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LAKE TROUT REPRODUCTION ON A MAN-MADE SPAWNING REEF[1]

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[1]Contribution from Dingell-Johnson Project F-35-R, Michigan.

Abstract

Lake trout reproduction on two man-made spawning reefs in Presque Isle Harbor, Lake Superior in 1977-1980 was qualitatively and quantitative described. Lake trout spawned during a 15- to 26-day period between 12 October - 14 November from sundown to at least midnight. Most of the spawners were of hatchery origin but wild trout increased from 4% to 25% during the period. Lake trout rarely visited the reefs more than once and may have deposited sex products on more than one reef. Number of spawners in 1979 was estimated to be 1,600 males and 600 females on the intake reef and 2,100 males and 1,100 females on the discharge reef. Egg deposition and swim-up fry production on the two reefs during 1977-1980 ranged 122-518/m^2 and 8-46/m^2, respectively. Physical characteristics, water chemistry, and biota indicated that these man-made reefs were favorable habitat for lake trout reproduction.

Introduction

Lake trout (*Salvelinus namaycush*) have been planted in lakes Superior and Michigan since the late 1950's in an effort to restore stocks depleted by commercial fishing and sea lamprey (*Petromyzon marinus*) predation. The planted fish, plus sea lamprey control and restricted fishing resulted in substantial recovery of adult fish abundance by the early 1970's (Pycha and King 1975, Rybicki and Keller 1978, Swanson and Swedberg 1980). Initially there was little or no observed natural reproduction by the hatchery fish and the ability of hatchery fish to locate suitable spawning reefs and reproduce in the Great Lakes was in doubt. However, Peck (1979) found concentrations of mature hatchery lake trout in spawning condition on traditional spawning reefs in lakes Superior and Michigan during 1973-1976 and successful natural reproduction by hatchery lake trout was confirmed in Presque Isle Harbor, Lake Superior, in 1975 on power plant water intake and discharge pipes (Hatch 1976, Peck 1982). Lake trout reproduction has also been documented on man-made structures in Lake Michigan in 1978 (Wagner 1981) and in 1980 (Jude et al. 1981).

There has been much published on lake trout populations (Martin and Olver 1980) but very little quantitative information is available on reproduction especially by stocks of hatchery fish. Reproduction by hatchery lake trout in inland lakes has been documented by Hacker 1957, Griest 1977, Olver and Lewis 1977, and Purych 1980. However, these reports provided little information on the magnitude of spawning populations and reproduction. For natural populations, Swanson and Swedberg (1980) estimated number of spawners on a reef in western Lake Superior but otherwise there are little quantitative data on number of spawners, egg deposition, and on survival and production of fry in the Great Lakes.

I studied lake trout reproduction on the power plant water intake and discharge pipes in Presque Isle Harbor during 1977-1980. The objectives of my study were (1) to describe spawning and estimate numbers of adult lake trout spawners, eggs deposited, fry produced, and egg-to-fry survival; and (2) to describe physical and other characteristics of this unique spawning area. Although the spawning reefs in Presque Isle Harbor are man-made, both hatchery and wild lake trout have reproduced on other man-made reefs, some installed specifically to create lake trout spawning reefs (Martin and Olver 1980). Quantitative data on lake trout reproduction on the man-made spawning reefs in Presque Isle Harbor provide a basis for evaluating man-made reefs as a lake trout management tool and these data may not be greatly different than those for a natural reef.

Methods

Study site.--Presque Isle Harbor (Fig. 1) is located on the south shore of Lake Superior at Marquette, Michigan (46°31'N; 87°24'W). Upper Peninsula Generating Company installed cooling water intake and discharge pipes in the harbor in 1974 to service a fossil fuel power plant (Presque Isle Power Station). Another discharge pipe was added in 1977. A rock overburden was used to anchor the pipes on the harbor floor. Lake trout were immediately attracted to this rock and spawned on it the same year as installed (Peck 1982).

Lake trout parameters.--I fished gill nets on the intake and discharge in Presque Isle Harbor during October-November 1977-1980 to determine duration of the spawning period (seasonal and daily), biological characteristics of the spawners (origin, length and age, composition, sex ratio, and fecundity), and to estimate their numbers. The gill nets were multifilament nylon, 30- to 90-m long and 6.5-cm stretched measure mesh. Lake trout were not gilled in these small-mesh nets but were caught by the teeth or jaw. This means of capture and net sets of only 1 hour, resulted in very little mortality. Netting was done 2-3 days each week during October-November with one or more sets made each day commencing at sundown. A few daytime sets (0900-1500 hours) were made but lake trout were rarely captured on the spawning areas during daylight hours. Bottom water temperatures on the spawning area were determined on each day of netting. I recorded total length, sex, maturity, fin clip for hatchery lake trout, and scale sampled unclipped lake trout. Lake trout spawning period was determined to be the inclusive dates when ripe to spent female fish were captured. Age of lake trout was determined from fin clips or from scale analysis for unclipped trout. Fish other than lake trout were measured and stomach contents examined for the presence of lake trout eggs. All live lake trout were marked and released. In 1977 and 1978, lake trout captured on the intake reef were marked with an upper caudal fin clip and those caught on the discharge reef were marked with lower caudal fin clip. The fin clip marking was done to recognize recaptured fish, to determine if there was any exchange of spawners between the intake and discharge, and to estimate the number of spawners by the multiple census mark and recapture method. In 1979, lake trout from both the intake and discharge were tagged in the epaxial muscle at the base of the dorsal fin with a red anchor tag (Floy FD-67F with flag removed). Recapture of these tagged fish in 1980 was used to estimate the number of lake trout present in 1979.

Fecundity of hatchery lake trout was determined from 20 lake trout collected in Lake Superior in and near Presque Isle Harbor during August-October 1977-1980. These fish were measured, weighed, and age determined. Eggs in each fish were counted and a random sample of two per 100 utilized for egg diameter measurement.

