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An Evaluation of Lake Trout Spawning Habitat Characteristics and Methods for Their Detection

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An Evaluation of Lake Trout Spawning Habitat Characteristics and Methods for Their Detection

by

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ABSTRACT

Fitzsimons, J.D. 1994. An evaluation of lake trout spawning habitat characteristics and methods for their detection. Can. Tech. Rep. Fish Aquat. Sci. No. 1962.

Spawning habitat characteristics of verified lake trout spawning sites in inland lakes and the Great Lakes were reviewed to provide a synthesis for use in identifying new Great Lakes sites. While sites can be characterized by physical, chemical, biological and hydrological features only physical and hydrological appear important in selection. Of greatest importance are the presence of multi-layered (>2) cobble (4-40 cm) substrates oriented parallel to prevailing currents and inclined (10-45°) downward and away from the direction of fall winds. Inland lakes and Great Lakes sites show a high degree of similarity of spawning habitat characteristics except for spawning depth which for 24 verified sites with over a 5 order of magnitude range in lake area, was related to lake area by the relationship spawning depth (m)= 0.07+0.93 log lake size (km^2) (r^2=0.79).

Use of buried egg entrapment gears for the detection of spawning habitat characteristics are superior to either gill net catches of spawners or egg traps/nets deployed on the surface of spawning substrates.

RÉSUMÉ

Fitzsimons, J.D. 1994. An evaluation of lake trout spawning habitat characteristics and methods for their detection. Can. Tech. Rep. Fish. Aquat. Sci. No. 1962.

Les caractéristiques des frayères vérifiées de touladi dans les lacs intérieurs et les Grands Lacs ont été étudiées d'une manière synthétique dans le but de déceler de nouvelles frayères dans les Grands Lacs. Bien que l'on puisse caractériser les frayères au moyen de caractéristiques physiques, chimiques, biologiques et hydrologiques, seules les caractéristiques physiques and hydrologiques semblent importante dans le choix du site. La présence de plusieurs couches (>2) des galets (4-40 cm) orientés parallèlement aux courants prédominants et avec inclinaison de 10 à 45° par rapport aux vents d'automne est la plus haute importance. Les caractéristiques des frayères des lacs intérieurs et des Grands Lacs sont très semblables sauf en ce qui concerne la profondeur de la frayère qui, pour 24 sites vérifiés dans des lacs dont la taille variait de plus de 5 ordres de grandeur, était liée à la taille du lac selon la formule: profondeur de la frayère (m) = 0,07+0,93 log [taille du lac] (km^2) (r^2=0,79).

L'utilisation d'engins de piégeage des oeufs pour la détection des caractéristiques des frayères est supérieure à la méthode qui consiste à capturer les géniteurs au filet maillant ou à la méthode de piégeage des oeufs à l'aide de filets déployés à la surface des substrats de la frayère.

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1.0 INTRODUCTION

Rehabilitation of lake trout stocks on the Great Lakes has been underway since 1950. This activity carried out primarily through stocking of hatchery-reared fish is considered an essential step toward rebuilding stocks that were eliminated through a combination of overfishing and lamprey predation (Eshenroder et al, 1983). Ultimately the goal is to restore self-sustaining populations. As a result of stocking trout abundance is at or in excess of historical levels although re-establishment of self-sustaining stocks has only occurred in Lake Superior (MacCallum and Selgeby, 1987). Since this was also the only lake with remnant lake trout stocks it is not clear what contribution hatchery lake trout made to the establishment of the self-sustaining stocks.

Although recovery of spawning stocks aided by stocking has contributed to increased recruitment in Lake Superior this has not been the case in the other Great Lakes. In Lake Ontario for example which has the highest lake trout stocking rate per unit area and effective lamprey control (Schneider et al, 1990), low numbers of spawners is an unlikely explanation for the lack of recruitment. During 1989 it was estimated that there were 3 billion eggs (Schneider et al, 1990) potentially deposited in Lake Ontario. Applying the average of body cavity to yearling survival rates that range from 0.3% for Lake Opeongo (D. Evans , Ontario Ministry of Natural Resources (OMNR), Maple, Ontario, pers. comm.) to 1.3% for the Apostle Islands in Lake Superior (B. Swanson, Wisconsin Department of Natural Resources (WDNR), Bayfield, Wisconsin, pers. comm.), or 0.8%, 2.4 billion yearlings should have been produced from the 1989 year class. Even if survival from body cavity to yearling in Lake Ontario was only 10% of that for the other lakes or 0.08%, the 240 million yearlings produced by the 1989 year class would still be sufficient to be detected in assessment gear (Elrod, 1987). It can be calculated based on Elrod (1987) that the minimum detectable number of yearlings in assessment gear is 10000 or .01 million based on the number of fish collected in index bottom trawls relative to the number stocked.

The ineffectiveness of the rehabilitation effort in producing significant numbers of natural recruits in Great Lakes other than Lake Superior was recognized as early as 1983. It was at that time a catalyst for a GLFC sponsored Conference on Lake Trout Research (CLAR) (Eshenroder et al, 1983) whose goal was to recommend research priorities among seven disciplines that may affect establishment of self-sustaining stocks. These disciplines included population dynamics and species interactions, stocking practices, genetics, physiology and behaviour, contaminants, habitat and socio-economic factors. Although assessment of the importance of all seven disciplines was to varying degrees dependent on knowing where lake trout spawn few active spawning sites had been identified. Furthermore the knowledge of what made these sites important was incomplete. However poor recruitment of naturally produced yearlings relative to hatchery-reared yearlings and the large population of mature adults suggested that factors active between the time of spawning and the first year when embryos were closely associated with spawning shoals were of prime importance to the lack of natural reproduction.

The deficiency in the state of knowledge regarding the location and dynamics of spawning shoals was most obvious to the habitat group at CLAR who identified a lack of specific information on the physical, chemical and biological habitat characteristics that limit lake trout

reproduction. More specifically spawning habitat information was needed to assess predation on eggs and larvae, to assess different stocking techniques, to understand spawning interactions between native and hatchery-reared fish, to assess the importance of genetically-linked factors on reproductive success, to assess periods of mortality that may or may not be contaminant linked and to avoid significant conflicts between sport and commercial fisheries and spawning lake trout.

Knowledge of lake trout spawning shoals has been confounded by a mass of anecdotal information that has accumulated over the years where habitat characteristics were discerned largely on the basis of associations with gill net collections of spawning fish (Goodyear et al, 1982a,b,c,d,e). Given the indirect nature of these observations it is perhaps not surprising that they comprise such a broad range of habitat characteristics. For example spawning has been documented over all substrate types ranging from fine material (eg. silt, clay and mud) to coarse rock to bedrock. Similarly depths of spawning were reported to range from 0 to 20 m generally and to depths greater than 100 m in Lake Superior.

Identification and study of spawning shoals is vital to future progress in lake trout rehabilitation. To provide a basis for synthesis of the current state of knowledge regarding lake trout spawning habitat in the Great Lakes and provide a sound basis for identifying new sites the following review of available information was conducted. This included a lake trout spawning habitat workshop, a literature review of lake trout spawning habitat characteristics and a critical review of methods used for the detection of lake trout spawning habitat.

2.0 METHODS

Since reproduction of lake trout in the Great Lakes is largely dependant on hatchery-reared fish it was important to first examine whether hatchery-reared lake trout were using the same spawning habitat as wild trout. For this the literature on establishment of self-sustaining populations with hatchery fish was reviewed along with a comparison of available information on spawning habitat characteristics of hatchery lake trout where they co-occurred with native lake trout.

