GREAT LAKES FISHERY COMMISSION
Research Completion Report *

COMPARISON OF LAKE TROUT-EGG SURVIVAL AT INSHORE AND OFFSHORE AND SHALLOW-WATER AND DEEPWATER SITES IN LAKE SUPERIOR

by

Randy L. Eshenroder
Great Lakes Fishery Commission
2100 Commonwealth Blvd., Suite 209
Ann Arbor, MI 48105

and

Charles R. Bronte
U.S. Fish and Wildlife Service
Great Lakes Center of the National Biological Survey
Ashland Biological Station
2800 Lake Shore Drive East
Ashland, WI 54806

and

James W. Peck
Michigan Department of Natural Resources
Marquette Fisheries Station
484 Cherry Creek Road
Marquette, MI 49855

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ABSTRACT. *We incubated lake trout* (Salvelinus namaycush) *eggs over winter at shallow and deep locations on Gull Island Shoal, Lake Superior; at a shallow-water site on the mainland (Bark Point); and in flowing Great Lakes water at two laboratories. Survival was highest in the laboratories and averaged 80.9%. In Lake Superior, survival at the shallow-water sites was significantly higher at Bark Point (44.6%) than at Gull Island Shoal (21%). Survival at the deep (15.1%) and shallow-water sites on Gull Island Shoal was not significantly different. The substantially lower survival at Gull Island Shoal, a well-known lake trout-spawning site, was not expected and may be related to where we placed the eggs or to meteorological conditions. Because of significantly higher survival of eggs in the laboratories, we concluded that survival of eggs in the lake was reduced by mechanical stress associated with water turbulence. We present a hypothesis suggesting that lake trout recruitment in the Great Lakes was limited by availability of spawning habitat.*

ADDITIONAL INDEX WORDS: Salvelinus namaycush, *survival, Lake Superior, egg survival.*

INTRODUCTION

Lake trout *(Salvelinus namaycush)* spawn typically in lakes over cobble- and rubble-sized rocks in autumn and their eggs incubate in these rocky substrates until spring. Native lake trout in the upper Great Lakes are reported to have spawned at a variety of sites: shallow, deep, inshore, and offshore (Eschmeyer 1955, Brown *et al.* 1981, Goodier 1981). How much each of these habitats contributed to historical recruitment is unknown. Populations of lake trout originating from hatcheries have been observed on numerous spawning reefs in Lake Superior, but mainly on sites that are contiguous with the shore or within 1-2 km of shore (Peck 1979, Krueger *et al.* 1986). Hatchery lake trout have not been found in abundance on shallow-water and deepwater sites in Lake Superior that are 5 km or more off shore, such as Gull Island Shoal (Krueger *et al.* 1986), Isle Royale (G. Curtis, Great Lakes Center of the National Biological Survey, 1993, pers. commun.), and Stannard Rock (Curtis 1990). Even at inshore sites, hatchery lake trout tend to be more abundant at depths <10 m (M. Ebener, Chippewa/Ottawa Treaty Fishery Management Authority, 1993, pers. commun.). Peck (1979) reported good spawner abundance at only two of seven sites in Lake Superior deeper than 10 m. These observations are consistent with other Great Lakes studies (Jude *et al.* 1981, Wagner 1981, Nester and Poe 1984, Peck 1986, Horns *et al.* 1989).

Use of shallow, inshore spawning sites by hatchery lake trout, when other kinds of sites are available, raises questions about the quality of different sites in the Great Lakes for lake trout reproduction. Among the Great Lakes, Lakes Michigan and Huron (main basin) were the biggest producers of lake trout on an areal basis (Christie and Regier 1988), and these lakes also possess major offshore reef complexes (Goodyear *et al.* 1982).