I used three methods to estimate number of spawners on the intake and discharge during 1977-1979. Fecundity, egg deposition, and sex ratio was one method used to estimate number of spawners on the intake in 1977, 1978, and 1979. To estimate the number of females, estimated egg deposition each year was divided by fecundity calculated for average total length of females captured on the reef. The 95% confidence limits on the number of females was based on pooled variance from the egg deposition estimate and fecundity estimate. The number of males was extrapolated from the estimate for females based on sample sex ratio. A Schnabel (Chapman modification) multiple census (Ricker 1975) was conducted on the intake and discharge during 19 October - 3 November in 1977 and during 10 October - 6 November in 1978. Approximate 95% confidence limits for these estimates were obtained by considering the number of recaptured fish as a Poisson variable. The number of age VII and older spawners of hatchery origin in 1979 was estimated using a Peterson (Bailey modification) single census (Ricker 1975). This estimate was based on recapture in 1980 of spawners tagged in 1979. No adjustments for tag loss were made because loss of this tag was reported as 4% or less (Bruce Swanson, Wisconsin Department of Natural Resources, personal communication). The number of recaptured fish was considered as a Poisson variable for calculation of 95% confidence limits. Lake trout younger than age VII were considered to be not fully recruited to the spawner population. An estimate of these young hatchery trout and wild trout was made based on their respective percentages of total catch.

I estimated egg deposition and swim-up fry production on the intake reef in 1977-1980 and on a 50-m segment of the discharge in 1979-1980. Egg deposition was estimated by extrapolation from the number deposited in egg-trap pails (Stauffer 1981) to the total spawning area sampled. Scuba divers buried 93 pairs of pails in the intake substrate and

18 pairs of pails in the discharge substrate prior to the spawning period. Pairs were placed at 6-m intervals (5-m intervals on the discharge) along the midline of longitudinal sections of the spawning reefs. One of each pair was lifted immediately after lake trout spawning to estimate egg deposition. Eggs from each pail were preserved in an aqueous solution containing 5% formalin, 4% glacial acetic acid, and 6% glycerin, and stage of development determined. Stages of development were unfertilized, dead-not eyed, dead-eyed, live-not eyed, and live-eyed. The remaining pail of each pair was left in the substrate for an estimate of fry production the following spring. I estimated the number of swim-up fry produced by extrapolation from the number of fry recovered from the pails. Fry emerging from the pails were captured in fry traps (Stauffer 1981) which were attached to the pails prior to lake trout emergence. Lake trout fry and other fish captured in the traps or recovered in the pails were preserved in 5% formalin, counted, and measured. Lake trout eggs were preserved in the aforementioned formalin-glacial acetic acid-glycerin solution and counted. However, stage of development could only rarely be determined because the eggs were badly decomposed. Fish other than lake trout were examined to determine if they had been eating lake trout eggs or fry.

Man-made reef parameters.--The rock overburden was granite on the intake and limestone on the discharge and consisted of a base layer of small crushed rock 1- to 2-cm in diameter upon which was added a layer of larger rock (Fig. 2). Physical characteristics were determined for 21 sites on the intake and 6 sites on the discharge. Scuba divers measured width (A), water depth (B), thickness of the large-rock layer (C), and photographed 0.5 m^2 of substrate at 30-m intervals (D) along the midline of the north, middle, and south longitudinal sections of the intake (Fig. 2). These same parameters were measured at each end of the 50-m segment on the discharge. I determined range and average diameter of rocks in the large-rock layer by measuring those in the photographs. I classified the rocks as boulders, cobbles, pebbles, or granules, based on particle diameter, according to Wentworth in Welch (1948).

I measured dissolved oxygen, alkalinity, pH, and turbidity on the intake and discharge reefs in the fall and spring during 1977 -1980. Water samples were collected with a Kemmerer water sampler within 1 m of the substrate. Dissolved oxygen was determined by the Winkler method, alkalinity by the phenolphthalein-methyl orange titration method, and pH by the colorimetric method (Welch 1948). Turbidity was measured with a Secchi disc in 1977-1978 and sedimentation was assessed from scuba diver observations and my observation of sediment in egg- and fry-trap pails.

Macroinvertebrate benthos was assessed in egg-trap pails on the intake in November 1977 and November 1978. In July 1979, benthos in egg-trap pails and on the reef proper were assessed both macro- and microscopically. Egg-trap pails were placed in plastic bags or covered pails, hauled to the surface and benthos removed by straining the enclosed water through a plankton net and picking organisms from the substrate particles. Benthos on the reef proper were sampled in July 1979 using a suction pump that vacuumed a 0.5 m^2 area with the pump discharge strained through a plankton net (No. 10) to recover the organisms.

Results

Spawning period.--The lake trout spawning period on the intake and discharge reefs, defined by the presence of ripe to spent females, was a 15- to 26-day period between 12 October and 14 November. Spawning occurred during 24 October - 02 November all 4 years. Males and females generally arrived at the spawning area about the same time, but males ripened earlier. Ripe males were captured on the reefs up to 13 days earlier than ripe females. Ripe males remained on the reefs as many as 15 days after the last female. The abundance of males peaked prior to the abundance of females. Water temperatures were 11 C or less at the onset of spawning then generally declined to near 5 C by the end of the period.

Most spawning apparently took place the first hours after sundown. Lake trout were rarely captured on the spawning areas during the day (0900-1500 hours) regardless of cloud cover, but scuba divers observed groups of 10-15 trout nearby on two occasions. Lake trout were abundant in net sets commencing at sundown (1900 hours), with abundance persisting for as little as 2 hours or at least 6 hours. Although the abundance of males generally remained constant during the nightly spawning periods, females were most abundant the first few hours after sundown. No fishing was done after 0100 hours.

Relative abundance, year-class composition, age, and length.--The number of wild lake trout caught per 30-m gill net (CPE) increased during 1977-1980 but hatchery trout CPE declined (Table 1). This decline occurred because decreasing abundance of the predominant 1969 and 1971 year classes was not compensated by recruitment from younger 1972-1974 year classes. Catch per effort of these young year classes on the spawning areas was much lower than CPE of the 1969 and 1971 year classes despite comparable stocking levels in and near Presque Isle Harbor. The 1972-1974 year classes may have experienced greater straying or prerecruitment mortality; or spawner populations in Presque Isle Harbor were influenced more by the number of lake trout planted in the remainder of Michigan waters, which have declined since 1970. For whatever reason, year class CPE was not well related to numbers of that year class planted in and near Presque Isle Harbor. The 1969 and 1971 year classes accounted for most of the catch in 1977 and 1978 and shared predominance only with the 1972 year class in 1979 and 1980. As a consequence, average age and total length of hatchery lake trout increased during 1977-1980 but the increase was only significant for males (Table 2). The youngest mature male and female hatchery trout was 4 and 6 years old, respectively, and the oldest was 17 years for both sexes.

