Biogeography of the deepwater sculpin (*Myoxocephalus thompsonii*), a Nearctic glacial relict

T.A. Sheldon, N.E. Mandrak, and N.R. Lovejoy

Abstract: Although the freshwater fish fauna of North America is relatively well studied, the biogeography of the deepwater sculpin (*Myoxocephalus thompsonii* (Girard, 1851)) remains poorly understood. Collections of the species are limited, both because of its relatively remote distribution and because its habitat at the bottom of very deep lakes presents considerable logistic challenges for sampling. To investigate the biogeography of the deepwater sculpin, we conducted a range-wide (excluding the Laurentian Great Lakes) survey for the species between May and October 2004. Deepwater sculpin were collected using a variety of sampling gears, including a trap that was specifically designed to capture the species. We hypothesized that deepwater sculpin would be found only in areas that were formerly occupied by glacial lakes or the Champlain Sea. We reconstructed the historical boundaries of these water bodies and found that nearly all lakes where deepwater sculpin were collected, including four new localities, were within those limits. Conversely, the species was not detected in sampled lakes that were beyond these boundaries. Our results clarify the distribution and biogeography of the deepwater sculpin and strengthen the view that the current distribution of the species was mediated by dispersal through glacial lakes and the Champlain Sea.

Résumé : Bien que la faune des poissons d’eau douce d’Amérique du Nord soit relativement bien connue, la biogéographie du chabot de profondeur (*Myoxocephalus thompsonii* (Girard, 1851)) reste mal comprise. Les récoltes de cette espèce sont peu nombreuses, tant à cause de sa répartition en milieu éloigné qu’à cause de son habitat au fond des lacs très profonds, qui compliquent considérablement la logistique d’échantillonnage. Afin d’étudier la biogéographie du chabot de profondeur, nous avons procédé à un inventaire à grande échelle (en excluant les Grands Lacs laurentiens) de l’espèce de mai à octobre 2004. Nous avons récolté les chabots de profondeur à l’aide de divers engins d’inventaire, y compris un piège spécialement conçu pour leur capture. Nous avons émis l’hypothèse que le chabot de profondeur ne serait retrouvé que dans les régions couvertes antérieurement par les lacs glaciaires ou la mer de Champlain. Nous avons reconstitué les frontières historiques de ces plans d’eau et observé que presque tous les lacs dans lesquels le chabot de profondeur a été retrouvé, dont quatre nouvelles localités, se situaient dans ces limites. À l’inverse, l’espèce n’a pas été retrouvée dans les lacs échantillonnés au-delà de ces frontières. Nos résultats précisent la répartition et la biogéographie du chabot de profondeur et appuient le point de vue qui veut que la répartition actuelle de l’espèce s’explique par une dispersion à travers les lacs glaciaires et la mer de Champlain.

[Traduit par la Rédaction]

Introduction

The deepwater sculpin, *Myoxocephalus thompsonii* (Girard, 1851), is one of the most poorly known freshwater fishes in North America (Girard 1852; Parker 1988). It lives at the bottom of deep, cold lakes, with the deepest specimens captured at ~366 m in both Great Bear Lake and Lake Superior (Scott and Crossman 1973). The species appears to occur only in oligotrophic lakes (Committee on the Status of Endangered Wildlife in Canada 2006), and can be an important part of the benthic community and deepwater lacustrine food chains (Scott and Crossman 1973). It is a primary consumer of the crustaceans *Diporeia* Bousfield, 1989 and *Mysis* Latreille, 1803, as well as larval chironomids (Black and Lankester 1981; Brandt 1986; Kraft and Kitchell 1986; Selgeby 1988; Geffen and Nash 1992). It is also an integral food item of deepwater piscivores such as lake trout (*Salvelinus namaycush* (Walbaum in Artedi, 1792)), burbot (*Lota lota* (L., 1758)), and alewife (*Alosa pseudoharengus* (Wilson, 1811)) (Day 1983; Madenjian et al. 2002; Murray et al. 2003; Stewart and Watkinson 2004). One of the primary determinants of deepwater sculpin abundance in Lake Michigan is predation by burbot on adults and by alewife on larvae (Madenjian et al. 2002; Madenjian et al. 2005). The deepwater sculpin is thought to be an ex-

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cellent indicator of the health or well-being of deepwater fish community and habitat (Casselman and Scott 2003; Mills et al. 2003), since it is negatively affected by contaminants and eutrophication of lakes (Parker 1988).

