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Updated distribution of four stenohaline fish species in Labrador, Canada

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Abstract
Distributions of freshwater fish species in Labrador are poorly documented as the region is remote and sparsely inhabited. Here, we update distributions of four species native to the Labrador Peninsula based on data collected over 10 years: Burbot (*Lota lota*), Round Whitefish (*Prosopium cylindraceum*), Lake Trout (*Salvelinus namaycush*), and Slimy Sculpin (*Cottus cognatus*). In northern Labrador, our findings extend their ranges inland and northwest of their formerly reported distributions. Their presence in previously unknown locations indicates an alternative post-glacial colonization pathway to one previously proposed that suggested an isolated pocket of Lake Trout in a northern coastal area colonized through marine invasion. Instead, we suggest that overland colonization occurred when glacial Lake Naskaupi withdrew across Quebec into several northern drainages. In southern Labrador, we found Lake Trout and Round Whitefish to the southeast of their previously reported ranges. The discovery of an isolated population of Lake Trout in a remote location of southeast Labrador implies that they may have existed in the area historically (6000 years ago), but have undergone a range contraction with a warming climate. In addition, 22 new locations are documented for Lake Trout within their established range.

Key words: Burbot; *Lota lota*; Round Whitefish; *Prosopium cylindraceum*; Lake Trout; *Salvelinus namaycush*; Slimy Sculpin; *Cottus cognatus*; occurrence; Labrador; colonization; range; glaciation

Introduction

The distribution of freshwater fish species in the Labrador region of Newfoundland and Labrador, Canada, is poorly defined. This is largely because of the inherent difficulties and costs associated with sampling remote locations. Despite the paucity of data, several attempts have been made to describe fish distributions and ichthyogeographic regions for Labrador (Bergeron and Brousseau 1981; Legendre and Legendre 1984; Black *et al.* 1986). Looking at individual distributional reports collated from over 100 years of records, Black *et al.* (1986) concluded that Labrador could be divided into three ichthyogeographic regions based on species composition: the Churchill River drainage comprising three subregions; the southeastern portion of Labrador; and northern Labrador (>55°N; Table 1). Their study led to considerable advancements in our understanding of the post-glacial distribution of fish species in Labrador; however, comprehensive records were not available, particularly for the north. For example, in recent years, updated freshwater species occurrence and range adjustments for Logperch (*Percina caprodes*), Lake Chub (*Cousius plumbeus*), and Longnose Dace (*Rhinichthys cataractae*) have been reported (Grant *et al.* 2000; Perry and Joyce 2003; Michaud *et al.* 2010). These reports highlighted the necessity for further fish surveys, particularly in more northern areas.

In 2001, the Government of Newfoundland and Labrador began working on a centralized georeferenced database and archive. This new Provincial Aquatics Database and Archive (PADA) contains freshwater fish data gathered from provincial standardized stock assessments, government reports (both federal and provincial), research studies, environmental assessments, and historical documents. In general, the information housed in PADA is a synthesis of over 100 years of data collection for the period 1909 through 2015.

To augment PADA and develop a better understanding of Labrador's ichthyofauna, a standardized sampling program was initiated throughout southern Labrador in 2002. This stock assessment program was implemented by the provincial government to address

TABLE 1. Principal fish species present in each of the three major ichthyogeographic regions in Labrador, Canada, as defined by Black *et al.* (1986).

Order/family	Species	Southeastern Labrador	Churchill River system	Northern Labrador (>55°N)
Anguilliformes/Anguillidae	American Eel *Anguilla rostrata*	X (coastal)		
Cypriniform/Catostomidae	Longnose Sucker *Catostomus catostomus*	X	X	X
	White Sucker *Catostomus commersonii*	X	X	
	Lake Chub *Couesius plumbeus*		X	X
	Northern Pearl Dace *Margariscus nachtriebi*		X	
	Longnose Dace *Rhinichthys cataractae*		X	
Esociformes/Esocidae	Northern Pike *Esox lucius*	X	X	
Gadiformes/Lotidae	Burbot *Lota lota*		X	X
Gasterosteiformes/ Gasterosteidae	Threespine Stickleback *Gasterosteus aculeatus*	X (coastal)	X	X
Osmeriformes/Osmeridae	Rainbow Smelt *Osmerus mordax*		X	
Perciformes/Percidae	Logperch *Percina caprodes*		X	
Salmoniformes/Salmonidae	Lake Whitefish *Coregonus clupeaformis*		X	X
	Round Whitefish *Prosopium cylindraceum*		X	X
	Atlantic Salmon *Salmo salar*	X	X	X
	Arctic Char *Salvelinus alpinus*	X (coastal)	X	X
	Brook Trout *Salvelinus fontinalis*	X	X	X
	Lake Trout *Salvelinus namaycush*		X	X
Scorpaeniformes/Cottidae	Slimy Sculpin *Cottus cognatus*		X	X
	Mottled Sculpin *Cottus bairdii*		X	

the public's concern over increased anthropogenic pressures on Labrador's fish resources, including road construction, hydroelectric development, and mineral exploration. In 2007, the province also began a climate-change study to determine the potential impacts that a warming climate may have on Labrador's northern fish populations. In combination, these two programs have contributed substantially to the data contained in PADA, allowing us to refine our knowledge of species distributions for both the southeastern and northern ichthyogeographic regions. Here, we use the old and new distributional records contained in PADA to update occurrence and distribution data of four stenohaline species native to the Labrador Peninsula: Burbot (*Lota lota*), Round Whitefish (*Prosopium cylindraceum*), Lake Trout (*Salvelinus namaycush*), and Slimy Sculpin (*Cottus cognatus*). We then use this new information to update the ichthyogeographic regions proposed by Black *et al.* (1986) by offering some refinements to the colonization pathways originally proposed. We chose these four species because their newly discovered presence above the Fraser Canyon in northern Labrador has led to our hypothesis that there were multiple colonization pathways from glacial Lake Naskaupi and not just one, as previously suggested by Black *et al.* (1986).

