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Lake trout in northern Lake Huron spawn on submerged drumlins

Stephen C. Riley [a,*], Thomas R. Binder [b], Nigel J. Wattrus [c], Matthew D. Faust [d], John Janssen [e], John Menzies [f], J. Ellen Marsden [g], Mark P. Ebener [h], Charles R. Bronte [i], Ji X. He [j], Taaja R. Tucker [a], Michael J. Hansen [k], Henry T. Thompson [k], Andrew M. Muir [d], Charles C. Krueger [l]

[a] U. S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA
[b] Michigan State University, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 49759, USA
[c] Large Lakes Observatory and Department of Geological Sciences, University of Minnesota-Duluth, 2205 E. 5th St., Research Laboratory Building 215, Duluth, MN 55812, USA
[d] Great Lakes Fishery Commission, 2100 Commonwealth Blvd., Suite 100, Ann Arbor, MI 48105, USA
[e] School of Freshwater Sciences, University of Wisconsin-Milwaukee, 600 E. Greenfield Ave., Milwaukee, WI 53204, USA
[f] Department of Earth Sciences, Brock University, 500 Glenridge Ave., St. Catharines, Ontario L2S 3A1, Canada
[g] Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Dr., Burlington, VT 05405, USA
[h] Chippewa-Ottawa Resource Authority, 179 W. Three Mile Road, Sault Ste. Marie, MI 49783, USA
[i] U. S. Fish and Wildlife Service, Green Bay National Wildlife and Fish Conservation Office, 2661 Scott Tower Drive, New Franken, WI 54229, USA
[j] Michigan Department of Natural Resources, Lake Huron Research Station, 160 East Fletcher Street, Alpena, MI 49707, USA
[k] U.S. Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 49759, USA
[l] Department of Fisheries and Wildlife, Center for Systems Integration and Sustainability, 115 Manly Miles Building, Michigan State University, East Lansing, MI 48824, USA

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ABSTRACT

Recent observations of spawning lake trout *Salvelinus namaycush* near Drummond Island in northern Lake Huron indicate that lake trout use drumlins, landforms created in subglacial environments by the action of ice sheets, as a primary spawning habitat. From these observations, we generated a hypothesis that may in part explain locations chosen by lake trout for spawning. Most salmonines spawn in streams where they rely on streamflows to sort and clean sediments to create good spawning habitat. Flows sufficient to sort larger sediment sizes are generally lacking in lakes, but some glacial bedforms contain large pockets of sorted sediments that can provide the interstitial spaces necessary for lake trout egg incubation, particularly if these bedforms are situated such that lake currents can penetrate these sediments. We hypothesize that sediment inclusions from glacial scavenging and sediment sorting that occurred during the creation of bedforms such as drumlins, end moraines, and eskers create suitable conditions for lake trout egg incubation, particularly where these bedforms interact with lake currents to remove fine sediments. Further, these bedforms may provide high-quality lake trout spawning habitat at many locations in the Great Lakes and may be especially important along the southern edge of the range of the species. A better understanding of the role of glacially-derived bedforms in the creation of lake trout spawning habitat may help develop powerful predictors of lake trout spawning locations, provide insight into the evolution of unique spawning behaviors by lake trout, and aid in lake trout restoration in the Great Lakes.

Lake trout *Salvelinus namaycush* historically were the dominant predator and supported a valuable commercial fishery in the Laurentian Great Lakes until the 1940s–1950s, when overfishing and predation by sea lamprey extirpated most lake trout stocks in the Great Lakes (Berst and Spangler, 1972; Krueger and Ebener, 2004; Muir et al., 2012a). Rehabilitation efforts including sea lamprey control, restrictive harvest regulations, and stocking began in the 1950s and 1960s, but aside from localized restoration in Lake Huron (Reid et al., 2001), wide-scale lake trout rehabilitation has occurred only in Lake Superior (Bronte et al., 2003; Eshenroder et al., 1995a, 1995b; Hansen et al., 1995).

The suitable spawning habitat which may be limiting in the Great Lakes (Eshenroder et al., 1995a) is an important consideration in lake trout restoration (Eshenroder et al., 1999). Quantification of the characteristics of lake trout spawning habitat is difficult in the Great Lakes as this species generally spawns at night (Esteve et al., 2008), often in deep waters during October–November, when sampling is difficult due to prevailing strong winds and the onset of winter weather conditions. Descriptions of Great Lakes populations in the late 1800s inferred that spawning occurred in October over rocky bottoms at depths from 2 to 25 m (e.g., Milner, 1874; see review by Muir et al., 2012b), but descriptions of spawning habitat advanced little over the next 100 years. Anecdotal descriptions of lake trout spawning locations and habitat types based on autumn catches in fishing gear were recorded during the 1970s from interviews of commercial fishermen who had fished in

* Corresponding author. Tel.: +1 734 214 7279.
E-mail address: sriley@usgs.gov (S.C. Riley).

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the first half of the 1900s before the demise of lake trout in the Great Lakes (Brown et al., 1981; Coberly and Horrall, 1980; Goodier, 1981). Based on this information, considerable variation occurred in spawning habitat; but actual data or direct observations on historically used habitats were few (see Kelso et al., 1995) compared to inland lakes (Martin, 1957; Martin and Olver, 1980). Several studies have since elucidated some of the characteristics of good lake trout spawning habitat in specific locations (Fitzsimons, 1995; Marsden and Krueger, 1991; Marsden et al., 1995a, 1995b, 2005; Sly and Evans, 1996), but no unifying framework exists to explain the structure and distribution of these habitats in the Great Lakes.