Wild lake trout averaged much younger than hatchery fish and average age of both males and females ranged between 5.6 and 7.4 years old (Table 2). There was no significant trend in average age and length during 1977-1980. The youngest mature male and female wild lake trout captured was 4 and 5 years old, respectively, and the oldest was 9 years for both sexes. The 1970-1975 year classes represented most of the wild trout with no year class being predominant for more than 2 years.

Origin.--Most (75-96%) lake trout spawners captured on the intake and discharge were of hatchery origin. However, the percentage of wild lake trout increased from less than 10% during 1977-1979 to 25% in 1980 with a corresponding four-fold increase in CPE (Table 1). Wild fish were more abundant on the discharge reef and during the early part of the spawning period on both reefs, comprising as much as 60-70% of some catches on the discharge in October 1980.

Sex ratio.--Males outnumbered females approximately 4 to 1 in gill net catches from the intake and discharge reefs in 1977-1980. Males outnumbered females in most daily samples and in those made at different hours on the same day. On the intake, the male component of the catch was 88% in 1977, 84% in 1978, 74% in 1979, and 79% in 1980. On the discharge, the male component was 90% in 1977, 83% in 1978, 84% in 1979, and 82% in 1980. Males were most predominant in the younger age groups; whereas in older age groups the split was nearly equal or favored females in a few cases. The wild trout catch was 100% males in 1977 and averaged 91% males during 1978-1980.

Fecundity.--The mean number of eggs produced by 20 females, ranging in total length from 673 to 876 mm, was 6,154 ± 787 and ranged from 3,174 (692-mm fish) to 8,646 (762-mm fish). The linear regression Y = 6,794 + 17.64X (where Y = estimated number of eggs and X = total length in mm) describes a significant (r = 0.54) relationship between fecundity and total length. A significant relationship was not obtained between fecundity and weight as only 8 fish were weighed. Average egg diameter in each of 20 random samples ranged from 3.95 to 5.59 mm but there was no significant relationship between egg diameter and fish length or weight.

Spawner population estimates.--My estimates for number of female lake trout spawners on the intake, based on fecundity-egg deposition, ranged from 54 in 1978 to 221 in 1977 (Table 3). Differences between years were mainly due to differences in egg deposition but none were statistically significant because of high variance for egg deposition estimates.

Spawner population estimates using the Schnabel multiple census method were considerably higher with wide confidence limits because of a low recapture rate (Table 3). Estimates for males + females ranged between 5-7 thousand on the intake and between 4-9 thousand on the discharge. Fish marked on one area were rarely recaptured on the other in 1977. However, in 1978 most recaptures on the discharge (9 of 15) had been marked on the intake. To take advantage of this recapture of stray marked fish, I used all recaptures and calculated a combined intake-discharge estimate for 1978 of 8,663 with limits of 13,614 and 5,775. This estimate based on a combined recapture rate of 3.6% was nearly identical to that for the discharge alone and confidence limits were much narrower.

The Petersen single census estimate of age VII and older spawners of hatchery origin in 1979 was 1,634 males, 567 females, and a combined male-female estimate of 2,349 on the intake; and 2,137 males, 1,127 females and a combined male-female estimate of 3,272 on the discharge (Table 3). I derived an estimate of all lake trout on the intake and discharge in 1979 by adjusting the combined male-female estimates of age VII and older hatchery trout for the percentages of hatchery trout less than age VII and wild trout in the catch. These total estimates were 2,466 (1.4% hatchery less than VII, 3.4% wild) on the intake and 4,197 (12.6% hatchery less than VII, 10.8% wild) on the discharge.

Egg deposition and fry production.--Annual estimates of egg deposition on the intake reef ranged from just over 0.3 million ($122 \pm 52/m^2$) to nearly 1.5 million ($518 \pm 348/m^2$) during 1977-1979 (Table 4). The number of eggs per trap ranged from 0 (33-51% of the traps) to 938 (one trap) with per pail averages of 34, 8, and 15 eggs for 1977, 1978, and 1979, respectively. Egg deposition was most dense on the middle longitudinal section and offshore half of the reef each year. However, due to variation in eggs per trap, differences in egg density between years and between most sections of the reef were not statistically significant. The exceptions were that deposition on the middle longitudinal section was significantly more than the south section in 1978, and significantly more than either the north or south sections in 1979.

Most lake trout eggs (68-74%) in the egg-trap pails on the intake in November-December were alive and a majority of the non-viable eggs observed at this time were unfertilized. Lake trout eggs spent most of their incubation on the intake as eyed eyes. Eyed eggs were present as early as 09 November and most eggs (70-80%) were eyed by December. Lake trout collected on the intake in mid-April were about equally divided between newly hatched sac fry and eggs about to hatch. All eggs had hatched by the end of April. Number of residual dead eggs in the pails ranged from 0 to 126 per pail and averaged 6.4, 4.1, and 2.3 per pail for 1978, 1979, and 1980. Most of the dead eggs were not eyed but their advanced state of decomposition prohibited determining a more precise stage of development. Dead fry were seldom found in the pails. Either there was little fry mortality between hatch and swim-up or the dead fry decomposed rapidly. Water temperatures during the incubation period ranged from 5-11 C at egg deposition in October-November, 2-5 C in December when most were eyed and 1-4 C during the March-April hatching period.

Annual estimates of swim-up fry production on the intake ranged from 56,670 ($20 \pm 10/m^2$) to 130,341 ($46 \pm 21/m^2$) for spring 1978-1980 (Table 4). There was no significant differences in fry density between years but there was between some sections. Fry density on the south longitudinal section was significantly less than either the north or middle sections in 1979 and less than the middle section in 1980. Number of fry per trap ranged from 0 (most traps) to 35, with per trap averages of 3.0, 1.3, and 1.7 fry/trap for 1978, 1979, and 1980, respectively. Most fry (85%) were caught in the pail fry traps in May and 99% of the total catch was made by 15 June. Water temperatures were 4-8 C during May-June.

