Highly productive native stocks of lake trout Salvelinus namaycush were severely depleted in Lake Superior and became extinct in the rest of the Great Lakes during the 1940s and 1950s due to predation by sea lamprey Petromyzon marinus and overfishing (Smith 1968). Although the sea lamprey is now largely under control, the goal of rebuilding self-sustaining populations of lake trout through stocking programs has not yet been achieved. Several hypotheses have been proposed to explain the poor natural reproduction by the stocked lake trout in lakes Michigan, Huron, and Ontario, where many millions have been planted (see reviews by Rybicki and Keller 1978; Martin and Olver 1980; Brown et al. 1981; Willford et al. 1981). Although many hatchery fish survive to maturity and appear to spawn at both traditional breeding grounds and artificial structures (Peck 1979, 1982), it is not clear how successful they are in locating areas with optimum conditions for survival of eggs and young (Brown et al. 1981; Horrall 1981; Foster 1984).

Lake trout do not excavate a redd and typically spawn in the fall over cobble, rubble, boulders, or “honeycomb” rock with abundant interstitial spaces (Eschmeyer 1964; Martin and Olver 1980). Males usually begin aggregating at spawning areas a week or more before females arrive (Miller and Kennedy 1948; Cuerrier and Schultz 1957; Martin 1957; McEachron 1958; Eschmeyer 1964; DeRoche 1969). During the spawning period, the sex ratio on the breeding grounds is usually two to three males per female. In some populations, at least, males “clean” specific areas of the spawning substrate (Merriman 1935; Royce 1951; DeRoche and Bond 1957; Martin 1957; Foster 1984), defend breeding areas from egg predators (Merriman 1935), and make “threatening motions” at other males even though no vigorous fighting is observed (Royce 1951). Overall, the reproductive behavior of lake trout appears to fit the definition and criteria for lekking, characterized by temporary aggregation of sexually active males on a traditional breeding ground (lek) where courtship and spawning subsequently occur (Loiselle and Barlow 1979).

No field observations of the lake trout’s reproductive behavior in any of the Great Lakes have been published. In other populations, spawning usually begins near dusk and continues until about 23:00 hours (Royce 1951; Martin 1957; Martin and Olver 1980). Such nocturnal spawning habits would favor the evolutionary development of nonvisual (acoustical, near-field displacement, electrical, tactile, or chemosensory) cues for location of spawning sites and partners and for synchronization of gamete release.
Martin (1955) suggested that spawning grounds used by native lake trout had "some characteristic odor" that attracted spawners. Field observations and results of Y-maze experiments and electrophysiological studies suggest the presence of species-specific (even race-specific) chemotactants in Arctic char *Salvelinus alpinus*, a close relative of the lake trout (Nordeng 1971; Hoglund and Astrand 1973; Døving et al. 1973; Døving et al. 1974). Water extracts of mucus elicited greater electrical responses in the Arctic char's olfactory bulb and telencephalon than either urine or milt which, in turn, elicited stronger responses than extracts of blood, muscle, decayed muscle, or fish food pellets. The active substance was stable, producing undiminished responses even after extracts had been stored for 1 month at room temperature or had been boiled for 15 min and cooled. It was discovered subsequently that the mucus extracts tested by Døving and his colleagues also contained intestinal fluid, and that the effective substance was present in one small fraction (0.035% of the dry weight of the water-soluble components) of intestinal contents of smolts (Døving et al. 1980; Selset 1980; Selset and Døving 1980; Stabell and Selset 1980). This fraction contained polar steroid molecules, primarily cholic acid. Later experiments showed that certain bile acids were potent olfactory stimuli for Arctic char; adults can detect them at a concentration of about $2 \times 10^{-10}$ M (Døving et al. 1980). However, gustatory receptors apparently also are involved in detecting bile acids. By recording the electrical activity of nerves innervating the upper lip and palate of rainbow trout *Salmo gairdneri*, Hara et al. (1984) found a threshold concentration ranging between $10^{-12}$ and $10^{-11}$ M for one of these steroids, indicating that such materials may be tasted as well as smelled at very low concentrations. The chemical stability of such compounds in the aquatic environment is not known, but Mackenzie et al. (1982) indicated that some steroids persist for years in marine sediments.