If, for instance, most of the historical recruitment in these lakes came from offshore (beyond the littoral zone) or deepwater sites (deeper than 20 m—see Martin and Olver (1980) for a review), then stocked lake trout cannot be expected to restore recruitment to historical levels except over very long periods of time. Therefore, the quality of spawning sites used by hatchery lake trout in comparison to other available sites is potentially an important variable in determining establishment of self-sustaining populations in whole lakes or in regions of lakes. Our study is an effort to assess differences in spawning-site quality by measuring lake trout-egg survival rates on an inshore shallow-water site, an offshore shallow-water site, and an offshore deepwater site in Lake Superior. Lake Superior was selected as the study site not because the bulk of its historical reproduction was suspected of recruiting from offshore locations, but because of logistical suitability. On the southern shore of Lake Superior, offshore spawning locations are only prevalent in eastern Wisconsin waters.

STUDY SITES

We selected one offshore site and one nearshore site in western Lake Superior (Fig. 1) that are known lake trout-spawning areas to compare lake trout-egg survival rates from fertilization to hatch. Gull Island Shoal (46°57′N, 90°24′W) is an offshore reef located about 33 km east of the Wisconsin mainland on the eastern edge of the Apostle Islands. This well-known spawning site is used by a self-sustaining population of lake trout that originated from a remanent stock of wild lake trout that survived the combined effects of intensive predation by sea lamprey *(Petromyzon marinus)* and overharvest (Swanson and Swedburg 1980). The reef is approximately 8 km long, 3 km wide, and composed of scattered rock rubble over sand and gravel with scattered rubble mounds and large boulders. The apex of the reef is a rubble mound of rocks of uniform size, and at its shallowest depth is 5.5 m under water. The majority of the reef is 18-35 m deep. We examined the reef with an underwater video camera mounted to a Mini-ROVER Mk II remotely operated submersible vehicle (Benthos, Inc., 47 Egerton Drive, North Falmouth, MA 02556, U.S.A.), and located one site at a depth of 10 m and another site at a depth of 20 m that had cobble-sized rubble deep enough for deployment of egg-incubating devices.

Bark Point reef (46°52´N, 91°11´W) is a small, nearshore, shallow reef (5-10 m) located at the northern end of the Bark Peninsula in western Wisconsin waters. This site has been described by Coberly and Horrall (1982) as a historically used, inshore spawning site, and recently, mostly hatchery-reared lake trout in spawning condition have been captured there each October (Red Cliff Fisheries Department, Red Cliff Band of Lake Superior Chippewas, Bayfield, WI, unpubl. data). This site is composed mainly of fractured-sandstone bedrock with cobble and boulder infilling at fracture points. With the use of divers and an underwater video camera, we identified an 8-m-wide expanse of cobble-sized rubble that ran parallel to the shoreline at the 10-m contour, and was deep enough for incubation of lake trout eggs.

METHODS

Lake trout eggs and milt were obtained from wild (unclipped) lake trout captured with gillnets on Gull Island Shoal by the Wisconsin Department of Natural Resources on 18 October 91. Eggs from each of 12 females were fertilized with milt from 2 wild males, allowed to water harden for 6 hours, then loaded into 168 egg incubators. We used the plexiglass egg incubator developed by Kennedy (1980), modified by Gunn and Keller (1984), and further described by Eshenroder (1988) and Manny *et al.* (1989). Each incubator contained 5 rows of 10 eggs; each (50 total) held singly in separate compartments (cells). The egg-filled incubators were held in a fiberglass raceway with flowing well water (approximately 38 L/min) at 8°C until they could be deployed on the reefs.

High winds and rough seas prevented deployment of incubators on 19 October. On 20 October, we transported 120 incubators and four sediment traps by boat to Gull Island Shoal. Each sediment trap consisted of four polyvinyl-chloride tubes (52-mm internal diameter, 370 mm high) attached vertically in the corners of a plastic milk crate and described by Manny *et al.* (1989). Each incubator was examined immediately prior to deployment to determine the number and location of cells with dead or missing eggs, and these data were used to adjust percent-hatch calculations at retrieval in spring. Scuba divers deployed 48 incubators and 2 sediment traps at the 10-m site and a like number at the 20-m site. The divers placed the incubators upright on the longitudinal edge, and either buried them in the rubble or armored them with surrounding rubble. The top edge of each incubator was previously marked so that all would be deployed top-up, allowing us to calculate survival relative to depth of burial. The incubators were attached to 3-m leader chains that were fastened to a 61-m center chain secured to the lake bottom with large trapnet anchors at each end. All leader chains, the center chain, and trapnet anchors were covered with rock to minimize movement caused by wave action and currents. Placement and anchoring of the chains were done in late July and early August 1991 when appropriate substrates were located. Sediment traps were deployed by chaining one to each trapnet anchor at the end of each center chain, placing rock in the sediment-trap crate, and partially burying the crate in the rubble. After the incubators and sediment traps had been deployed, the deployment sites of each incubator and sediment trap were filmed with an underwater video camera. Water temperature was 8°C on both reefs when incubators were deployed.