Survival from deposited egg to swim-up fry was 9-16% on the intake during 1977-1980 (Table 4). Survival was highest the year of lowest egg deposition and lowest the year of highest egg deposition. In 1977, I attached a fish-tight cover to every other egg-trap pail that was to be left in the substrate overwinter in an attempt to increase survival by excluding egg predators. I found that there was no difference in egg-to-fry survival between covered and uncovered pails.

Egg deposition on the 450 m^2 segment of the discharge was 64,350 extrapolated from an estimated egg density of $143 \pm 101/m^2$. This density was not significantly different from that which occurred on the intake (Table 4). However, 65% of the eggs examined in November were non-viable and badly decomposed. Condition and stage of development were

13.2% unfertilized, 0.6% dead-eyed, 47.8 dead-unknown, 20.4% live-eyed and 15.0% live-not eyed. Fry production was 3,600 extrapolated from an estimated density of 8±11/m^2. Egg-to-fry survival was 6%.

Characteristics of the man-made spawning area.--The 2,834 m^2 intake spawning reef was a rectangular mound, approximately 15 m x 180 m, oriented east-west perpendicular to shore (Fig. 1 and Table 5). The average gradient on the sides of the mound was 12% on the north and 8% on the south. Water depth over the area ranged from 2 m on the inshore (west) end to 8 m near the offshore (east) end. Thickness of the large-rock layer (crevice depth) ranged from 45 to 60 cm over 81% of the area and 3 to 23 cm over the remaining 19%. The diameter of rocks in this surface layer ranged from 1 cm (pebble) to 35 cm (boulder) and average diameter at 21 sampling sites ranged from 7 to 20 cm (cobble). Wagner (1982) presented a photograph and physical description of the intake substrate.

The 50-m segment near the offshore end of the discharge was oriented north-south, averaged 9-m wide and included 450 m^2 (Fig. 1 and Table 5). Water depth over this entire area was about 8 m. Thickness of the large-rock layer ranged 11 to 38 cm. The diameter of rocks ranged 1 cm (pebble) to 40 cm (boulder) and averaged 6 cm (pebble) to 16 cm (cobble) at six sampling sites. I found that dissolved oxygen on the intake and discharge reefs ranged between 10 and 14 ppm (average 13 ppm) during March-May and October-December (1977-1980) sampling periods. Alkalinity was 43-64 ppm (average 52 ppm) during these periods except for a 22 ppm reading in March on the inshore end of the intake. This reading was in the plume of the Dead River which was discharging copious amounts of dark tannin-colored water. Turbidity on the intake was occasionally quite high during April-June when ore and coal boat traffic was frequent and the boat slips were being dredged. Secchi disc readings varied from less than 1 m to nearly 5 m on the intake during this period. Readings were 3 to 5 m on the discharge which was farther removed from the river and the boat traffic. Very little sediment accumulated in egg-trap pails on the intake during August-November 1977 and divers reported a clean substrate just prior to spawning. Although most pails lifted the following June were clean, some had filled with enough sediment to smother eggs and fry and a sandbar encroached upon the inshore 30 m of the intake which was subsequently eliminated from the study. No significant sedimentation occurred in pails set on the reef in 1978 or 1979 and no further encroachment by the sandbar was noted. No significant sedimentation occurred in egg- and fry-trap pails set on the discharge during 1979-1980 and scuba divers reported a clean looking substrate.

Slimy and mottled sculpins (*Cottus cognatus* and *C. bairdi*), burbot (*Lota lota*), and round whitefish (*Prosopium cylindraceum*) were the most common fish found on the intake and discharge. The former two appeared to be year-round residents in and about the rock substrate. Other fishes that were less frequently captured or observed on the spawning area were brown trout (*Salmo trutta*), coho salmon (*Oncorhynchus kisutch*), splake (*Salvelinus fontinalis* x *S. namaycush*), white sucker (*Catostomus commersoni*), rock bass (*Ambloplites rupestris*), bullhead (*Ictalurus* sp.), yellow perch (*Perca flavescens*), and smallmouth bass (*Micropterus dolomieui*).

Round whitefish, burbot, and sculpins preyed on the lake trout eggs. Egg predation by round whitefish and burbot occurred mainly during the spawning period when eggs were abundant but sculpins found in egg-trap pails lifted 2-4 weeks after deposition were still preying on eggs. A total of 74 sculpins were found in egg-trap pails lifted after the spawning period in 1977-1979. No more than one sculpin was found per pail. Nineteen of 23 sculpins 50 mm and longer had eaten eggs but none of the 51 smaller sculpins were egg eaters. Two burbot were found in the pails but they contained no lake trout eggs.

Invertebrate benthos on the intake in July 1979 were mostly Copepoda (Harpacticoida and Cyclopoida), Cladocera, and Diptera (Chironomidae) in samples from both buckets and the reef proper. Other organisms present in lesser numbers were Amphipoda, Ostracoda, Hydracarina, Ephemoptera, Trichoptera, Isopoda, and Odonata. Macroinvertebrate benthos from egg-trap pails examined in 1977 and 1978 included all of the above plus Hirudinea, Pelecypoda, and four genera of Gastropoda At least two families of Trichoptera (Psychomyiidae and Hydropsychidae) and one genus of Isopoda (Asellus sp.) were typical of flowing water and may have originated from the nearby Dead River.

Discussion

The behavior and characteristics of lake trout spawners on man-made reefs in Presque Isle Harbor were similar to that of contemporary and former spawning stocks on natural reefs in Lake Superior. Peck (1979) sampled natural reefs in 1973-1976 and found that the mostly hatchery-origin stocks spawned roughly from 20 October until at least 5 November at temperatures of 8-12 C, 71-81% were males and the average age was 8-9 years old for both sexes. Eschmeyer (1955) reported that spawning by native stocks in 1944-1953 started in early October, peaked in late October, and ended in mid-November. These stocks were 60-69% males and 9-, 10-, and 11-year-old fish made up 90% of the population. On the man-made reefs in Presque Isle Harbor, spawning started anywhere from early to late October but the 24 October - 02 November period of spawning common to all 4 years would apparently be common for all contemporary or former inshore stocks of lean lake trout in Michigan waters of Lake Superior. Average age of spawners in Presque Isle Harbor in 1977 was similar to that on natural reefs sampled in

1973-1976 but by 1980 the average age had increased and was approaching that reported by Eschmeyer for former native stocks. Although similar in average age, the youngest male and female spawners in Presque Isle Harbor were 4 and 5 years old compared to 7 and 9 years old for former native populations. These younger ages were mostly males which would explain the male component in Presque Isle Harbor being higher than that for native populations.