The known range of deepwater sculpin in Canada extends from the Gatineau region of Quebec through the Laurentian Great Lakes, continuing through Manitoba and Saskatchewan, and northwest to Great Slave and Great Bear lakes (Scott and Crossman 1973; Parker 1988; Committee on the Status of Endangered Wildlife in Canada 2006). A disjunct population occurs in Upper Waterton Lake in southwestern Alberta (McAllister and Ward 1972; Parker 1988). Distribution records indicate that the deepwater sculpin is almost entirely confined to Canada; prior to this study, the deepwater sculpin had been reported from 55 lakes in Canada and only 4 lakes in the United States. The deepwater sculpin has been recorded from all of the Laurentian Great Lakes; however, the presence of a reproducing population within Lake Erie has never been reported. Juveniles recorded within Lake Erie are most likely due to larval drift from Lake Huron, as Lake Erie is probably too shallow and eutrophic to sustain reproducing populations (Roseman et al. 1998). The deepwater sculpin was thought to be extirpated from Lake Ontario, but has since been reported in extremely low numbers (Brandt 1986; Casselman and Scott 2003).

Although the current distributions of most Canadian fish species were affected by advancing and retreating continental glaciers, the deepwater sculpin is thought to owe both its origin and its current distribution to glacial effects (McAllister 1961; Scott and Crossman 1973; Kontula and Vainola 2003). The sister species of the deepwater sculpin is the Arctic marine fourhorn sculpin (*Myoxocephalus quadricornis* (L., 1758)). This curious relationship led researchers to call the deepwater sculpin a “glacial relict”, a species derived from an Arctic marine lineage that was driven south into freshwater habitats by early glacial advances (McAllister 1961; Dadswell 1972; Kontula and Vainola 2003). This origin is thought to be shared with other freshwater glacial relicts, such as the crustaceans *Mysis* spp. and *Diporeia* spp., that similarly have close relationships with Arctic marine taxa (Ricker 1959; Martin and Chapman 1965; Audzijonyte et al. 2005). Once established in freshwater, the deepwater sculpin would have been subjected to any subsequent glacial advances, presumably surviving in glacial refugia along with other North American freshwater fish species. Dispersal from these refugia into formerly glaciated regions was facilitated by extensive melt-water lakes that formed along the margins of the retreating glaciers, and also by the Champlain Sea, a brackish inundation of the St. Lawrence and Ottawa river valleys that was present 13 000 – 10 000 years ago (Dadswell 1974). Thus, the highly scattered locality records of deepwater sculpin are thought to be a result of the patchy occurrence of lakes with suitable environmental conditions (very deep and cold) that were also accessible by routes of dispersal via glacial lakes or the Champlain Sea (Dadswell 1974; Parker 1988). However, this dispersal hypothesis has not yet been explicitly tested with distributional data and glacial lake reconstructions.

Despite the biogeographic novelty of the deepwater sculpin, details regarding the distribution of the species across most of its range remain poorly understood, and known localities outside the Laurentian Great Lakes may not adequately reflect the actual distribution of the species. Information gaps are due, in part, to the remote locations and associated logistic challenges of sampling ecologically suitable lakes, as well as the restriction of the species to the greatest depths within lakes (Scott and Crossman 1973; Murray et al. 2003). However, complete knowledge of the distribution of a species is essential for understanding its biogeographic and evolutionary histories (Mandrak and Crossman 1992).

In this study, we examine the biogeography of the deepwater sculpin. In light of the limited distribution data for the species across its entire range, we conducted a range-wide sampling survey. We checked historical records of deepwater sculpin and sampled lakes with suitable habitat to identify new localities for the species outside the Laurentian Great Lakes. We also test the hypothesis that the distribution of the deepwater sculpin is the result of post-Pleistocene dispersal via large glacial lakes and the Champlain Sea (McPhail and Lindsey 1970; McAllister and Ward 1972; Kontula and Vainola 2003). This hypothesis predicts that lakes with deepwater sculpin should be found only in areas that were formerly occupied by glacial lakes or the Champlain Sea, or were in close proximity to them and directly connected to their former outlets (Karrow and Calkin 1985; Eschman and Karrow 1985; Dyke and Prest 1987; Barnett and Bajc 2002). To test this prediction, we sampled several lakes that were ecologically suitable (deep, cold, oligotrophic) but were outside former glacial lake boundaries.

Materials and methods

We conducted an intensive field sampling program targeting deepwater sculpin between May and October 2004. Our sampling effort encompassed most of the known distribution of the deepwater sculpin, ranging from Alexie Lake in the northwest, to Thirty-One Mile Lake in the east, and Upper Waterton Lake in the southwest. The survey included lakes where deepwater sculpin had previously been recorded, allowing us to confirm their presence. It also included lakes where deepwater sculpin had not previously been recorded, but were expected to occur, based on known habitat requirements (deep, cold, oligotrophic lakes) and distribution (within the reconstructed range of glacial lake boundaries).