A second part of this review was a workshop organized to draw together people with either extensive knowledge of Great Lakes lake trout spawning characteristics or intensive knowledge of individual spawning site characteristics. In so doing it was intended that the workshop would provide a basis for developing a list of testable criteria. As a greater number of spawning sites have been identified in inland lakes, many with direct observations, and these sites appear similar to those used in the Great Lakes this perspective was also included. By comparing spawning habitat characteristics for inland lakes to those known for the Great Lakes it may be possible to use inland lake data to make predictions about spawning behaviour in the Great Lakes. To facilitate discussion, factors potentially affecting lake trout spawning habitat selection were divided into physical, chemical, biological and hydrological factors (Table 1) and speakers were instructed to emphasize the parts of their work that addressed the importance or lack of importance of these factors.

An assessment of spawning habitat characteristics was also made by evaluation of habitat manipulation studies. Studies were rather broadly defined and included selective modification of existing spawning shoals or creation of new shoals either deliberately or incidental to the construction of underwater engineering structures. Determination of spawning characteristics

important at newly created shoals was facilitated by comparing them to existing natural shoals.

Given the importance sampling methods have on the identification of spawning habitats and their characteristics (Marsden and Krueger, 1991) a review of existing methods was conducted. This included historical and present day methods along with recommendations.

Finally each of the individual habitat characteristics was reviewed. An attempt was made to separate those characteristics that were important for the spawning process itself from those that were important more for subsequent survival of eggs and fry.

3.0 RESULTS AND DISCUSSION

3.1 NATURAL REPRODUCTION AND SELECTION OF SPAWNING HABITAT BY HATCHERY-REARED LAKE TROUT

In using spawning characteristics of non-native hatchery-reared lake trout to provide insights into those used by native fish there is the assumption that at the very least hatchery reared fish are capable of finding and using substrates that will provide at the very least adequate short-term survival of embryos. The assumption that hatchery experience has not altered spawning behaviour is implicit in stocking hatchery-reared lake trout to rehabilitate self-sustaining stocks. In the conspecific brook trout a long period of domestication has been associated with the domestic strain losing much of its ability to locate and use suitable spawning areas (Fraser, 1989).

While there have been many instances of lake trout stocking of inland lakes there has been little assessment with respect to the establishment of self-sustaining populations (Olver and Lewis, 1977). What assessment has been done (Olver and Lewis, 1977; Purych, 1980; Hitchins and Samis, 1986) indicates that natural reproduction generally occurs after the initial plantings, usually yearlings, reach the first year of maturity which generally occurs at age five. Consequently rearing the eggs of feral brood stocks in a hatchery for one year appears to have little effect on the ability of at least some of these fish to locate and use suitable spawning areas.

Not only is there the assumption that non-native hatchery-reared lake trout are capable of natural reproduction but that they have similar spawning characteristics to native lake trout. It is believed that much of the original genetic differentiation present in lake trout stocks (Dehring et al, 1981) was associated with adaptation to different habitats. Consequently with the loss of many of the original genetic strains from Lake Superior and practically all of the genetic strains from the other Great Lakes some of the adaptations to local environments may have been lost. As a consequence it may be difficult to re-establish new donor strains by transplanting them into non-native Great Lakes environments. There is evidence from both inland lakes (Plosila, 1977) and Lake Superior (B. Swanson, pers. comm.) that the failure of some transplants may result from lower fitness of the donor stock in the non-native environment. Similarly failure may also result from reduced reproductive activity of transplanted lake trout in non-native environments (Krueger et al, 1986).

The question then is whether there are enough coarse grained characteristics associated with the lake trout species itself to permit non-native strains to find and use spawning habitat that will provide adequate survival of eggs and fry. Alternatively are fine grain characteristics associated with individual strains more important such that successful spawning by non-native strains is unlikely. If the latter prevails, spawning characteristics of contemporary non-native strains may

not emulate those used by the historic but now extinct strains such that they may be entirely inappropriate for successful spawning.

Superficially, spawning habitat characteristics used by non-native hatchery-reared spawners show a lot of similarities or overlap with native spawners. The minimum depth used by spawning native lake trout in Lake Superior (Swanson and Swedburg, 1980; Curtis, 1990) is similar to that for hatchery-reared lake trout (Peck, 1986). Also there is considerable overlap with the size of substrate used by native (Swanson and Swedburg, 1980) and non-native spawners (Peck, 1986). At this level of resolution the non-native hatchery spawners have retained some of the spawning traits of their native counterparts. That sufficient traits have been retained is indicated by successful reproduction by hatchery-reared fish at least one location in Lake Superior (Peck, 1986). Furthermore a general similarity in the habitat characteristics used by divergent strains of hatchery reared lake trout is indicated by the spawning of multiple non-native strains at a shoal in Lake Ontario (Marsden and Krueger, 1989). On the basis of the above then there seems to be insufficient evidence at present to indicate that selection of spawning habitat characteristics is at the strain level. Consequently characteristics used by non-native hatchery-reared spawners can be treated as similar to those of native spawners.

Spawning habitat characteristics used by hatchery reared lake trout may be similar to those of native spawners to the extent that survival of eggs and fry are comparable. However there may also be a need for close physical proximity of spawning, nursery and rearing habitat. While a site may be appropriate for spawning it may be inappropriate for the transition of fry to juvenile because of excessive distance to deepwater habitat and exposure to predators. Whether the ability to discern contiguous spawning-nursery-rearing habitat is any better in native fish than non-native hatchery reared fish is not known. Several investigators have reported that wild young-of-the-year lake trout migrate to deep water soon after yolk-sac absorption (Royce, 1951; Martin, 1957; DeRoche, 1967) whereas Peck (1982) reported extended shallow water residence for the young-of-the-year of hatchery-reared spawners. While this would seem to be a disadvantage subjecting young-of-the-year to greater predation there is evidence of wild young lake trout exhibiting extended shallow water residence in Great Bear Lake (Miller and Kennedy, 1948). Moreover one of the stimuli for movement of young-of-the-year to deeper water appears to be temperatures in excess of 15°C (Peck, 1982). Therefore extended residence in shallow water may be one of a number of strategies employed to avoid predation. With this strategy low spring temperatures in keeping young-of-the-year close to shore may allow sufficient time for growth such that their larger size may reduce predation when they do move to deeper water.

3.2 SYNOPSIS OF PAPERS

The papers (see Appendix 1) presented at the workshop covered assessment of habitat characteristics used in inland lakes, a summary of spawning locations in the Great Lakes, and accounts of spawning at two spawning sites in Lake Ontario, Yorkshire Island and Stony Island.

Neal Maclean (OMNR) provided a review of a lake trout spawning habitat model that was based on information for 282 shoals in 95 lakes across Ontario. This review subsequently formed part of a synthesis on environmental and genetic factors affecting the physiology and ecology of lake trout (MacLean et al, 1990). The model developed from information taken from

questionnaires completed by local fishery biologists of direct observations of known spawning shoals has yet to be extensively tested. Six rules were derived from the information and are:

1. Depth of the shoal was less than 4 m (98% of the shoals were less than 4.8 m deep with the average 1.5 m deep).

2. The shoal was located within 10 m of the shoreline (95% of the shoals were within 10 m of the shoreline).

3. The shoal was located greater than 20 m from an inlet (Over 99% of the shoals were greater than 20 m from an inlet).

4. The wind fetch for the shoal was greater than 0.5 km (Only 2% of the shoals had a fetch of 0.25 km while 10% had a fetch of <1 km. There appeared to be no relationship between the prevailing wind direction and location of spawning shoals).

5. The shoal was exposed to the prevailing wind direction (> 80% of the shoals were exposed to the prevailing wind direction).

6. Substrate at the shoal consisted of rubble 5-30 cm in diameter (> 50% of the shoals had substrate in this size range.

The rules above were tested in Devil Lake where 16 actively used shoals were known to exist. Application of the six rules to the lake identified the 16 shoals plus an additional 6 although spawning on the additional shoals has not been confirmed.

Marla Thibodeau (DFO) gave a summary of a compilation of putative Great Lakes lake trout spawning locations up to the present (Thibodeau and Kelso, 1990). Although approximately 827 lake trout spawning locations have been documented in the Great Lakes only 31 or 3.8% were based on direct evidence and over 50% of these sites were man-made.