Here we hypothesize that certain glacial bedforms such as drumlins may provide suitable lake trout spawning habitat, and we suggest that a better understanding of the location and structure of submerged glacial bedforms in the Great Lakes may provide a new framework for the identification and location of lake trout spawning habitat. Drumlins are landforms created in subglacial environments by the action of advancing and receding ice sheets (Johnson et al., 2010). On land, drumlins appear as small hills ranging from approximately 100 m to >1 km long, and they tend to occur in clusters called “fields” or “swarms.” Although the mechanisms of drumlin formation are controversial (Krüger, 1994; Menzies, 1979; Menzies and Shilts, 2002; Shaw et al., 1989; Stokes et al., 2011), many drumlins contain layers or zones of sorted sediments ranging in size from silt to boulders. In the Great Lakes, layers of sorted large sediment within submerged drumlins could potentially provide high-quality spawning habitat for lake trout, particularly where drumlins are situated such that water currents penetrate these layers. Here we report evidence that lake trout in northern Lake Huron spawn on drumlins, and we develop and advance the hypothesis that drumlins and other submerged glacial bedforms such as end moraines, fluted moraines, and eskers may be widely distributed along the southern edge of the species' distribution and may be highly suitable for lake trout spawning due to sediment sorting that occurred during their formation.

Methods

High resolution multibeam bathymetric surveys conducted in 2010 and 2011 were used to characterize the lake bed to the south of Drummond Island in northern Lake Huron. The multibeam system used was a Reson Seabat 7101 operating at 240 kHz, which uses 511 beams spanning an angular range of $\pm 75°$ about nadir to measure bathymetry at a resolution of 1.25 cm. The lateral resolution is dependent on water depth and number of beams retained in the processed data. Post-acquisition processing of bathymetric and backscatter data was performed using CARIS HIPS and SIPS, a full-featured hydrographic package. Processing removed outliers from the data and applied appropriate corrections for vessel motion and ray bending due to sound velocity variations. Processed data were used to produce high-resolution bathymetric and backscatter maps at 1 m intervals.

During September–November 2010–2012, an acoustic telemetry array was deployed within the Drummond Island Refuge in northern Lake Huron to study the spawning behavior of lake trout. Each year, a positional (Vemco Positioning System—VPS) array of 131–150 Vemco VR2W receivers was deployed such that nearly complete acoustic coverage of an 18.9 km^2 area within the array was achieved during the autumn spawning period. During August–September 2010–2011, 400 adult lake trout of wild and hatchery origin were implanted with Vemco V16 acoustic tags and released prior to spawning near the array. The tags pinged every 50–130 s and 2-D positions of each fish were recorded continuously to an accuracy of 15–20 m while fish were within the array. The distribution of recorded positions was visualized using Python (v. 2.6.5, Python Software Foundation) to identify areas of greatest lake trout activity during the spawning season. Locations suspected of supporting successful spawning on the basis of telemetry data were verified visually by SCUBA divers and by collection of fry using emergent fry traps (Stauffer, 1981).

Results

High-resolution bathymetry revealed that the lake bed off the southern shore of Drummond Island is a submerged drumlin field formed beneath the Laurentide Ice Sheet during the last glaciation (Fig. 1). This drumlin field consists of a series of elongate ridges (drumlins) that rise 10 to 20 m above the surrounding lake bed. The drumlins range from 200 to 500 m wide and 500 to 1500 m long and are oriented in a north–south direction, which reflects the flow direction of the ice sheet during their formation (Fig. 1B). The surficial substrate on the drumlins is composed of coarse gravel and boulders, while sediments in areas between the drumlins are fine-grained, having a sand or silt composition. Fluted moraines, which are often found in association with drumlins, also occur interspersed among the drumlins at Drummond Island. Fluted moraines are streamlined ridges and grooves, often smaller and narrower than drumlins, that trend at right angles to the ice front.

Behavioral data gathered with acoustic tags implanted in spawning lake trout and diver observations within the Drummond Island drumlin field indicated that lake trout in this area spawned primarily on drumlins (Fig. 2). The movement and aggregation of acoustically-tagged lake trout in this study area indicated that these fish tended to aggregate on or near drumlins. Three sites were verified as spawning sites in fall 2011 by the presence of fertilized eggs found by divers in the fall and the presence of viable lake trout fry captured in emergent fry traps in spring 2012 (Figs. 1, 2). Three additional sites were similarly verified as spawning sites in fall 2012; five of these six sites are on drumlins (Fig. 1).