Contemporary female hatchery lake trout may be more fecund than the former native fish. My estimate for hatchery-origin females averaged about 1,000 eggs more than comparable size native females sampled in 1950-1953 by Eschmeyer (1955).

Lake trout spawning parameters in smaller inland lakes were not as easily comparable to those in Presque Isle Harbor. Spawning period varies with latitude, occurring as early as August in higher latitudes and as late as January in the lowest part of the range (Martin and Olver 1980). Climatic factors such as heavy cloud cover prior to spawning, a decline in temperature to about 10 C, and strong winds are reported to trigger the onset of spawning. I did not evaluate cloud cover and discounted wind because reefs in the harbor were protected from the prevailing winds. Temperatures had generally fallen to near or below 10 C with the onset of spawning on the intake and discharge in Presque Isle Harbor. Thereafter slight increases in temperature, even to above 10 C, did not deter spawning.

There is no prior documentation of lake trout daily spawning activity in the Great Lakes. However, the time of day that most lake trout spawned on Presque Isle Harbor corresponded to that documented in most inland lakes. In previous studies, most lake trout spawning took place during hours of darkness beginning about dusk and continuing to about midnight (Royce 1943, Martin 1957, DeRoche 1969, Martin and Olver 1980). Royce (1943) reported that most spawning activity occurred during the early portion of this period right after dusk. On the other hand a tagging study by MacLean et al. (1981) indicated that adults visited spawning reefs during daylight hours. I found lake trout abundant on the man-made reefs in the harbor from dusk through midnight with females most abundant in the early part of this period. I found very few lake trout on these reefs during daylight hours.

Individual lake trout apparently visit more than one spawning reef, spend little time on any one of them, deposit sex products over a period of a week or more, and therefore may spawn on more than one reef during a single season. MacLean et al. (1981) found that male and female lake trout in a Canadian inland lake moved constantly during the spawning season, visiting more than one reef on the same night and as many as 10 reefs in a 2-week period. DeRoche (1969) reported that lake trout captured in a Maine inland lake on one spawning site were subsequently recaptured on another spawning site that same season and that while some returned to the same spawning beds each year, others strayed to beds many miles away. In the Great Lakes, some lake trout tagged and released in Presque Isle Harbor, Lake Superior, and Charlevoix, Lake Michigan, were recaptured several days later on natural reefs 10-35 km away (Peck 1979). My observations in Presque Isle Harbor generally support these other studies. Lake trout rarely made more than a 1-night visit to the intake and discharge spawning reef as evidenced by the low recapture rate of marked fish in my rather intense sampling effort. The first spent female lake trout were always encountered 9-12 days after capture of the first ripe female and significantly more spent females were captured during the second half of the spawning period on both intake (X^2 = 16.17, df = 1) and discharge (X^2 = 5.95, df = 1) indicating that eggs are not all released at once. Also I found no relationship between number of eggs deposited and spawner CPE on the intake. I would expect to see a direct relationship between these parameters if females on the intake had deposited their entire egg complement there. This evidence suggests that the individual lake trout sampled on intake and discharge deposited sex products over a period of days and on more than one reef.

The apparent and suspected spawning behavior of lake trout in Presque Isle Harbor very likely adversely affected my spawner population estimates. Estimates from fecundity and multiple census methods would be most affected. Egg deposition would not be suitable to estimate number of spawners nor could number of spawners be used to estimate egg deposition if individual lake trout spread their egg complement over more than one reef. Spawner estimates based on fecundity and egg deposition were much lower than by either census method and were lower than the actual number of spawners captured in 1978 and 1979. The Schnabel multiple census was also unsuitable for estimating spawning populations of lake trout in Presque Isle Harbor. Exceptionally low recapture rates (1-2%), even with sequential net sets the same night, indicated continuous immigration and emigration which violated the methods no recruitment requirement (Ricker 1975). The Schnabel multiple census estimates were not well related to egg deposition and not at all to spawner CPE. Multiple censuses may not be suitable for estimating spawner populations on natural reefs considering continuous movement of spawners reported by MacLean et al. (1981).

The Petersen single census appears to be the best method for estimating spawning populations of lake trout. Recapture rates 1 year after marking were two to three times higher than for the multiple censuses conducted over a 2- to 3-week period. This would indicate that while trout may visit a number of reefs during a spawning period, they visit the same reefs each year. Restricting the estimate to recognizable recruited year classes of hatchery fish (fin clip) satisfied the no recruitment requirement of this method. Although the Petersen single census appeared to be the best method; on the intake, the potential egg deposition (2,352,684) from the lower limit of the female estimate (354) was 2.5 times larger than the upper limit of the egg deposition estimate. This may be further evidence that lake trout deposit their sex products on more than one reef. Swanson and Swedberg (1980) used the Petersen method to estimate native male spawners on Gull Island Reef in western Lake Superior during 1964-1979. Swanson and Swedberg relied on wild males because they were most abundant, were considered least likely to stray, and there was some evidence that females did not spawn every year. In contrast I used the more abundant recruited year classes of hatchery trout of both sexes and obtained a higher rate of recapture (9.5%) on the intake reef than Swanson and Swedberg did for wild males on Gull Island Reef (8.6%). I also found that return of hatchery females (8%) was not greatly different from hatchery males (10%) and that the return of wild lake trout (2%) was much lower than that of hatchery trout. The higher rate of return for hatchery trout in Presque Isle Harbor than for wild trout on Gull Island Reef (9.5% vs 8.6%) was likely due in part to the much smaller area of the intake and discharge (less than 1 km^2) relative to Gull Island Reef (more than 25 km^2) and because Presque Isle Harbor is a planting site and some homing was likely. Most wild trout on the intake and discharge were strays which may account for the low rate of recapture. The man-made reefs were too recent to be natal reefs for wild trout except for the 1975 year class in 1980. The similar recapture rates for hatchery males and females on intake and discharge reefs indicate that both produced sex products with equal frequency, at least in 1979 and 1980.

