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The Isolation of Atlantic Cod, *Gadus morhua* (Gadiformes), Populations in Northern Meromictic Lakes—A Recurrent Arctic Phenomenon[1]

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Abstract—Although it has previously been considered to be a rare phenomenon, this paper provides evidence of eight occurrences of Atlantic cod in northern coastal saline lakes in Arctic Canada, Greenland, Norway, and Russia. Historic and current habitat features that are necessary for Atlantic cod to colonize and persist in Arctic meromictic lakes are discussed. Data analyses confirm that the persistence of Atlantic cod in Arctic lakes is a recurrent phenomenon, and these populations represent an important component of intraspecific biodiversity.

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Atlantic cod is widely distributed in the North Atlantic from Cape Hatteras, North Carolina (35° N), northward to the tip of Labrador at Cape Chidley (60° N), and continues with scattered records as far north as Upernavik on the west coast of Greenland and in Davis Strait (~73°N). To the east the range extends still further north, reaching or exceeding the 75th parallel. From eastern Greenland into the Barents Sea off Norway and northern Russia (Fig. 1). Although the species typically inhabits cold (10–15°C) and very cold waters (0–5°C) in coastal areas and in offshore waters, it can persist in coastal lakes under certain conditions. These include brackish embayments with perennial connections to the sea[2] and partially isolated coastal lakes that receive seawater inflows only during tidal events that exceed the height of the river and/or ridge separating the lake from the adjacent sea. The latter cases can include groups of cod that have been carried into coastal lakes and trapped there, or true resident populations that spawn in the lake, maintaining little to no gene flow with oceanic stocks. In rare cases, this can occur in areas outside of the species' contemporary range in marine waters, particularly at the northern extreme of the species' distribution. The historical factors and ecological mechanisms underlying the establishment and/or persistence of these highly unusual populations are not well known. Not only are they fascinating in their own right, but they also provide a microcosm for the study of a species of significant conservation, economic, and cultural concern which has been depleted or extirpated throughout much of its range, yet persists in these harsh and unusual settings. Some of these populations appear to thrive in the absence of human influence, while others appear to cling to the very extreme of their biological tolerances. Due in part to the paucity of peer-reviewed publications on this subject, previous researchers have tended to consider these populations to be quite unique phenomena. It is significant that the latest compilation of biological information on Atlantic cod (Cohen et al., 1990) only mentioned the well-studied Lake Mogilnoe population in Russia.

Closer examination reveals that the isolation of Atlantic cod in coastal saline lakes is a recurrent Arctic phenomenon, which may have repeated itself on at least eight occasions (Fig. 1). In the Annual Report of the Fisheries Research Board of Canada for 1952 (Anonymous, 1953), mention was made of another case of cod, possibly Atlantic cod, in a lake (“Winton Lake” in McLaren 1967b) in the Canadian Arctic, on Beekman Peninsula, Baffin Island, between Frobisher Bay and Cumberland Sound. However, a later investigation of this lake found no cod (I.A. McLaren, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, personal communication).

The purpose of this paper is to compile and contrast existing information about this phenomenon and to advance knowledge about the historical and contempo-

[1] The text was submitted by the authors in English.
[2] For example, Bras d'Or Lakes, Nova Scotia, Canada, Lambert et al., 2000.