Spawning depths ranged from 1 to 27 m at the 31 sites. However the prime method of collection of eggs at these sites was with the use of surface or diver operated pumps operated either during or after spawning. Given the post-spawning dispersal of eggs that occurs, usually from shallower to deeper depths, spawning depths indicated by this type of gear may be relatively crude and indicate the extent of dispersal from the original spawning location. Variation in spawning depths for the individual sites ranged up to 25 m although the range for the shallowest depth used across all sites was 1 to 18.3 m. The 18.3 m, based on the collection of one egg, is probably not representative such that the range is more likely 1 to 3 m. Consequently there appears to be a high degree of similarity between spawning depths used in the Great Lakes and inland lakes as indicated by Maclean et al (1991).

Dispersal of eggs after deposition also affects the range of substrate types indicated as being used, which ranged in size from sand to boulders. The requirement of eggs to remain immobilized and well oxygenated during embryogenesis would preclude sand and pebbles as suitable substrates owing to their reduced interstitial space and potential for remobilization. In fact in their review Thibodeau and Kelso (1990) found that aggregate materials of 4 to 64 mm

comprised over 50% of the reported spawning shoals and close to 100% of the shoals where direct observations were made. Hence as for spawning depth there is a high degree of similarity between size of substrate used in the Great Lakes and inland lakes.

John Casselman (OMNR) provided a detailed account based on two years of monitoring lake trout spawning dynamics at Yorkshire Bar adjacent to Yorkshire Island in eastern Lake Ontario (Casselman, 1989). The bar runs in a northeasterly direction perpendicular to the prevailing fall north-westerlies but parallel to prevailing lake currents. During the summer the bar is covered by heavy growths of Cladophora but by the fall the majority of these growths have detached and been dispersed by storms. At this site divers reported male lake trout to be closely associated with the top and steep eastern (20°) slope of the bar in water ranging in depth from 3 to 6 m. and over rubble ranging in size from 5 to 40 cm. Gill net catches of spawning fish were considerably less precise in delineating spawning substrate in that large numbers of fish were observed over a much broader area than seen by divers.

Attempts to determine the relationship between egg deposition and habitat characteristics using two types of traps deployed from the surface, one an open net design (Horns et al, 1989) and one a closed trap design (Marsden et al, 1991) were largely unsuccessful. Of the few eggs sampled indications were that these two gears caught not only depositing eggs but drifting eggs as well. Diver conducted surveys indicated a range of egg deposition from 65 to 100 eggs/m^2 in the top 10 to 30 cm of substrate at water depths of 3 to 6 m, with greatest egg deposition at 3 m. Eggs found at greater water depths were located primarily down the eastern slope of the bar presumably as a result of drift by currents. Also observed during the collections were large numbers of small crayfish and sculpins, potential predators of lake trout eggs.

Ellen Marsden (Cornell University) working at Stony Island, 20 km to the east of Yorkshire Island, provided details of four years of lake trout spawning assessment at this site (Marsden et al, 1988; Marsden and Krueger, 1991). This is the only site in Lake Ontario where significant survival to the fry stage has been observed (Marsden et al, 1988). The spawning area is located along a steep dropoff that lies along the eastern edge of a reef extending 18 m northeast of Stony Island. Contours on the drop-off run in a NNE-SSW direction parallel to the prevailing lake currents but perpendicular to the prevailing fall northwesterlies. Depth at the top of the dropoff is 5 m and at the bottom 8 to 10 m. Substrate at the north end of the dropoff consists of large cobbles and boulders (13-40 cm) with deep interstitial spaces (45 cm) but becomes progressively smaller and infilled with sand moving to the south. Much of the larger substrate is covered with Cladophora during the summer but by fall currents and storms have removed the remaining growths of this algae from the area.

Eggs were collected using a combination of open net and closed trap designs as used by Casselman (1989). Despite considerable lateral and downslope movement of eggs post deposition the majority (70%) of the 6000 eggs collected were found on large cobble with deep interstitial spaces along the steep dropoff at the north end of the shoal. Associated with this substrate were large numbers of crayfish and sculpins. Considerably fewer (20%) eggs were collected on the infilled and smaller substrate at the south end of the dropoff. Fewer eggs still were collected on top of the reef proper (<2%) and on the sandy plain (<5%) at the base of the dropoff. After storms from the northwest windrows of eggs were observed by divers at the base of the dropoff emphasizing how mobile eggs can be at times, potentially confounding spawning-habitat relationships. Egg deposition at Stony Island occurs on a relatively small area approximately 4.5

X 60 m comprising less than 10% of the total reef area.

As at Yorkshire Bar, divers at Stony Island noted a close correspondence between where eggs were collected and spawning fish occurred. Fish were primarily observed to be associated with the steep slope at the north end and only rarely with the reef proper, the south end of the dropoff or the sandy area at the base of the reef.

3.3 DETERMINATION OF SPAWNING SHOAL CHARACTERISTICS THROUGH CONSTRUCTION OF SPAWNING SUBSTRATES

There are two lines of evidence that indicate that creation of artificial spawning shoals are possible: the deliberate creation of spawning beds and the construction of underwater structures for engineering purposes that are subsequently used for spawning.

One of three shoals constructed by Martin (1955) in Shirley Lake to offset the effects of a 1.1 m prespawning drawdown was used by spawning lake trout. The shoals built on the windward side of the lake in 1.0 m of water, had areas of approximately 63 m^2, 0.3 to 0.8 m thick. Martin suspected that the reason only one shoal was used was because of its close proximity to a small active traditional reef.

Use by lake trout of an artificial spawning shoal constructed in Green Lake, Wisconsin was demonstrated indirectly by the presence of lake trout eggs in the stomachs of mud puppies at the shoal (Hacker, 1956). The shoal, consisting of a layer of angular granite 0.6 m thick, 570 m^2 in area, was created adjacent to a traditional spawning ground. The traditional spawning shoal was located off a point in 19 m of water and consisted of silt, clay and sand with some limestone fragments. Currents were sufficient to maintain the artificial spawning bed sediment-free for the eight month period of observation.

In both of the above instances spawning occurred on new substrate located close to existing spawning shoals that had either minimal or non-existent quantities of cobble/boulder substrate. For Shirley Lake the existing spawning shoal was quite small and other spawning areas in the lake were reduced by a hydraulic drawdown that occurred prior to spawning. In Green Lake typical spawning material consisting of cobble/rubble was non-existent prior to construction of the artificial shoal. Consequently use of the artificial shoals in these two studies may have been influenced by a relatively small amount of substrate relative to available spawning fish and the artificial shoals location in the lake relative to existing shoals. This may be reflected in Shirley Lake in the relatively high egg deposition rate on the artificial shoal (892 eggs/m^2) and the three-fold higher deposition rate on the small natural shoal in this same lake (55 eggs/m^2) relative to a shoal in adjacent Louisa Lake (18 eggs/m^2) where drawdown does not occur.

Use of man-made engineering structures by spawning lake trout have been documented in both Lakes Michigan (Wagner, 1981) and Superior (Peck, 1986). In Grand Traverse Bay, Lake Michigan, considerable egg deposition was evident on the southern open-water and leeward side of the Elmwood Marina boat basin breakwall that consisted of 5-30 cm crushed rock inclined at 45°. In contrast, relatively little egg deposition occurred on the northern, enclosed and windward side of the same breakwall where considerable silt deposition was evident. Similarly, significant egg deposition was evident at a submerged powerplant crib in Grand Traverse Bay consisting of 5-115 cm rounded rock. The number of eggs collected per unit diver effort at this crib was ten-fold higher than at the breakwall. At another breakwall in Grand Traverse Bay consisting of >25

cm rounded rock but with the windward side facing open water and the leeward side surrounding a boat basin, little egg deposition was evident on the windward slope. In Presque Isle Harbour, Lake Superior spawning was documented at a submerged power plant intake pipe covered with 7 to 20 cm crushed rock in 5 m of water, and having an east-west orientation (Peck, 1986). Eggs were five times more abundant on the top of the intake than on the sides.

