ABSTRACT. Behavior of lake trout (Salvelinus namaycush) fry is not well understood but could affect the role of predation on recruitment. Movement out of the substrate as sac fry could expose fry to predation. The purpose of this study was to compare vertical movement of lake trout sac fry at different developmental stages, to describe their diel movement patterns, and to examine the distance that sac fry will swim off the bottom. Fry traps set at three heights were used to capture fry moving out of rock substrate in laboratory tanks. Movement out of the substrate occurred at the sac fry stage, steadily increased as fry advanced developmentally, and peaked at swimbladder filling. Catch of fry was always greatest at night. Few to no fry were captured during daylight hours. Catch of fry was usually greatest in traps near the bottom (17 cm off the bottom), but sac fry were regularly captured in traps set 37 and 57 cm off the bottom during all stages of development. These results show that lake trout sac fry move out of the substrate at night before swimbladder filling and thus, could suffer from predation by fishes that feed at night near the bottom.

INDEX WORDS: Emergence, swimbladder, larval fish, Great Lakes, predation, lake trout.

INTRODUCTION
Lake trout (Salvelinus namaycush) are native to the Great Lakes and were historically an abundant fish. By the 1960s, near-shore populations of lake trout were greatly reduced or extinct in all of the Great Lakes. This decline of lake trout populations has been attributed to overfishing, sea lamprey (Pertromyzon marinus) predation, and habitat degradation (Elrod et al. 1995, Hansen et al. 1995). Programs to rehabilitate naturally reproducing populations of lake trout in the Great Lakes were started in the 1950s through the 1970s with management actions aimed at the stocking of hatchery-reared lake trout and sea lamprey control. Stocked juvenile lake trout survive to maturity and large populations of mature hatchery-origin fish have been established throughout the Great Lakes. Despite the survival success of stocked fish, little natural recruitment has occurred except in Lake Superior. In Lake Ontario, stocked adult lake trout spawn over substrate suitable for egg and fry survival (Marsden and Krueger 1991) and some eggs survive and develop to the emergent stage (Perkins and Krueger 1995). However, almost no fry ever survived to age 1 (Elrod et al. 1995) until recently, when catches of naturally spawned lake trout have increased (O’Gorman et al. 1998), but still remain relatively low. Predation by a non-native species, the alewife (Alosa pseudoharengus), on lake trout fry has been identified as one possible cause for the absence of natural recruitment at some locations in the Great Lakes (Johnson and VanAmberg 1995, Jones et al. 1995, Krueger et al. 1995).

Lake trout spawn in the fall over rocky substrate with open interstices. Eggs are distributed over the bottom and develop over winter in interstitial spaces (Martin and Olver 1980). After hatching sac fry remain in the interstices and continue to develop by absorbing their yolk sacs for nutrition. Sac fry swimbladders contain no gas and fry are negatively buoyant. To regulate buoyancy, fry fill their swimbladders with gas by swimming to the surface to gulp air (Tait 1960). Swimbladder filling occurs when the yolk sac is fully absorbed (Balon 1980). The start of feeding and free swimming above the
substrate occurs at approximately the time of swim- 
bladder filling (Godin 1981). Salmonids typically 
emerge and fill their swimbladders at night (Hoar 
1956, Godin 1981, Gustafson-Marjanen and Dowse 
1983). Moving out of the substrate and swimming 
to the surface to fill the swimbladder probably in-
creases the vulnerability of fry to predation, espe-
cially by fishes. Predation by alewife on lake trout 
fry has been proposed to occur as fry are swimming 
to the surface to fill their swimbladders (Krueger et 
al. 1995) and may be a major impediment to natural 
reproduction by lake trout in the Great Lakes (Jones 
et al. 1995). Predation on fry can also result from 
benthic predators such as sculpins (Cottus spp.), 
burbot (Lota lota), and mudpuppies (Necturus mac-
ulosus) (Hacker 1956, Stauffer and Wagner 1979, 

The extent and timing of lake trout fry move-
ments out of the substrate are unknown, and thus 
the potential risk of predation by fish feeding in the 
water column above spawning substrate cannot be 
assessed. Some movement of lake trout fry out of 
the substrate occurs before swimbladder filling be-
cause sac fry, in addition to emergent fry, were reg-
ularly caught over several years in fry traps set on a 
Lake Ontario reef (Marsden et al. 1988, Marsden 
and Krueger 1991, Krueger et al. 1995). Capture of 
fry in traps has also been reported at other locations 
in the Great Lakes (Wagner 1981, Stauffer 1981, 
Nester and Poe 1984, Peck 1986), but the specific 
development stage of the captured fry was not re-
ported. Sac fry stage fish moving above the sub-
strate may be highly vulnerable to predation 
because their large yolk sacs and negative buoyancy 
made them poor swimmers and probably easy prey 
for predators found above the substrate. The poten-
tial for alewife predation would be greater if many 
sac fry frequently swim above the substrate prior to 
swimbladder filling, than if fry remained in the sub-
strate. Understanding the extent and duration of sac 
fry movement above the substrate will help deter-
mine the potential vulnerability of lake trout fry to 
predation by species such as alewife.