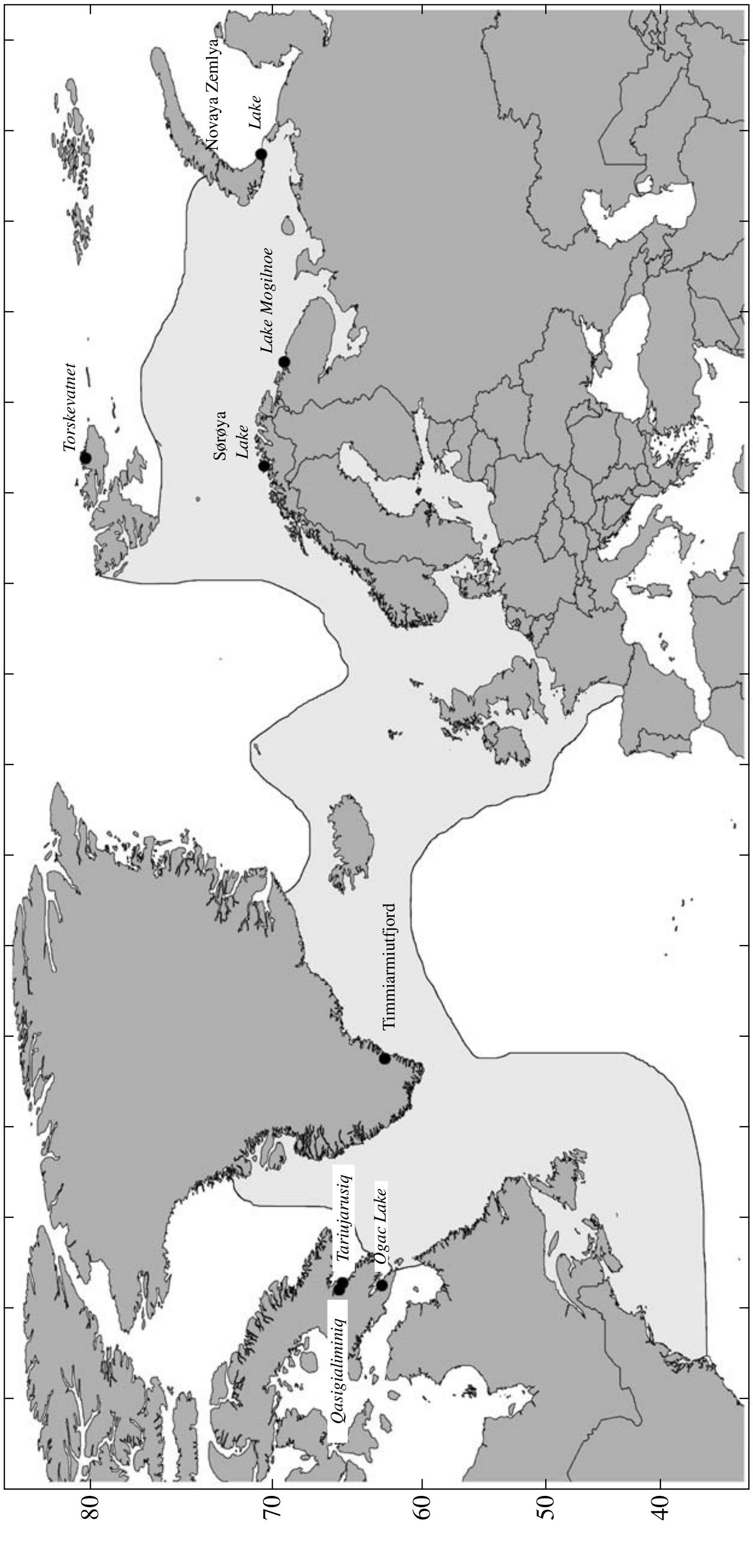

Fig. 1. Map of the range of oceanic Atlantic cod, *Gadus morhua*, populations (shaded area), compiled from Svetovidov (1948), Jensen (1948), Demel and Rutkowicz (1966), and Cohen et al. (1990), with the locations (dots) of the eight lacustrine Atlantic cod populations superimposed. Following Renaud (1989b) and contrary to Svetovidov (1948), *Gadus ogac* and *G. macrocephalus* are considered as distinct species from *G. morhua*, and therefore, their ranges are not included.