The remaining 24 incubators transported to Gull Island Shoal were transported back to land, and 12 each were delivered to control incubation sites at Lake Superior State College, Sault Ste. Marie, Michigan, and at the U.S. Fish and Wildlife Service, Hammond Bay Biological Station, Millersburg, Michigan, on 21 October.

At Lake Superior State College, 12 control incubators were placed in a 58-L aquarium that received water at 1.9 L/min. Water temperature was 8°C at the start of incubation. The water source was Lake Superior via a canal that supplied water to the Edison-Sault Electric power generating facility. At Hammond Bay Biological Station, 12 control incubators were placed into a 813-L circular, fiberglass tank that received water at a rate of 1.5 L/min. The source was Lake Huron water pumped from a depth of 24 m. Water temperature at the start of incubation was 7°C. On 21 October, we transported the 48 remaining incubators and two sediment traps by boat to Bark Point, but could only deploy 36 incubators and one sediment trap because of deteriorating weather. The second sediment trap was deployed on 15 November. Incubators and sediment traps were deployed in the same manner as on Gull Island Shoal.

Incubators and sediment traps were retrieved by divers from Bark Point on 17 May 92, and from Gull Island Shoal on 21 June 92. Weather, diver availability, and other research priorities prevented gear retrieval from both sites at the same time. Before the incubators were retrieved, divers again filmed the deployment site of each incubator to determine the number of incubators that were completely dislodged from the substrate (completely exposed), partially exposed, or that remained buried throughout the study period. Incubators were transported to the laboratory in coolers filled with lake water, and examined within 18 hours of retrieval. Water temperatures at each site were approximately 5.5°C at retrieval, and lake water in the transportation coolers was 5.5°-6.0°C. We examined control incubators at Lake Superior State College on 25 March 92 and at Hammond Bay Biological Station on 23 April 92, after hatching had been completed.

We calculated percentage survival of eggs in each incubator as the number of hatched eggs at retrieval (this includes live fry, dead fry, and live eggs about to hatch) divided by the number of live eggs present at deployment. Comparisons of survival among control and experimental sites were made using analysis of variance after normalizing the distribution of survival rates by arcsine transformation (Zar 1974). Pairwise comparisons of means by site to determine which means differed were made using Tukey's multiple range test. Only experimental incubators that remained buried throughout the duration of the field exposure were included in the statistical analysis.

RESULTS

At Bark Point, 44.5% of the incubators remained completely buried in the substrate and undisturbed, while at Gull Island Shoal 70.8% remained undisturbed at the 10-m location, and 83.3% remained undisturbed at the 20-m location (Table 1). Substrate at Bark Point was generally clean with little periphyton growth on rocks. Periphyton growth was more pronounced at the Gull Island Shoal sites with interstitial infilling by loose periphyton, especially at the 20-m location. Incubators at this location exhibited some periphyton growths when they were retrieved. Incubators retrieved from Bark Point and the 10-m site at Gull Island Shoal were relatively clean.

TABLE 1. Mean percent hatch (survival value) and standard deviation (parentheses) of lake trout eggs incubated in western Lake Superior and at control sites during the winter of 1991-92. Numbers under survival value indicate the number of incubators. Percent-hatch estimates (buried or control incubators only) with the same letter superscript are not significantly different: analysis of variance, P = 0.05, arcsine transformation.