This paper describes experimental tests of the hypothesis that prior "conditioning" of spawning sites by chemical residues from previously hatched young of the year increases the subsequent occurrence of reproductive behavior of adults at these sites. The logical extension of results, should the hypothesis be supported, is that such chemical residues at traditional spawning grounds decomposed or dissipated when native lake trout stocks became extinct in most of the Great Lakes, thereby breaking an important link in the natural chain of reproductive events that fishery managers are trying to restore.

**Single-Pool Egg Deposition Experiment**

**Methods**

In 1979 a conventional above-ground, vinyl-lined, circular swimming pool, 5.3 m in diameter, was used for behavioral observations. A 2.5-cm thick layer of Styrofoam placed beneath the plastic pool liner reduced heat gain and noise transmission from the concrete floor. A perforated polyvinyl chloride water intake pipe ran along the middle of the pool bottom (Fig. 1). A pump withdrew about 100 L/min from the pool through the intake pipe, of which 55 were pumped to the overhead cooling and aeration reservoir and 45 were bypassed back to the pool. The ad-
dition of 11–26 L/min of processed laboratory well water resulted in continuous flushing through a surface overflow drain that maintained water depth at 1 m and water volume at about 22,100 L. Simulating autumnal cooling in the lake environment, water temperature decreased gradually from 12.6 to 7.8°C. The direction of the inflows produced a gentle counterclockwise flow. Current velocities along the wall of the pool, about 10 cm above the bottom and 30 cm from the inner surface of the wall, ranged from 3.1 to 6.1 cm/s. Dye tests with methylene blue confirmed that the only substantial water movement was around the periphery of the pool and that the water just above the center of each reef and in the center of the pool was still. Chemical and physical characteristics of the processed water were given by Berlin et al. (1981).

Four experimental spawning reefs were constructed by resting 90 x 120-cm rectangular sections of plastic “egg-crate” grating (commonly used as diffusers for fluorescent ceiling lights) on unglazed brick supports. Two of the four reefs, designated S-1 and S-4, were covered with large stones (10–25-cm diameter) and the other two, designated B-2 and B-3, with 24 unglazed bricks (20.5 x 9.5 x 6 cm). Parallel sides of adjacent reefs were 80 cm apart. Spaces between stones or bricks on top of each reef were 2.5–8 cm wide, to allow eggs to fall through the grating (Benoit 1974). Two wood-framed, screen-bottom drawers, 77 x 52 x 4.5 cm, with attached rollers made of polyvinyl chloride pipe, were placed beneath each reef to collect eggs. The plastic screen bottom of the drawers was 5 cm below the underside of the grating and 1.5 cm above the vinyl bottom of the pool. Vertical folds stapled in the screen kept eggs from rolling about. The drawers were buoyant and floated slowly to the surface when pulled from beneath a reef with a hooked pole.

Eggs were removed from drawers daily. Volitionally spawned eggs were distinguished from eggs spontaneously expelled in midwater by relative transparency, shape, number, and clumped distribution pattern in the paired drawers beneath each reef. Because Benoit (1974) found that spawn-catching substrates such as those that I used did not provide sufficient contact time between eggs and milt for optimum fertilization rates, I did not use fertilization (development of embryos subsequent to collection) as a distinguishing criterion for volitional spawning. Viable-looking (translucent) eggs were counted individuively or their numbers were estimated volumetrically, and subsamples were placed in a Heath incubator to be checked for subsequent development.

Daytime light intensity, measured with an underwater light meter, was 97–161 lux at the surface, 65–129 lux at the bottom, and 16 lux beneath a floating rectangular section of Styrofoam (60 x 180 x 2 cm) anchored against the north side of the pool to provide shade for the fish. Fluorescent ceiling lights were controlled by a timer to simulate the local outdoor photoperiod. Windows near the laboratory ceiling allowed some natural light to enter the room.

A Javelin Night Viewing Device, Model 221, facilitated night observations when the only illumination was provided by two rheostat-controlled, 100-W, red, outdoor-type floodlights mounted 3 m above the center of the pool. The intensity of the red light was set so low that fish could not be seen in the pools without the aid of the device.