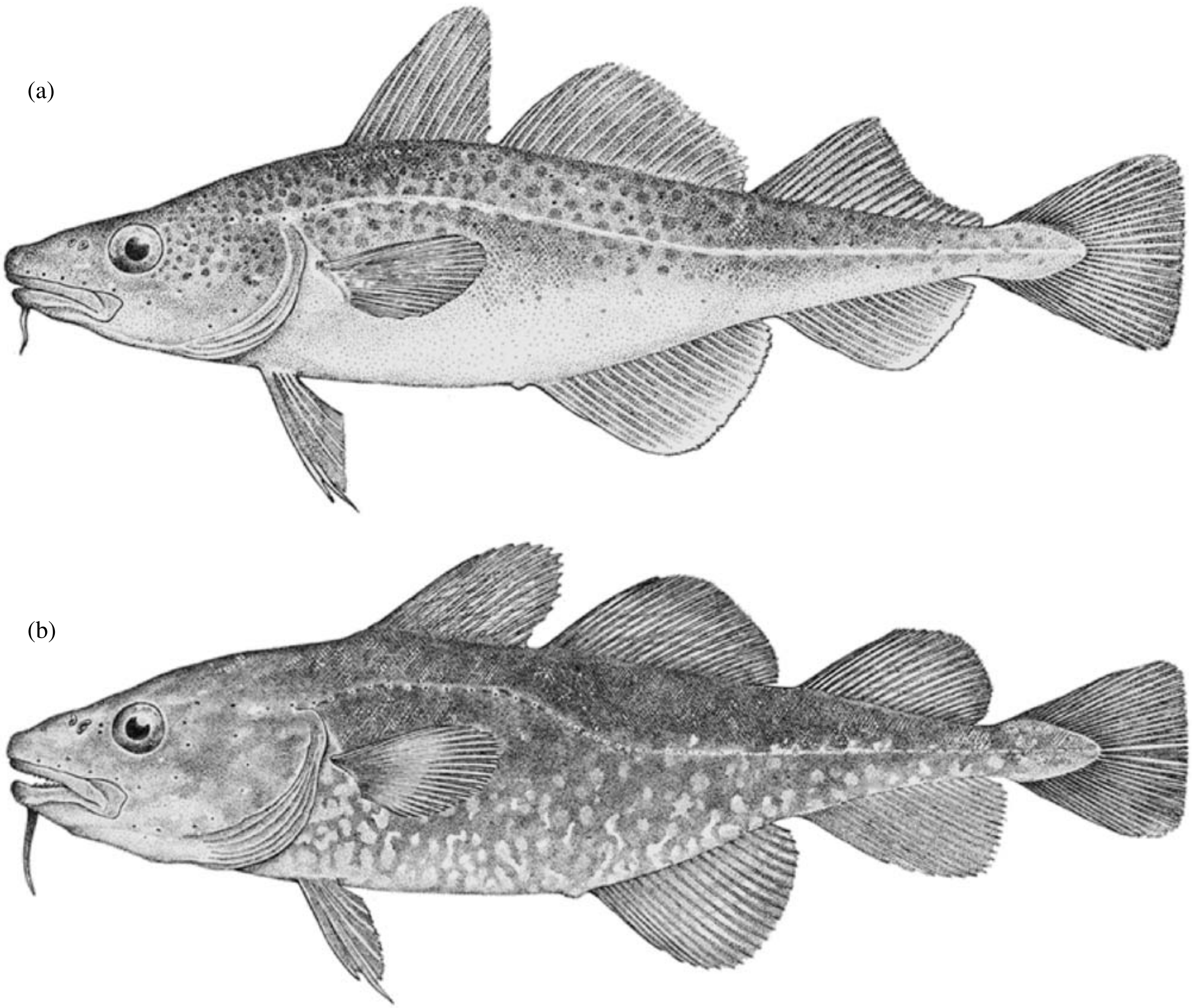

Fig. 2. Atlantic cod, *Gadus morhua*, 261 mm standard length (a) and ogac or Greenland cod, *G. ogac*, 374 mm standard length (b) in side view. Both individuals were collected sympatrically in the Strait of Belle Isle at Red Bay, Labrador, Canada, in 1982 and drawn by C.H. Douglas, Canadian Museum of Nature. Courtesy Canadian Museum of Nature.

rary conditions that account for the persistence of Atlantic cod populations in coastal Arctic saline lakes.

MATERIAL AND METHODS

All cod specimens in this study were identified as Atlantic cod, *Gadus morhua*. The main diagnostic characters of *G. morhua* are the presence of a white lateral line contrasting sharply with dark spots on the dorsal and lateral aspects of the body. On the other hand, in *G. ogac* and *G. macrocephalus*, the dorsal and lateral aspects of the body have light vermiculations on a dark background and this light and dark pigmentation blends in with the lateral line (Fig. 2).

Since the taxonomy of this species group has been the subject of much debate, it is important here to make some comments. Vladykov (1933) was the first to remark on the morphological similarity between Greenland cod (*Gadus ogac*) and White Sea coastal cod (*Gadus morhua marisalbi*). Walters (1955) went further and suggested that the two should probably be synonymized. Cohen et al. (1990) accepted this view and placed *G. morhua marisalbi* as the synonymy of *G. ogac*. However, Renaud (1989a) conducted a multivariate analysis of 51 taxonomic characters on 199 specimens of *Gadus* from across its wide geographic range and comprising all six subspecies of *G. morhua* recognized by Svetovidov (1948) as follows: 55 *G. m. morhua*, 15 *G. m. callarias*, 56 *G. m. macrocephalus*, 51 *G. m. ogac*, 1 *G. m. kildinensis*, and 21 *G. m. marisalbi.* The principal coordinates analysis showed three distinct groupings: *morhua–callarias-kildinensis–marisalbi, macrocephalus*, and *ogac*. Furthermore, 18 specimens that clustered within the newly defined *G. morhua* group and 22 that clustered within the *G. ogac* group were collected sympatrically at eight Canadian localities between Miramichi Bay, New Brunswick (47°08′ N, 64°58′ W), and Ungava Bay, Northwest Territories (60°25′ N, 64°51′ W). The characters that gave the best separation between the two groups were the external pigmentation of the ovaries (100% separation), the body pigmentation (98%), and the lateral line pigmentation (94%). Additionally, Renaud et al. (1986) conducted an electrophoretic study of *G. morhua* and *G. ogac* collected sympatrically in the Strait of Belle Isle at Red Bay, Labrador (51°44′ N 56°26′ W), and showed the two to be fixed for alternate alleles at seven loci (Aat-1, Ck-1, Est-1, Est-2, Est-4, G3pdh-2, and Mdh-3), further evidence for their specific distinctiveness. Renaud (1989a), therefore, recognized three species within the genus, namely, *G. morhua*, *G. macrocephalus*, and *G. ogac*, and rejected the notion that *G. ogac* and *G. m. marisalbi* were synonyms. The idea that the genus comprises three species is also independently supported by the study of Vladykov et al. (1985), who found distinct differences in the "breeding tubercles" of *G. morhua, G. macrocephalus*, and *G. ogac*. These breeding tubercles should properly be called contact organs, as was pointed out by Renaud and Morrison (1992), because they are of dermal origin and not epidermal origin. Additionally, Evseenko and Pobalkova (2001) compared contact organs in White Sea coastal cod with those of Greenland cod and found them to be quite distinctive from each other. The eggs of these two taxa are also distinctive. In the former, they are pelagic and the chorion is nonadhesive, while in the latter, they are demersal and the chorion is adhesive (Makhotin et al., 1984; Evseenko et al., 2006).

RESULTS

Canada: Ogac Lake, Baffin Island, Nunavut (62°52′ N, 67°21′ W)

Ogac (Inuktitut for *cod*) Lake is a small (148 ha) meromictic lake at the head of a small fiord in Frobisher Bay[3] (McLaren, 1967b). The first recorded observation of cod in this lake was by the Porter–Shaw expedition of 1896–1897 (Porter 1898), confirmed further in a series of publications (Dunbar, 1958; McLaren, 1967a, 1967b, 1969; Patriquin, 1967; Woods, 1969). On March 27, 1987, 14 Atlantic cod were jigged from Ogac Lake and four of these were analyzed as part of a taxonomic revision of the genus *Gadus* (Renaud, 1989a). These four individuals clustered within the *G. morhua* group in principal coordinates space.