	Condition of incubators at retrieval		
Location	Completely exposed	Partially exposed	Buried or control
Control sites			
Hammond Bay Biological Station	-	-	85.9^{a} (10.2) 12 incubators
Lake Superior State College	-	-	76.2^{a} (19.9) 12 incubators
Experimental sites			
Bark Point			
10-m depth	13.4 (13.5) 12 incubators	10.2 (14.6) 8 incubators	44.6^{b} (21.7) 16 incubators
Gull Island Shoal			
10-m depth	5.8 (5.8) 9 incubators	9.9 (8.4) 4 incubators	21.0^{c} (16.0) 34 incubators
20-m depth	1.0 (1.4) 2 incubators	10.1 (10.1) 4 incubators	14.5^{c} (14.4) 42 incubators

All sediment traps were overturned or lost with the exception of one sediment trap recovered at Bark Point; therefore, no comparisons of sedimentation among sites or depths were possible. In the Bark Point trap, sediment levels ranged between 1.9 cm and 2.7 cm among the four tubes and averaged 2.3 cm.

Survival of eggs to hatch in the control incubators at Hammond Bay Biological Station (85.5%) and at Lake Superior State College (76.2%) was not significantly different (Table 1). However, survival to hatch was significantly higher in control incubators than in incubators at either Bark Point or Gull Island Shoal (analysis of variance, F = 75.70 for 4 and 109 d.f., $P<0.01$). In general, eggs in incubators that were partially exposed and completely exposed had lower survival than eggs in incubators that remained buried throughout the experiment. We focus on data from the incubators that remained buried, because the period of partial or complete exposure (which likely differs among sites) adds another variable to the analysis. Percent hatch for incubators that remained buried in the substrate were significantly higher at Bark Point (44.6%) than at either the shallow-water (21.0%) or deepwater (15.1%) sites at Gull Island Shoal; but percent hatch was not significantly different between the two depths at Gull Island Shoal (Table 1). The mean coefficient (CV) of variation for the two sites at Gull Island Shoal (CV = 88) was nearly twice as great (CV = 49) as at Bark Point, and among the controls (CV = 19) was less than half that observed at Bark Point.

Because each row of eggs in the plexiglass incubators was at a slightly different elevation from the lake bottom (each adjacent row was 2 cm apart), we tested for a row effect on survival. No significant difference was found (analysis of variance, P = 0.15).

DISCUSSION

We did not expect the substantially lower survival of eggs on Gull Island Shoal (15.1-21.0%) compared to Bark Point (44.6%). Habitat quality was presumed to be exceptional on Gull Island Shoal, because it was one of the sites where a very small population of spawners (suppressed by sea lampreys and intensive fishing) was able to quickly rebound in response to a commercial-fishing closure and initiation of sea lamprey control (Dryer and King 1968). We are cautious about viewing our research as a thorough assessment of quality of lake trout spawning habitat at Bark Point or Gull Island Shoal, especially at shallower depths where decaying periphyton was probably not a factor. In this, a field experiment, we could not control all variables. The inshore site (Bark Point) and the offshore shallow site on Gull Island Shoal were not exposed to identical hydrological conditions. Because of the configuration of the west end of the lake, Gull Island Shoal is exposed to more wind fetch from more directions than is Bark Point. Despite less vulnerability to storms, proportionately more of the incubators at Bark Point were exposed or dislodged and they appear to have been buffeted by more currents than at Gull Island Shoal. Paradoxically, the incubators at Bark Point that remained buried had the highest survival (excluding the controls). The relatively small amount of sediment (2.3 cm) in the sediment traps at Bark Point, suggests that the frequency of onshore storms there was low or that resuspendable material was relatively scarce. Manny *et al.* (1989) reported 15 cm of mostly sand sediments from identical traps deployed at a very-exposed area of Lake Huron. Likewise, identical traps deployed overwinter on a reef north of Presque Isle Harbor, Lake Superior, in 1989 by J. W. Peck yielded 21.0 cm of sediments. More-protected traps deployed inside Presque Isle Harbor contained only 2.2 cm of sediments. We surmise that because Bark Point is much more exposed than the inside of Presque Isle Harbor, the low yield of sediments at Bark Point is indicative of a scarcity of resuspendable material (the adjacent shoreline is solid rock), and that this scarcity may be a factor in the higher survival of lake trout eggs at this site.