Lake trout egg deposition on the intake and discharge was somewhat less than that reported on natural reefs in other studies. It was within the range reported in Otsego Lake, New York (215-238/m^2) by Royce (1943). However, these data were from shallow water where few trout were seen spawning. Martin (1957) reported an average of 538/m^2 from egg containers buried in Ontario lakes. Only deposition on the intake in 1977 was comparable to this latter figure.

Egg survival on the intake within 6-8 weeks after deposition was comparable to that reported in other waters but fertilization efficiency and survival from fertilized egg to hatching appeared to be less. Royce (1943) found 79% live eggs 25 days after spawning with 5.8% unfertilized. Martin (1957) reported 92% viable eggs 2 weeks after spawning and 73% alive 4 weeks later. I found 68-74% egg survival on the intake in 1977-1979, 2-6 weeks after spawning, but a higher percentage of the non-viable eggs were unfertilized (10-25%). However, I may have underestimated fertilization because decomposed eggs did not clear properly and fertilization may have been obscured. Martin and Olver (1980) reported that survival of fertilized eggs to hatch may be at least 50% based on unpublished survival in an incubation tray in an Ontario lake. Although I did not determine survival to hatch, I concluded that it was not much different than survival to swim-up because dead fry were rarely found in the fry-trap pails. The estimated fertilized egg to swim-up fry survival on the intake was only 12-19%, which was only about one-third that reported by Martin and Olver. This lower survival rate may reflect lower reproductive efficiency, which has been inferred for spawners of hatchery origin (Brown et al. 1981), or it may be that eggs in fry-trap pails experienced higher mortality than those outside the pails. Two factors which reduced egg to fry survival in my study but apparently not in the Ontario incubation tray, were predation and fungal infection. Although egg predation is not considered a serious problem on suitable lake trout spawning substrate (Martin and Olver 1980), some did occur on the intake spawning area (this study and Stauffer and Wagner 1979). Sculpins 50 mm and longer found in egg-trap pails were averaging 1-2 eggs per stomach 2-5 weeks after spawning period. It is probable that some predation continued until fry-trap covers were installed about 4 months later. Martin (1957) considered fungal infection (Saprolegnia) to be a prime mortality factor for lake trout eggs. Fungal infection rates of 35-80% have been reported (Martin and Olver 1980). I observed fungal infection on some eggs recovered from egg-trap pails shortly after deposition and practically all eggs in pails checked 6-7 months later were infected. Initial fungal infection was most noticeable in pails containing the most eggs. It is possible that the pails prohibited adequate dispersal of larger numbers of eggs and fungal infection mortality and predation were higher in the pails than on the reef proper.

Physical, chemical, and invertebrate benthos parameters on the intake and discharge spawning reefs indicated a healthy environment for incubation of lake trout eggs. Rock diameter and interstice depth were comparable to other substrate (natural and man-made) in the Great Lakes where lake trout eggs have successfully incubated (Wagner 1982). Currents kept the area relatively silt-free despite commercial boat traffic and discharge from the Dead River. Dissolved oxygen reported in this study and monthly values reported by Hatch (1976) were all near or above saturation. The intake spawning reef was within the thermal plume of a shoreline discharge of power plant cooling water, but water temperatures during egg deposition to swim-up fry stage in this study and in 1976 (Peck 1982) were within limits for early life history stages of lake trout. Perhaps the biggest threat to lake trout reproduction, especially on the intake spawning reef is entrainment of lake trout alevins in the power plant intake. Hatch (1976) estimated entrainment of the 1976 year class at nearly 110,000. Although the total production of alevins in 1976 was not determined, the number entrained is within the range of estimated total swim-up fry production on the intake in 1978-1980.

Man's industrial activities generally do not contribute positively to the welfare of fish and wildlife. However, in Presque Isle Harbor, installation of water-pipe overburden has provided suitable lake trout spawning habitat on an otherwise sand bottom immediately adjacent to a planting site. This has resulted in increased lake trout reproduction in Lake Superior despite a possible significant loss of alevins through entrainment. Future installation of man-made structures in the Great Lakes, involving rock rubble, might be guided by rock diameter and other parameters reported in this study and Wagner (1982), thereby providing suitable lake trout spawning habitat in addition to achieving industrial goals. Man-made reefs installed strictly for lake trout reproduction may be a valuable management tool near planting sites which lack suitable natural substrate but possess suitable hydrology, chemistry, and biology.

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Table 1. Number of mature lake trout captured per 30-m gill net set (CPE) for hatchery and wild trout year classes on intake and discharge spawning reefs in Presque Isle Harbor, Lake Superior, 1977-1980; and number planted as yearlings in the immediate vicinity (within 10 k) of Presque Isle Harbor.

Year class	Number planted (x 10^3)	Year 1977	1978	1979	1980	Total
1963	156	0.41	0.43	0.07	0.06	0.97
1964	79	0.32	0.17	0.06	0.08	0.63
1965	126	0.23	0.26	0.11	0.12	0.76
1966	0	0.73	0.51	0.28	0.28	1.80
1967	0	1.32	0.83	0.40	0.45	3.00
1968	203	0.95	0.79	0.49	0.44	2.67
1969	150	2.80	2.57	0.88	0.95	7.20
1970	0	0.29	0.06	0.07	0.08	0.05
1971	109	2.46	4.47	1.83	1.89	10.65
1972	100	0.49	1.79	1.04	1.26	4.58
1973	168	0.07	0.49	0.33	0.31	1.20
1974	150	---	0.02	0.19	0.16	0.37
1975	156	---	---	0.01	0.19	0.20
1976	174	---	---	---	0.01	0.01
Hatchery trout CPE	---	10.07	12.39	5.76	6.28	---
Wild trout CPE	---	0.41	0.78	0.54	2.15	---
Grand Total CPE	---	10.47	13.19	6.26	8.38	---

Table 2. Average age and total length (mm), with 95% confidence limits, of mature hatchery and wild lake trout captured on the intake and discharge spawning reefs in Presque Isle Harbor, Lake Superior, October-November 1977-1980.