Methods

Study area

The study area includes the entire Labrador Peninsula (Figure 1), an area of ~293 000 km^2, which represents 3% of Canada's total land mass (Anderson 1985). Labrador's topography was shaped by glacial activity during the Laurentide ice sheet recession of the late Wisconsinan period, which ended ~6500 years ago (Kleman *et al.* 1994). An older, undated ice sheet also contributed to these land formations (Kleman *et al.* 1994).

The provincial standardized stock assessment and climate-change studies (2007–2015) focussed on the southeastern and northern ichthyogeographic regions. The northern sample sites were situated in the high subarctic tundra (Kingurutik–Fraser River) and alpine

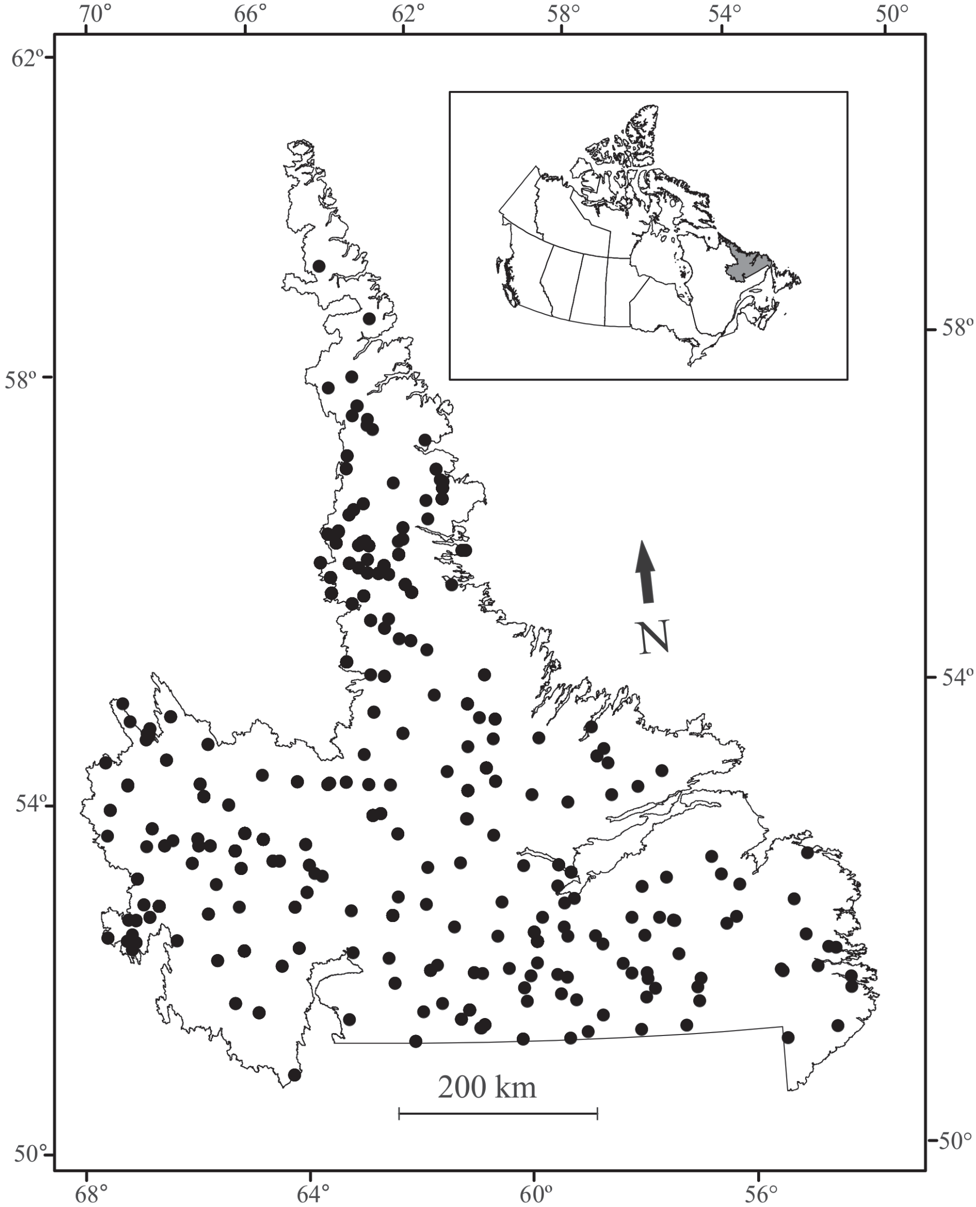

Figure 1. Location of waterbodies (solid circles) associated with freshwater fish distribution data for Labrador, Canada, collected from 1909 through 2015 from the Department of Fisheries and Oceans, Government of Newfoundland and Labrador, and Black *et al.* (1986).

tundra (Torngat) ecoregions. The southeast sites were in the low subarctic forest (Mecatina River), mid-boreal forest (Paradise River), and the string bog ecoregions (Meades 1990).