Discussion

Our hypothesis that drumlins and other glacial bedforms are important sites for lake trout spawning is supported by the movement and aggregation of spawning fish near Drummond Island and the association of other known lake trout spawning areas with drumlin fields. The drumlins at Drummond Island are part of a larger drumlin field that extends across Drummond Island and west along the mainland Upper Peninsula of Michigan, which includes the Les Cheneaux Islands (Fig. 1A: also see Berquist, 1941; Karrow, 1987; Lotan and Shetron, 1968; Russell, 1906), and lake trout are suspected to spawn on other submerged drumlins within this drumlin field according to commercial fishers (M. P. Ebener, personal observation; Fig. 1A). A drumlin field also extends down the northeastern Lower Peninsula from near Cheboygan to Alpena, Michigan (Fig. 1A: also see Berquist, 1943; Karrow, 1987), and includes drumlins that are historical lake trout spawning reefs in Thunder Bay (Johnson and Van Amberg, 1995; Nester and Poe, 1984; Fig. 1A) and which may also support several lake trout spawning reefs that occur just offshore (e.g., Nester and Poe, 1987; Organ et al., 1978; Peck, 1979; Fig. 1A). Other historical lake trout spawning areas in the Great Lakes are located near known drumlin fields, including reefs in Grand Traverse Bay, Green Bay, Georgian Bay, and the Apostle Islands (Coberly and Horrall, 1980; Dawson et al., 1997; Holey et al., 1995; cf. Kerr and Eyles, 2007; Leverett, 1906), and drumlins are among the features used for spawning by lake trout in Lake Simcoe (Sly and Evans, 1996; Todd et al., 2008). Moreover, high-resolution laser bathymetry of several spawning reefs in Lake Michigan suggests that most suspected lake trout spawning areas are former glacial outwash plains that may include drumlins and other glacial bedforms (Barnes et al., 2005). Taken together, these observations suggest that drumlins may function as lake trout spawning habitat throughout the Great Lakes.

Drumlins are found throughout the parts of the world that were covered by Quaternary and pre-Quaternary ice sheets, although their spatial distribution within any glaciated area can be highly variable (Menzies, 1979; Patterson and Hooke, 1995). Drumlin composition varies widely from stratified sand to unstratified till to solid bedrock, and drumlins may have a core composed of rock, sand, boulders, or