The Elmwood Marina breakwall and Presque Isle Harbour intake have certain similarities with the Stony Island and Yorkshire Bar sites respectively that collectively provide insights into the functioning of spawning shoals. Both the Elmwood Harbour and Stony Island spawning sites are oriented near perpendicular to prevailing fall winds with similarly sized cobble on a 45° slope. Prevailing currents at both Stony Island and the Elmwood Harbour sites run from south to north parallel to the slope. The lengths of the cobble slopes where most egg deposition was occurring was similar with 7 m for the Elmwood Marina site and 5 m for the Stony Island site. Prevailing winds and currents have the effect of keeping both sites clean as evidenced by significant sedimentation immediately adjacent to the spawning area at both sites.

Like the Elmwood Harbour Marina and Stony Island sites, the Yorkshire Bar and Presque Isle Harbour intake are also oriented perpendicular to the prevailing fall winds. However they differ in that they are more like bars than reefs, being comprised of similarly sized cobbles sloping upwind and downwind at approximately 10°. Prevailing winds and currents were sufficient to prevent sedimentation in the spawning areas. At Yorkshire Bar the prevailing current runs south to north parallel to the slope while current direction at the Presque Isle Harbour site is west to east parallel to the orientation of the intake pipe. Egg deposition appeared to be heaviest along the top of both of these structures (Peck, 1986; Casselman, 1990).

In summary, spawning at all of the above sites appears to be associated with cobble structures of varying inclination (10-45°) at least 2 m in height and lying perpendicular to prevailing winds but parallel to prevailing currents. These characteristics are consistent with observations made at a natural shoal in Lake Opeongo (P. Sly, Rawson Academy, Ottawa, Ontario, pers. comm.) and a man-made shoal at Burlington pier on Lake Ontario (pers. obs.) The reason that these sites are preferred are not known but may have to do with fine scale changes in current, temperature and light at these structures that cause spawning lake trout to congregate. The association with currents also appears to result in reduced sedimentation that would favour egg survival.

3.4 METHODS FOR THE DETECTION OF SPAWNING AND HABITAT RELATIONSHIPS

Knowledge regarding lake trout spawning in inland lakes is considerably more advanced than in the Great Lakes. Part of this stems from the shallow spawning depths used in inland lakes, that averaged 1.5 m for the data set of Maclean et al (1990). In inland lakes observations of spawning lake trout can be made directly from the surface whereas in the Great Lakes few if any open lake spawning sites are observable from the surface because of the greater spawning depths used. Consequently, historically, observations of spawning locations was dependent on more indirect methods such as gill net catches. According to Thibodeau and Kelso (1990) over 800 sites were thought to exist historically many of which were based on gill net collections. While it is not known whether all these sites were used historically the fact that only 31 actively used sites have been found and of these 14 were man-made suggests that the 800 was an overestimate and that gill net catches may not be a reliable indicator of spawning locations.

Although gill nets are potentially useful in pinpointing large spawning aggregations of fish they are limited in indicating where fish will actually spawn. Their usefulness can be increased somewhat by the inclusion of other methods. Side scan sonar mapping (Edsall et al, 1979) has been used to describe large scale distributions of substrates and bathymetry on historic spawning shoals in the Great Lakes. Tracking of fish using ultrasonic transmitters has proven useful in inland lakes (MacLean et al, 1982) in delineating lake trout spawning shoals but its usefulness in the Great Lakes has not yet been demonstrated (pers. obs.). Using both of the above along with gill net catch data will aid in the gross delineation of spawning areas. However this must be backed up with ground truthing to confirm that spawning is taking place.

Several gears have been used to collect eggs, some more direct than others. Surface operated pumps have been tried and showed varying levels of success at collecting eggs (Stauffer, 1981). However they were limited in accurately defining spawning habitat characteristics by the limited depth of substrate from which eggs can be removed, the imprecise information available on substrate condition at the surface and the lack of quantitative information on habitat sampled. In addition eggs are collected after deposition so depending on currents may not accurately reflect spawning habitat relationships. While diver operated pumps (Stauffer, 1981) permit observations of habitat and an increase in substrate sampling depth and hence number of eggs collected, their use is still limited by the current induced dispersal of eggs that occurs post spawning.

Pails buried in the substrate prior to spawning (Stauffer, 1981) eliminates some of the problems of post deposition egg dispersal since some eggs will remain where initially deposited. At the same time pails allow detailed observations of spawning-habitat relationships. Pails proved very effective in delineating the zone of egg deposition in Marquette Harbour (Peck, 1986) with numbers ranging from 130 to 553 eggs/m^2 over 3 spawning seasons. They are somewhat limited however in requiring divers to deploy and retrieve them with repetitive sampling not very practical.

The next development in egg trapping was an egg net placed on the substrate (Horns et al, 1989) either by divers or from the surface in arrays fastened together with rope or chain. By setting the net from the surface there was not the same requirement for divers as with pails especially if deeper spawning shoals were being sampled. Also repetitive sampling throughout the course of the spawning period was possible. Given that the egg net was one sided and could be easily overturned in currents potentially losing and/or damaging its contents it had limited utility especially in shallow high energy zones and there was no way of knowing the actual fishing effort. This may have been part of the reason that Casselman (1989) was unable to collect many eggs using this device at Yorkshire Bar whereas Marsden and Krueger (1991) used this net with considerable success at Stony Island. Stony Island is considerably more protected from prevailing winds than Yorkshire Bar such that fewer nets were overturned.

To eliminate some of the problems of the egg net an egg trap was developed (Marsden et al, 1991) that consisted of a double-sided hollow disc with 2 cones on either side such that it could collect eggs on either side. As with the net this trap could be deployed either from the surface or by divers. In extensive field applications of the egg nets for two years and the egg trap for one year (Marsden and Krueger, 1991) egg nets collected three to five times more eggs using comparable numbers of nets/traps. Casselman (1989) did not find this trap to be any more effective in collecting eggs than the egg net.

Common to both of these gears is their potential for movement and actual loss during the

spawning period. While movement as Marsden and Krueger (1991) observed did not preclude the capture of eggs it makes the delineation of habitat-spawning relationships difficult especially if movement has been extensive. Although some of the problems of movement of transect lines and their attached traps can be overcome by weighting the transect line this puts excessive strain on the trap or net and fasteners used and as was found by both Casselman (1989) and Marsden and Krueger (1991) can result in either loss or destruction of the gear.

Another drawback with both these gears when deployed on transect lines especially on uneven ground is orientation. If transect lines whether rope or chain are set too tight the trap/net collection surface may be oriented vertically reducing its effectiveness to near zero. Similarly if the trap/net is placed on substrate comprised of large cobbles or boulders it may not lie horizontal again reducing its effectiveness.

Obviously there is a need for improvement in the methods used for collecting eggs if detailed assessments of spawning habitat relationships are to be conducted in Great Lakes environments. The convenience offered by surface deployed gear appears to be at the expense of maintaining the gear in place once deployed especially in high energy environments. In addition with traps there is the additional disadvantage of collecting fewer eggs potentially limiting the resolution of important habitat variables. The perceived advantage of being able to use these devices in deep waters without diver support does not appear justified by the relatively shallow spawning depths used by Great Lakes lake trout as indicated by Thibodeau and Kelso (1990). At present the best gear appears to be one buried in the substrate such as pails where location can be maintained throughout the spawning period, and egg collections can be related to a known set of habitat parameters. However owing to the difficulty in repetitively sampling pails over the spawning period to look at the importance of such factors as current direction, time of day or temperature fluctuations, there is a need to modify the pails such that they can be more readily be sampled repetitively. The ability to repetitively sample is particularly important when strong currents or storms are present as were noted by Marsden and Krueger (1991). These events tend to redistribute eggs from the initial spawning location potentially masking the delineation of spawning habitat relationships. By successively emptying the sampler through the course of the spawning period which may last several weeks several opportunities exist to look at the importance of different habitat variables. Alternatively there is room for development of a new sampler that can be buried in the substrate but sampled repetitively.