This study used a laboratory approach to investi-
gate upward movement of lake trout fry as they de-
veloped from early sac fry to swimbladder filling. 
The objectives of this study were to 1) compare the 
vertical upward movement at different developmen-
tal stages from after hatching to swimbladder fill-
ing, 2) describe the diel (24 h) movement pattern of 
sac fry, and 3) examine the height that sac fry will 
swim off the bottom.

**METHODS**

Traps set at different heights above the bottom of 
laboratory tanks were used to catch lake trout fry as 
they moved off the bottom. Two trials were con-
ducted. In each trial, sac fry were stocked into tanks 
and periodic 24 h trapping was conducted over ap-
proximately a 1 month period until all fry had filled 
their swimbladders.

**Laboratory Tanks**

Sac fry were placed in six 1.22 m diameter circu-
lar fiberglass tanks set up at the Resource Ecology 
and Management (REM) Facility at Cornell Univer-
sity, Ithaca, New York. Water depth in the tanks 
was 0.72 m. Tanks had a flow-through water supply 
at a rate of approximately 1 L/min. Water was 
drawn from Cayuga Lake at a depth of about 19 m, 
chlorinated by the Town of Ithaca, New York, and 
then dechlorinated at the REM Facility. Inflow 
water was delivered from a 25-cm-long horizontal 
pipe located about 20 cm above the water surface; 
water discharged through multiple small holes on 
the underside of the pipe. Water drained from a 
screened standpipe located in the center of the 
tanks. A plastic grid, 1.0 cm high with 1.3 cm2 
openings, was placed in the bottom of each tank to 
increase small interstitial spaces. Rocks covered the 
grid to an approximate depth of 10 cm. Rocks were 
primarily cobble (70 to 80%, 6.4 to 20 cm) with 
some pebble (20 to 30%, 1.6 to 6.4 cm) and gravel 
(< 10%, 0.2 to 1.6 cm). The temperature of each 
tank was recorded daily with a mercury thermome-
ter or an electronic thermometer calibrated with a 
mercury thermometer. Tanks were exposed to the 
natural photoperiod of February and April through 
windows of the facility.

**Experimental Fish**

In both trials, each tank was stocked with 153 
lake trout sac fry to provide a density of 131 fry per 
m2, the density of alevins and emergent fry esti-
mated by Perkins and Krueger (1995) for Stony Is-
land Reef in Lake Ontario. The first group of fry 
was obtained from the New York State Department 
of Environmental Conservation Fish Hatchery at 
Bath, New York as recently hatched sac fry (stage 
F19; Balon 1980) and originated from lake trout 
captured from Seneca Lake, New York on 16 Octo-
ber 1995, and artificially fertilized. All eggs of this 
lot hatched by 15 December 1995 at 534 degree 
days of development (mean temperature 8.9°C).
Sac fry were transported to the REM facility on 22 December 1995. The sac fry were kept in a full dark photoperiod at 0.1 to 3.0°C until 6 February 1996 (day 1 of first trial) when the sac fry were stocked into the six experimental tanks at 654 degree days of development. The second group of fry were progeny of a hatchery broodstock derived from Seneca Lake, New York, obtained as eyed eggs from the Allegheny National Fish Hatchery, Warren, Pennsylvania (U. S. Fish and Wildlife Service). Gametes were fertilized on 21 November 1995. Eyed eggs (mean temperature 2.7°C) were shipped to the REM facility on 5 March 1996 and kept at 3.4 to 5.1°C in a full dark photoperiod. Most eggs had hatched by 10 April 1996 when the fry were stocked into the experimental tanks at 400 degree days (day 1 of second trial).

The classification system of Balon (1980) for the early development of lake trout was used to place fry into development stages for comparison. In this paper, sac fry were used for stages F1g to F210 (Balon’s (1980) free embryo or eleutheroembryo) and alevin for fish whose swimbladders were filled at the A111 stage. All fry caught in traps were classified by this system.