Previous authors have proposed that the distribution of deepwater sculpin is the result of post-Pleistocene dispersal only through, and not beyond, large glacial lakes (McPhail and Lindsey 1970; Dadswell 1974; Kontula and Vainola 2003). If this is the case, deepwater sculpin should not occur in lakes outside the former boundaries of glacial lakes, the Champlain Sea, or their outlets. To test this idea, we reconstructed the boundaries of glacial lakes and the Champlain Sea by overlaying metadata layers of previous glacial lake boundaries from Dyke et al. (2003). This online data set represents the most up-to-date outline of North American glacial lake boundaries from the Wisconsinan glaciation (18 000 to 5 000 years before present). We combined glacial lake outlines from 52 individual periods (metadata sets) during this timeframe to create a total glacial lake and Champlain Sea extent for the entire deglaciation period. We then selected several lakes that were clearly outside these reconstructed boundaries. Because the expense of traveling and sampling imposed limitations on the number and location of lakes that we could investigate, we tested the glacial lake boundary hypothesis in only a limited area. We examined three lakes in the Rocky Mountains (Upper Kananaskis Lake, Lake Minnewanka, and Emerald Lake) and two lakes in northern Alberta and Saskatchewan (Peerless Lake and Cold Lake). These lakes were deemed ecologically suitable for deepwater sculpin (all had maximum depths >35 m and benthic water temperatures <8 °C during the summer), but were determined to lie outside historic glacial lake boundaries.

To specifically target the benthic deepwater sculpin, we designed custom collapsible fish traps, and used gillnets and trawls. The benthic fish traps were designed to lie flat on the bottom and offer the maximum possible catchment area at 0–15 cm above the lake bed. It was important that the benthic fish traps be collapsible to reduce volume during transport. The traps were made out of 6 mm wire mesh. Their dimensions were 90 cm long × 45 cm wide × 15 cm high (Sheldon 2006). The mouth of the catchment area was 45 cm wide × 15 cm high, and this funneled into the trap with a final entrance size of 6.25 cm × 5 cm. The funnel length was 25 cm. The reduced height of the trap, combined with the length of the funnel, caused the slope angle of the funnels to be 11.5°. This slope minimized the vertical travel distance for the fishes entering the trap. We predicted that this, along with the large trap catchment area, would significantly increase catch per unit effort of deepwater sculpin relative to traditional basket minnow traps. During a trial period, equal numbers of our benthic fish traps and traditional basket minnow traps were deployed randomly throughout the sampling area in the first 11 lakes. Of 46 deepwater sculpin captured in the traps, 40 were captured in the benthic fish traps. Subsequent to this trial period, only benthic fish traps were used (Sheldon 2006).

In each lake, 15–30 traps were baited with dog biscuits and cyalume (glow) sticks, and set for at least 12 h. These traps were re-set up to five times, with each set lasting ~12 h, until a minimum of five deepwater sculpin were captured (number required for a concurrent genetics study). A 1.0 cm stretched mesh gillnet (1 m high × 15 m long panel) was set on the bottom for 12 h, and a minimum of two bottom trawls of 10 min in duration were also conducted in each lake weather permitting. Trawling methods were modeled after Dadswell (1974), using an exact replicate of a small otter trawl that was successfully employed during the course of his work on benthic crustaceans and fishes in eastern North America. In our study, the trawl was towed across the lake bottom at ~3–5 km/h. A ratio of approximately 3:1 was used to gauge tow rope length to trawling depth (Dadswell 1974). All sampling was conducted in the deeper regions of each lake as indicated by bathymetric maps and local knowledge. Depths were confirmed using a Garmin® sonar depth finder. Trawls were conducted in two transects across the deepest part of each lake whenever possible. A minimum of 900 h of benthic minnow trap, 12 h of gillnet, and 0.5 h of benthic trawling effort were expended while sampling each lake.

Upon capture, deepwater sculpin were removed from fishing gear and anaesthetized in 0.5–0.6 mL/L of 2-phenoxyethanol. Gill and fin clips were then taken from all deepwater sculpin for genetic analyses. Deepwater sculpin were fixed in a 10% buffered formalin solution and then transferred to 70% ethanol for long-term storage. This allowed immediate preservation of gut contents, while ensuring the otoliths remained undamaged. We also collected habitat data at each sampling point (described in detail in Sheldon 2006).