3.5 A SUMMARY AND REVIEW OF HABITAT CHARACTERISTICS INFLUENCING LAKE TROUT SPAWNING

3.5.1 Physical

Substrate Type and Size: Lake trout use rounded or angular cobble/rubble (4-40 cm) to spawn on in inland and Great Lakes (Martin and Olver, 1980; Marsden and Krueger, 1991). DeRoche (1969) reported some preference for angular over rounded cobbles which Prevost(1956) found provided less protection for eggs against fish predators. This was also the conclusion of the four speakers at the workshop. Although Thibodeau and Kelso (1990) found historical references to

spawning on fine materials these could not be confirmed. Such materials would provide little protection from currents and predators as was found by Hacker (1956) who documented considerable predation on eggs when deposited on fine grained substrates. There is insufficient information to judge whether there is a preferred cobble size although size of cobbles tends to be larger on exposed Lake Superior shoals (B. Swanson, pers. comm.).

Depth of Cobbles: Both Marsden and Krueger (1991) and Casselman (1989) observed the greatest egg deposition at Stony Island and Yorkshire Island respectively in areas with the greatest depth of cobbles (> 30 cm) and having the least amount of sediment infilling. Patterns of egg deposition at a shoal at Burlington Pier (pers. obs.) are in support of these observations. Wagner (1981) in his studies at Elmwood Marina in Grand Traverse Bay also found the greatest egg deposition on the non-sedimented portion of a breakwall with little egg deposition on an area where silt had infilled the cobble substrate. Sedimentation of material may be correlated with currents (Sly and Widmer, 1984) such that it is difficult to separate their individual importance.

Whether there is a critical depth of cobbles required before lake trout will spawn is not known although both Martin (1956) and Hacker (1956) observed spawning on artificial shoals 0.6 m deep.

Slope of Cobbles: As indicated by the studies of Marsden and Krueger (1991), Casselman (1989), Wagner (1981) and Peck (1986) in the Great Lakes and studies in the Finger Lakes (Royce, 1943, 1951; Sly and Widmer, 1984) lake trout tend to spawn in areas associated with a sloping substrate. Spawning occurs either on the top of the slope or somewhere along the slope with angle of inclination ranging from 10 to 45 degrees. Depending on the angle there may be changes in light, pressure and temperature such that the association with slope may reflect the importance of other co-occurring factors. Aggregation of spawning fish may also be favoured by the slope. Marsden and Krueger (1991) observed that spawning fish were associated with the top of the slope which was accessed by fish moving up the slope itself. Slope may also be important in acting as a conduit for emergent fry to quickly move to deepwater nursery and rearing habitat (Casselman, 1991) although it's primarily only in the Finger Lakes where because of the steep slope that spawning, nursery and rearing habitat are near contiguous.

Sedimentation Rate: While sedimentation rate may limit the success of natural reproduction (Sly and Widmer, 1984) it does not necessarily control spawning provided it does not result in significant infilling of cobble substrates. Sly (1988) observed egg deposition in a number of inland and Great Lakes where fall sedimentation rates ranged over three orders of magnitude.

Colour and Type of Cobbles: On the Canadian Shield, lake trout spawn on granitic material while in the Great Lakes substrates may be of limestone (Martin and Olver, 1980). With this variation in colour it is unlikely that colour plays a large role in spawning habitat selection.

Size of Shoal: Shoals may vary in size from a few square meters in inland lakes (D. Jefferies, Ontario Ministry of Natural Resources, Picton, Ontario, pers. comm.) to several square kilometers in Lake Superior (Swanson and Swedberg, 1980). Whether the size of the shoal imposes a limit

on the number of fish that will spawn there is not known. Martin (1956) found significant egg deposition on a small (63 m^2) artificial shoal in Shirley Lake. There are some indications that egg deposition may be inversely proportional to the amount of habitat. In Shirley Lake where spawning shoals were shallow and associated with the shoreline Martin (1956) noted that when water levels were drawn down prior to spawning, egg deposition on the remaining submerged spawning substrate was three-fold higher than that for shoals in an adjacent unregulated lake. Similarly egg deposition at Stony Island is 20-fold less than at a site at Burlington in western Lake Ontario where there is approximately 10-fold less spawning habitat (pers. obs.) although similar numbers of spawners.

3.5.2 Chemical

Dissolved Oxygen/Ammonia: Like sedimentation rate which could contribute to low dissolved oxygen/elevated ammonia these two factors may limit reproductive success but do not appear to control spawning. Sly (1988) measured dissolved oxygen at spawning at Stony and Yorkshire Islands in Lake Ontario, and Seneca Lake that are below the dissolved oxygen levels considered lethal to lake trout embryos (Garside, 1959; Carlson and Sieffert, 1974; Fitzsimons, 1989).

Conspecific Odours: A lab study has reported preferential attraction of spawning lake trout to artificial reefs containing young-of-the-year fecal material (Foster, 1985). While odour substances may enhance selection of a particular spawning site it is unlikely they are an absolute requirement since self-sustaining lake trout populations have become established in lakes that were previously devoid of lake trout (Olver and Lewis, 1977; Purych, 1980; Hitchins and Samis, 1986).

3.5.3 Biological

Predators: Although predators may limit the success of reproduction their presence doesn't prevent spawning. Predators including slimy sculpins, white suckers, brown bullheads and burbot appear to be quite common both during and after spawning (Martin and Olver, 1980) perhaps attesting to the limited aggression shown by lake trout males (J. Gunn, Laurentian University, Sudbury, Ontario, pers. comm.). Round whitefish in Opeongo Lake have been observed consuming lake trout eggs while lake trout spawning was underway (H. Don, Department of the Environment, Burlington, Ontario, pers. comm.)

Competitors: As it is a lake spawning species that spawns in the fall the lake trout has little opportunity for competitive interactions at spawning time with salmonids or other reef spawning fish. However in the Great Lakes chinook salmon have recently been reported to spawn extensively on shoals in Lake Huron and in one case on the same shoal as lake trout (Powell and Miller, 1990). In this report the authors reported seeing non-lamprey scars which they suggested might be due to aggression between the chinook salmon and lake trout. It's not known whether the presence of chinook salmon reduced spawning activity by lake trout.

Macrophytes/Cladophora: Sly (1988) has noted aquatic plants associated with but not directly on

spawning shoals at both Yorkshire and Stony Islands during the spawning period. During the summer both of these sites had extensive coverage of Cladophora on the spawning material itself, sometimes to a depth of 20 cm (pers. obs.; E. Marsden, Illinois Natural History Survey, Zion, Illinois, pers. comm.). These deposits detach and are removed by spawning time however by strong waves and currents. While standing stocks of these plants and associated fouling of shoals do not appear to prevent spawning they may result in reduced egg survival through fouling of interstitial spaces with decaying plant material, contributing to reduced dissolved oxygen and elevated ammonia (Sly, 1988)

Genetics/Stocks: Marsden et al (1989) found through electrophoretic analysis of eggs deposited, a predominance of egg deposition by Seneca Lake strain (78%) lake trout at Stony Island despite the presence of spawners of eight other strains some of which were numerically 10-fold more abundant. At Yorkshire Island egg deposition was dominated by Manitou Lake strain (50%) (P. Grewe, pers. comm.) while egg deposition at Burlington Pier in western Lake Ontario was dominated by Clearwater Lake (55%) and Lake Manitou (30%) strain lake trout. Clearwater Lake strain lake trout would not be expected to spawn at this location since the closest stocking location was 100 km away, with large areas of apparently superior quality spawning habitat in between (pers. obs.). While not definitive, these shoal-to-shoal differences suggest a recognition of unique habitat characteristics at the strain level although spawning was observed to occur within a depth range of less than 1 m and on similarly sized spawning substrate across all three of the above Lake Ontario spawning sites. Segregation of stocks by spawning shoals was suggested for lake trout in Lake Simcoe (MacLean et al, 1981).