All of the adult lake trout used in these studies were of the Marquette Hatchery (Lake Superior “lean”) strain. This strain is the principal one stocked in the Great Lakes at the present time.

On October 9, 1979, seven male and five female lake trout were placed in the pool. They were 10–11 years old and 596–706 mm long (fork length). About half the adults of each sex had been reared at the Great Lakes Fishery Laboratory and the other half at the Marquette State Fish Hatchery. Four males and eight females were added on November 9, and six males and one female on November 14 (Table 1). All of the fish added in November had been reared at the Great Lakes Fishery Laboratory; the other half at the Marquette State Fish Hatchery. Four males and eight females were added on November 9, and six males and one female on November 14 (Table 1). All of the fish added in November had been reared at the laboratory; they were 593–685 mm long and 6 years old.

Potential sources of conspecific chemostimuli consisted of screen envelopes containing polyester fiber masses with four kinds of materials collected between late January and late April 1979 from incubators or troughs in which Marquette-strain lake trout had been hatched or reared: (1) egg membranes; (2) sediment (mostly diatomsaceous earth, possibly mixed with sloughed mucus) from a trough containing yolk-sac larvae; (3) sediment (including feces) from a trough in which 75% of the young had attained the swim-up stage; and (4) feces and possibly uneaten food caught over a 3-week period in the matrix of a polyester fiber mass that had been placed in the drain (standpipe) compartment of a trough in which
Table 1.—Spawning by lake trout on artificial reefs (S = stone; B = brick) in a 22,000-L pool in relation to placement of source envelopes for chemosensory cues emanating from sediment with yolk-sac larvae (Y), feces (F), or egg membranes (E) from young of the year, 1979.

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a Envelopes containing two possible cues are tabulated in two columns. The cumulative total of envelopes was four: egg membranes only; membranes + sediment; membranes + feces; feces only.
b Envelopes were transferred between reefs B-3 and B-2 (November 12) and back (November 26). Both envelopes (the second added November 13) contained feces.
c No envelopes were added to reef S-4.
d Seven male and five female fish present.
e Four males and eight females added; milt and ovarian fluid added.
f Six males and one female added.
g Screen-bottomed egg-collecting drawers were lined with plastic sheeting to improve egg-milt contact time in drawers. Ten fertilized eggs were recovered from reef S-1 between November 30 and December 15.

Young had been feeding for 2 months. These materials had been frozen in plastic and glass containers after their collection. The wet weight of the materials in each type (sediment, egg membranes, or feces) of chemosensory stimulus source (polyester fiber excepted) was estimated to be 5 g or less. After materials were thawed, they were spread (types 1–3) onto clean polyester fiber, which was stapled into an envelope of plastic-coated fiberglass window screening. Comparable amounts of type-4 fiber masses also were enclosed in plastic screen envelopes. Edges of envelopes were wedged beneath bricks or rocks atop appropriate reefs. One envelope (egg membranes and feces) was placed on stone reef S-1 on October 23, augmented with a second (egg membranes) on November 1, with a third (egg membranes and sediment) on November 2, and with a fourth (feces and fiber) on November 13. No envelopes were placed on stone reef S-4. One envelope (feces) was placed on brick reef B-3 on November 1, and shifted on November 12 to brick reef B-2 where it was augmented by a second envelope on November 13. Both envelopes were shifted back to brick reef B-3 on November 26.

On November 9, at 2220 hours, 200 mL of an aqueous mixture of milt and ovarian fluid (stripped earlier that day from laboratory-reared adults) were introduced into the peripheral cur-
rent of the pool. This material seemed to repel the fish; those downstream from the introduction point swam rapidly out of the area, and the general activity level of all fish declined markedly. These effects were not quantified and were transitory (behavior returned to normal within 20 min). No other additions of milt or ovarian fluid, either singly or combined, were tested, and these observations are presented only for the sake of completeness.

