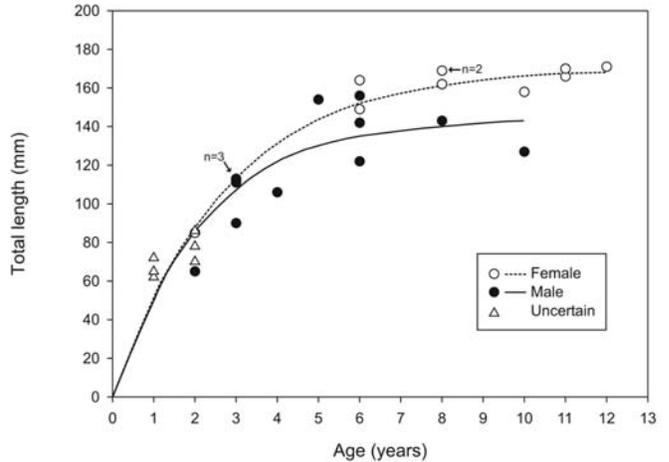


FIG. 4. Relationship between age and total length for Lake Tuborg fourhorn sculpin. All symbols represent individual fish except where indicated by number.

the male:female ratio was 1.0:0.8. For each sex, the von Bertalanffy growth curve estimate was as follows (Fig. 4):

$$\text{Male: } TL_t = 145.32 [1 - \exp^{-0.44(t-0.0)}];$$

$$\text{Female: } TL_t = 171.61 [1 - \exp^{-0.36(t-0.0)}].$$

Differences in growth between the sexes were evident in the third year of life where females started to show faster growth, reaching a theoretical maximum total length of 171.61 mm, whereas the males had a theoretical maximum total length of 145.32 mm. The growth curves of Lake Tuborg sculpin differed significantly between the sexes (F test: $p < 0.05$) (Fig. 4).

Stomach Contents

Of the seven fourhorn sculpin stomachs examined, all contained the crustacean *Mysis segerstralei* (formerly *Mysis relicta*). The mysids were identified according to Audzijonyte and Väinölä (2005) and R. Väinölä (University of Helsinki, Helsinki, Finland, pers. comm. 2021). The number of mysids in the stomachs ranged from one to eight. A complete, preserved specimen of *M. segerstralei* from Lake Tuborg has been deposited into the permanent collection at the Canadian Museum of Nature (catalogue no. CMNC 2021-0098). Several of the sculpin stomachs also contained other prey items: one contained 102 fertilized Arctic charr eggs with a mean diameter of 4.0 mm (Arctic charr egg diameter range = 3.2–4.5 mm; Johnson, 1980); one contained a fourhorn sculpin (~55 mm TL); and another contained a spider (Family: Linyphiidae) (D. Shorthouse, Agriculture and Agri-Food Canada, Ottawa, Ontario pers. comm. 2021).

Habitat

For Lake Tuborg's southwest basin, Hattersley-Smith and Serson (1964) reported salinities of 0.46‰ (conductivity

~935 $\mu\text{S}\cdot\text{cm}^{-1}$, converted from ‰) for the freshwater layer and 25.59‰ (~40,101 $\mu\text{S}\cdot\text{cm}^{-1}$, converted) for the seawater layer. Lewis et al. (2007) measured conductivities and reported similar values for the layers of ~900 $\mu\text{S}\cdot\text{cm}^{-1}$ and ~41,850 $\mu\text{S}\cdot\text{cm}^{-1}$, respectively. Water samples collected and analyzed for this study yielded values of 611 $\mu\text{S}\cdot\text{cm}^{-1}$ at 3.0 m depth and 29,003 $\mu\text{S}\cdot\text{cm}^{-1}$ at 70.0 m depth. Conductivities from the lake's freshwater northeastern basin (Fig. 2) is freshwater throughout its ~80 m water column (Smith et al., 2004). Conductivities for this basin ranged from ~500 $\mu\text{S}\cdot\text{cm}^{-1}$ to 800 $\mu\text{S}\cdot\text{cm}^{-1}$ (Smith et al., 2004; Lewis et al. 2007). Therefore, the fourhorn sculpin of Lake Tuborg comprise a totally freshwater dwelling population.

DISCUSSION

Age and Growth

The Lake Tuborg fourhorn sculpin in our study ranged from 62 mm to 171 mm in total length and in age from 1–12 years old. The only comparable data available for fourhorn sculpin from Canadian lacustrine waters are from Garrow Lake, Little Cornwallis Island, Nunavut, where the sculpin ranged in total length from 118 mm to 199 mm and in age from 4–10 years (Fallis and Harbicht, 1980). Few studies on age and growth of Scandinavian populations of the glacial relict freshwater form of the fourhorn sculpin have been conducted (Timola and Luotonen, 1986). However, Timola and Luotonen (1986), using similar age estimation methods as we did, found that the fourhorn sculpin of northeastern Bothnian Bay, Finland and Sweden, essentially a freshwater body (Kautsky and Kautsky, 2000), had a size range from ~115 mm to 275 mm total length and an age range of 2–11 years.