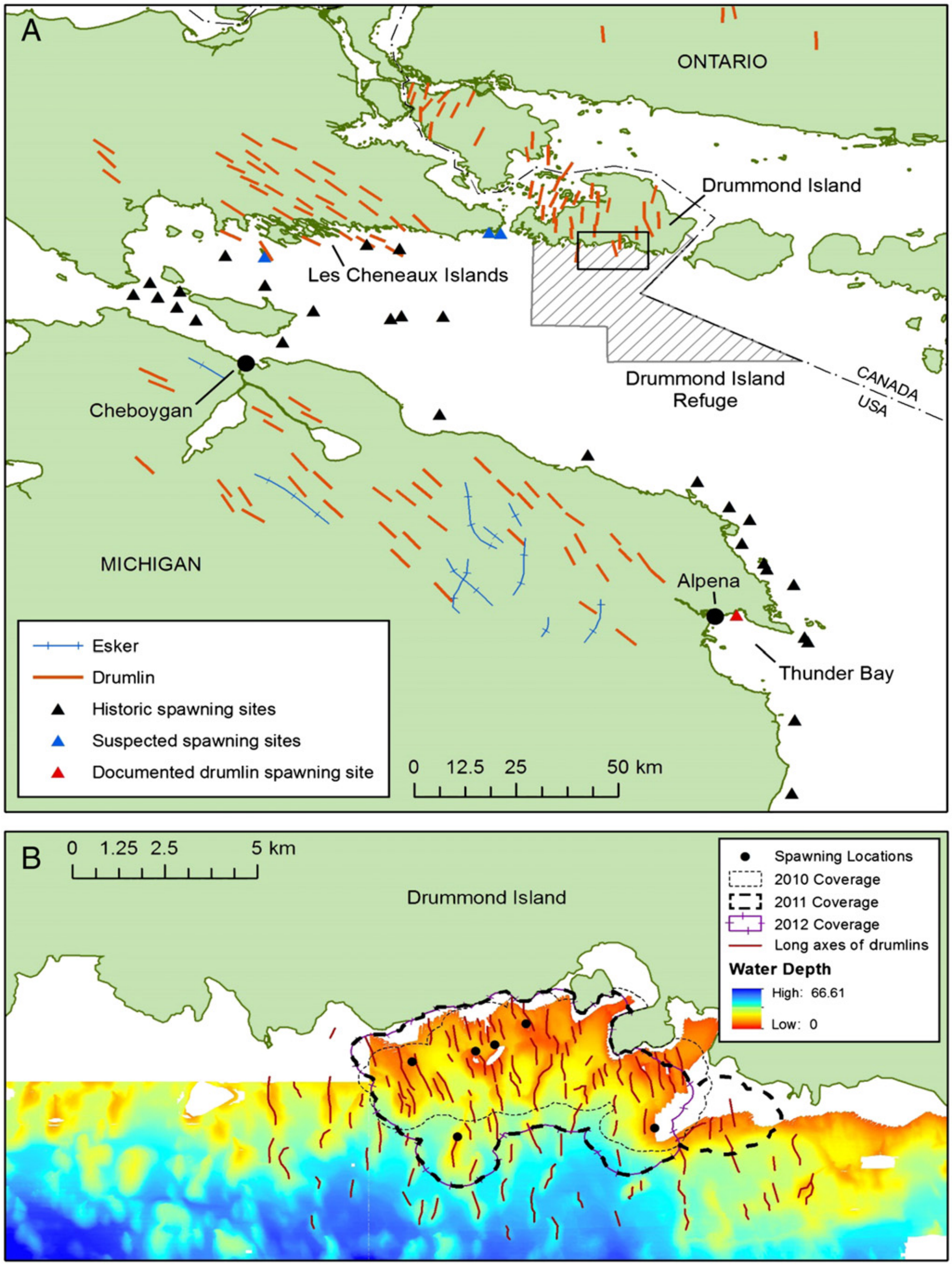

Fig. 1. A: Drumlins and eskers in the northern Lake Huron region (redrawn after Karrow, 1987). The purple area represents the Drummond Island Refuge. The black rectangle within the refuge delineates the inset panel below, where multibeam bathymetry data were collected. The drumlin field to the lower left extends into and supports lake trout spawning reefs in Thunder Bay. The location of a known spawning site located on a drumlin in Thunder Bay is indicated (red triangle; J. E. Marsden, unpublished data), as well as other known (black triangles; Nester and Poe, 1987; Organ et al., 1978; Peck, 1979) and suspected (blue triangles; M. P. Ebener, personal communication) spawning sites in northern Lake Huron; although these sites may also occur on drumlins, the extent of the drumlin fields within the lake are unknown due to the lack of sufficiently detailed bathymetry. B: Multibeam bathymetry of the area south of Drummond Island revealed an extensive drumlin field oriented in a north–south direction. The long axes of drumlins and fluted moraines south of Drummond Island are shown. Blue, dashed black and purple outlines delineate the extent of the acoustic telemetry array in 2010, 2011, and 2012, respectively. Black circles represent the location of lake trout spawning areas inferred from acoustically-tagged lake trout behavior and confirmed by diver location of lake trout eggs or fry.

laminated clay, along with a superficial carapace or veneer of till (Benn and Evans, 2010; Menzies, 1979, 1987). The drumlins of most interest here are those composed of large amounts of till and sorted sediments, such as stratified glaciofluvial sediments (Stokes et al., 2011). The presence of sorted, stratified sediments within drumlins is well-described in the literature (Lemke, 1958; Meehan et al., 1997; Menzies, 1979, 1984; Menzies and Brand, 2007; Munro-Stasiuk, 2000; Sharpe, 1987; Shaw, 1983; Shaw et al., 1989). Drumlins contain a wide range of sediment types, some of glacial origin picked up in subglacial or proglacial environments and some pre-glacial sediments. As drumlins are formed, sediments available within the subglacial environment are simply incorporated into the drumlin developmental process. In many cases these sediments are further deformed and structurally altered during streamlining and overriding ice and sediment action (Menzies et al., 1997; Slater, 1929).

In addition to drumlins, we hypothesize that other glacial bedforms may also serve as spawning habitat for lake trout in the Great Lakes. The sorted large sediments incorporated during the formation of drumlins

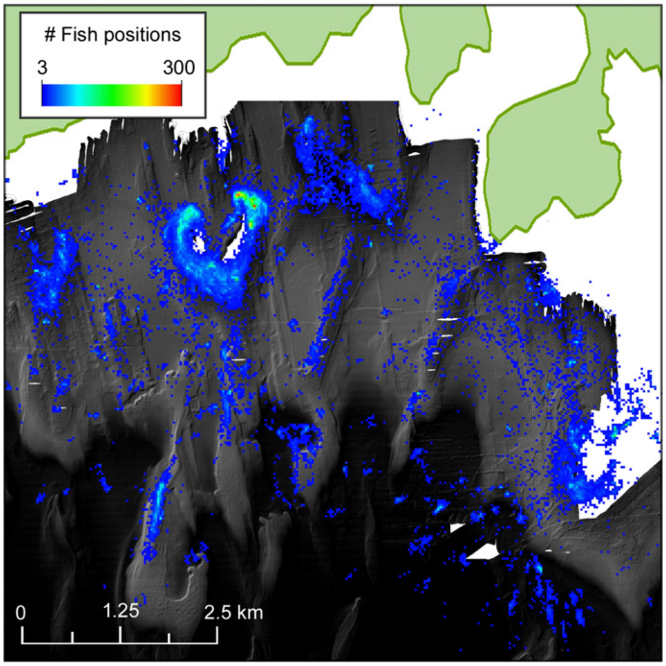

Fig. 2. An example of acoustic telemetry data that were used to identify spawning sites used by lake trout near Drummond Island. Data shown are from 2011; points represent the positions of adult lake trout recorded by the acoustic telemetry array near Drummond Island during the spawning season. These position data clearly show that most lake trout activity occurs along the top of submerged drumlins. Combined data from 2010–2012 were used to identify the primary spawning locations depicted in Fig. 1, which were verified by diver sampling of eggs or fry (see text).

and other glacial bedforms are the most likely lake bed feature within the Great Lakes that would provide large pockets of suitable spawning substrate for lake trout, especially for those non-Canadian Shield shorelines along the southern edge of the geographic distribution of lake trout (Crossman, 1995; Lindsey, 1964). Few other plausible physical processes could produce extensive pockets of sorted large substrates within the Great Lakes. Other glacial bedforms that could provide spawning habitat include eskers (remnants of meltwater streams that flowed beneath ice sheets), end moraines (piles of unconsolidated glaciogenic debris that mark the margins of past ice advances or stillstands), fluted moraines (moraines with a surface of streamlined ridges and grooves trending at right angles to the ice front), and outwash fans and kame deltas formed in front of or at the edge of past ice sheet margins. Lake trout may also use other types of features for spawning, including karst bedrock at the offshore reefs in Lake Huron (Edsall et al., 1992) and steep talus slopes along the western and northern shores of Lake Superior and lakes of the Canadian Shield further north (C. Krueger, personal observation). Other features, such as beach ridges, bars, spits and submerged beaches formed by wave action and littoral drift when the Great Lakes were at lower than current water levels, could potentially support spawning habitat, but the forces involved in their formation are unlikely to have sorted sediments as large or as extensively as those sorted by ice sheets.