Sampling

Fish distribution data for lakes was compiled using data archived in PADA, which includes entries used by Black *et al.* (1986). However, since the publication of their paper, species occurrence records have been augmented. Collection dates for all data housed in PADA now range from 1909 through 2015.

The PADA data come from various reports and studies; therefore, the collection methods include a variety of active and passive fish-capture techniques, such as seine nets, gill nets, fyke nets, electrofishing, and angling; stomach contents of predators were also examined. Species occurrence data for all lakes were digitally georeferenced using a geographical information system (ArcMap version 10.3.1; ESRI, Redlands, California, USA).

The most recent occurrence data for Labrador were collected by the Government of Newfoundland and Labrador during both the climate-change study and index netting surveys for 2002–2015. A total of 37 lakes were selected for sampling in the northern region, and 27 lakes (representing nine major watersheds) were sampled in the southeastern region. Sampling programs used standardized multi-mesh nylon monofilament gill nets increasing in mesh size from 1.27 cm stretch to 13.97 cm, in 1.27-cm increments. Net locations were chosen randomly for each lake surveyed and all sets were placed perpendicular to the shoreline and allowed to soak overnight.

Stomach contents of sampled piscivores, such as Northern Pike (*Esox lucius*), Brook Trout (*Salvelinus fontinalis*), and Lake Trout, were also examined and prey fish species identified when possible.

Results

Burbot

Burbot was identified in 21 new locations (Tables 2 and 3; Figure 2a), 16 inside and five outside its previously known range. Four of the five lakes where Burbot was found are within the high subarctic tundra ecoregion: Langille, Iglusuatahrusuak, Alliger, and Sabrina (Table 3; Figure 2a). Burbot was also found in Lake LB50 on the southern fringe of the alpine tundra ecoregion (Table 3; Figure 2a).

Round Whitefish

We identified 13 new locations for Round Whitefish inside and six outside its previously known distribution, for a total of 19 new sites. Of the six sites outside its known range, three are in the high subarctic tundra ecoregion and three are in southern Labrador (Tables 2 and 3; Figure 2b). Two of the locations in the high subarctic tundra ecosystem, Iglusuatahrusuak Lake and Alliger Lake, are near the Labrador coastline, while the third, Lake Langille, is ~15 km north of the Fraser River, near the Labrador–Quebec border. All three new records in southern Labrador, Lac Avert, Little Guines, and Unknown Lake, are located in the low subarctic forest ecoregion (Table 3; Figure 2b).

Lake Trout

We document 22 new locations for Lake Trout inside and 10 sites outside the previously known range in Labrador (Tables 2 and 3; Figure 2c). Seven occurrences expand the known species distribution into the high subarctic ecoregion and the alpine tundra ecoregion. Lakes Sabrina, Tracy, and LB20 are found near the northeastern tip of the high subarctic tundra ecoregion, ~125 km north of the Fraser River, while Lake LB50 extends into the southern portion of the alpine tundra ecoregion (Figure 2c). Lake Tracy is part of an unnamed tributary (drainage 104; Anderson 1985) that flows northward into the Hebron Fjord. Lake LB20 (drainage 103; Anderson 1985) is also found in separate drainage that flows into the Hebron Fjord (Figure 2c).

The discovery of three previously unknown sites in southern Labrador represents expansion of the known range of Lake Trout farther into the southeast of the low subarctic forest ecoregion (Table 3; Figure 2c). Lake Trout sampled in the southeastern region were collected from Lac Mercier, Lac Avert, and Little Guines Lake. Lac Avert and Little Guines Lake are in the Little Mecatina River watershed (Table 3). Lac Mercier is ~50 km southwest of the town of Happy Valley-Goose Bay and is part of the Kenamu watershed (Figure 2c).

Slimy Sculpin

Slimy Sculpin was found at 12 new locations (Tables 2 and 3; Figure 2d), seven inside and five outside its previously reported range. New species occurrences for Slimy Sculpin were recorded in three lakes of the high subarctic tundra ecoregion in northern Labrador (Lakes Alliger, Sabrina, and Tracy) and two were in the alpine tundra ecoregion: Lake LB50 (Table 3; Figure 2d) and an unnamed stream near the Hebron Fjord (three living specimens; Table 3; Figure 2d). All Slimy Sculpin discoveries were the result of examining the stomach contents of lethally sampled Lake Trout. The specimens were not in an advanced state of decomposition and the absence of palatine teeth made it possible to identify these fish as Slimy Sculpin rather than Mottled Sculpin (*Cottus bairdii*; Scott and Crossman 1998).

TABLE 2. Locations of 30 lakes that highlight a new occurrence within previously established ranges* of four stenohaline freshwater fish species native to Labrador, Canada, collected during sampling by gill net from 2007 to 2015.