The length-at-age analysis of the Lake Tuborg fourhorn sculpin (Fig. 4), while an approximation due to a relatively small sample size, does offer some insight into growth of the fish. Sexual dimorphism in growth was indicated at approximately age three years where females began to grow faster and to a greater theoretical maximum length than males. There are no comparable data from other freshwater forms of fourhorn sculpin from Canadian waters, although similar sexual dimorphism in growth has been reported in the marine form in Arctic Canada (e.g., Lawrence et al., 1984) and in northern Europe (e.g., Bengtsson, 1993). Timola and Luotonen (1986) did not segregate the sexes in their sample of Bothnian Bay fourhorn sculpin, thus gave mean total length-at-age values for the combined sexes. Not surprisingly, the Bothnian Bay sculpin were larger at a given age than Lake Tuborg sculpin (e.g., Bothnian Bay: age two are ~115 mm, age six are ~190 mm; Lake Tuborg: age two are ~65–80 mm, age six are ~120–160 mm). Bothnian Bay sculpin grew to a greater observed maximum size (~275 mm) than did those from Lake Tuborg (171 mm). Growth of fish is primarily dependent on food (quality and quantity) and temperature. Bothnian Bay is a

more productive habitat than Lake Tuborg with its warmer climate, and greater species diversity and abundance (Kautsky and Kautsky, 2000; Bowman and Long, 1968, respectively).

Diet

What is currently known of the diet of the freshwater form of fourhorn sculpin is primarily limited to the populations from Scandinavia. In a study of fourhorn sculpin from 11 Finnish lakes, Savolainen (1975) found that 84% of sculpin examined contained crustaceans with *Mysis relicta* being the dominant prey species followed by *Pallasea quadrispinosa* and *Limnocalanus macrurus*. Trichoptera (caddisfly) pupae, halacarid (mites) larvae, *Coregonus* spp. (whitefishes) eggs, and *Cyclops* spp. were also found in sculpin stomachs. Fourhorn sculpin in Swedish lakes fed on a wide range of benthic and semi-pelagic crustaceans such as the sympatric *M. relicta* and *Mysis salemaai* (Audzijonyte and Väinölä, 2005), *P. quadrispinosa*, *Gammaracanthus lacustris*, *Pontoporeia affinis* (now *Monoporeia affinis*), and *Mesidotea entomon* (now *Saduria entomon*) (Westin, 1968). In Lake Vättern, Sweden, Hammar et al. (1996) found that cyclopods were the main prey item of fourhorn sculpin followed by *M. relicta* and *M. salemaai*, *G. lacustris*, and *S. entomon*. They also fed on chironomid larvae and pupae and ostracods.

There is a dearth of information on the food of freshwater fourhorn sculpin in Canada. The only available information is from Fallis and Harbicht (1980) who reported that the fourhorn sculpin of Garrow Lake fed on amphipods, copepods, and sculpin eggs. Compared to relatively nearby and more studied Lake Hazen (~90 km to the northeast of Lake Tuborg; Fig. 1 inset) (Oliver, 1963; McLaren, 1964), very little is known about the benthic invertebrates and zooplankton (potential food for the fourhorn sculpin) in Lake Tuborg. The only previously reported zooplankton in Lake Tuborg are the copepods *L. macrurus*, *D. bungei*, and *T. borealis* (Bowman and Long, 1968). The only pelagic and the main prey of the Lake Tuborg sculpin was *M. segerstralei*, which suggests that the copepods reported from the lake (*L. macrurus* in particular, which has been reported in Scandinavian sculpin stomachs) are not abundant, at least at the time of sculpin capture (early August). The fertilized Arctic charr eggs in the stomach of one of the sculpin capture suggested that it was an opportunistic benthic feeder. The timing of the sculpin capture also suggested that the Arctic charr in Lake Tuborg were spawning at that time. Arctic charr typically spawn in autumn. However, some populations are known to spawn at other times of the year including summer (Klemetsen et al., 1997). The small sculpin in the stomach of one of the sculpin indicated cannibalistic behaviour and coupled with the charr egg-eating, suggested that charr larvae and fry may also be susceptible to predation by the sculpin. While piscivory has been reported for the marine form of fourhorn sculpin (e.g., Lawrence et al., 1984), there are no

previous reports of cannibalism or piscivorous behaviour for Scandinavian freshwater fourhorn sculpin (e.g., Westin, 1968; Savolainen, 1975; Hammar et al., 1996). Fallis and Harbicht (1980) referred to sculpin eggs in the stomach of one of their sculpin specimens. The presence of a spider in one Lake Tuborg sculpin stomach also indicated opportunistic feeding behaviour. The spider was likely made available to the sculpin after the drop in Lake Tuborg water levels (post-jökulhlaup) exposed more of the deltas of the inlet streams.