Ogac Lake is meromictic and displays the characteristics of coastal lakes from previously glaciated areas described by Livingstone (1966). These include strong vertical stability of thermal and salinity strata, which consist of a warmer freshwater layer above a deep saline layer, which is often anoxic at the bottom. The surface layer of Ogac Lake is almost fresh, approaching ~23‰ at 5 m and 27‰ between 10 and 40 m, depending on the season and proximity to freshwater/tidal inflow sources (table). Most of the freshwater supply to Ogac Lake derives from a river draining a large catchment area into the inner basin, although four smaller streams also enter the lake. The lake is anoxic below ~28 m, which is probably the "compensation depth" where phytoplankton productivity matches consumption (McLaren, 1967b), and where the bottom is rich in hydrogen sulfide (Dunbar, 1958). There are three distinct basins, ranging from 30 to 60 m in depth, each separated from the other by a shallow sill. The small size of the lake, its division into basins, and the shelter of steep surrounding topography combine to inhibit vertical mixing, resulting in permanent meromixis (McLaren, 1967b). The only outflow is a river approximately 250 m long, which is about 100 m wide at the lake, narrowing to less than 10 m in the final 75 m, where it cascades down almost 10 m at low tide.

The highest spring tides, which can reach 12 m in this area, supply seawater to Ogac Lake monthly during the open-water season (McLaren, 1967b). In 1957, these tides were as much as 1.2 m above lake level, which fluctuates due to tidal input, spring runoff, and rain (McLaren, 1967b). In 2003 and 2004, it was observed that seawater only entered the lake during tides 11.16 m or higher (July–August 2003–2004). The observation that the tide height required to breach the lake is now about 35 cm higher than was observed in the 1960s is consistent with evidence of ongoing postglacial crustal emergence at this site (Doner, 2001) and suggests a rebound rate of approximately 0.8 cm/year. Data from a temperature data logger deployed from July 23, 2004, to July 25, 2005, detected pulses of cold seawater during 96 inflowing tides between 11.13 and 11.81 meters in height throughout the year, confirming reports by local Inuit that the river remains open throughout the winter months in some years.

As is often the case for this class of lake, the aquatic community in Ogac Lake is simple, composed of marine species that either persist as marine relicts, or are dispersed into the lake during tidal inflows, or both. The zooplankton community is dominated by two copepods, *Pseudocalanus minutus* and *Oithona similis*; a chaetognath, *Sagitta elegans*; and a medusa, *Aglantha digitale* (McLaren, 1969). The copepod nauplii are assumed to be the principal food of the larval cod (Patriquin, 1967). Benthic species found in the stomachs of cod 30 cm and greater included the sea urchin *Strongylocentrotus droebachiensis*, the mollusc *Saxicava arctica*, and the polychaete *Cistenides granulata* (Patriquin, 1967).

[3] There are no reports of Atlantic cod in Frobisher Bay (McLaren, 1967a; Patriquin, 1967). The nearest to Ogac Lake that Atlantic cod are found is in the region of Resolution Island off the southern end of Baffin Island, a distance of about 150 km (Kennedy, 1953).

Summary of available biotic and abiotic limnological information from four Arctic lakes containing Atlantic cod

Indices	Lake			
	Ogac	Qasigialiminiq	Tariujarusiq	Mogilnoe
Surface layer:	(July 17, 2003)	(July 28, 2003)	(Aug. 4, 2003)	(June 25, 1999)
depth, m	0–4	0–4	0–3	0–4.5
salinity, ‰	0.9–2.2	0.4–0.7	5.8	3.0–6.0
temperature, °C	5.7–7.1	8.8–10.5	11.6–12.0	10–13
mg O_2 l^{-1}	11.7–13.4	9.0–10.5	9.8–10.0	7.69–7.72
Intermediate layer:	(July 17, 2003)	(July 28, 2003)	(Aug. 4, 2003)	(June 25, 1999)
depth, m	4–28	4–23	3–28	4.5–8.75
salinity, ‰	23–27	26.5–28.8	21.5–27.6	20.7–27.8
temperature, °C	2.4–7.0	4.9–11.0	7.9–9.2	6–9
mg O_2 l^{-1}	2.5–12.1	3.0–11.0	2.6–12.3	6.47–8.21
Bottom layer:	(July 17, 2003)	(July 28, 2003)	(Aug. 4, 2003)	(June 25, 1999)
depth, m	28–bottom	23–bottom	28–bottom	9.0–15.5
salinity, ‰	26.9–33	28.8–30.1	28.6–30.1	29.4–30.9
temperature, °C	1.9–2.6	<4.9	9.5–9.9	6–7
mg O_2 l^{-1}	<2.5	<2.9	<0.1	0
Tides, m:				
range, m	12.05	7.12	7.12	3.1
breaching tide height, m	11.16	6.40	6.64	not applicable
Cod abundance, kg $hook^{-1}$ h^{-1}	2.5–57.0	1.5–5.0	0.5–5.0	1.1–3.5
Cod size, cm:				
mean TL	59	52	53	52.5
Max TL	133	82	111	72
mean Fulton's K	0.75	0.72	0.69	0.67
Number sampled	103	106	92	35

Note: Dates of observations are given in brackets.

Using data collected on marine fish larvae and crustaceans being washed upriver[4] and combining these data with measurements of the total volume of the tidal inflow, it was estimated that a minimum of 256 kg of marine fish larvae and crustaceans had been washed into Ogac Lake during this tide. Clearly, these large influxes of rich nutrients are very valuable to the cod, which can be observed feeding heavily near the river mouth long after the tide has subsided. Kennedy (1953) reported that McCall and Dawson saw hundreds of 20-mm sculpins enter Ogac Lake on a particularly high tide on August 6, 1952. The cod congregated at the outlet, now temporarily an inlet, to feed on them and the sculpin were completely consumed within one day.