Lake trout are unique among salmonines in that they spawn almost exclusively in lakes. All other salmonines spawn primarily in streams and rely on stream flows to sort and clean sediments to create suitable spawning habitat. Seasonal high stream flows may be particularly important for sediment sorting and maintenance of spawning beds (Poff et al., 1997). These flows are lacking in lakes, but glacial bedforms such as drumlins often contain large units of sorted glaciofluvial sediments that could provide the interstitial spaces necessary for lake trout egg incubation, particularly when the bedforms are situated such that lake currents or wave action penetrate these sediments to remove fine sediment (cf. Menzies and Brand, 2007). In other words, given the general lack of currents sufficient to move and sort coarse sediments of gravel and cobble size in the Great Lakes, lake trout must use spawning sediments that were sorted by forces other than currents (e.g., ice sheets), but probably rely on lake currents to ventilate and clean these sediments of finer sedimentary particles. Lake trout spawning habitat quality may be affected by a variety of variables (Marsden et al., 1995a), but sediment size and the depth and cleanliness of interstitial spaces are perhaps the most critical to protect eggs from physical forces as well as predators and to maintain oxygen. Therefore, we suggest that certain glacial bedforms may provide the sorted large sediment substrata necessary for successful lake trout reproduction.

Great Lakes levels have been both much lower (ca. 100 m for lakes Huron and Michigan) and significantly higher since the last glaciers receded (Lewis et al., 1994, 2007; Rea et al., 1994), and the distribution of suitable lake trout spawning habitat on glacially-derived bedforms has therefore likely changed drastically over time (Power, 2002), but these features would most likely have been consistently available. A robust model to predict lake trout spawning habitat distribution would require an understanding of how glaciers concentrated suitable material and also how hydrodynamic flows restructure and clean sediments in glacial deposits to provide interstitial spaces needed for incubating lake trout eggs.

The suitability of drumlins and other submerged glacial bedforms as lake trout spawning habitat may be related to the fact that they rise above the lake bed and intercept lake currents. When interacting with longshore coastal currents, these features should generate interstitial flow via the Bernoulli effect (e.g., Thibodeaux and Boyle, 1987). The abrupt topography of a feature such as a drumlin accelerates flow, creating a lowered pressure just downstream of the summit, thereby pumping surface water through sediments. The actual interstitial flows for any particular drumlin will depend on currents, the porosity of the sediments, and the amount of infill that impedes interstitial flow. The oscillating flows of wave surge also might tend to erode the till carapace of drumlins, increasing penetration into the substrates, while longshore currents that flow over the top of a drumlin may create turbulence. Thus, the spawning habitat quality of a glacial bedform such as a drumlin will be spatially and temporally variable and associated with complex multiscale effects of climate, water currents, wave surge, and lake levels.

While the distribution of drumlins, eskers, and moraines on land is relatively well-understood, little is known about the locations of submerged glacial bedforms within the Great Lakes due to the relative lack of resolution of existing bathymetric data compared to terrestrial topographic data. Drumlins, eskers, and moraines can be identified by shape parameters from fine-scale topographic data, as we have done here, but sufficiently fine-scale bathymetry is not available for most areas of the Great Lakes. Where such data exist, the locations of known historical lake trout spawning areas could be overlain on these bathymetry data to determine the role of glacial bedforms as spawning habitat for lake trout. Complete mapping of submerged glacial bedforms within the Great Lakes would increase our understanding of the glacial history of the region and might ultimately contribute to predictive models of the location of suitable lake trout spawning habitat.

In Lake Huron, wild fry and yearling lake trout have been captured by trawl surveys in most years since 2004 (Riley et al., 2007), and these fish are now recruiting to gill-net surveys (He et al., 2012), which suggests that successful natural reproduction and recruitment of lake trout is now occurring. Although sampling was conducted throughout the Michigan waters of the main basin, the majority of these juvenile lake trout were captured near the Drummond Island Refuge (Riley et al., 2007; S. C. Riley, unpublished data), indicating the presence of high-quality spawning habitat in this area. Moreover, the Drummond Island area has long been recognized as an important spawning area for lake trout in Lake Huron based on historical records (Eshenroder et al., 1995a, 1995b; Organ et al. 1978; Peck, 1979; Wagner, 1982). Here we suggest that spawning habitat quality may be particularly high at Drummond Island due to the presence of relict glacial bedforms such as drumlins. Further underwater habitat mapping could be used to identify similar high-quality habitat elsewhere, potentially aiding lake trout rehabilitation in Lake Michigan and beyond.