Results

We collected 155 deepwater sculpin specimens. The species was recorded from 20 of the 35 lakes sampled (Table 1, Fig. 1). Deepwater sculpin were collected in lakes throughout their range within Canada, outside of the Laurentian Great Lakes. Lakes where deepwater sculpin were captured near the boundary of the known species range included Alexie Lake in the Northwest Territories in the northwestern portion of its range, Thirty-One Mile Lake in Quebec in the extreme east, and Upper Waterton Lake in Alberta in the extreme southwest (Fig. 1). In addition, deepwater sculpin were discovered in four lakes where they have not previously been recorded: Eagle and Teggau lakes in northwestern Ontario, and Clearwater and Second Cranberry lakes in northwestern Manitoba (Table 1, Fig. 1). The occurrence of deepwater sculpin in Second Cranberry Lake is the first record of deepwater sculpin from the Nelson River watershed of Manitoba.

Our sampling failed to find deepwater sculpin in 15 lakes. These included eight lakes where the species had not previously been collected, including all five lakes (Upper Kananaskis Lake, Lake Minnewanka, Emerald Lake, Peerless Lake, and Cold Lake) that were outside the reconstructed glacial lake boundaries, as well as three other lakes (Chitty Lake, Lake 258, and High Lake). We also failed to find deepwater sculpin in seven lakes where the species had previously been documented, including Lac des Iles and Heney Lake in the Gatineau region of Quebec, Cedar Lake in Algonquin Provincial Park in Ontario, Lake 310 and Lake of the Woods in northwestern Ontario, and Mirond Lake and Lac La Ronge in northeastern Saskatchewan.

Figure 2 shows the map of reconstructed late Pleistocene Champlain Sea and glacial lake boundaries in relation to all known deepwater sculpin locations (those indicated by this study and by previous reports). In nearly all cases, lakes where deepwater sculpin were caught historically or during this study were found to be within the maximum extent of glacial lakes or the Champlain Sea, or immediately adjacent to these water bodies. However, Upper Waterton Lake seems to be an exception to this rule. The five lakes that were clearly outside glacial boundaries and chosen to test the glacial lake dispersal hypothesis yielded no deepwater sculpin specimens.

Discussion

Our results support the hypothesis that the current distribution of the deepwater sculpin was mediated by post-Pleistocene dispersal through large glacial lakes or the Champlain Sea (McPhail and Lindsey 1970; McAllister and Ward 1972; Kontula and Vainola 2003). Each of the four lakes where deepwater sculpin were newly discovered (Eagle, Teggau, Clearwater, and Second Cranberry lakes) are present in a geographic area formerly occupied by

Table 1. Results of 2004 survey for deepwater sculpin (*Myoxocephalus thompsonii*) from inland lakes across their range.

No.[*]	Lake	Province	Latitude (N)	Longitude (W)	Historical presence[†]	2004 survey presence	*N*[‡]
1	Roddick Lake	Quebec	46°14′54.4″	75°53′30.9″	Yes	Yes	8
2	Lac des Iles		46°27′36.0″	75°31′59.2″	Yes	No	0
3	Thirty-One mile		46°12′43.1″	75°48′46.4″	Yes	Yes	6
4	Heney Lake		46°01′16.4″	75°55′29.2″	Yes	No	0
5	Lake 259 (ELA)	Ontario	49°41′19.9″	93°47′08.2″	Yes	Yes	6
6	Teggau (ELA)[§]		49°42′07.7″	93°38′53.1″	No	Yes	2
7	Lake 310 (ELA)		49°39′42.3″	93°38′13.6″	Yes	No	0
8	Lake 258 (ELA)		49°41′41.6″	93°48′02.9″	No	No	0
9	Eagle Lake[§]		49°46′15.5″	93°36′44.0″	No	Yes	11
10	Burchell Lake		48°35′07.6″	90°37′37.6″	Yes	Yes	17
11	Fairbank Lake		46°27′35.0″	81°25′37.0″	Yes	Yes	6
12	Cedar Lake		46°02′46.7″	78°33′11.9″	Yes	No	0
13	Saganaga Lake		48°14′32.7″	90°56′02.7″	Yes	Yes	10
14	Lake Nipigon		49°27′37.0″	88°09′57.6″	Yes	Yes	2
15	High Lake	Manitoba–Ontario	49°42′05.2″	95°08′01.2″	No	No	0
16	Westhawk Lake	Manitoba	49°45′32.0″	95°11′28.0″	Yes	Yes	6
17	George Lake		50°15′49.6″	95°28′16.2″	Yes	Yes	1
18	Lake of the Woods		49°41′28.7″	94°48′53.3″	Yes	No	0
19	Clearwater Lake[§]		54°04′05.5″	101°05′33.7″	No	Yes	5
20	Second Cranberry Lake[§]		54°39′08.5″	101°09′58.2″	No	Yes	18
21	Lake Athapapuskow		54°33′01.2″	101°39′05.4″	Yes	Yes	9
22	Mirond Lake	Saskatchewan	55°07′20.3″	102°48′07.6″	Yes	No	0
23	Lac La Ronge		55°12′06.9″	105°03′59.2″	Yes	No	0
24	Reindeer Lake		56°23′34.7″	102°58′22.2″	Yes	Yes	4
25	Wollaston Lake		58°14′59.3″	103°29′44.4″	Yes	Yes	4
26	Lac La Plonge		55°08′16.8″	107°15′43.2″	Yes	Yes	2
27	Chitty Lake	Northwest Territories	62°43′42.0″	114°07′57.2″	No	No	0
28	Alexie Lake		62°40′36.0″	114°06′08.0″	Yes	Yes	1
29	Great Slave Lake		62°29′15.0″	110°52′44.0″	Yes	Yes	9
30	Cold Lake	Alberta	54°31′23.0″	110°06′30.8″	No	No	0
31	Peerless Lake		56°40′23.0″	114°41′04.0″	No	No	0
32	Upper Waterton Lake		49°00′17.9″	113°54′16.8″	Yes	Yes	28
33	Upper Kananaskis		50°36′41.4″	115°09′55.9″	No	No	0
34	Lake Minnewanka		51°16′02.2″	115°25′57.4″	No	No	0
35	Emerald Lake	British Columbia	51°26′25.1″	116°31′39.8″	No	No	0