The size of the Ogac Lake cod population was estimated by mark-recapture and direct observation in 1957 and 1962 as being on the order of 500 individuals longer than 60 cm and 10000 individuals longer than 25 cm (Patriquin, 1967). Our observations and collections, as well as genetic analysis used to estimate effective population size, suggest that this remains a reasonable estimate (Hardie et al., 2006).

Notably, cod in Ogac Lake can grow to very large sizes, well in excess of what is commonly encountered in contemporary marine stocks of this species. In July 2003, 12 individuals between 110 and 133 cm total length were tagged, which was consistent with records from early collections that reported cod up to 144 cm (Patriquin, 1967). The fact that no untagged individuals in this size class were subsequently observed over a three-week period following tagging, despite many hours of observation by snorkeling and remote underwater video, as well as extensive collection efforts angling and netting cod over a five-week period in 2004, suggests that the number of cod of this size does not greatly exceed the number that were tagged. The largest cod ever recorded in Ogac Lake measured 157 cm and was released alive (Hardie, July 25, 2005).

Patriquin (1967) found that cod in Ogac Lake displayed unusually high growth rate variability among

[4] Samples were taken in July–August 2004, using stationary placements of 15 cm^2 aquarium nets (model 11276, Rolf C. Hagen (USA) Corp., Mansfield, MA) at various depths across a transect of the river during a 60-min tidal inflow.

individuals, compared to oceanic populations. While slow growth rates in Ogac Lake cod are not unexpected, given that cod 30 cm and greater feed predominantly on sea urchins, the extremely high growth rates experienced by some individuals is notable and implies the genetic potential for high growth rates under better feeding conditions (Patriquin, 1967). Unusually high rates of cannibalism by cod 50 cm and greater (Patriquin, 1967; Hardie and Hutchings, unpublished data) might also account for the rapid growth observed in some individuals. Patriquin (1967) reported that maturity is reached at large size in both females (80–90 cm, age 9 or older) and males (60–70 cm, age 7 or older). In contrast, Hardie and Hutchings recorded evidence of past maturity in most females larger than 50 cm and in most males larger than 40 cm. It is unlikely that this difference represents a change in age at maturity during the period between studies. Rather, it seems that improper assignment of maturity status was made during data collection in the 1950s and 1960s, such that late-recovery stage, post-reproductive cod were classified as immature.

Canada: Qasigialiminiq, Baffin Island, Nunavut (65°48′ N, 68°10′ W)

The cod population in Qasigialiminiq (Inuktitut for *there used to be seals*) was known to Pangnirtung (Nunavut, Canada) fishermen for several generations, although it had never been of particular cultural, subsistence, or economic significance. In 1985, Atlantic cod were caught in Cumberland Sound, at Nettilling Fiord (Stewart and Bernier, 1988). However, L.W. Dahlke (Fisheries and Oceans Canada, Iqaluit, Nunavut, personal communication) has informed us that this report referred to one of the two lakes we report on here. In 2003, Hardie confirmed that the cod in Qasigialiminiq and Tariujarusiq (see below) were *G. morhua*.

Qasigialiminiq is approximately 10 km long and 1 km wide (~1000 ha) and is made up of one basin (maximum depth = 38 m). The lake is strongly stratified, including anoxic hypersaline pockets at all depths below 30 m, overlain by a seawater layer up to 3–5 m and a freshwater layer at the surface (July 2003). The lake is supplied with freshwater from one large river and several small springs. Based on our observations that only tide heights above 6.4 m enter this lake, coupled with predicted maximum local tide height of 7.1 m, approximately 70 tides as much as 60 cm over lake level would have entered the lake between June 1 and November 30, 2003.[5] One important difference between Qasigialiminiq and Ogac Lake is the nature of the outflow; in the former lake, the water percolates through and flows over a gravel and boulder ridge approximately a kilometer wide onto a shallow, rocky tidal flat that extends several hundred meters from the lake before dropping to deeper water. This feature may strongly affect the influx of nutrients and biological material during inflowing tides if they sieve slowly through the boulders rather than rushing up a narrow river as they do at Ogac Lake. There were no urchins present in Qasigialiminiq in 2003, in contrast to their predominance in the benthos and cod stomach contents in Ogac Lake. The cod in Qasigialiminiq were smaller and appeared to be less abundant than in Ogac Lake (table).

[5] Temperature data-logger data.

Canada: Tariujarusiq, Baffin Island, Nunavut (65°33′ N, 67°25′ W)

Tariujarusiq (Inuktitut for *slightly saline*) is approximately 3 km long and 1.8 km wide (~540 ha) and is made up of one basin (maximum depth = 80 m). The lake is less strongly stratified than Ogac Lake or Qasigialiminiq, due in part to the fact that the lake is only supplied with freshwater from five small creeks, in contrast to the significant river basins draining into Ogac Lake and Qasigialiminiq. Surface salinity is 7‰ to a depth of 3 m, at which point it increases abruptly to 23‰, thereafter increasing gradually to 27‰ by 28 m; the entire lake is anoxic below that depth (August 2003). Based on observations in August 2003 that only tide heights greater than 6.6 m enter this lake, coupled with a predicted maximum local tide height of 7.1 m, approximately 33 tides as much as 50 cm over lake level would have entered the lake between June 1 and November 30, 2003. Data from a temperature data logger deployed from August 6, 2003, to July 25, 2005, detected pulses of cold seawater during 24 inflowing tides between 6.64 and 7.02 meters in height between August 6 and December 2, 2003. No further tides were detected entering the lake until August 30, 2004, after which point 17 tides from 6.64–6.90 m entered until October 20, 2004. The outflow and adjacent intertidal area of Tariujarusiq were similar to those described at Qasigialiminiq, although the outflow was narrower (~250 m). Sea urchins were highly abundant in this lake. Although some large cod (>100 cm) were observed, catch rates were lowest in this lake (table).