Freshwater Form of Fourhorn Sculpin in Canada in Relation to Habitat Type

The formation of the majority of Canadian Arctic lakes containing fourhorn sculpin was the result of post-glacial uplift (isostatic rebound) of land previously covered by the ice during the Wisconsinan glaciation period (Clayton and Moran, 1982). After thinning and retreat of the ice sheet, coastal areas were initially covered by encroaching sea water. This would have been followed by an uplifting of the land which eventually would have isolated newly formed lakes (e.g., Garrow Lake, formed ~3000 BP; Dickman and Ouellet, 1987). Another form of post-glacier lake formation resulted in fiord-type lakes, of which Lake Tuborg is an example (formed ~3000 BP; Bowman and Long, 1968). In these cases, lakes were formed as a result of glaciers advancing and pinching off the fiord. In both types of lake formation, seawater and marine biota (fish and invertebrates) would have been trapped in the resultant lake. Over time the salinity of the waters in these lakes would have been reduced by varying degrees depending on geographical factors such as size and morphology of the lake's drainage basin and precipitation and snow melt. Gradual desalination would have provided an ideal milieu for the evolution of freshwater adaptation in isolated marine lineages. Most likely, freshwater populations of the fourhorn sculpin originated independently in different lakes. Preliminary genetic analyses, not presented here, indicated that the Lake Tuborg population is distinct from marine fourhorn sculpin, based on the possession of a distinct mitochondrial haplotype (N. Lovejoy, University of Toronto, pers. comm. 2022).

Lake forms of the fourhorn sculpin may occur in waters with a variety of salinities. The habitats of Lake Tuborg potentially occupiable by fish are exclusively freshwater, thus this population of fourhorn sculpin is most likely fully adapted to freshwater. The inland lakes on Victoria Island containing fourhorn sculpin such as Ferguson (now called Tahiryuaq), Washburn, and Zeta Lakes are also freshwater, as implied by their inland locations and low Cl^- values (Johnson, 1964). However, fourhorn sculpin also occur in Garrow Lake, Little Cornwallis Island (Dickman, 1995), which has a measured conductivity of ~1000 $\mu S \cdot cm^{-1}$ in its surface waters (0–1 m), 3100 $\mu S \cdot cm^{-1}$ at 2 m, 10,000 $\mu S \cdot cm^{-1}$ between 5m and 12 m, and 79,800 $\mu S \cdot cm^{-1}$ at 17 m (Ouellet

et al., 1989). All fourhorn sculpin captured in Garrow Lake were taken from the 5m to 15 m depth range (Dickman, 1995) where the conductivity was ~10,000 $\mu S \cdot cm^{-1}$. For comparison, the conductivity of seawater just off the coast of Little Cornwallis Island in the general vicinity of Garrow Lake is between 52,100 and 53,000 $\mu S \cdot cm^{-1}$ (converted from salinities of 34.3‰ and 35.0‰ reported by Dickman and Ouellet, 1987). Fourhorn sculpin also appear to inhabit Romulus Lake, Ellesmere Island. No sculpin have been captured in the lake, but they were observed close to shore in the brackish mixolimnion layer of the lake (Davidge, 1994). The conductivity of the mixolimnion is ~17,000 $\mu S \cdot cm^{-1}$ (Davidge, 1994; Van Hove et al., 2006). The fourhorn sculpin populations from Romulus, Garrow, and Tuborg Lakes respectively may represent different stages in the adaptation of the populations from marine forms to exclusively freshwater forms.

The relatively rare, totally freshwater fourhorn sculpin of Lake Tuborg may be susceptible to potential changes in habitat as a result of climate change. The Antoinette Glacier of the Agassiz Ice Cap was advancing when it isolated Lake Tuborg from the sea ~3000 years BP (Long, 1967). However, the Agassiz Ice Cap is currently experiencing rapid melt and negative mass balance (Sharp et al., 2011; Burgess, 2017). Lake Tuborg may be vulnerable to the current recession of the Antoinette Glacier at its outlet. The glacier's terminal moraine currently controls the lake outlet to the sea. The subsequent deposited sediments from the continually receding glacier may impact water quality (e.g., turbidity) in its vicinity as well as allowing for potential changes to the outlet of the lake.

COSEWIC (2003) lists the freshwater form of fourhorn sculpin as being present in fewer than 20 lakes in the Canadian Arctic, the majority of which are freshwater (e.g., Lake Tuborg, the Victoria Island lakes, Stanwell-Fletcher Lake). However, because of the relatively high conductivities of several of the lakes listed in COSEWIC (2003) (e.g., Garrow, Romulus, and Husky Lakes), some of these fourhorn sculpin populations should be considered more likely to be brackish forms rather than true freshwater forms. We suggest that the current COSEWIC list of lakes inhabited by the freshwater form of fourhorn sculpin should be revised based on a more careful evaluation of the habitat occupancy and conductivity of each lake and towards that, we present a list of the known lacustrine and riverine populations of fourhorn sculpin in Canadian waters (Supplementary Appendix: Table S1). Our list is based on a re-examination of the museum records used for the COSEWIC (2003) list and the limited, pertinent literature (e.g., Johnson, 1964; Dickman, 1995). Because the fourhorn sculpin is of interest to researchers studying post-glacial dispersion and zoogeography of aquatic species (COSEWIC, 2003), and some populations may be susceptible to climate change, consideration should also be given to a more thorough study of the species including at least one each of freshwater and brackish populations.

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