Results

Lake trout deposited 6,858 eggs at the four reefs in the pool during the period November 9–December 25, 1979 (Table 1): 71% at stone reef S-1 (egg membranes and feces) and 27% at brick reef B-3 (feces). After the envelope was removed from reef B-3 on November 12, this reef soon lost its attractiveness as a spawning site. However, the fish did not shift egg deposition to the other brick reef (B-2) where the envelope had been newly placed, nor did they resume spawning on B-3 when envelopes (now two of them) were placed there. Only once during the study was there evidence of volitional spawning (75 eggs) at stone reef S-4, upon which no envelope had ever been placed. Altogether, 92% of the 6,858 eggs recovered were found beneath reefs where envelopes containing feces were present (Table 1); only 13 eggs among the subsampled lots were found to be fertilized, but these eggs represent the first record of volitionally spawned and fertilized eggs for lake trout in a laboratory environment.

There were several evenings when females approached and appeared to investigate stone reef S-1 (sediment from yolk sac larvae, egg membranes, and feces), their behavior characterized by very slow swimming near the center of the reef with their bodies tilted at about a 45° angle, head downward.

Male lake trout also were seen contacting the stones on this reef with the undersides of their bodies. Although such “cleaning” by males was noted only five times, it occurred only at the treated reefs. Cleaning was first seen and photographed on brick reef B-3 on the evening of November 1, 1979, about 5 h after an envelope containing feces of young of the year had been placed there, and the behavior was noted at stone reef S-1 four times during the period November 5–14. The time lag between removal of the single envelope (feces) from reef B-3 on November 12 and the beginning of reduced use of this reef as a spawning site (Table 1) about 2 d later could be either a residual treatment effect or the effect of the temporary presence of a chemical mark applied earlier to the brick substrate by cleaning males.

Spawning was not directly observed. It presumably took place in total darkness; no eggs were found after periods of dim light, but newly spawned eggs were found twice immediately after 1–2-h periods of darkness. Also, judged by the temporal pattern and total number of eggs deposited (Table 1), probably only 2 or 3 of the 14 females actually spawned.

Double-Pool Videotaped Behavior Experiment

Methods

In 1980, two smaller (3.7-m diameter) vinyl-lined circular pools were used, each with its own water-chilling reservoir and a processed well water inflow of 20–24 L/min. Recirculation flows to each pool consisted of a bypass rate of 38–47 L/min and a reservoir flow-through rate of 19–20 L/min. Water depth was 1 m and volume was about 10,500 L in each pool. Inflows were directed across the center of each pool, perpendicular to the axis along which the reefs were aligned, so that the current regime was symmetrical and no circular current was produced. There was no exchange of water between pools. Two brick reefs, similar to those in 1979 except that they were 91 x 72 cm, were positioned in each pool about 65 cm apart, and a floating Styrofoam cover was anchored equidistant from the two reefs at the side opposite from the inflows.

Because of unexpected delays in obtaining the smaller pools, I attempted to delay ripening of the experimental fish by supplementing the natural declining (autumnal) photoperiod with artificial light. Later, the light port, a square opening in the cover over each holding tank, was covered with boards for several weeks before the fish were put into pools. These efforts to manipulate ripening failed. Females released eggs in both the holding tanks and test pools, but males developed only weak nuptial coloration and rarely showed courtship quivering. No volitional spawnings occurred.

Thirty-three laboratory- and hatchery-reared adult lake trout (approximate sex ratio, two males per female; all of the Marquette strain and 7 to
12 years old) were placed in each pool on December 12, 1980, and three dummy envelopes (containing polyester fiber only) and one test envelope (containing fiber and feces of young of the year that had been feeding for 60 d) were wedged beneath the bricks on the four reefs in the two pools the next day. In pool 1 were control reef A (dummy envelope) and experimental reef B (test envelope); in pool 2 were two control reefs, C and D (both with dummy envelopes).

Visual observations of the nocturnal behavior of lake trout at the four reefs were made with the night-viewing device and dim red illumination, totaling 2 h over December 13, 14, and 16, 1980. Subsequently, the behavior was videotaped (again with night-viewing device and dim red light) on various nights between December 19, 1980, and January 6, 1981. Water temperatures ranged from 9.7 to 10.2°C on visual observation dates and from 8.4 to 9.3°C on videotaping dates. At least one 5-min segment was taped for each reef on each of 11 nights. On 4 nights, a second 5-min segment was taped at one reef 30-60 min after the first to examine temporal variability (least-squares regression and one-way analysis of variance).