Note: ELA, Experimental Lakes Area.

[*] Corresponds to the numbers on Fig. 1.

[†] Constitutes a minimum of one record for deepwater sculpin prior to the 2004 survey.

[‡] Number of deepwater sculpins captured in 2004.

[§] New distribution record of deepwater sculpin.

both the Wisconsinan ice sheet and glacial Lake Agassiz (Dyke and Prest 1987). Thus, nearly all lakes with deepwater sculpin, including the new distribution records, are located in areas that were formerly occupied by glacial lakes or the Champlain Sea (Karrow and Calkin 1985; Eschman and Karrow 1985; Dyke and Prest 1987; Barnett and Bajc 2002) (Fig. 2). The populations of deepwater sculpin show a relatively continuous distribution in ecologically suitable lakes across Canada in an area once covered by glacial lakes (Mandrak and Crossman 1992) (Fig. 2). Although the deepwater sculpin always co-occurs with at least one other member of the Nearctic glacial fauna (such as *Mysis relicta* Lovén, 1862 or *Diporeia affinis*), it is found in relatively fewer lakes than other relict species (Dadswell 1974). This could be either a result of difficulty detecting deepwater sculpin, or stricter ecological conditions necessary for their persistence (Sheldon 2006).

Our sampling of ecologically suitable lakes beyond former glacial lake margins failed to detect deepwater sculpin (for further clarification regarding a possible exception see the Upper Waterton Lake discussion below). This supports the hypothesis that the continental distribution of deepwater sculpin resulted from post-glacial dispersal opportunities limited by the maximum extent of glacial lakes and their immediate outlets. It also suggests that secondary dispersal, subsequent to initial invasion via glacial lake corridors, has not occurred and that the distribution of deepwater sculpin has been stable over the past several thousand years. Our test of the glacial lake dispersal hypothesis was limited by logistical and financial constraints — we were only able to investigate the absence of the species in a few chosen lakes.

Fig. 1. Results of the 2004 survey for deepwater sculpin (*Myoxocephalus thompsonii*) from inland lakes across their range. See Table 1 for lake names.