Data Collection

Traps to catch fry were constructed of plastic funnels that led into the inside of cylindrical plastic containers. Funnels had a 19.5 cm diameter opening and the narrow end was inserted 6 cm into a container (diameter 6.4 cm, height 9 cm) through a hole in the bottom. Traps were weighted to make them negatively buoyant. Traps were suspended with nylon twine from bars which rested on the tank rims. Five traps were attached to a bar at approximately 25 cm intervals. Four bars of five traps (20 traps total) were set horizontally across each tank to capture fry, except in the first trial until day 10 when only 10 traps per tank were used. Traps were set with the opening facing down toward the substrate at three depths: either resting on the bottom, midway in the tank (trap mouth 20 cm above the substrate), or as close to the surface as possible (trap mouth 40 cm above the substrate). Due to the height of the funnels (17 cm), effective trapping distances were 17, 37, and 57 cm above the substrate for the three trap heights (designated bottom, middle, and high). In each tank, all traps were suspended at the same height to avoid trap interference that would occur if multiple trap heights were used in a single tank. Two tanks were used for each of the three trap heights. Trap heights used in each tank were changed prior to each sampling day so that each tank received each trap height the same number of times each trial.

Two types of trap monitoring were done. Daily monitoring (traps checked every 24 hours) was used to determine the change in the amount of vertical movement as fry developed (objective 1). Hourly monitoring was used to determine diel patterns of movement (objective 2). In hourly trapping, traps were checked every 2 hours during the night and approximately every 6 hours during the day. To determine the number of fry captured after a trapping period, the four bars of traps were simultaneously removed from a tank, the number of fry in each trap was recorded, and the traps were reset. Captured fry were released back into the tanks immediately after traps were checked. The container part of the trap held water, thus traps could be out of the tanks without undue stress to the captured fry.

Eight daily and five hourly trappings were done in the first trial. Fourteen daily and two hourly trappings were performed in the second trial. The first trial was concluded after 30 days when most (97%) of the fry had filled their swimbladders (804 degree days). The second trial lasted 32 days and concluded when all fry had filled swimbladders (658 degree days). Trial “days” started and ended at approximately 12:00, and not at midnight, so that the nighttime catch, when peak fry movement occurred, was not split between two periods. During the first trial, daylight length ranged from 10.2 h to 11.5 h and changed approximately +2 min per day. During the second trial, daylight length ranged from 13.2 h to 14.5 h and changed approximately +2 min per day.

The filling of the swimbladder in fry was monitored in both trials. Captured fry were held in a glass pipette in front of a light to determine if the swimbladder was filled with gas (Tait 1960). The swimbladder was recorded as filled if a very-clear sac was seen dorsal to the gut and ventral to the vertebral column. In the first trial, swimbladder status was only determined during the last trapping period (day 30). Swimbladder status was determined throughout the second trial from day 27 of the trial (mid F210 stage). A sample of 25 to 92 fry per trapping day was used for this determination.

At the conclusion of the first trial, all six tanks were drained and the remaining fry removed and counted to calculate survival of fry in the experimental tanks. At the conclusion of the second trial,
four of the six tanks were drained and the fry removed and counted.

Data Analysis

Difference in water temperature among the six tanks was tested with an ANOVA (Zar 1984) to determine if fry in each of the six tanks had similar conditions for development. Mean number of fry caught per tank was calculated by summing all fry caught in each tank for a sample period and dividing the sum of the tank totals by the number of tanks (6). Comparison of the total number of fry captured during the day versus at night was tested with a chi-square goodness of fit test for an uniform distribution (Ho: equal number of fry of captured in day and night) (Zar 1984). Expected catches were calculated by multiplying the number of hours trapped during the day or night by the ratio of the total number of fry caught to the total number of hours trapped. Catch rates (mean number of fry per tank per hour) were determined by dividing the mean number of fry captured per tank by the number of hours traps were set. Mean catch rate was calculated as the average of the catch rates for each trapping period in the day or night for each trial. Trapping periods that were not exclusively during the day or night (sunrise or sunset occurred between setting and checking) were excluded from these analyses. Differences in catch among the three trap heights were tested with a chi-square goodness of fit test for an uniform distribution among heights (Ho: equal number captured at the three trap heights). Differences in the total number of fry captured in the outer two trap positions (near tank walls) versus the inner three positions on the suspending bars was also compared to test for an equal catch between the outer and inner trap positions. This test was done to determine if the tank walls guided fry movement. The outer traps were located close to the side of the tanks and thus could catch more fry than the inner traps if fry were being led into the traps by the sides of the tanks.