Frequencies of various activities at each of the four reefs were transcribed from the videotapes. Videotape segments were timed with a stopwatch, then scored for the following characteristics: number of passes per minute over center (brick-covered) or edge (brick-free) portion of a reef; passing speed; and number of times one fish followed another. Frequencies of edge passes, center passes, and follows at each reef were compared by analysis of covariance, with date as the covariate (SAS 1982).

**Results**

Although no spawning occurred in either pool, attraction of both males and females to experimental reef B was observed immediately after an envelope containing feces of young of the year was placed there, but no comparable attraction of fish to the three control reefs was observed. This pattern persisted throughout the visual observation period.

In the subsequent videotaped observations, pass speeds over the reefs varied little from an average of 25.5 cm/s. Sequential segments taped 30-60 min apart at control reef A on four dates showed no significant differences ($P > 0.05$) in numbers of center passes, edge passes, or follows per minute indicating that the order in which each of the reefs was videotaped on a given night had little effect on the amount of activity observed. The cumulative number of center passes over any reef was linearly related to cumulative seconds of observation at that reef ($r = 0.97; P < 0.01$), indicating that standardizing the behavioral data as numbers per minute should not have biased the results. Fish passed over reef centers and followed one another significantly more often in pool 1 than they did in pool 2 ($P \leq 0.05$, Table 2). There was no significant difference between pools for edge passes. Within pool 1, however, edge passes were significantly higher at the experimental reef ($P = 0.03$). No other significant differences between reefs within pools were observed in the videotapes.

**Discussion**

The results of the 1979 and, to a lesser extent, the 1980 experiments suggest that chemosensory cues emanating from the residue of feces in substrate areas previously occupied by young of the year act as chemoattractants and affect pre-spawning movements so that adults tend to aggregate and spawn where such materials are detected. While these results also seem relevant to pheromonal and other chemosensory hypotheses of long-distance homing movements of lake trout (Nordeng 1977; Brown et al. 1981; Horrall 1981; Hasler and Scholz 1983), it is inappropriate to pursue such ideas here, considering the degree to which the behavior pools constrained the movements of the experimental fish.

The practical management implications of such chemoattractants are that appropriate source materials might attract ripe lake trout to specific reef or shoal areas in the Great Lakes. If residues of feces from young of the year significantly increased the probability that a given site would be used for spawning, then management agencies might expect some difficulties in reestablishing spawning populations on traditional but long unused sites where interstitial accumulations of such residues, once annually renewed, had decomposed or dissipated. On the other hand, where successful plantings of eggs or young fish, or hatches of eggs from spawnings by native or planted adults, have occurred in the recent past, one would predict that the chemoattractants emanating from those substrates might attract hatchery fish to aggregate and spawn there. Egg plantings could seed a traditional or artificial
TABLE 2.—Frequencies of three types of adult lake trout behaviors during observations videotaped on 11 nights in 1980 with respect to presence or absence of feces of young of the year, with results of analysis of covariance for relationships between pools, reefs within pools, and dates. Asterisk denotes significant difference at $P = 0.05$.

<table>
<thead>
<tr>
<th>Site or comparison</th>
<th>Behavior</th>
<th>Site or comparison</th>
<th>Frequency (number per minute ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Edge passes</td>
<td>Center passes</td>
</tr>
<tr>
<td>Pool 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control reef A</td>
<td></td>
<td>1.14 ± 0.65</td>
<td>5.81 ± 1.90</td>
</tr>
<tr>
<td>Experimental reef B (feces)</td>
<td></td>
<td>1.82 ± 1.09</td>
<td>5.78 ± 2.30</td>
</tr>
<tr>
<td>Pool 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control reef C</td>
<td></td>
<td>1.03 ± 0.51</td>
<td>3.54 ± 1.60</td>
</tr>
<tr>
<td>Control reef D</td>
<td></td>
<td>0.60 ± 0.40</td>
<td>3.12 ± 2.19</td>
</tr>
</tbody>
</table>

**Observed probability value**

|                    |          |                   |                                   |           |
| Between pools      |          | 0.24              | 0.01*                            | 0.05*     |
| Within pool 1      |          | 0.03*             | 0.94                             | 0.75      |
| Within pool 2      |          | 0.16              | 0.38                             | 0.32      |
| Date               |          | 0.24              | 0.01*                            | 0.12      |
| Date × pool interaction | 0.59 | 0.01*     |                                   | 0.13      |

* Each control reef had only a dummy envelope.

spawning site with surviving young. These young presumably not only would leave some feces deep in reef interstices but also would have ample time to imprint upon various sensory cues associated with the site, cues that could be used when they homed back to the site when ready to spawn (Horrell 1981; Swanson 1982).