The observation that lake trout spawn on glacial bedforms such as drumlins may provide a new framework for our understanding of lake trout spawning habitat in the Great Lakes. The association of lake trout spawning with glacial features has been previously noted (e.g., Eshenroder et al., 1995a, 1995b; Sly and Evans, 1996), but to our knowledge the telemetry data from Drummond Island are the first to directly implicate drumlins specifically as a primary lake trout spawning habitat. Eshenroder et al. (1995b) suggested that some glacially-formed features may provide habitats that protect eggs from physical disturbance and that currents may remove fine sediments from egg deposition areas. We further suggest that drumlins and other glacial features may provide such spawning habitat for lake trout in the Great Lakes and may be particularly important for populations at the southern edge of the species' range, south of the Canadian Shield. Systematic examination of the glacial features used by lake trout for spawning may yield insight into the design of artificial reefs, facilitate the maintenance of existing reefs at risk from overlying invasive mussels (*Dreissena* spp.), algal fouling (e.g., *Cladophora*), and egg predators (e.g., invasive round gobies *Neogobius melanostomus*), and aid in lake trout restoration by facilitating the identification of areas that are rich in potential spawning habitat. Once glacial bedforms with potential spawning habitat have been identified, targeted stocking of lake trout early life stages (Bronte et al., 2002; Negus, 2010) may initiate quicker colonization of these potentially productive areas. A better understanding of the role of glacial bedforms in the creation of high-quality lake trout spawning habitat might also aid in the identification of habitats that should be protected from the potential negative effects of offshore development, including wind farms or offshore dumping of dredge spoils, and this will be possible only when fine-scale bathymetry data are available for large areas of the Great Lakes.

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References

Barnes, P.W., Fleisher, G.W., Gardner, J.V., Lee, K.M., 2005. Using laser technology to characterize substrate morphology and geology of selected lake trout spawning habitat in northern Lake Michigan. Am. Fish. Soc. Symp. 41, 165–169.

Benn, D.I., Evans, D.J.A., 2010. Glaciers and glaciation. Second ed., Hodder Education.

Berquist, S.G., 1941. The distribution of drumlins in Michigan. Mich. Acad. Sci. Arts Lett. 28, 451–464.

Berquist, S.G., 1943. New drumlin areas in Cheboygan and Presque Isle Counties, Michigan. Mich. Acad. Sci. Arts Lett. 28, 481–485.

Berst, A.H., Spangler, G.R., 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29, 877–887.

Bronte, C.R., Schram, S.T., Selgeby, J.H., Swanson, B.L., 2002. Reestablishing a spawning population of lake trout in Lake Superior with fertilized eggs in artificial turf incubators. N. Am. J. Fish Manag. 22, 796–805.

Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., Lozano, S.J., 2003. Fish community change in Lake Superior, 1970–2000. Can. J. Fish. Aquat. Sci. 60, 1552–1574.

Brown Jr., E.H., Eck, G.W., Foster, N.R., Horrall, R.M., Coberly, C.E., 1981. Historical evidence for discrete stocks of lake trout (*Salvelinus namaycush*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 38, 1747–1758.

Coberly, C.E., Horrall, R.M., 1980. Fish spawning grounds in Wisconsin waters of the Great Lakes. Univ. Wisconsin Sea Grant Institute, Madison, Wisconsin.

Crossman, E.J., 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside its native distribution: a review. J. Great Lakes Res. (Supple. 1), 17–29.

Dawson, K.A., Eshenroder, R.L., Holey, M.E., Ward, C., 1997. Quantification of historic lake trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. Can. J. Fish. Aquat. Sci. 54, 2290–2302.

Edsall, T.A., Brown, C.L., Kennedy, G.W., Poe, T.P., 1992. Lake trout spawning habitat in the Six Fathom Bank-Yankee Reef lake trout sanctuary, Lake Huron. J. Great Lakes Res. 18, 70–90.

Eshenroder, R.L., Payne, N.R., Johnson, J.E., Bowen II, C., Ebener, M.E., 1995a. Lake trout rehabilitation in Lake Huron. J. Great Lakes Res. 21 (Suppl. 1), 108–127.

Eshenroder, R.L., Bronte, C.R., Peck, J.W., 1995b. Comparison of lake trout egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. J. Great Lakes Res. 21 (Suppl. 1), 313–322.

Eshenroder, R.L., Peck, J.W., Olver, C.H., 1999. Research priorities for lake trout rehabilitation in the Great Lakes: a 15-year retrospective. Great Lakes Fishery Commission Technical Report 64, Ann Arbor, MI.

Esteve, M., McLennan, D.A., Gunn, J.M., 2008. Lake trout (*Salvelinus namaycush*) spawning behaviour: the evolution of a new female strategy. Environ. Biol. Fish 83, 69–76.

Fitzsimons, J.D., 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. J. Great Lakes Res. 21 (Suppl. 1), 337–347.

Goodier, J.L., 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. Can. J. Fish. Aquat. Sci. 39, 1721–1737.

Hansen, M.J., Peck, J.W., Schorfhaar, R.G., Selgeby, J.H., Scheiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W., Young, R.J., 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. J. Great Lakes Res. 21 (Suppl. 1), 152–175.

He, J.X., Ebener, M.P., Riley, S.C., Cottrill, A., Kowalski, A., Koproski, S., Mohr, L., Johnson, J.E., 2012. Lake trout status in the main basin of Lake Huron, 1973–2010. N. Am. J. Fish Manag. 32, 402–412.