Lake	Latitude, °N	Longitude, °W	BUR	RWF	LT	SSC
Crystal Lake	55.5116	63.6734	X	X	X	X
Lac Joseph	52.8294	65.1878	X	X	—	X
Konrad Lake	56.2224	62.7156	X	—	X	X
Khongnekh Lake	56.3974	63.0700	X	X	X	X
Strange Lake	56.2853	63.9475	—	X	X	X
Cabot Lake	56.1500	62.6064	—	—	—	X
Genetics H†	56.6048	63.8682	X	X	X	—
Lake B6†	56.3288	63.3420	X	X	X	—
Slushy Lake†	56.4189	64.1230	X	X	X	—
Walkabout Lake†	56.3277	63.1565	X	X	X	—
WP152†	56.3779	63.4900	X	X	X	—
Hawk Lake	56.0437	63.5880	X	—	X	—
Lac Arvert	52.3020	61.7683	X	—	—	—
Little Guines†	52.1634	61.5447	X	—	—	—
Anak2†	56.5814	63.3234	X	—	X	—
Wanker Lake†	56.5828	63.4904	X	—	X	—
Lac Mercier	52.9183	60.7238	X	—	—	—
Alligar Lake	57.1074	62.0749	—	—	X	—
Unkown Lake†	52.6689	62.3518	X	—	—	—
Lake 1†	56.6817	64.0053	—	X	X	—
Esker Lake†	56.4171	63.6394	—	X	X	—
T-Bone Lake†	56.1404	63.9328	—	X	X	—
Mistastin Lake	55.8949	63.2865	—	X	—	—
Lake A4†	56.3168	62.9895	—	—	X	—
Lake B2†	56.6231	63.3826	—	—	X	—
Lake B5†	56.4531	63.3456	—	—	X	—
Genetics B†	56.1193	63.4008	—	—	X	—
Toilet Seat Lake†	55.8237	63.0595	—	—	X	—
Lake Karen†	55.7076	62.6299	—	—	X	—
Anaktalik Lake	56.5016	62.8229	—	—	—	X

Note: BUR = Burbot (*Lota lota*); RWF = Round Whitefish (*Prosopium cylindraceum*); LT= Lake Trout (*Salvelinus namaycush*); SSC = Slimy Sculpin (*Cottus cognatus*). X indicates fish present.
*Black *et al.* (1986).
†Ungazetted name.

Discussion

Our findings have extended the range of four stenohaline species (Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin) northwest of their formerly reported distributions. Lake Trout is now documented ~125 km north of the Fraser River drainage (former range limit) and inland ~90 km from coastal lakes. In southern Labrador, Round Whitefish and Lake Trout, were found 65 km farther to the southeast than their formerly reported range limits.

Northern Labrador

In the north, expansion of the range for Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin may indicate an alternative explanation for colonization than that described by Black *et al.* (1986) to account for the presence of an isolated pocket of Lake Trout in the Puttuaala Brook watershed, near Okak Bay.

Black *et al.* (1986) proposed that Lake Trout and other species likely dispersed through an overland pathway from Quebec that drained southward into the Fraser River watershed and on to the Labrador Sea, from where they moved northward by way of coastal invasions. Our findings show that overland invasion was likely not confined to the Fraser River drainage basin but also occurred in drainages farther north.

TABLE 3. Number of individuals of each species captured during sampling events from 2007 to 2015 at previously undescribed locations for freshwater fish species in Labrador, Canada. Location numbers correspond to points shown in Figure 2.

Location	Year	Ecoregion	Latitude, °N	Longitude, °W	Sample method	LNS	WS	LC	NP	BUR	LWF	RWF	AC	BT	LT	SSC
1. Little Guines*	2011	LSF	52.1634	61.5447	Gill net	11	69	2	18	11	59	3†	—	—	49†	—
2. Lac Avert	2011	LSF	52.3020	61.7683	Gill net	10	100	1	36	16	86	3†	—	—	66†	—
3. Unknown lake*	2011	LSF	52.6689	62.3518	Gill net	—	176	—	24	1	129	3†	—	—	28	—
4. Lac Mercier	2007	LSF	52.9183	60.7238	Gill net	66	21	—	6	2	—	—	—	12	54†	—
5. Lake Langille*	2012	HST	56.8649	63.6539	Gill net	—	—	—	—	1†	—	32†	5	—	59†	3‡
6. Lake C3*	2012	HST	56.9128	63.5762	Angled	—	—	—	—	—	—	—	—	—	1†	—
7. Lake Rhonda*	2012	HST	56.9676	63.4141	Gill net	—	—	—	—	—	—	—	1	—	119†	—
8. Lake Sabrina*	2012	HST	57.2858	63.7134	Gill net	—	—	—	—	2†	—	—	50	—	27†	—
9. Lake Tracy*	2012	HST	57.4071	63.7007	Gill net	—	—	—	—	—	—	—	5	—	59†	3‡
10. Iglusuatahrusuak	2007	HST	57.0105	62.0857	Gill net	—	—	—	—	4†	—	27†	8	—	119	—
11. Alliger Lake	2009	HST	57.1074	62.0749	Gill net	—	—	—	—	8†	—	104†	135	8	264	8‡
12. Unnamed stream*	2013	AT	57.8668	63.5386	Electro.	—	—	—	—	—	—	—	113	—	—	3†
13. Lake LB20*	2015	HST	57.7443	63.3666	Gill net	—	—	—	—	—	—	—	22	—	8†	—
14. Lake LB50*	2015	AT	57.7731	63.6157	Gill net	—	—	—	—	1†	—	—	3	3	32†	2‡

