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Lake trout in northern Lake Huron spawn on submerged drumlins

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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.

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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

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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 ±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