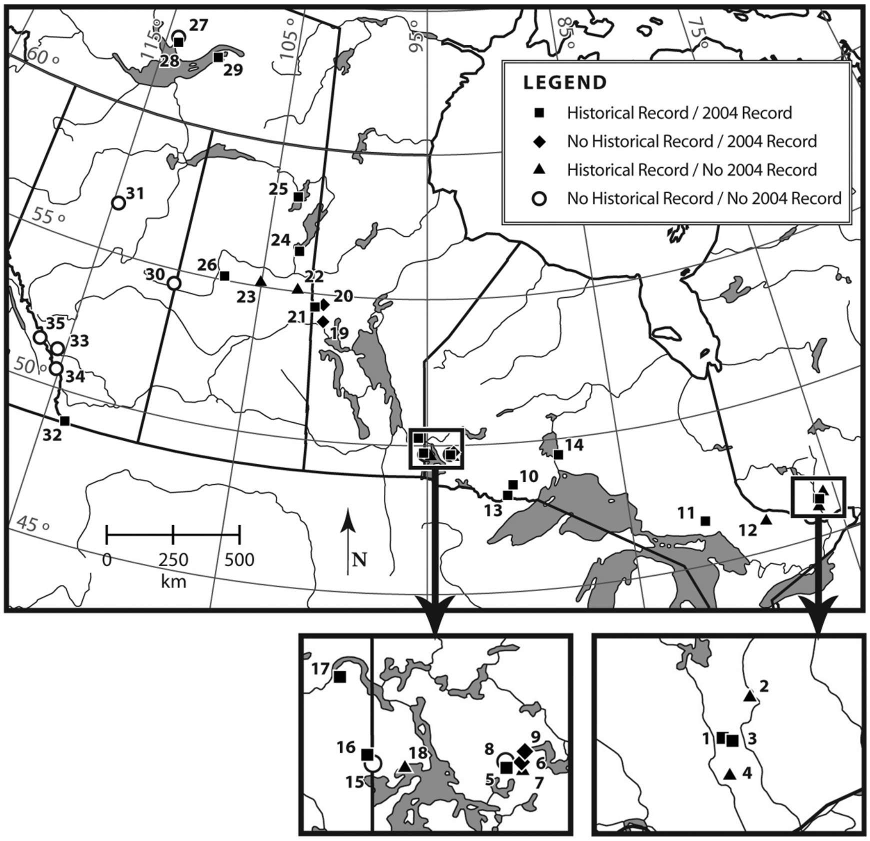
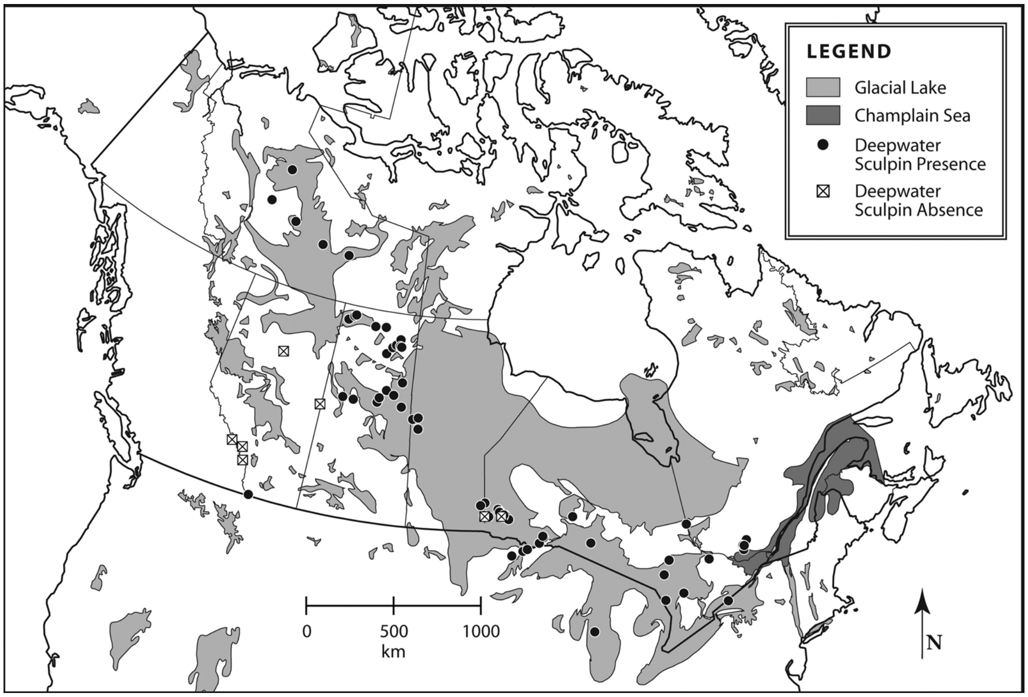


Fig. 2. The distribution of deepwater sculpin (*Myoxocephalus thompsonii*) relative to the reconstructed maximum extent of glacial lakes and the Champlain Sea from 18 000 to 5 000 years before present (adapted from Dyke et al. 2003). Sculpin presence is based on published historical records (including technical reports) and (or) records from this study. Sculpin absence refers to localities where deepwater sculpin were not found during this study, or were not recorded in the published literature or technical reports.



However, previous sampling (albeit not specifically targeting deepwater sculpin) of hundreds of lakes outside glacial lake boundaries (e.g., Nelson and Paetz 1992; Mandrak and Crossman 1992; Stewart and Watkinson 2004) also failed to detect the species, providing additional support for the hypothesis. Ongoing ichthyological surveys and more exhaustive sampling, particularly of benthic habitats using suitable gears, should allow further evaluation of the glacial dispersal scenario. Standardized benthic surveys across large numbers of lakes would also allow the application of more statistical approaches to distribution modeling.