Note: LNS = Longnose Sucker (*Catostomus catostomus*); WS = White Sucker (*Catostomus commersonii*); LC = Lake Chub (*Couesius plumbeus*); NP = Northern Pike (*Esox lucius*); BUR = Burbot (*Lota lota*); LWF = Lake Whitefish (*Coregonis clupeaformis*); RWF = Round Whitefish (*Prosopium cylindraceum*); AC = Arctic Char (*Salvelinus alpinus*); BT = Brook Trout (*Salvelinus fontinalis*); LT = Lake Trout (*Salvelinus namaycush*); SSC = Slimy Sculpin (*Cottus cognatus*). LSF = low subarctic forest, HST = high subarctic tundra, AT = alpine tundra. Electro. = electrofishing.
*Ungazetted name.
†New occurrence for this species.
‡New occurrence for this species, found in stomach of Lake Trout.

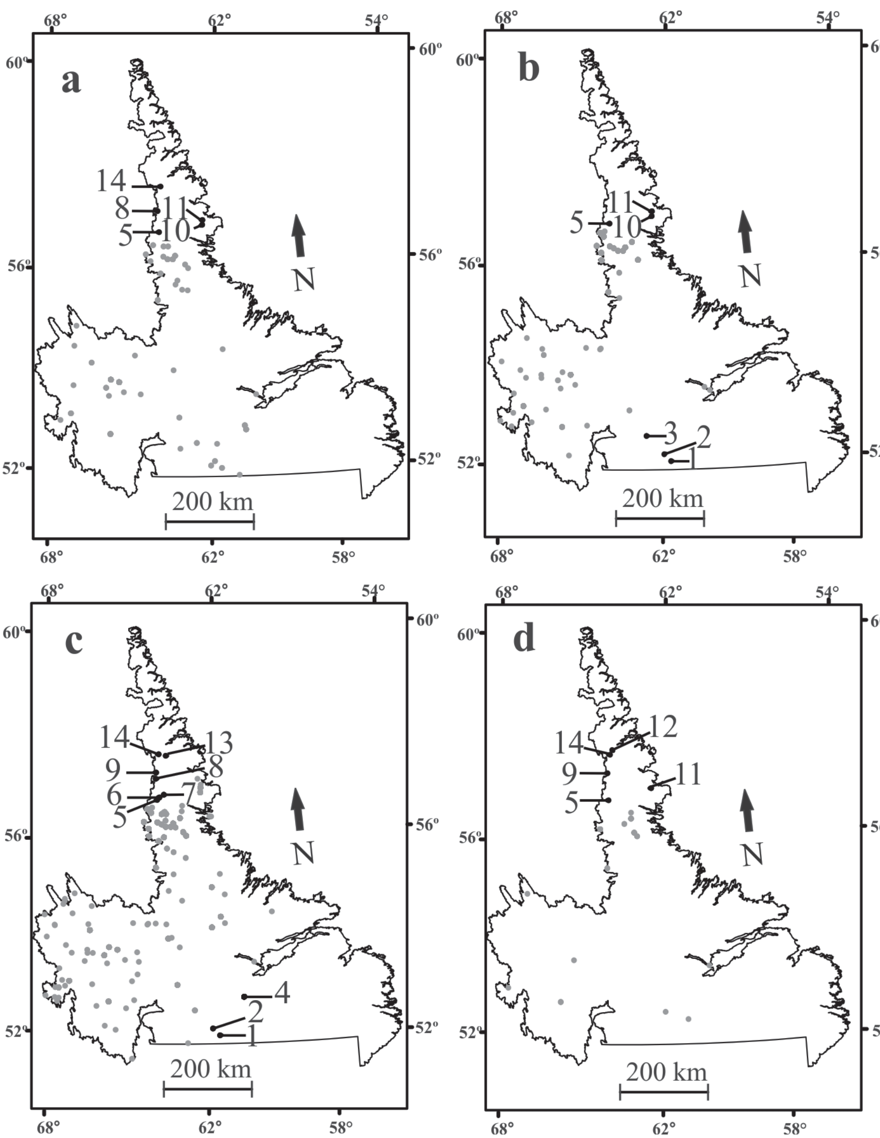

FIGURE 2. Previously known ranges (grey circles; Black *et al*. 1986) and new locations (black circles) for a. Burbot (*Lota lota*), b. Round Whitefish (*Prosopium cylindraceum*), c. Lake Trout (*Salvelinus namaycush*), and d. Slimy Sculpin (*Cottus cognatus*) in Labrador, extending species ranges north or southeast. 1 = Little Guines Lake; 2 = Lac Avert; 3 = unknown lake; 4 = Lac Mercier; 5 = Lake Langille; 6 = Lake C3; 7 = Lake Rhonda; 8 = Lake Sabrina; 9 = Lake Tracy; 10 = Iglusuatahrusuak Lake; 11 = Alliger Lake; 12 = unnamed stream; 13 = LB20; 14 = LB50.