Spawner Density: Theoretically only two fish need be present at a shoal to result in natural reproduction although whether a critical number is needed is not known. Stocking of yearling lake trout in Gamitagama Lake, a lake previously devoid of lake trout, resulted in natural reproduction four years later (Olver and Lewis, 1977). Based on the initial planting of 1000 yearlings that reached maturity at age 5+ and using an estimated annual mortality rate of 0.5 as few as 30 male and female lake trout may have been using a spawning shoal in this lake. The number may have been even less since six potential spawning shoals existed in the lake.

Whether there is an upper limit to the number of spawning lake trout a particular shoal will support is not known. Casselman (1989) found that while numbers of lake trout in the Outlet Basin of eastern Lake Ontario have increased almost 50-fold between 1975 and 1989, numbers at Yorkshire Bar a spawning shoal show similar increases suggesting that if an upper limit exists it hasn't been reached yet. However whether this increasing number of spawners is reflected in increased spawning and egg deposition is not known. While not the same as an increasing number of spawners relative to a fixed amount of spawning material Martin (1956) reported three-fold more egg deposition in Shirley Lake after a pre-spawning drawdown that exposed most of the shoreline spawning material than in adjacent Louisa Lake where no drawdown had occurred. Egg deposition on a spawning shoal at Burlington Pier in western Lake Ontario, where numbers of spawning lake trout are similar (pers. obs.) to those at Stony Island (C. Schneider, New York Department of Environmental Conservation, Cape Vincent, N.Y., pers. comm.), was 20-fold higher (pers. obs.) than egg deposition at Stony Island (E. Marsden, pers. comm.) where there is ten times the amount of potential spawning material. While it is not known what effects

large populations of spawners relative to a small spawning area have on spawning physiology, Peck (1986) found that survival from egg to swim-up fry was highest the year of lowest egg deposition.

Proximity to Stocking Site: Lake trout appear capable of finding suitable spawning sites at great distances from where they are initially stocked. As indicated earlier Clearwater Lake lake trout were found to spawn at Burlington Pier (pers. obs.) even though the closest they could have been stocked as yearlings was 100 km away. Similarly the closest stocking site to Stony Island for Seneca Lake strain lake trout which have successfully reproduced at this site is 7 km (Marsden et al, 1989). In inland lakes there is also evidence that lake trout select appropriate spawning habitat far from stocking sites (MacLean et al, 1981). Thus some stocked lake trout at least have the ability to seek out and select appropriate spawning habitat independent of stocking site.

3.5.4 Hydrological

Currents: That current may be important factor in initiating spawning habitat selection is suggested by the presence of some river spawning strains (Loftus, 1954), although this is an extreme form of selection. The importance of currents to spawning at Yorkshire Bar and Stony Island is suggested by the failure of interstitial spaces at these sites to become fouled despite the potential at these sites for significant sedimentation and infilling (Sly, 1988). Whether the same currrents that maintain interstitial spaces free of sediment are active during the spawning act is not known. Observations of egg deposition at Burlington Pier in western Lake Ontario indicate that currents may be important during spawning is suggested (pers. obs.). Although maximum egg deposition occurred at the top of this shoal elevated egg peak egg deposition could be followed downslope in a 2 m wide swath for a distance of approximately 15 m in a near straight line. Such a pattern conceivably would not be possible had eggs been deposited in the absence of currents then remobilized by currents.

Fetch: In inland lakes MacLean et al (1990) found fetch to be important such that 98% of shoals had a fetch greater than 0.5 km. Fetches of less than this have been noted at spawning time in the Great Lakes at Presque Isle Harbour (Peck, 1986) and Burlington Pier (pers. obs.) where lake currents may moderate the requirement for longer fetches. Very long fetches may be counterproductive to spawning in the Great Lakes through excessive turbulence resulting in avoidance by fish or in the extreme, destruction of the spawning shoal.

Seepage: There is no evidence that ground water seepage is important to lake trout spawning (Martin and Olver, 1980).

Ice Scour and Cover: Extensive ice scour has been noted on spawning shoals at Yorkshire Bar (pers. obs.) and at Stony Island (E. Marsden, pers. comm.) Therefore its absence does not appear to be a prerequisite for spawning although it may limit survival by dislodging eggs prior to hatching.

Proximity to Tributaries: Although MacLean et al (1991) were unable to find lake trout spawning

shoals located adjacent to tributary inputs in inland lakes, there are several reports of river spawning by lake trout (Martin and Olver, 1980) including Lake Superior. Failure to spawn in inland lake tributaries may be due to the variable nature of stream bed or stream flow.

Water Depth, Lake Size and Water Level Fluctuations: These three factors appear to act together in affecting lake trout spawning habitat selection. Based on a survey of reported spawning depths for 24 lakes (see Appendix 2) and associated lake size (Fig. 1), there was a trend for increasing spawning depth with lake size. This relationship is described by the equation:

spawning depth(m)=0.07+0.93 log lake size (km^2)(r^2=.79)

Although the reported spawning at 20 m in Lake Superior (Eschmyer, 1955) would not fit this relationship neither has this report, where a single egg was found entrained in bottom material snagged by a gill net, ever been confirmed either. Also not fitting and not included in this relationship is the confirmed presence of lake trout eggs at 4.5 m at Peach Orchard Pt. in southern Seneca Lake (Storr, 1962). Slope at this site was quite steep ranging from 30 to 43 degrees. This in combination with strong seiche and wind driven currents would tend to obscure any spawning-habitat relationships. Eggs found at 4.5 m by Storr may well have been deposited at shallower depths. Recent observations in northern Seneca Lake adjacent to Geneva have found evidence of lake trout spawning at a breakwall in 2.5 m of water (E. Marsden, pers. comm.) which is consistent with the above relationship

The above relationship may represent a point at which for a particular lake size there is sufficient scouring of bottom materials to prevent sedimentation and infilling of interstitial spaces, yet incubating eggs remain undisturbed. While water level drawdowns of 0.6 m in Lake Opeongo where lake trout spawn at 1 m (Martin, 1956) did not appear to affect recruitment wave turbulence at 0.4 m in this relatively small inland lake would be expected to be much less than in a Great Lake. Within Lake Ontario across three geographically distinct spawning shoals, maximum egg deposition is occurring within a depth range of less than 1 m.

Selection of water depth by spawning lake trout appears to be a dynamic process. Prior to the late 1930's when the level of Bark Lake was raised 11 m lake trout spawned at approximately 1 m depth in this lake (Wilton, 1985). After the level was raised lake trout continued to spawn at approximately 1 m depth even though this location was now 11 m up the original shoreline.

DeRoche, S.E. and L.H. Bond.1957. The lake trout of Cold Stream Pond, Enfield, Maine. Trans. Am. Fish. Soc. 85: 257-270.

Dorr, J.A. III, D.V. O'Connor, N.R. Foster and D.J. Jude. 1981. Substrate conditions and abundance of lake trout eggs in a traditional spawning area in southeastern Lake Michigan. N. Am. J. Fish. Manage. 1: 165-172.

Edsall, T.A., P.T. Poe, R.T. Nester, and C.L. Brown. 1989. Side-scan sonar mapping of lake trout spawning habitat in Northern Lake Michigan. N. Am. J. Fish. Manage. 9: 269-279.

Elrod, J.H. 1987. Dispersal of three strains of hatchery-reared lake trout in Lake Ontario. J. Great Lakes Res. 13: 157-167.

Eschmyer, P.H. 1955. The reproduction of lake trout in southern Lake Superior. Trans. Am. Fish. Soc. 84: 47-74.