The presence of deepwater sculpin in Upper Waterton Lake seems to be an exception to the hypothesis that the distribution of the species is exclusively the result of dispersal through glacial lakes, inland seas, and their outlets (Fig. 2). There is evidence of two separate glacial advances of the continental ice sheet to within 10 km of Upper Waterton Lake during the last glacial maximum (Jackson and Little 2004). Within the Upper Waterton area itself, there are scattered Canadian Shield clasts and glaciolacustrine sediments that were deposited in glacial lakes by continental ice sheet margins during the last glaciation (Jackson and Little 2004). This suggests that dispersal of deepwater sculpin into Upper Waterton Lake via glacial lake avenues and their immediate outlets subsequent to the last continental ice sheet advance is a possibility.

The new records of deepwater sculpin from Eagle Lake in northwestern Ontario, as well as Clearwater and Second Cranberry lakes in northwestern Manitoba, suggest that deepwater sculpin may be present in fairly accessible and popular fishing lakes. Each of these lakes has a substantial number of fishing lodges, some of which are active for over 5 months of the year. However, deepwater sculpin had remained undetected in all three lakes. This was most likely due to emphasis on sport-fishing species, such as lake trout and burbot, and the difficulties associated with the identification of sculpin species from the gut contents of these deepwater piscivores, if gut contents were examined at all. The presence of deepwater sculpin in both Teggau and Eagle lakes within the Experimental Lakes Area (ELA) of northwestern Ontario suggests that deepwater sculpin may remain undetected in lakes where targeted sampling has not occurred. Scientific fish surveys have been carried out in both of these lakes, yet deepwater sculpin had not been recorded in either (K. Mills, personal communication (2004)). This is most likely due to the difficulty inherent in catching smaller fish at the bottom of these very deep lakes. Sampling for deepwater sculpin must be targeted, as general fish surveys without the appropriate sampling equipment may not yield true indications of occurrence. These four new distribution records also suggest that the deepwater sculpin may be present in other deep, remote lakes in areas formerly occupied by glacial lakes.

During the 2004 survey, we failed to capture deepwater sculpin in seven lakes from where they were previously reported. There are a number of possible explanations for this failure to detect their presence. First, some previous records may be the result of erroneous identifications of species of sculpin. This is likely the case for Cedar Lake, Ontario, where a single juvenile deepwater sculpin (10 mm in length) had been reported from a bottom trawl over 40 years ago (Martin and Chapman 1965), and none have been captured since. Intense sampling of this lake over a 3-day period in August 2004 yielded 113 sculpins, all of which were spoonhead sculpin (*Cottus ricei* (Nelson, 1876)). We never found deepwater and spoonhead sculpins in the same lakes together, suggesting that competitive exclusion may occur between these species outside of the Great Lakes.

Second, deepwater sculpin may persist in these lakes, but sampling during the 2004 survey may have been inadequate to detect their presence (false negatives). This may be the case for Lac La Ronge and Mirond Lake. Both lakes, especially Lac La Ronge, are very large and sampling a small proportion of lake area may simply indicate the absence of deepwater sculpin from that specific area rather than the lake as a whole.

Finally, the absence of deepwater sculpin from some lakes in which they were previously documented may be that changing lake conditions have resulted in their extirpation. All lakes where deepwater sculpin were captured had relatively low nutrient concentrations and low biological production rates (Sheldon 2006). However, Lac des Iles and Heney Lake in the Gatineau region of Quebec, two localities where deepwater sculpin were previously recorded, were found to be relatively eutrophic or mesotrophic (Sheldon 2006). Both these lakes were sampled without success. This suggests that deepwater sculpin may be extirpated in these lakes because of changing environmental conditions (for more detailed analysis see Sheldon 2006).

The biogeography of deepwater sculpin has conservation and management implications. The absence of the species beyond Wisconsinan glacial lake and Champlain Sea boundaries indicates that dispersal of deepwater sculpin between lakes has most likely not occurred since the late stages of the glacial lake phase of the Wisconsinan glaciation. This further emphasizes that the current distribution of deepwater sculpin in Canada is static, rather than dynamic. Dispersal from lake to lake, resulting in newly founded reproducing populations or a rescue effect, is highly unlikely. This suggests that deepwater sculpin are unable to expand their range or exploit newly suitable habitat should it become available. This makes the species extremely vulnerable to local extirpation should their current habitats become eutrophied or otherwise disturbed.