Origin and parameters	Year 1977	1978	1979	1980
		Age		
Hatchery				
Male				
Mean	8.2±0.2	8.2±0.2	8.8±0.2	9.6±0.2
Range	4-14	5-15	4-16	4-17
Number	354	521	382	432
Female				
Mean	9.8±0.7	9.3±0.5	10.3±0.5	10.7±0.4
Range	6-14	6-15	7-15	6-17
Number	44	99	89	133
Wild				
Male				
Mean	6.7±0.7	6.4±0.5	5.7±0.3	5.6±0.1
Range	5-9	5-9	5-9	4-9
Number	12	28	36	175
Female				
Mean	---	7.4±0.4	6.8±1.1	7.1±0.9
Range	---	7-8	6-7	5-9
Number	0	9	5	11
		Total length		
Hatchery				
Male				
Mean	699±8	710±6	715±7	733±16
Range	555-950	540-940	565-945	545-925
Number	354	527	388	434
Female				
Mean	744±20	754±12	763±12	766±11
Range	643-885	650-920	660-910	635-975
Number	44	99	90	134
Wild				
Male				
Mean	674±30	690±21	648±17	640±8
Range	587-772	610-820	560-775	540-880
Number	18	28	40	176
Female				
Mean	---	717±25	750±87	712±39
Range	---	650-750	715-807	650-805
Number	0	9	5	11

Table 3. Population estimates, with 95% confidence limits (CL), of sexually mature lake trout on intake and discharge spawning reefs in Presque Isle Harbor, Lake Superior, October-November 1977-1979.

	Fecundity, egg deposition method, intake				
Year	Average fecundity ±95% CL	Estimated egg deposition ±95% CL	Estimated number of females[1] ±95% CL	Sex ratio (% males)	Total estimate[2] (male + female)
1977	6,646 ±782	1,467,753 ±986,058	221 ±151	88 --	1,842 ±1,258
1978	6,346 ±698	345,687 ±147,342	54 ±24	84 --	338 ±150
1979	6,646 ±782	651,705 ±300,351	98 ±47	74 --	377 ±181

	Multiple census method, intake and discharge				
	Estimated number	95% CL			
Year	(male + female)	upper	lower	Number marked	Recapture rate (%)
Intake					
1977	6,914	17,285	2,529	207	1.0
1978	5,070	11,091	2,517	262	2.3
Discharge					
1977	4,405	11,013	1,798	188	1.6
1978	8,652	18,982	4,296	313	1.9
Intake + Discharge					
1978	8,663	13,614	5,775	575	3.6

Table 3. Continued:

	Petersen single census method, intake and discharge 1979				
	Estimated number	95% CL upper	95% CL lower	Number tagged	Recapture rate (%)
Intake					
Male	1,634	4,810	1,110	101	9.9
Female	597	6,000	354	35	8.6
Male & female	2,349	5,480	1,651	136	9.6
Discharge					
Male	2,137	4,475	1,517	179	8.4
Female	1,127	4,333	703	52	3.8
Male & female	3,272	6,417	2,357	231	7.4

[1] Estimate = egg deposition divided by fecundity with 95% CL based on pooled variance.

[2] Extrapolated from number of females based on sex ratio.

Table 4. Estimated number of lake trout eggs deposited, fry produced, and deposited egg-to-fry survival with 95% confidence limits (CL), on longitudinal sections (north, middle, south) and inshore and offshore halves of the intake reef, Presque Isle Harbor, Lake Superior, 1977-1980.

Year and section	Area (m^2)	Number of eggs: Per m^2 ±95% CL	Number of eggs: Total estimate	Number of fry: Per m^2 ±95% CL	Number of fry: Total estimate	Egg-to-fry survival (%)
1977-1978						
North	944.5	315±271	297,518	24±19	22,668	8
Middle	944.5	905±942	854,772	86±54	81,227	10
South	944.5	319±364	301,296	27±23	25,502	8
Inshore	1,328.5	313±199	415,820	41±26	54,468	13
Offshore	1,505.0	733±675	1,103,165	51±34	76,662	7
Total	2,833.5	518±348	1,467,753	46±21	130,341	9
1978-1979						
North	944.5	136±101	128,452	28±19	26,446	21
Middle	944.5	200±111	188,900	30±23	28,335	15
South	944.5	30±38	28,336	2±4	1,889	7
Inshore	1,328.5	55±28	73,068	23±15	30,556	42
Offshore	1,505.0	183±95	275,415	18±14	27,090	10
Total	2,833.5	122±52	345,687	20±10	56,670	16
1979-1980						
North	944.5	95±61	89,728	21±16	19,834	22
Middle	944.5	508±292	479,806	54±35	51,003	11
South	944.5	87±59	82,172	6±4	5,667	7
Inshore	1,328.5	103±67	136,836	12±7	15,942	14
Offshore	1,505.0	349±192	525,245	39±23	58,695	13
Total	2,833.5	230±106	651,705	27±13	76,504	12

Table 5. Width, water depth, and thickness of the large-rock layer at sampling sites on longitudinal sections of intake and discharge spawning reefs, Presque Isle Harbor, Lake Superior, 1977-1980.

	Intake						
Reef interval (m)	Bottom width (m)	Water depth (m)			Thickness of large-rock layer (cm)		
		North	Middle	South	North	Middle	South
0	12	2.4	1.8	2.1	45	45	45
30	13	2.7	2.4	3.0	45	45	50
60	16	4.0	3.4	4.0	45	45	50
90	15	6.1	4.9	5.2	23	15	50
120	15	7.6	5.8	6.4	45	45	45
150	16	7.9	6.1	7.3	50	45	3
180	21	5.2	4.9	5.5	60	20	60
Average	15	5.1	4.2	4.8	45	37	43

	Discharge (50-m segment)						
Reef interval (m)	Bottom width (m)	Water depth (m)			Thickness of large-rock layer (cm)		
		East	Middle	West	East	Middle	West
0	6	8.2	7.9	8.2	11	25	23
50	12	8.2	7.6	8.5	38	34	33
Average	9	8.2	7.8	8.4	24	30	28