Holey, M.E., Rybicki, R.W., Eck, G.W., Brown, E.H., Marsden, J.E., Lavis, D.S., Toneys, M.L., Trudeau, T.N., Horrall, R.M., 1995. Progress toward lake trout restoration in Lake Michigan. J. Great Lakes Res. 21 (Suppl. 1), 128–151.

Johnson, J.E., Van Amberg, J.P., 1995. Evidence of natural reproduction of lake trout in western Lake Huron. J. Great Lakes Res. 21, 253–259.

Johnson, M.D., Schomacker, A., Benediktsson, Í.Ö., Geiger, A.J., Ferguson, A., Ingólfsson, Ó., 2010. Active drumlin field revealed at the margin of Múlajökull, Iceland: a surge-type glacier. Geol. Soc. Am. 38, 943–946.

Karrow, P.F., 1987. Glacial and glaciolacustrine events in northwestern Lake Huron, Michigan and Ontario. Geol. Soc. Am. Bull. 98, 113–120.

Kelso, J.R.M., MacCallum, W.R., Thibodeau, M.L., 1995. Lake trout spawning at five sites in Ontario waters of Lake Superior. J. Great Lakes Res. 21 (Suppl. 1), 202–211.

Kerr, M., Eyles, N., 2007. Origin of drumlins on the floor of Lake Ontario and in upper New York state. Sediment. Geol. 193, 7–20.

Krueger, C.C., Ebener, M.P., 2004. Rehabilitation of lake trout in the Great Lakes: past lessons and future challenges. In: Gunn, J.M., Stedman, R.J., Ryder, R.A. (Eds.), Boreal Shield watersheds. Lake trout ecosystems in a changing environment. Lewis Publishers, Boca Raton, Florida, pp. 37–56.

Krüger, J., 1994. Glacial processes, sediments, landforms and stratigraphy in the terminus region of Myrdalsjökull, Iceland. Folia Geogr. Dan. 21, 233.

Lemke, R.W., 1958. Narrow linear drumlins near Velva, North Dakota. Am. J. Sci. 256, 270–283.

Leverett, F., 1906. Drumlins in the Grand Traverse region of Michigan. (abst.) Geol. Soc. Am. Bull. 16, 577.

Lewis, C.F.M., Moore, T.C., Rea, D.K., Dettman, D.L., Smith, A.M., Mayer, L.A., 1994. Lakes of the Huron basin: their record of runoff from the Laurentide ice sheet. Quat. Sci. Rev. 13, 891–922.

Lewis, C.F.M., Heil, C.W., Hubeny, J.B., King, J.W., Moore, T.C., Rea, D.K., 2007. The Stanley unconformity in Lake Huron basin: evidence for a climate-driven closed lowstand about 7900 ^{14}C BP, with similar implications for the Chippewa lowstand in Lake Michigan basin. J. Paleolimnol. 37, 135–452.

Lindsey, C.C., 1964. Problems in zoogeography of the lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 21, 977–994.

Lotan, J.E., Shetron, S.G., 1968. Characteristics of drumlins in Leelanau County, Michigan. Mich. Acad. Sci. Arts Lett. 53, 79–89.

Marsden, J.E., Krueger, C.C., 1991. Spawning by hatchery-origin lake trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. Can. J. Fish. Aquat. Sci. 48, 2377–2384.

Marsden, J.E., Casselman, J.M., Edsall, T.A., Elliot, R.F., Fitzsimons, J.D., Horns, W.H., Manny, B.A., McAughey, S.C., Sly, P.G., Swanson, B.L., 1995a. Lake trout spawning habitat in the Great Lakes: a review of current knowledge. J. Great Lakes Res. 21 (Supplement 1), 487–497.

Marsden, J.E., Perkins, D.L., Krueger, C.C., 1995b. Recognition of spawning areas by lake trout: deposition and survival of eggs on small, man-made rock piles. J. Great Lakes Res. 21 (Suppl. 1), 330–336.

Marsden, J.E., Ellrott, B.J., Claramunt, R.M., Jonas, J.L., Fitzsimons, J.D., 2005. A comparison of lake trout spawning, fry emergence, and habitat use in lakes Michigan, Huron, and Champlain. J. Great Lakes Res. 31, 492–508.

Martin, N.V., 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86, 231–244.

Martin, N.V., Olver, C.H., 1980. The lake charr, *Salvelinus namaycush*. In: Balon, E.K. (Ed.), Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishing, The Hague, Netherlands, pp. 205–277.

Meehan, R.T., Warren, W.P., Gallagher, C.J.D., 1997. The sedimentology of a Late Pleistocene drumlin near Kingscourt, Ireland. Sediment. Geol. 111, 91–105.

Menzies, J., 1979. A review of the literature on the formation and location of drumlins. Earth Sci. Rev. 14, 315–359.

Menzies, J., 1984. Drumlins: a bibliography. Geobooks, Norwich p. 117.

Menzies, J., 1987. Towards a general hypothesis on the formation of drumlins. In: Menzies, J., Rose, J. (Eds.), Drumlin Symposium. A.A. Balkema, Rotterdam, pp. 9–24.

Menzies, J., Brand, U., 2007. The internal sediment architecture of a drumlin, Port Byron, New York State, USA. Quat. Sci. Rev. 26, 322–335.

Menzies, J., Shilts, W.W., 2002. Subglacial environments. In: Menzies, J. (Ed.), Modern and Past Glacial Environments. Butterworth-Heineman, Oxford, pp. 183–278.