For example, Burbot, Lake Trout, and Slimy Sculpin specimens were identified from three lakes in two unnamed tributaries (Lake Tracy, Lake LB50, Lake LB20, Rivers 103 and 104). Both of these tributaries drain northward into the Hebron Fjord, which is much farther north than the Fraser Canyon (Anderson 1985). Further, lakes Sabrina and Langille are part of the Kingurutik River drainage, which flows south into Tikkoatokak Bay, a separate watershed located above the Fraser Canyon. This finding is supported by Jansson and Kleman (2004) who determined that there were large numbers of glacial lakes present in Labrador during the retreat of the Laurentide Ice Sheet. Water spillage from these lakes led to ~30 meltwater injection events spilling into the Labrador Sea. Thus, many overland colonization events could have occurred across northern Labrador. Using geomorphic maps and the direction of esker deposits, Jansson and

Kleman (2004) described several drainage routes, in addition to the Fraser Canyon route. Some extended farther north and included the Kingurutik, Hebron, and Koruc drainage basins (Figure 3). It is noteworthy that we sampled the isolated coastal lakes, which are part of Puttuaala Brook, near Okak Bay (Lake Alliger and Iglusuatahrusuak Lake), and discovered that Burbot, Round Whitefish, and Slimy Sculpin also existed with Lake Trout. These species were also present in lakes Langille and Sabrina, located on the Kingurutik watershed, bordering Puttuaala Brook. Therefore, it is probable that all four species dispersed into Puttuaala Brook from the Kingurutik watershed when glacial lakes, such as Naskaupi, released their waters, causing spillages from the Kingurutik drainage into neighbouring Pattuaala Brook.

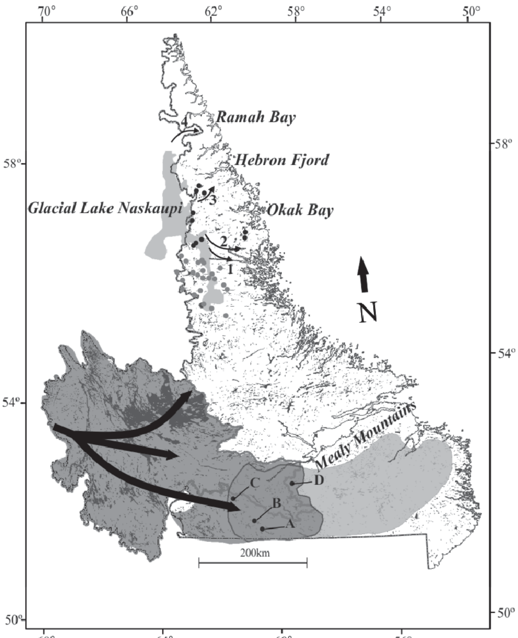

FIGURE 3. Possible colonization routes of freshwater fish species into areas of northern Labrador and location of the four sampled lakes in the transition zone: A. Little Guines Lake; B. Lac Avert; C. unknown lake; and D. Lac Mercier. The shaded dark and light grey areas represent the approximate locations of the Churchill and southeast Ichthyogeographic regions, respectively. The medium grey area, in northern Labrador represents glacial Lake Naskaupi, and the black arrows represent drainage routes adopted from Jansson and Kleman (2004): 1. Fraser River; 2. Kingurutik River; 3. Hebron Fjord; 4. Koruc River. Grey dots indicate locations of 25 lakes that highlight new occurrences within previously established ranges (Black *et al.* 1986) of four stenohaline freshwater fish species native to Labrador, Canada, collected during sampling events from 2007 to 2015. The large black arrows represent the overland dispersal routes taken by freshwater fish from Glacial Lake Barlow-Ojibway.

Waterways formerly connected following glacial retreat may have provided pathways for species dispersal into coastal areas. Thus, future investigations may extend the range of stenohaline species considerably northward. For example, we speculate that, following a pattern of drainage from Quebec, it is also likely that water spilled northward from glacial Lake Naskaupi, through the Koroc River system in Quebec, then eastward into Ramah Bay. This glacial spillway may have provided colonization routes. This is of particular interest because the lakes that may contain these species fall within the boundaries of the recently established Torngat Mountains National Park. Determining the postglacial movement of freshwater fish species in this region would provide an addition to the natural history database of the park.

Southern Labrador

The southerly collections of both Round Whitefish and Lake Trout demonstrate a range extension of ~65 km into the southeastern portion of Labrador. Of special interest is the discovery of Lake Trout in Lac Mercier, a small isolated lake that abuts the southwestern boundary of the Mealy Mountain Range and is ~50 km southeast of Happy Valley-Goose Bay. Many lakes near Lac Mercier have been sampled, and the occurrence of Lake Trout at this location represents a local anomaly. In general, the weather and geomorphology favour species tolerant of warmer waters, because most lakes are shallow and exhibit warm water temperatures in the summer (Meades 1990; Spence and Perry 2010; R.C.P. unpubl. data), and Longnose Sucker (*Catostomus catostomus*), White Sucker (*Catostomus commersonii*), Northern Pike, and Brook Trout, predominate (Black *et al.* 1986; R.C.P. unpubl. data). Lake Trout requires cold, well-oxygenated waters (Martin and Oliver 1980) with a thermal optimum of 10 ± 2°C (Magnuson *et al.* 1990).