Greenland: Unnamed Lake Close to Timmiarmiutfjord (Precise Geographic Coordinates Unknown)

In 1996, Atlantic cod were caught in a lake close to Timmiarmiutfjord on the southeastern coast of Greenland. The hydrography of this lake, including the frequency of tidal inflows, is unknown. Although this lake is connected to the ocean at high tide, local fishermen claimed that the cod population spawns in the lake and resides there permanently. They also reported that the sampling in 1996 was the first time that the lake has been fished since the 1950s, when cod were also present. Tissue samples from the 1996 survey are kept at the University of Bergen, where they may be available for genetic comparisons to coastal Greenland populations of the species to test hypotheses concerning gene flow (T. Johansen, University of Bergen, Norway, personal communication).

Norway: Torskevatnet, Nordaustlandet, Svalbard Archipelago (80°16′ N, 22°35′ E)

The name Torskevatnet refers to cod (*torsk* is Norwegian for *cod*), but the name is rather new and not officially recognized. The following information was reported by Gulliksen and Svensen (2004). The lake is about 100–200 ha in area, 35–40 m deep, and is meromictic. The top 11–12 m is fresh to slightly brackish and well oxygenated. Below 11–12 m, the salinity is 50–52‰ and the water is anoxic and rich in hydrogen sulfide. The top layer is cooler (3.5–4.8°C) than the deeper saline layer (6.5–7.0°C) when measured in August–September. A river approximately 500 m long joins the lake to the sea, where it terminates in a ridge of sand, gravel, and boulders. At high tide, seawater overflows the ridge and seawater reverses the flow of the river, whereafter it enters the lake. The top oxygenated layer contains *Mysis relicta* and *Gammaracanthus locusta* (B. Gulliksen, Norwegian College of Fishery Science, University of Tromso, Norway, personal communication). In 1997, three cod and one Arctic char (*Salvelinus alpinus*) were caught at the same time (M.-A. Svenning, NINA—Norwegian Institute for Nature Research, Tromso, Norway, personal communication). Thus, both Atlantic cod and Arctic char probably inhabit the lake, the former in the upper reaches of the saline layer near or around the halocline, and the latter fully in the freshwater surface layer. One of the cod captured in 1997 had eaten *Mysis* (M-A. Svenning, personal communication), which are only found in the freshwater layer. When the occurrence of cod in this lake was first reported circa 1990, the Norwegian Polar Institute caught 10–15 individuals. J. Mork (Norwegian University of Science and Technology, Trondheim, Norway) used 10–11 isozyme markers to compare these cod to samples obtained from the Barents Sea; he could not detect any genetic differentiation between the two samples. Although alternative genetic tools such as microsatellites may reveal more subtle genetic differences, this result, along with the anoxic and hypersaline nature of the deeper saline layers, suggests that suitable habitat for proper egg development may be extremely limited or nonexistent. This is curious, since cod do not inhabit local waters. One possible explanation for their occurrence in the lake is that, on rare occasions, strong inflows of Atlantic water (following the west coast of Spitzbergen and bending east at the northwestern corner) may penetrate as far east as Nordaustlandet, carrying cod larvae. If this event coincides with a high tide flowing into the lake, cod larvae may be carried in, where some manage to survive despite the difficult conditions. No cod or char were collected during a survey in autumn 2004.

Norway: Unnamed Lake on Soroya (70°35′ N, 22°25′ E)

This small lake is also meromictic, having oxygenated freshwater surface and intermediate brackish (10–15‰) layers over an anoxic saline (30‰) bottom layer. Only the very highest spring tides enter the lake, approximately twice per year. In 1988, 3–4 Atlantic cod and pollock (*Pollachius virens*) were caught from the brackish layer. The cod were all small (15–25 cm) and immature (T. Pedersen, Norwegian College of Fishery Science, University of Tromso, Norway, personal communication).

Russia: Lake Mogilnoe (67°50′ N, 37°22′ E)

Lake Mogilnoe is on Kildin Island, near the Kola Peninsula in the Barents Sea, which appears in 17th century English and Dutch marine documents (Linschoten-van, 1601). Atlantic cod have likely been isolated in the lake since it was formed by glacioisostatic rebound about 10000 years before present (ybp). The lake itself has been studied for two centuries (Ozeretskovsky, 1804; Knipowitsch, 1895; Derjugin, 1920; Guryevitsch, 1975), including a recent report on hydrological, hydro-optic, hydroacoustic, microbial, parasite, toxicological, and ichthyological research carried out in 1997–2000 (Titov, 2002). Lake Mogilnoe is only 562 m long by 275 meter wide and is separated from the Barents Sea by a low (3.7–5.4 m) narrow (63–70 m) barrier that is somewhat permeable to the exchange of fresh and sea water. A high tide of 3.1 meters outside the lake produces a rise in lake level of 81 mm. No marine tides enter Lake Mogilnoe directly. The lake is perennially stratified, from fresh at the surface to 30.9‰ at the bottom, which corresponds to a depth of 14 m (Guryevitsch and Shirokolobov, 1975; Antziferov and Trofimov, 2002). The stagnant hydrogen sulfide rich anaerobic layer begins at depths between 8 and 13 m (Guryevitsch, 1975; Titov, 2002).