Eshenroder, R.L. T.P. Poe, and C.H. Olver. 1983. Strategies for rehabilitation of lake trout in the Great Lakes: Proceedings of a conference on lake trout research (CLAR), August 1983. Great lakes Fishery Commission Technical Report No. 40. pp 1-63.

Fitzsimons, J.D. 1989. The effects of short-and long-term exposures to low dissolved oxygen-elevated ammonia on lake trout eggs. Abstract. 32nd Conference on Great Lakes Research, Madison, Wisconsin.

Fitzsimons, J.D. 1992. Lake trout spawning in Mazinaw Lake 1991. Draft.

Foster, N.R. 1985. Lake trout reproductive behaviour: influence of chemosensory cues from young-of-the-year by-products. Trans. Am. Fish. Soc. 114: 794-803.

Fraser, J.M. 1989. Establishment of reproducing populations of brook trout after stocking of interstrain hybrids in Precambrian Shield lakes. N. Am. J. Fish. Manage. 9: 352-363.

Garside, E.T. 1959. Some effects of oxygen in relation to temperature on the development of the trout embryos. Can. J. Zool. 37: 383-386.

Goodyear, C.S., T.A. Edsall, D.M. Ormsby, G.D. Ross, and P.E. Polanski. 1982b. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume four: Lake Michigan. Wildl. Serv. Washington, D.C. FWS/OBS-82/52. 201 p.

Goodyear, C.S., T.A. Edsall, D.M. Ormsby, G.C. Ross and P.E. Polanski. 1982d. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume nine: Lake Erie.

Wildl. Serv., Washington, D.C. FWS/OBS-82/52. 193 p.

Goodyear, C.S., T.A. Edsall, D.M. Ormsby, G.C. Ross, and P.E. Polanski. 1982c. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume five: Lake Huron. Wildl. Serv., Washington, D.C. FWS/OBS-82-52. 113 p.

Goodyear, C.S., T.A. Edsall, D.M. Ormsby, G.C. Ross and P.E. Polanski. 1982e. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume eleven: Lake Ontario. Wildl. Serv., Washington, D.C FWS/OBS-82-52. 109 p.

Goodyear, C.S., T.A. Edsall, and D.M. Ormsby. 1982a. Spawning and nursery areas of Great Lakes fishes. Volume two: Lake Superior. Wildl. Serv., Washington, D.C. FWS/OBS-82/52. 114 p.

Gunn, J.M. and W. Keller. 1981. Emergence and survival of lake trout (Salvelinus namaycush) and brook trout (Salvelinus fontinalis) from artificial substrates in an acid lake. Ont. Fish. Tech. Rep. Ser.No. 1. 9 p.

Hacker, V. A. 1957.Biology and management of lake trout in Green Lake, Wisconsin. Trans. Am. Fish. Soc. 86: 71-83.

Hitchins, J.R. and W.G.A. Samis. 1986. Successful reproduction by introduced lake trout in 10 Northeastern Ontario lakes. N. Am. J. Fish. Manage. 6: 372-375.

Horns, W.H., J.E. Marsden and C.C. Krueger. 1989. Inexpensive method for quantitative assessment of lake trout egg deposition. N. Am. J. Fish. Manage. 9: 280-286.

Krueger, C.C., B.L. Swanson, and J.H. Selgeby. 1986. Evaluation of hatchery-reared lake trout for reestablishment of populations in the Apostle Islands region of Lake Superior, 1960-1984. Pages 93-107. In R.H. Stroud (ed.) "Fish Culture in Fisheries Management". American Fisheries Society, Bethesda, Maryland.

Loftus, K.H. 1958. Studies on river-spawning lake trout in eastern Lake Superior. Trans. Am. Fish. Soc. 87: 259-277.

MacCallum, W. R. and J.H. Selgeby. Lake Superior revisited 1984. Can. J. Fish. Aquat. Sci. 44: 23-36.

MacLean, N.G. J.M. Gunn, F.J. Hicks, P.E. Ihssen, M. Malhiot, T.E. Mosindy and W. Wilson. 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. Lake Trout Synthesis, Ontario Ministry of Natural Resources, Toronto, Ontario. 84 p.

MacLean, J.A., D.O. Evans, N.V. Martin and R.L. Desjardine. 1981. Survival, growth,

spawning distribution and movements of introduced and native lake trout (Salvelinus namaycush) in two inland lakes. Can. J. Fish. Aquat. Sci. 38: 1685-1700.

Marsden , J.E., C.C. Krueger and B. May. 1989. Identification of parental origins of naturally produced lake trout in Lake Ontario: Application of mixed-stock analysis to a second generation. N. Am. J. Fish. Manage. 9: 257-268.

Marsden, J.E., C.C. Krueger, and C.P. Schneider. 1988. Evidence of natural reproduction by stocked lake trout in lake Ontario. J. Great Lakes Res. 14: 3-8.

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

Marsden, J.E., C.C. Krueger and H.M. Hawkins. 1991. An improved trap for passive capture of demersal eggs during spawning: An efficiency comparison with egg nets. N. Am. J. Fish. Manage. 11: 364-368.

Martin, N.V. 1955. The effect of drawdown on lake trout reproduction and the use of artificial spawning beds. Trans. N.A. Wildl. Conf. 20: 263-271.

Martin, N.V. 1956. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231-244.

Martin, N.V. and C.H. Olver. 1980. The lake charr, Salvelinus namaycush, pp205-207. In E.K. Balon [ed.] Charrs:salmonid fishes of the genus Salvelinus. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

McCrimmon, H.R. 1958. Observations on the spawning of lake trout, Salvelinus namaycush, and the post spawning movement in Lake Simcoe. Can. Fish. Cult. 23: 3-11.

Miller, R.B. and W. A. Kennedy. 1948. Observations on the lake trout of Great Bear Lake. J. Fish. Res. Bd. Can. 7: 176-189.

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

Olver, C.H. and C.A. Lewis. 1977. Reproduction of planted lake trout, Salvelinus namaycush, in Gamitagama Lake, a small Precambrian lake in Ontario. J. Fish. Res. Bd. Can. 34: 1419-1422.

Peck, J.W. 1986. Dynamics of reproduction by hatchery lake trout on a man-made

Storr, J.F. 1962. Delta structures in the New York Finger Lakes and their relation to the effects of currents on sediment distribution and aquatic organisms. Great Lakes Res. Div., Univ. of Michigan, Pub. No. 9., pp 129-138.

Swanson, B.L. and D.V. Swedberg. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (Salvelinus namaycush) population and the role of sea lamprey (Petromyzon marinus) predation. Can. J. Fish. Aquat. Sci. 37: 2074-2080.

Thibodeau, M.L. and J.R.M. Kelso. 1990. An evaluation of putative lake trout (Salvelinus namaycush) spawning sites in the Great Lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1739.

Wagner, W.C. 1981. Reproduction of planted lake trout in Lake Michigan. N. Am. J. Fish. Manage. 1: 159-164.

Wilton, M.L. 1985. Water drawdown and its effects on lake trout reproduction in three south-central Ontario lakes. Ontario Fisheries Technical Report Series No. 20, 9 p.

Table 2. An overview of lake trout spawning habitat characteristics in inland and Great Lakes and their relative importance.