Lake Trout in Lac Mercier are likely sustained because of a set of locally unique conditions that provide these optimal conditions. The lake is fed by three cool, well-oxygenated streams and has a small pocket of deep water that establishes a thermocline during the warm summer months (R.C.P. unpubl. data). To date, the closest lake reported to contain Lake Trout is over 100 km away from Lac Mercier. Therefore, their presence in this isolated deepwater lake suggests that, in the past, Lake Trout may have occurred across the entire region. It is possible that Lake Trout existed in southern Labrador following the final retreat of the Laurentide Ice Sheet into Ungava Bay, ~6000 years ago, when postglacial meltwaters produced cold water temperatures and much cooler mean atmospheric temperatures. Lake Trout may have been extirpated from most of this range by a warmer contemporary climate. Snucins and Gunn (1995) reported a similar situation for an isolated population of adult Lake Trout in Pedro Lake, Ontario. There, Lake Trout were sustained, in an otherwise unsuitable environment, by groundwater seepage that maintained a small pocket of cold water.

Although it is possible that Lake Trout were introduced to Lac Mercier, it is not probable. With a human population of less than 30 000, Labrador is sparsely populated (Newfoundland Labrador Census 2016). At the time of this discovery, Lac Mercier was separated from Happy Valley-Goose Bay by the Churchill River and an absence of roads. This small lake was located in an isolated area of Labrador and surrounded by pristine old-growth forest that had never been harvested. The absence of infrastructure meant that the only way into Lac Mercier was by float plane and, as Mercier is not recognized as a quality fishing destination, the potential for human introduction is minimal. Furthermore, the species complement in Lac Mercier included most of the species that co-occur with Lake Trout in the Churchill drainage, including Longnose Sucker, White Sucker, Northern Pike, Burbot, Longnose Dace, and Brook Trout.

Black *et al.* (1986) theorized that the main postglacial dispersal route into Labrador was from Quebec. The most probable pathway was via glacial Lake Barlow-Ojibway, moving across Quebec, north and south of the Otish Mountains, through proglacial lakes and watershed transfers during postglacial rebound. This route gave fish access to the headwaters of the Churchill River and to tributaries in Labrador. From there, species moved southeasterly, colonizing via tributary headwaters or through main stem migrations, moving up the Churchill drainage tributaries. At the bottom of the Churchill drainage, only a few species successfully colonized the furthest southeastern portion of Labrador, because the Mealy Mountains or sea dispersals served as barriers to most.

However, the Lake Trout population in Lac Mercier indicates another explanation is possible for the impoverished species composition in the southeast ichthyogeographic region. Black *et al.* (1986) suggested that the paucity of species found below Lake Melville and east of the Little Mecatina River could be attributed to the Mealy Mountains, which served as a barrier to species potentially arriving from the Churchill drainage.

Nevertheless, some Churchill drainage species are present, including Longnose Sucker, White Sucker, and Northern Pike. These are considered cool water species tolerant of warmer waters than Lake Trout and Lake Whitefish (*Coregonus clupeaformis*; Wismer and Christie 1987). The presence of these cool-water-tolerant species provides some indirect evidence that, at one time in the distant past, Lake Trout may have also been present in southeastern Labrador. If the Mealy Mountains were not a barrier to colonization of the area by warmer water species, it is unlikely that they were for coldwater species. The idea that the Mealy Mountains served as a barrier to some species, while allowing others to pass is predicated on varying swimming performance. The swimming ability of Lake Trout falls well within the ranges of all the warmer water tolerant species listed above and matches that of Brook Trout (Peake 2008). Therefore, it is more probable that a gradual conversion to unsuitable habitat, and not topographic barriers, led to the impoverished species complement. Supporting this assertion is the observation that lakes become shallower and summer temperatures warmer in a southwest to southeast direction (Figure 4). Thus, this combination of relatively shallow waters and warm temperatures likely created the observed species complement in southeastern Labrador.

The species complement in the deep lakes of southwestern Labrador includes both cool water and coldwater species such as Lake Whitefish, Brook Trout, Burbot, Lake Trout, Longnose Sucker, Northern Pike, Round Whitefish, and White Sucker. In contrast, we sampled many large lakes in all the major watersheds of the southeast region, including Traverspine, Kenamu, Eagle, and Paradise River watersheds, and found that most lakes were shallow (Spence and Perry 2010). The Eagle and Paradise Rivers watersheds comprise a large area of the southeastern region and drain areas of 10 824 km^2 and 5276 km^2, respectively. Both rivers have as their source shallow string bogs and glides (Anderson 1985). These shallow lakes contain fishes that have greater thermal tolerances for warmer waters or, in the case of Brook Trout, have adaptive strategies to sustain themselves during critically warm events (Petty *et al.* 2012). Thus, cool water species such as Longnose Sucker, White Sucker, Northern Pike, and Brook Trout were present while Burbot, Lake Whitefish, and Lake Trout were absent.