Atlantic cod are found in the narrow saline layer between the fresh and anaerobic levels, although they have been observed for prolonged periods in the shallow freshwater layer. The cod mature at around 4.5 years old and do not appear to live beyond 8–9 years of age (Tzeb and Pozdnyakov, 1975; Mukhina et al., 2002). Growth analysis from otolith annuli shows evidence of unusually rapid growth during the first two years. Juvenile cod feed almost exclusively on *Daphnia* spp. (90.54% of the food bolus weight), while larger individuals consume a much broader range of prey, mostly conspecific juveniles (69.07%) and gammarid amphipods (10.72%) (Mukhina et al., 2002). Cod in Lake Mogilnoe average 50 cm in length, 1112 g total weight, and 2.33% hepatosomatic index (Mukhina et al., 2002). Although length and weight increase with age, the hepatosomatic index decreases in older cod, which is a common phenomenon in small water bodies with low prey availability for adult individuals. Svetovidov (1948) recognized the Atlantic cod population inhabiting this lake as subspecifically distinct, *Gadus morhua kildinensis* Derjugin 1920.

Russia: Lake on Novaya Zemlya (Precise Geographic Coordinates Unknown, Approximately between 70°30′–71°00′ N and 55°30′–57°30′ E)

This lake is located on the southeastern tip of Novaya Zemlya near Krotov Bay (Bukhta Krotova). This site is outside of the species' range of Atlantic cod, which only reach the location during the warmest years, when they can pass through Karskie Vorota Strait (Proliv Karskie Vorota) into the Kara Sea. In the winter of 1939–1940, a Russian expedition overwintering near Krotov Bay found cod in a lake that was separated from the sea by a cobble bar. Between December 1939 and June 1940, expedition members caught more than 300 cod for food. All of the fish weighed less than 2.5 kg. No ichthyologists participated in the expedition and no scientific information was collected. This incident has been documented in unpublished manuscripts of N. Maslov and I. Agapov and referred to in Ponomarenko (1994) and Ponomarenko et al. (2003). The most probable interpretation is that prior to 1939, migrating cod trying to escape subzero water in the Kara Sea went to the surface and accidentally entered the brackish lake. During storm events with strong northeast and east winds (which are common in late summer), the lake became separated from the sea by a cobble bar and the cod were trapped. A less probable explanation is that the Novaya Zemlya population existed in this lake for a much longer time. The fate of this cod population is unknown, although it is unlikely that it has persisted. Cod that were not harvested by the 1939–1940 overwintering expedition probably died during the unusually cold season of 1940–1941. After the Second World War, this island was closed to research and therefore no information is available.

DISCUSSION

The occurrence of Atlantic cod in coastal Arctic lakes is of interest from diverse perspectives. Not only is Atlantic cod a significant species from cultural, economic, and conservation viewpoints, but the study of species at the edges of their ranges often yields insight into diverse aspects of their biology. Furthermore, the remoteness of most of these lakes ensures that the populations persist in a relatively pristine environment, which, coupled with their limited size and complexity, can provide a useful microcosm of oceanic cod populations. One important distinction among occurrences of cod in Arctic lakes concerns their degree of isolation from marine stocks, and it will be important to differentiate truly isolated lake-resident populations from occurrences of cod dispersed into coastal lakes at some life stage. Molecular tools can be used to reveal aspects of the colonization history and genetic structure of true resident populations. In either case, a comparative approach can be used to reveal possible habitat constraints (e.g., temperature/salinity/dissolved oxygen stratification, tidal influence, surrounding topography, species composition) necessary for Atlantic cod to persist in lentic Arctic habitats.

Isolation and colonization history. The most obvious question concerns whether or not the lacustrine populations fall within the contemporary distribution of Atlantic cod. For those populations falling outside the species' range, we must address how and when the lakes were colonized and strive to understand what evolutionary and ecological effects this has had relative to oceanic populations. For lacustrine populations within the species' range, we must take steps to quantify historic and contemporary gene flow between lacustrine and oceanic populations, and to understand mechanisms, if any, that limit migration. Among the eight lakes described in this manuscript, only the Lake Mogilnoe population and those near Timmiarmiutfjord and on Soroya fall within the contemporary distribution of Atlantic cod (Fig. 1). Based on current information, it is not possible to quantify the degree of isolation of the cod in these lakes, because very little data are available. More work needs to be done at the lake on Soroya to ascertain whether the 3–4 juvenile cod and pollock observed were simply washed into the lake as larvae or juveniles during one of the few high tides that enter the lake per year. An analysis of genetic characteristics of the cod collected in the lake near Timmiarmiutfjord relative to Eastern Greenland oceanic cod samples is needed to test the local belief that the cod in this lake are locally spawning residents that are distinct from oceanic stocks in the area. Lake Mogilnoe is distinct from the remaining lakes in that it does not receive influxes of seawater freely at high tides, but depends on subterranean percolation for water exchange with adjacent marine waters. In contrast, the remaining five lakes are outside of the contemporary distribution of Atlantic cod. Because very little data are available for the lake on Novaya Zemlya, a new survey of the lake is required to confirm whether or not this population has persisted.