If lake trout passively or actively mark their spawning grounds with chemical substances, this could occur at two times: while recently hatched young reside on the spawning ground, before and after swimup; and during the cleaning activity of adult males. After deposition in the lake environment, lake trout eggs develop for 4 to 5 months before hatching. Hatched young spend an additional 1 to 2 months hidden in the substrate. Until emergence, they exhibit a strong photophobia, hiding in dark or shadowed areas at least during the day (Balon 1980). The young emerge from the substrate and soon migrate to the surface, where they fill their swimbladders with air (Tait 1960). The first feces production is not apparent until after the first feeding, which occurs shortly after emergence. Balon (1980) observed that "yellow bile" persists in the gut until gradually displaced by the first exogenous food. Recent field studies in Marquette Harbor in southern Lake Superior showed that larvae began hatching in mid-April and some remained in or near the spawning area 1 to 2 months after emergence, from May to mid-July (Peck 1982). Eschmeyer (1956) found that young of the year near Laughing Fish Point, also in southern Lake Superior, spent their first summer in relatively shallow water, at or near the spawning grounds where they hatched, but moved into deeper water during equinoctial storms in September.

During the days immediately before spawning, males perform an activity that has been described by Royce (1951) and Eschmeyer (1964) as cleaning of the spawning ground. In Royce's account, males cruised along close to the bottom, occasionally giving stones sudden, snapping movements with their tails, and several showed considerable abrasion on the lower jaw and underside of the tail. Martin (1957) described cleaning as "a twist of the tail or body over the bottom or occasionally rubbing with the snout [in] the interstices between the rocks." According to Merriman's (1935) description, "They work over the bottom slowly and carefully, rubbing it with their bellies, until it becomes a clean white color, sharply contrasting with the surrounding areas." The traditional explanation of cleaning is that it removes superficial debris, algal growths, and detritus from the spawning ground. However, cleaning might also be similar to scent-marking, a specialized behavior pattern during which a chemoattractant is directly applied to the substrate by the male. Although I did not specifically test this hypothesis in the present experiments, such a phenomenon could have influenced the 1979 results, when an envelope containing feces of young was moved from one reef to another yet spawning persisted for an additional night at the former location of that odor source. Selection
of spawning sites in nature appears to be closely associated with the location of cleaned areas. Royce (1943) observed that lake trout "mated at random all over the area which had been cleaned off," and Merriman (1935) also implied that spawning was restricted to cleaned areas. My suggestion that male scent-marking of the substrate may occur during cleaning stems from two considerations: cleaning fish make direct contact with the substrate; and male lake trout may possess epidermal pearl organs (Vladykov 1954, 1970; Martin 1957; Paterson 1968). Noakes (1980) used histological techniques to test whether mature males developed more thickened skin than females during the spawning season but found no significant difference. His attempts to confirm the presence of epidermal pearl organs were inconclusive. Vladykov (1970) described the pearl organs as minute, whitish tubercles on the scales, particularly abundant over the lower surface around the anal region. This part of the body also contacts the bottom during cleaning.

Ovarian fluid exuding from ripe females arriving at the spawning ground probably facilitates their location by males. Although presence of an attractant pheromone in ovarian fluid of lake trout has not been tested, it was demonstrated for rainbow trout in experiments conducted by Emanuel and Dodson (1979) and by Honda (1980). The release of attractant pheromones by ripe females is widespread among teleost fishes (Liley 1982).

Lake trout thus might use several chemosensory cues in their reproductive behavior, but the possible use of such supplemental signals does not diminish this study's finding. The presence of feces from young of the year in substrates significantly increases the probability that adults will be attracted to and use those substrates as spawning sites.

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