Lac Mercier is situated at a longitude that we consider to be part of a larger transition zone between the Churchill and southeast ichthyogeographic regions. In this zone, the topography of the land begins to change, with lakes becoming shallower from west to east (Government of Newfoundland and Labrador unpubl. data). In the area, coldwater species persist only in lakes that consistently maintain the appropriate thermal properties, while species with higher thermal tolerance are present in most lakes. For example, Lac Mercier was not the only location where we found a remnant population of a coldwater species. To the south of Lac Mercier, we sampled two lakes

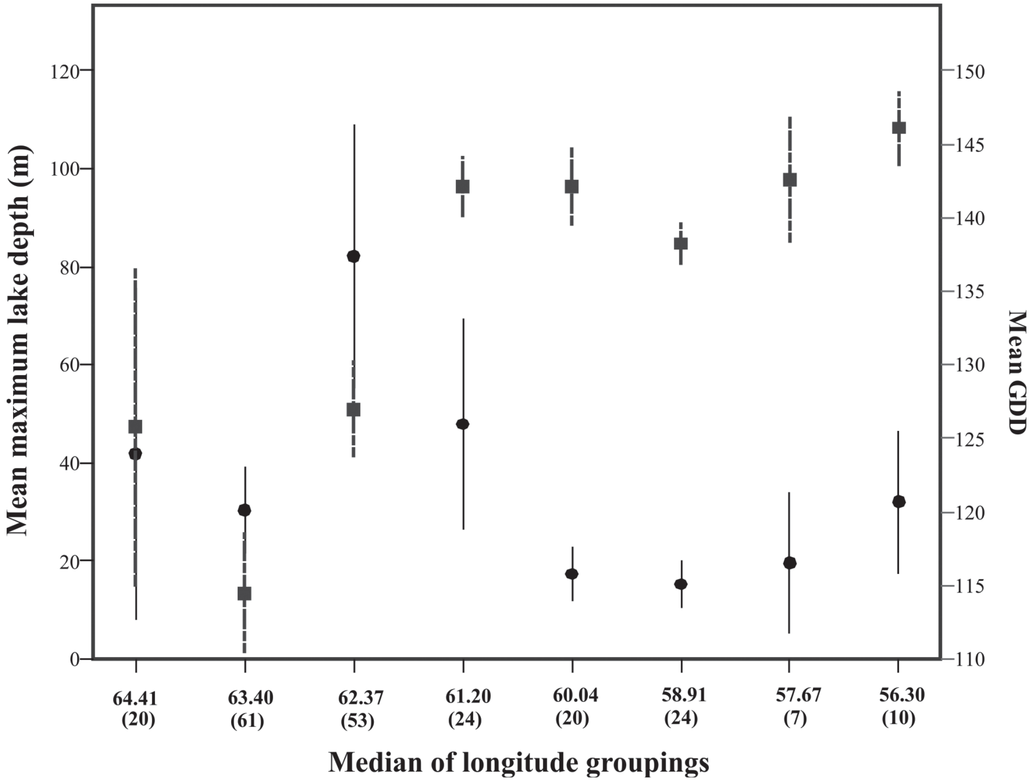

FIGURE 4. Mean maximum lake depths (●; calculated using model of Hollister *et al.* 2011) and mean growing degree-days (■; GDD; NRCan 2020), with 95% CI, for lakes in southern Labrador (all sampled lakes were below 53° latitude). Lakes were grouped longitudinally by depth (from west to east); number of lakes in each grouping is shown in parentheses under median for lakes in the group. Shape data from Natural Resources Canada (http://cfs.nrcan.gc.ca/projects/3) were used to assign mean annual temperature norms to each lake.

that contained Lake Whitefish and Round Whitefish, but not Lake Trout. Both species of whitefishes have slightly higher optimum thermal growth temperatures than Lake Trout (Hasnain *et al.* 2010). To the east of Mercier, we sampled several lakes that had Burbot but no other coldwater species. Burbot has a warmer optimum thermal growth temperature than either the whitefishes or Lake Trout (Hasnain *et al.* 2010).

Our study supports the hypothesis of three ichthyogeographic regions formulated by Black *et al.* (1986). However, our discovery of Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin in other drainages above the Fraser River watershed in northern Labrador suggests that an alternative explanation of colonization pathways may be required. Rather than marine dispersal accounting for the presence of stenohaline species in coastal lakes near Okak Bay, it is more probable that an overland pathway led to their presence.

In southern Labrador, Round Whitefish and Lake Trout have been found farther to the southeast, beyond their formerly reported range limits. In addition, the discovery of an isolated pocket of coldwater species in Lac Mercier suggests that Lake Trout were present in the region since the last ice age, but environmental warming might have led to range contraction. This contraction may have led to the impoverished species complement currently found in the southeastern portion of Labrador. The isolation of this Lake Trout population (~100 km from the nearest Lake Trout lake population) may indicate that it is genetically distinct and deserves special conservation status. Future studies investigating the genetic structure of Lake Trout in Labrador may provide insights into this interesting fish population. Furthermore, the examination of genetic structure across all freshwater species would assist in validating colonization patterns as well as help identify evolutionarily distinct lineages.

Author Contributions

Writing – Original Draft: R.C.P. and D.G.K.; Writing – Review & Editing: R.C.P. and D.G.K.;

Conceptualization: R.C.P.; Investigation: R.C.P. and D.G.K.; Methodology: R.C.P. and D.G.K.

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Data accessibility

The Government of Newfoundland and Labrador Provincial Aquatics Database and Archive (PADA) houses the data contained in this manuscript. Access to data contained in PADA may be gained by submitting a written request to the Department of Fisheries, Forestry and Agriculture, Forestry and Wildlife Branch, P.O. Box 2006 Corner Brook, Newfoundland and Labrador A2H 6J8.

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