The contemporary occurrence of cod in Torskevatnet on Svalbard seems uncertain, since no cod were collected there in the most recent survey (2004). Genetic evidence and habitat characteristics (i.e., absence of a seawater layer that is not anoxic and hypersaline) suggest that this is not a locally spawning resident population, and there exists a possible mechanism for occasional immigration of larval cod under certain conditions of oceanic currents and tide heights. In contrast, collections of cod eggs and larvae (Patriquin, 1967; Hardie and Hutchings, unpublished data), as well as genetic analysis of samples of cod from the three lakes on Baffin Island, Canada (Hardie et al., 2006), strongly support that these are true resident populations which have been isolated from each other and from oceanic stocks for 5000 to 8000 years. This is consistent with several lines of evidence highlighting a period of ameliorated Arctic Ocean conditions associated with the shrinking of the Laurentide ice sheet in North America, including warmer temperatures and diminished landfast ice between 10000 and 7000 ybp (Lindberg, 1970, 1972; Dyke, 1979; Stewart and England, 1983; Pielou, 1991). Five subarctic marine mollusk species expanded their range northward during this period, arriving in Cumberland Sound, Nunavut, around 8700 ybp (Aitken and Gilbert, 1989). Interestingly, two of these species' ranges had retreated southward by 3000 ybp, providing a plausible mechanism for the occurrence of Atlantic cod in Arctic lakes despite their current absence from adjacent marine waters at these latitudes. Furthermore, Eastern Baffin Island has been emerging from sea levels about 70 meters higher than present due to glacioisostatic processes since about 8000 ybp (Doner, 2001; references in Dyke, 1979), which provides support for the creation of these partially isolated lakes during the same period that Atlantic cod were likely to be present in the area. Additionally, the latitudinal range of Atlantic cod can change dramatically in a relatively short period of time. Jensen (1948) documented such a shift northward off the west coast of Greenland. Between 1917 and 1931, Atlantic cod increased its range almost 11° of latitude from Paamiut (then known as Frederikshåb, 62°00′ N) in the south and Upernavik (72°45′ N) in the north. Jensen (1948) suggested that this latitudinal dispersal northwards was in response to changes in the ocean currents such that the warm Irminger current exerted a greater influence than the cold East Greenland current, resulting in increases of 1 or 2°C in the water temperature of the cold West Greenland current. Jensen (1948) added that these latitudinal shifts are not restricted to the waters off western Greenland but are also known from other areas of the Arctic Ocean such as Jan Mayen, Spitzbergen, the Barents Sea, and the Kara Sea.

Habitat considerations. All Arctic lakes that contain, or have contained, Atlantic cod are coastal and meromictic. Permanent stratification provides a saline habitat for cod and maintains lake temperatures greater than the seawater outside by various mechanisms (McLaren, 1967b), allowing cod to persist in some lakes at latitudes beyond the contemporary northern limit of the species' distribution. In most cases, influxes of seawater from high tides are required to maintain salinity in the deeper layers, although subterranean percolation can also achieve this. The free influx of the highest spring tides through a reversing river, as is the case at Ogac Lake, provides a valuable source of food for noncannibalistic cod and may explain why this lake has the largest numbers and the largest individual cod relative to lakes where tides enter less freely or by subterranean percolation.

Although some inflow of seawater is all that is required, most of the lakes occur in areas with moderately to extremely high tidal amplitude. This may ensure continued tidal inflows over adequate time periods for cod populations to become established in a milieu of rapidly changing relative sea level in recently glaciated areas. The greater the local tidal amplitude, the longer the lake will exist in a partially isolated state (i.e., connected to the sea only at high or the highest tides).

Species composition varies among Arctic lakes that contain Atlantic cod, although diversity is generally low. Since much of the species composition in these lakes is allochthonous, diversity probably depends to some degree on the nature, extent, and frequency of tidal inflows, as well on local marine diversity and available lake habitat. Clearly, noncannibalistic cod must have other food sources in true resident populations, which appear to vary from exclusively mysids in Torskevatnet, to copepods, urchins, polychaetes, and mollusks in the Canadian lakes, to water fleas and amphipods in Lake Mogilnoe. Most of the lakes do not contain any other fish species, with the exception of Torskevatnet, which also contains Arctic char; Lake Mogilnoe, which also contains rock gunnel (*Pholis gunnelus*) and threespine stickleback (*Gasterosteus aculeatus*) (Tzeb, 1975); and Ogac Lake, which also contains small numbers of fourline snakeblenny (*Eumesogrammus praecisus*). In any case, cannibalism is quite common among larger cod in some of the lakes.

CONCLUSIONS

The persistence of Atlantic cod in Arctic lakes is a recurrent phenomenon. Much remains to be learned about the eight known occurrences described in this study in order to fully understand the historical and contemporary biotic and abiotic conditions required for the colonization and persistence of true resident cod populations. It is likely that other such populations exist elsewhere in the circumpolar Arctic. Not only do these populations represent an important component of intraspecific genetic biodiversity, but they also provide a unique opportunity to study various aspects of the biology of a species of significant economic, cultural, and conservation concern that has been depleted or extirpated throughout much of its range.

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