Another variable in this experiment is our choice of the specific locations where the incubators were deployed at each site. In particular, Gull Island Shoal is huge (approximately 3,100 ha) compared to Bark Point, and we don't know exactly where lake trout spawned on either site. Being smaller, Bark Point was much easier to survey for what appeared to us to be the best spawning habitat. Perhaps a different site on Gull Island Shoal, where many are available, would have yielded different results. One interpretation of the higher coefficients of variation at Gull Island Shoal compared to Bark Point is that only small differences in the placement of an individual incubator can profoundly affect egg survival. After all, the surficial substrates at both sites appeared similar, and why some incubators produced much higher survival rates than others was not apparent visually. This problem of scale is daunting for lake trout researchers on the Great Lakes.

How well the plexiglass incubator that we used to assess egg survival mimics the survival of naturally spawned lake trout eggs remains uncertain. This incubator has been used in the Great Lakes since 1986 (Manny *et al.* 1989), but it was not evaluated until Perkins and Krueger (in press) undertook comparative studies in Lake Ontario in 1991-92. They assessed survival of naturally spawned and artificially seeded lake trout eggs in small-mesh nylon bags that contained natural substrates and of eggs in plexiglass incubators like we used. Survival in the bags, which appear to more closely represent natural conditions, was an order of magnitude lower than in the plexiglass incubators. If the plexiglass incubators enhance survival this much, none of the sites that we assessed could be considered good spawning habitats. Actual survival rates of only 1-4% do not seemingly leave much slack for additional losses due to egg dislodgment or predation, which the incubators prevent.

Survival among the laboratory controls, which averaged 81%, clearly indicated much lower survival (15.1-44.6%) on eggs incubated in the lake. We conclude that survival of lake trout eggs in the lake was reduced by exposure to mechanical stress caused directly by water turbulence or indirectly by particles entrained in turbulent water. No other factor such as predation could be identified as a cause of mortality. Trout eggs are known to be particularly sensitive to mechanical stress during a period from 48 h after fertilization until eye-up (Piper *et al.* 1982). The exact length of this period for lake trout is not known. The rocky substrates that lake trout spawn over may serve to dissipate water turbulence, and thereby protect eggs from mechanical stress. The control eggs were incubated in a quiescent environment, but in the lake some turbulence is required to clean the substrates and provide a flow of well-oxygenated water. J. W. Peck found that lake trout eggs survived better at locations in Presque Isle Harbor, Lake Superior, where exposure to water turbulence was reduced. In fact, survival of his least-exposed eggs approached that of unexposed laboratory controls. Using similar apparatus, Manny *et al.* (1989) reported survival rates of 10% and 24% for lake trout eggs incubated in central Lake Huron. Their control eggs also survived better (40%) than eggs incubated in the lake, but the difference was significant for only one of two sites. Martin and Olver (1980) noted that lake trout spawned deeper in larger lakes. Although this behavior has adaptive significance in avoiding unstable (beach) substrates, it may also serve to reduce stress associated with excessive water turbulence. Spawning-site selection by lake trout in the Great Lakes may be a function of trade-offs between reducing mechanical stress on and obtaining well-oxygenated water for eggs.

CONCLUSIONS AND SPECULATIONS

The lake trout rehabilitation program in the Great Lakes represents a massive, sustained effort that began more than three decades ago in Lake Superior (Pycha and King

1975). Yet managers and researchers lack a robust hypothesis that accounts for three observations: 1) the results from rehabilitation, 2) the among-lake differences in yield from historical populations, and 3) the success with which lake trout have been introduced in inland lakes. Our interest in lake trout reproduction in the Great Lakes and in the difficulty in achieving self-sustaining populations of lake trout except in Lake Superior has caused us to look for fundamental explanations that account for these phenomena. Here we identify one such explanation with the belief that its dissemination and scrutiny will stimulate discussion and accelerate the understanding of lake trout reproductive biology.