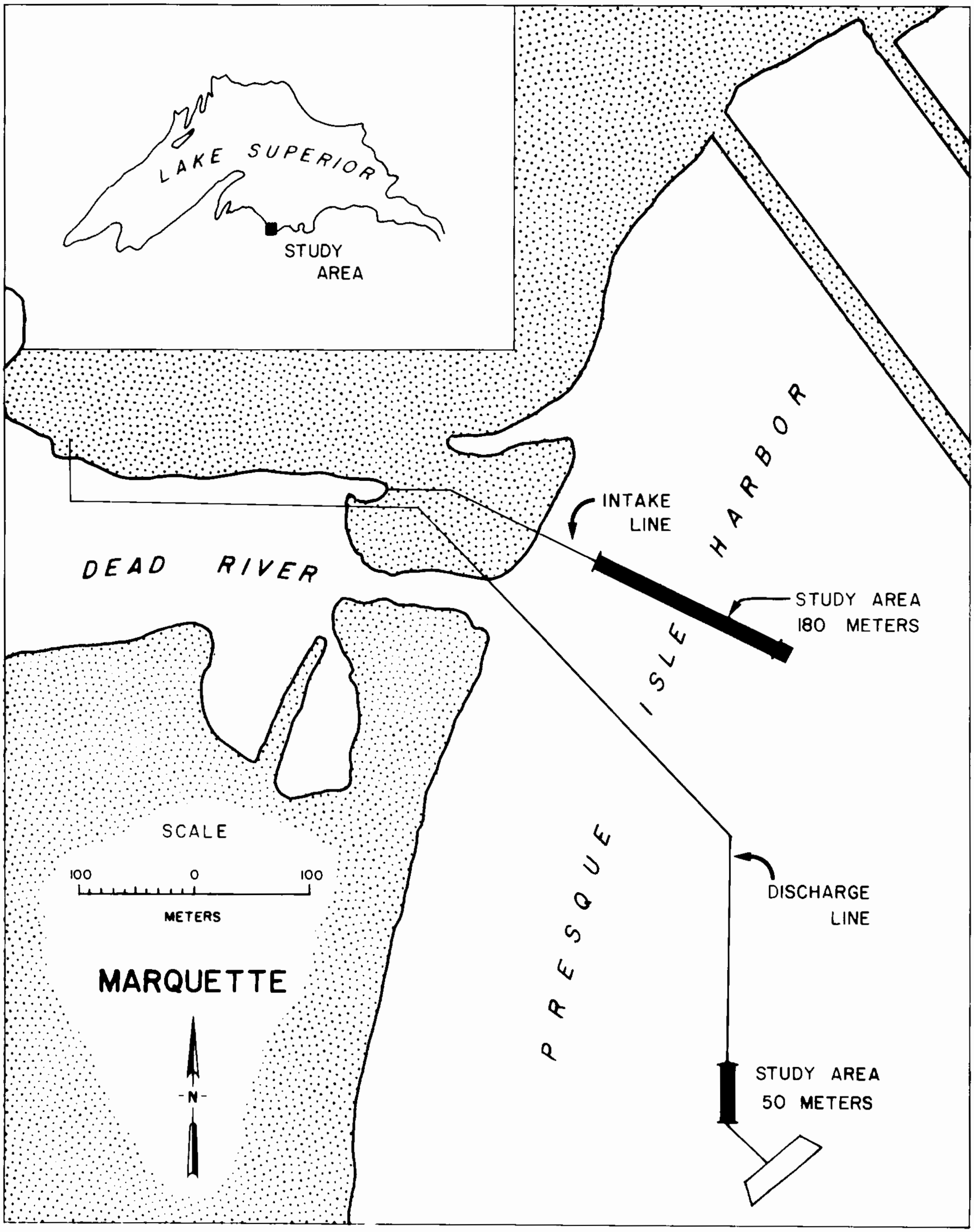

Figure 1. Presque Isle Power Station intake and discharge spawning areas in Presque Isle Harbor, Lake Superior, with study areas indicated.

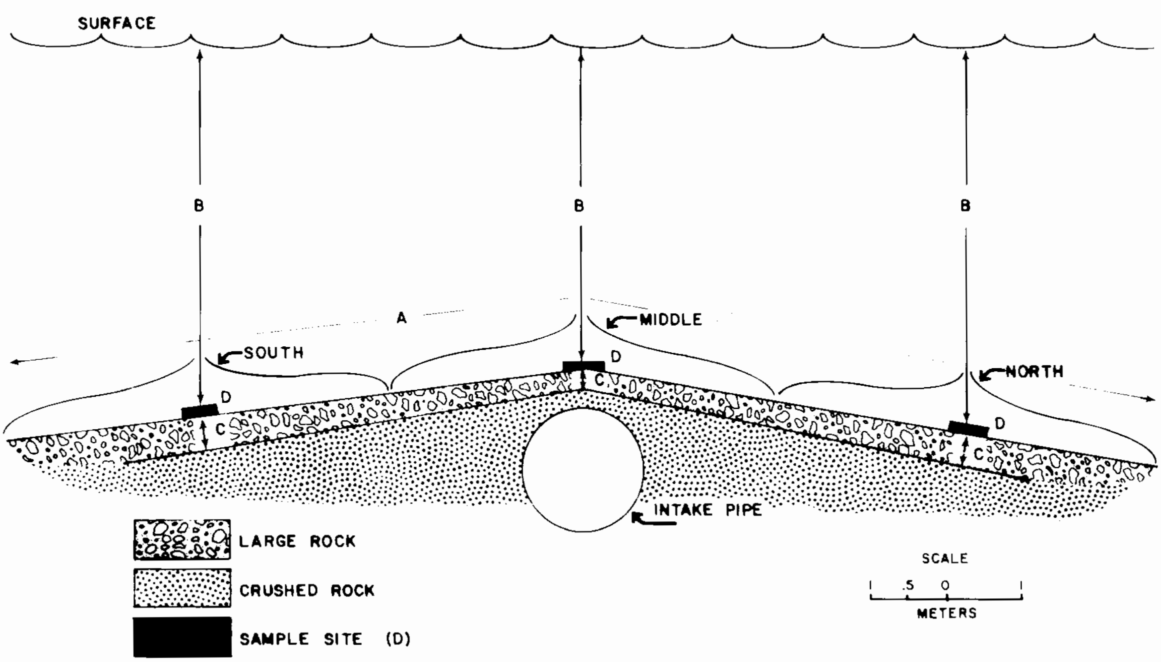

Figure 2. Cross section of intake spawning area in Presque Isle Harbor, Lake Superior, depicting physical parameters [width (A), water depth (B), thickness of large-rock layer (C)] measured at sampling sites (D). Scale represents the parameter averages presented in Table 5.

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