FACTOR CATEGORY	FACTOR CODE	FACTOR	SIMILAR FOR INLAND AND GREAT LAKES	REQUIRED FOR SPAWNING	REQUIRED FOR OPTIMAL SURVIVAL	RELATED TO
PHYSICAL	P1	presence of 4 to 40 cm cobble/rubble	yes	yes	ND	
	P2	multiple layers of cobbles	yes	yes	yes	P4
	P3	moderate to high slope of cobbles	yes	yes	ND	H1
	P4	low sedimentation rate	ND	no	yes	C1,B3,H1
	P5	colour and type of cobbles	yes	no	no	
	P6	moderate to large size of shoal	yes	no	no	
CHEMICAL	C1	high dissolved oxygen/ low ammonia	ND	no	yes	P2,P4,B3,H1
	C2	presence of conspecific odours	ND	no	no	
BIOLOGICAL	B1	low numbers of predators	yes	no	yes	
	B2	low numbers of competitors	yes	no	yes	
	B3	absence of macrophytes/ Cladophora	ND	no	yes	P4,C1,H1
	B4	presence of native stocks	NA	no	ND	
	B5	high spawner density	ND	no	ND	
	B6	close proximity to stocking site	yes	no	ND	
HYDROLOGICAL	H1	presence of currents	ND	yes	yes	
	H2	long fetch	no	no	no	P2,P4,C1
	H3	presence of seepage	yes	no	no	
	H4	absence of ice scour and cover	ND	no	yes	
	H5	remote from tributaries	no	no	ND	
	H6	critical water depth	yes[1]	yes	yes	H7,H8
	H7	critical lake size	NA	NA	NA	H6,H8
	H8	lack of water level fluctuations	ND	no	yes	H6, H7

[1]related to lake size
ND no data
NA not applicable

Table 1. Factors potentially affecting lake trout spawning habitat selection.

Physical	**Chemical**	**Biological**	**Hydrological**
-substrate type	-dissolved oxygen	-predators	-currents
-size of cobbles	-ammonia	-competitors	-fetch
-shape of cobbles	-hydrogen sulphide	-macrophytes/	-seepage
-depth of cobbles	-odour substances	Cladophora	-water depth
-slope of cobbles		-genetics/stocks	-temperature
-colour of cobbles		-spawner density	-ice scour
-type of cobble		-proximity to	-lake size
-infilling		stocking site	-proximity to tributaries
-sedimentation rate			-water level fluctuations
-proximity to drop-off			
--light levels			
-interstitial space			

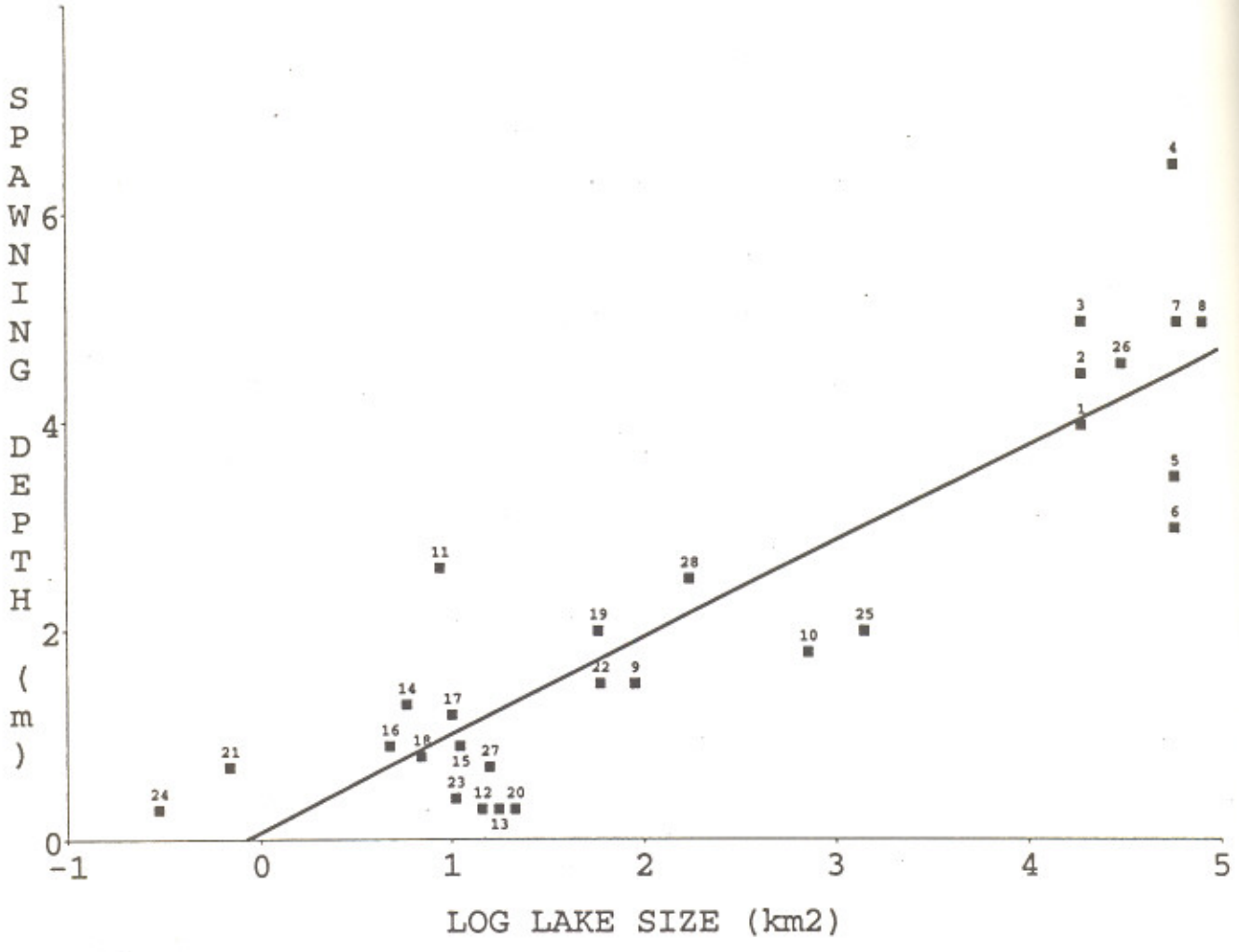

Figure 1. Relationship between lake size (km^2, log10 scale) and lake trout spawning depth (m). Numbers on top (bottom) of symbols refer to lakes listed in Appendix 2.

Appendix 2. Summary of lakes used to assess the relationship between lake size and lake trout spawning depth.

No	Lake	Area (km^2)	Spawning depth (m)	Reference
1	Lake Ontario	18960.0	4.0	Marsden and Krueger, 1991
2	Lake Ontario	18960.0	4.5	Casselman, 1990
3	Lake Ontario	18960.0	5.0	J. Fitzsimons, unpublished
4	Lake Michigan	57800.0	6.5	Wagner, 1981
5	Lake Michigan	57800.0	3.5	Wagner, 1981
6	Lake Michigan	57800.0	3.0	Dorr et al, 1981
7	Lake Huron	59600.0	5.0	Nester and Poe, 1984
8	Lake Superior	82100.0	5.0	Peck, 1986
9	South Bay	90.9	1.5	J. Collins, OMNR, Tehkumah, Ontario, pers. comm.
10	Lake Simcoe	725.0	1.8	MacCrimmon, 1958
11	Otsego Lake	8.9	2.6	Royce, 1943
12	Cold Stream Pond	14.5	0.3	DeRoche and Bond, 1955
13	Thompson Lake	17.7	0.3	DeRoche, 1969
14	Louisa Lake	5.9	1.3	Martin, 1956
15	Hay Lake	11.2	0.9	Martin, 1956
16	Shirley Lake	4.8	0.9	Martin, 1956
17	Happy Isle Lake	10.2	1.2	Martin, 1956
18	Merchants Lake	7.0	0.8	Martin, 1956
19	Opeongo Lake	58.6	2.0	Martin, 1956
20	Massawippi Lake	21.5	0.3	Prevost, 1956
21	Whitepine Lake	0.7	0.7	Gunn and Keller, 1984
22	Bark Lake	60.0	1.5	Wilton, 1985
23	Mary Lake	10.6	0.4	Wilton, 1985
24	Bella Lake	0.3	0.3	Wilton, 1985
25	Lac la Ronge	1425.0	2.0	Rawson, 1961
26	Great Bear Lake	30680.0	4.6	Miller and Kennedy, 1948
27	Mazinaw Lake	15.9	0.7	Fitzsimons, 1992
28	Seneca Lake	175.4	2.5	E. Marsden, pers. comm.