Our study has improved understanding of the biogeography of the deepwater sculpin. It will provide a baseline for further effective research on the history, management, and conservation of the deepwater sculpin. The discovery of four new locality records is important, as current information about the species outside the Laurentian Great Lakes basin is extremely limited. Results from our survey, combined with historical distribution records, bring the total number of lakes where deepwater sculpin have been found to 63 (Table A1), although deepwater sculpin may be extirpated or falsely recorded from a few of these lakes. The range of deepwater sculpin throughout Canada corresponds closely to glacial lake and Champlain Sea boundaries, suggesting that the distribution of the species is the result of dispersal through these water bodies or their outlets. The study confirms that, because of their restrictive requirements, dispersal of deepwater sculpin has likely not occurred since the late stages of the glacial lake phase, nor is it likely to occur in the future. Thus, the deepwater sculpin offers a tremendous opportunity to study the influence of glaciation on a widespread fish species within Canada that has not been affected by secondary dispersal subsequent to initial invasion. However, without the proper conservation measures, this opportunity may be lost.

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Appendix A

Table A1. All lakes where deepwater sculpin (*Myoxocephalus thompsonii*) have been reported.

Region	Lake	Latitude (N)	Longitude (W)
Northwest Territories	Great Slave Lake	62°29′15″	110°52′44″
	Lac La Martre	63°21′48″	117°57′47″
	Keller Lake	63°57′00″	121°35′00″
	Great Bear Lake	65°50′00″	120°45′00″
	Alexie Lake	62°40′36″	114°06′08″
Alberta	Upper Waterton Lake	49°00′18″	113°54′17″
Saskatchewan	Reindeer Lake	56°23′35″	102°58′22″
	Wollaston Lake	58°14′59″	103°29′44″
	Lac La Ronge	55°12′07″	105°03′59″
	Lac La Plonge	55°08′17″	107°15′43″
	Mirond Lake	55°07′20″	102°48′08″
	Lake Athabasca	59°15′30″	109°28′00″
	Black Lake	59°10′00″	105°20′00″
	Riou Lake	59°07′00″	106°25′00″
	Beaverlodge Lake	59°31′00″	108°35′00″
	Canoe Lake	55°10′00″	108°15′00″
	East Lake	58°17′00″	103°38′00″
	Hatchet Lake	58°38′00″	103°34′00″
	Laonil Lake	55°41′00″	103°38′00″
	Mackay Lake	55°27′00″	104°56′00″
	McLennan Lake	55°53′00″	104°22′00″
	Milliken Lake	59°27′00″	108°45′00″
	Waterbury Lake	58°10′00″	104°22′00″
	Yalowega Lake	57°48′00″	104°53′00″
	Lake C1	58°19′00″	104°02′00″
Manitoba	Westhawk Lake	49°45′32″	95°11′28″
	George Lake	50°15′50″	95°28′16″
	Lake Athapapuskow	54°33′01″	101°39′05″
	Second Cranberry Lake	54°39′09″	101°09′58″
	Clearwater Lake	54°04′06″	101°05′34″
Ontario	Lake Ontario	43°45′00″	78°00′00″
	Lake Huron	44°30′00″	82°15′00″
	Lake Superior	48°00′00″	87°00′00″
	Lake Erie	42°15′00″	81°00′00″
	Cedar Lake	46°02′47″	78°33′12″
	Raven Lake	48°03′31″	79°33′09″
	Fairbank Lake	46°27′35″	81°25′37″
	Burchell Lake	48°35′08″	90°37′38″
	Lake Saganaga	48°14′33″	90°56′03″
	Lake 259 (ELA)	49°41′20″	93°47′08″
	Lake 310 (ELA)	49°39′42″	93°38′14″
	Lake of the Woods	49°41′29″	94°48′53″
	William Lake	50°04′00″	94°04′00″
	Horseshoe Lake	49°55′00″	93°57′00″
	Dicker Lake	49°57′00″	93°55′00″
	Passover Lake	49°32′00″	93°14′00″
	Trout Lake	49°45′00″	93°29′00″
	Burton Lake	49°41′00″	93°47′00″
	Squeers Lake	48°31′00″	90°34′00″
	Lake Nipigon	49°27′37″	88°09′58″
	Huston Lake	50°24′00″	95°07′00″
	Notellum Lake	44°40′00″	80°54′00″
	Lake Manitou	45°47′00″	82°00′00″
	Eagle Lake	49°46′16″	93°36′44″
	Teggau Lake	49°42′08″	93°38′53″
Quebec	Roddick Lake	46°14′54″	75°53′31″
	Lac des Iles	46°27′36″	75°31′59″
	Thirty-one Mile Lake	46°12′43″	75°48′46″
	Heney Lake	46°01′16″	75°55′29″
U.S.A.	Lake Michigan	43°30′00″	87°30′00″
	Lake Vermillion	47°52′15″	92°13′01″
	Dry Lake	47°57′18″	91°52′29″
	Sturgeon Lake	47°39′17″	93°04′27″

Note: ELA, Experimental Lakes Area.