Our hypothesis is based on the notion that physical processes, especially waves and water currents, limit lake trout recruitment in the Great Lakes. We propose that these physical processes limit recruitment by making marginal what would qualify otherwise as good spawning habitats in inland lakes. Hitchins and Samis (1986) reported remarkable success in introducing lake trout in Ontario's inland lakes. Our experimental finding that lake trout eggs appear to have been killed directly by water turbulence in Lake Superior is one indication of how physical processes shape lake trout reproduction in the Great Lakes. Beeton (1984) lists the role of physical processes as one of the characteristics separating large lakes from small, and thus a hypothesis emphasizing them is conceptually appealing. Also, lake trout evolved well before the end of the Pliestocene (Benke 1972), survived in refugia [which were probably small] during the Wisconsin glaciation (Ihssen *et* *al.* 1988), and considerable adaption may have been required for them to colonize the Great Lakes.

Rocky surficial substrates utilized by spawning lake trout arise from various geological processes such as weathering or glacial deposition. Lake trout in inland lakes generally use such substrates when they occur at depths <6 m (Martin and Olver 1980). In the Great Lakes, however, potential spawning substrates associated with shore can be degraded in the shallowest depths by wave action or ice scour and in adjacent depths by infilling from resuspended fines (mostly sand). Fines are resuspended and transported great distances during storms. For example, Boyce *et al.* (1990) reported that one particular storm episode completely filled a 550-mm-long sediment tube placed at the 8-m contour in Lake Ontario. Also, Hands (1983) calculated that a persistent wind of 25 knots (12.4 m/s) over a fetch of 100 km would disturb sand down to a depth of 46 m. Once resuspended, fines travel great distances as evidenced by their presence well off the bottom on offshore reefs (Edsall *et al.* 1989, Edsall *et al.* 1992). Suitable spawning habitat likely occurs in narrow habitat envelopes where water turbulence is moderate enough for substrate stability, but intense enough to remove fines and provide the interstitial depth needed both to prevent eggs from being dislodged and to dissipate mechanical stress associated with egg mortality.

We speculate that two geological features combine to enlarge the envelope of suitable spawning habitats, and that their occurrence is crucial to lake trout reproduction in the Great Lakes. These features are: 1) extensive reaches of rocky littoral zone that provide meager amounts of resuspendable fines, and 2) submerged structures that outcrop from the lake bottom and act as venturies causing water masses to accelerate and scour fines at extended depths. This venturi effect is evident on offshore, submerged spawning reefs in Lakes Michigan and Huron where patches of what appear to be good habitat extend 15-35 m downward from the shallowest point (Edsall *et al.* 1989, Edsall *et al.* 1992). In contrast, shore sites in western Lake Huron surveyed by Nester and Poe (1987) occur in a much smaller band of depths, most commonly between the 2- to 9-m depth contours. Sand deposits do occur on submerged reefs, but below the upper reaches where the best spawning substrates occur (Edsall *et al.* 1989, Edsall *et al.* 1992). In contrast, littoral beaches provide a source of resuspendable fines that are the last particles to settle following turbulence. Their dispersal results in degradation of spawning habitat.

Historical yields of lake trout from the Great Lakes are consistent with our hypothesis. Christie and Regier (1988) provide estimates of thermal habitat volume appropriate for lake trout in each Great Lake (excluding Erie) and corresponding mean yields during periods of stable catch. The ratio of mean yield to thermal habitat volume corrects for habitat size and growing season allowing direct comparison of productivity among the lakes, assuming comparable fishing rates. Lake Michigan has the highest productivity; productivity of the other lakes as a fraction of Lake Michigan's was: Lake Huron (main basin), 0.78; Lake Superior, 0.42; and Lake Ontario, 0.37. Lakes Michigan and Huron (main basin) were most productive and have prominent submerged reef complexes as well as extensive littoral-zone spawning habitat associated with an arc of Silurian dolomite that extends along their northern shores (Hough, 1958, Brown *et al.* 1981, Eshenroder *et al.* in press). Lake Superior has extensive littoral areas of Precambrian rocks (Hough 1958) and prominent offshore reefs (Swanson and Swedberg 1980, Goodier 1981, Curtis 1990), but lacks a centrally located ridge of sedimentary rocks comparable to the Milwaukee Reef complex in Lake Michigan or the Six Fathom Bank-Yankee Reef complex in Lake Huron. Lake Ontario appears to have less of each feature than do the other lakes. Its most prominent structure is a sill of Ordovician limestone that separates the Kingston Basin from the main lake (Sly 1988).