Menzies, J., Zaniewski, K., Dreger, D., 1997. Evidence, from microstructures, of deformable bed conditions within drumlins, Chimney Bluffs, New York State. Sediment. Geol. 111, 161–176.

Milner, J.W., 1874. Report on the fisheries of the Great Lakes; the result of inquiries prosecuted in 1871 and 1872. Rept. U.S. Comm. Fish., 1872–1873, pp. 1–78.

Muir, A.M., Krueger, C.C., Hansen, M.J., 2012a. Re-establishing lake trout in the Laurentian Great Lakes: past, present, and future. In: Taylor, W.W., Lynch, A.J., Leonard, N.J. (Eds.), Great Lakes fisheries policy and management: a binational perspective. Michigan State University Press, East Lansing, pp. 533–588.

Muir, A.M., Blackie, C.T., Marsden, J.E., Krueger, C.C., 2012b. Lake charr *Salvelinus namaycush* spawning behaviour: new field observations and a review of current knowledge. Rev. Fish Biol. Fish. 22, 575–593.

Munro-Stasiuk, M.J., 2000. Rhythmic till sedimentation: evidence for repeated hydraulic lifting of a stagnant ice mass. J. Sediment. Res. 70, 94–106.

Negus, M.T., 2010. Contribution of lake trout stocked as fry to an adult population in Lake Superior. J. Great Lakes Res. 36, 380–386.

Nester, R.T., Poe, T.P., 1984. First evidence of successful natural reproduction of planted lake trout in Lake Huron. N. Am. J. Fish Manag. 4, 126–128.

Nester, R.T., Poe, T.P., 1987. Visual observations of historical lake trout spawning grounds in western Lake Huron. N. Am. J. Fish Manag. 7, 418–424.

Organ, W.L., Towns, G.L., Walter, M.O., Pelletier, R.B., Riege, D.A., 1978. Past and presently known spawning grounds of fishes in Michigan coastal waters of the Great Lakes. Michigan Department of Natural Resources, Fisheries Division, Technical Report 78-7, Lansing.

Patterson, C.J., Hooke, R.L., 1995. Physical environment of drumlin formation. J. Glaciol. 41, 30–38.

Peck, J.W., 1979. Utilization of traditional spawning reefs by hatchery lake trout in the upper Great Lakes. Michigan Department of Natural Resources, Fisheries Research Report 1871, Lansing.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. Bioscience 47, 769–784.

Power, G., 2002. Charrs, glaciations and seasonal ice. Environ. Biol. Fish 64, 17–35.

Rea, D.K., Moore, T.C., Lewis, C.F.M., Mayer, L.A., Dettman, D.L., Smith, A.J., Dobson, D.M., 1994. Stratigraphy and paleolimnologic record of lower Holocene sediments in northern Lake Huron and Georgian Bay. Can. J. Earth Sci. 31, 1586–1605.

Reid, D.M., Anderson, D.M., Henderson, B.A., 2001. Restoration of lake trout in Parry Sound, Lake Huron. N. Am. J. Fish Manag. 21, 156–169.

Riley, S.C., He, J.X., Johnson, J.E., O'Brien, T.P., Schaeffer, J.S., 2007. Evidence of widespread natural reproduction by lake trout *Salvelinus namaycush* in the Michigan waters of Lake Huron. J. Great Lakes Res. 33, 917–921.

Russell, I.C., 1906. Drumlin areas in northern Michigan. Geol. Soc. Am. Bull. 16, 577–578.

Sharpe, D.R., 1987. The stratified nature of drumlins from Victoria Island and southern Ontario, Canada. In: Menzies, J., Rose, J. (Eds.), Drumlin Symposium. A.A. Balkema Publishers, Rotterdam, pp. 185–214.

Shaw, J., 1983. Drumlin formation related to inverted meltwater erosional marks. J. Glaciol. 29, 461–479.

Shaw, J., Kvill, D., Rains, B., 1989. Drumlins and catastrophic subglacial floods. Sediment. Geol. 62, 177–202.

Slater, G., 1929. Structure of drumlins on the southern shore of Lake Ontario. N. Y. State Mus. Bull. 281, 3–19.

Sly, P.G., Evans, D.O., 1996. Suitability of habitat for spawning lake trout. J. Aquat. Ecosyst. Health 5, 153–175.

Stauffer, T.M., 1981. Collecting gear for lake trout eggs and fry. Progress. Fish Cult. 43, 186–193.

Stokes, C.R., Spagnolo, M., Clark, C.D., 2011. The composition and internal structure of drumlins: complexity, commonality, and implications for a unifying theory of their formation. Earth-Sci. Rev. 107, 398–422.

Thibodeaux, L.J., Boyle, J.D., 1987. Bedform-generated convective transport in bottom sediment. Nature 325, 341–343.

Todd, B.J., Lewis, C.F.M., Anderson, T.W., 2008. Quaternary features beneath Lake Simcoe, Ontario, Canada: drumlins, tunnel channels, and records of proglacial to postglacial closed and overflowing lakes. J. Paleolimnol. 39, 361–380.

Wagner, W.C., 1982. Lake trout spawning habitat in the Great Lakes. Fisheries Research Report 1904. Michigan Department of Natural Resources, Fisheries Division.