If lake trout productivity among the lakes was a function of the availability of spawning habitat, lake trout within a lake may have been distributed similarly. In Lake Superior, lake trout were abundant in offshore waters, for example at Isle Royale and Stannard Rock (Hile 1951, Curtis 1990), where spawning habitat was available. In Michigan's waters of Lake Huron, lake trout yields were highest in the northernmost districts (Hile 1946) that also produced 90% of the take of spawn-run lake trout during 1929-32, a special period investigated by Eshenroder *et al.* (in press). Within these districts the catch of spawn-run lake trout was associated with only two geological formations, one a Silurian-dolomite littoral zone and the other a complex of Devonian (Bois Blanc Formation) reefs (Eshenroder *et al.* in press). The reef area (Beaver Island refuge) where lake trout stocking is currently focused in northern Lake Michigan is also associated with the Bois Blanc Formation (Hough 1958). These observations support the notion that lake trout would have been more abundant had spawning habitat been more uniformly distributed. An examination of lake trout yield within the lakes in relation to geology is needed. Such an exercise should consider the type of substrate (igneous or sedimentary) as well as amount. Weathering processes associated with dewatering following the Lake Algonquin stage, about 9,500 B.P. (Hough 1958), should have produced more spawning habitats from softer sedimentary than from harder igneous or metamorphic rocks.

The tendency of stocked lake trout to spawn inshore in shallow water (discussed earlier) may be associated with their successful reproduction in Lake Superior. In Minnesota and Michigan waters adjacent to extensive reaches of rocky littoral zone, hatchery fish spawned successfully (Hansen *et al.* in press). In Wisconsin's waters, hatchery lake trout have not contributed significantly to recruitment (Hansen *et al.* in press). Poor performance of hatchery lake trout in the other lakes may relate to our hypothesis. The waters adjacent to the arc of Silurian dolomite that forms the northern shores of Lakes Michigan and Huron are only lightly stocked. Stocking programs in Lakes Michigan and Huron include stocking of offshore reefs, but more time is required for evaluation. Hatchery trout have reproduced successfully in South Bay, Lake Huron (Anderson and

Collins, in press), which has a physical environment like an inland lake and is formed of Silurian dolomite. We do not hold that reproduction inshore in all but Lake Superior is nearly impossible, but do suggest that it may be difficult except where rocky substrates predominate.

Our hypothesis on how physical processes affect lake trout reproduction in the Great Lakes is reasonably consistent with observation. Its most provoking element is the inference that lake trout in the Great Lakes may have been limited by the availability of spawning habitat rather than edaphic conditions. Sly and Christie (1992) explain some of the interlake variation in lake trout productivity as being caused by benthic food-web effects mediated by nutrient chemistry. Their analysis does not account for the scale of differences expressed in the lake trout yield to thermal habitat volume ratios, and their historical food-web analysis if confounded by the presence of abundant alewife *(Alosa pseudoharengus)* populations in Lake Ontario, which were not fished when the historical yield data were being recorded. More research will be required to clearly define what limits lake trout reproduction in the Great Lakes. Questions raised here about the potential significance of different types of lake trout spawning habitats in the Great Lakes are speculative. A better understanding of what exactly constitutes quality spawning habitat for lake trout in the Great Lakes is important for assessing the performance of planted fish. Our study is one step towards conducting this assessment.

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FIGURE CAPTION

FIG. 1. Map of study area in western Lake Superior.