RESULTS

Experimental Conditions

Water Temperature

No difference in mean water temperature occurred among the six experimental tanks in the first (P > 0.99) or second trials (P > 0.99). The average water temperature during the first trial in the six tanks was 5.3°C (range 4.1 to 6.3°C), in the second trial the average water temperature was 8.5°C (range 5.9 to 10.6°C). The maximum water temperature difference on any day between the six tanks in the first trial was 0.4°C, and 0.8°C in the second trial.

Fry Development and Survival

The fry that were stocked in the first trial were classified as early in the F210 stage (Balon’s (1980) free embryo or eleutheroembryo; the yolk sac was partially absorbed and elongated in shape, with minimal differentiation of the adipose, caudal, and anal fin from the embryonic fin fold, 24 mm TL; Table 1). On the fourteenth day of the first trial, fry were midway through the F210 stage and had a length of 26 mm. On the twenty-first day, fry were advanced in the F210 stage (yolk sac more absorbed, increased differentiation of embryonic fin fold, 27 mm). Approximately three or four neutrally buoyant (assumed to have filled swimbladders) fry were observed swimming near the surface of one tank on day 25. On day 29, many free-swimming emergent fry were observed in all tanks. On the final, thirtieth day, 97% of the fry had filled swimbladders, and were classified as alevins (A111; little yolk sac remaining, fin fold almost fully differentiated, 27 mm).

The fry used in the second trial were recently hatched when stocked into the experimental tanks at the F19 stage (yolk sac large and nearly spherical, thin body, no differentiation of the embryonic fin fold, 19 mm). On the fifteenth day, fry were in the transition from late F19 to early F210 (yolk sac partially absorbed but still prominent). Two fry (4%) had filled swimbladders on day 27 (27 mm). On the twenty-eighth day, fry were at an advanced F210 stage and 57% of the fry had filled their swimbladders. On the thirty-second day of the second trial, all fry had filled swimbladders and were in the A111 stage (yolk sac nearly absorbed, 28 mm, Table 1).

Fry survival was high in the experimental tanks with an average of 147.7 fry (96.5% survival) recovered alive per tank at the end of the first trial (range 144 to 151 fry), and an average of 144.5 fry (94.4% survival) recovered alive per tank at the end of the second trial (range 138 to 152).

Movement in Association with Developmental Stage

Movement out of the substrate was detected at the earliest life stages used (F19), increased as fry
Movement of Lake Trout Fry

TABLE 1. Mean number of fry captured per tank per 24 h period in the six experimental tanks (three trap heights pooled). In hourly trapping, traps were checked every 2 hours during the night and approximately every 6 hours during the day. In daily monitoring the traps were checked approximately every 24 hours.

<table>
<thead>
<tr>
<th>Trial</th>
<th>Sample type</th>
<th>Day</th>
<th>Degree Days</th>
<th>Balon (1980) Stage</th>
<th>Percent of fish with filled swimbladders (number/tank/day)</th>
<th>Mean no. caught/tank/day (standard error)</th>
<th>Figure 1 panel for hourly sample days</th>
</tr>
</thead>
<tbody>
<tr>
<td>First Daily</td>
<td>3</td>
<td>659</td>
<td>early F210</td>
<td>–</td>
<td>0.2 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>8</td>
<td>687</td>
<td>F210</td>
<td>–</td>
<td>0.5 (0.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>9</td>
<td>691</td>
<td>F210</td>
<td>–</td>
<td>0.2 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>10</td>
<td>696</td>
<td>F210</td>
<td>–</td>
<td>0.5 (0.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>11</td>
<td>701</td>
<td>F210</td>
<td>–</td>
<td>2.3 (0.56)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>15</td>
<td>720</td>
<td>F210</td>
<td>–</td>
<td>4.0 (1.53)</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>16</td>
<td>726</td>
<td>F210</td>
<td>–</td>
<td>3.7 (1.23)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>17</td>
<td>732</td>
<td>F210</td>
<td>–</td>
<td>6.0 (1.15)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>18</td>
<td>738</td>
<td>F210</td>
<td>–</td>
<td>1.5 (0.43)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>19</td>
<td>744</td>
<td>F210</td>
<td>–</td>
<td>11.7 (3.03)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>22</td>
<td>760</td>
<td>advanced F210</td>
<td>–</td>
<td>17.0 (2.18)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>24</td>
<td>772</td>
<td>advanced F210</td>
<td>–</td>
<td>23.7 (3.69)</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>30</td>
<td>804</td>
<td>A111</td>
<td>97% (27)</td>
<td>65.8 (8.54)</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Second Daily</td>
<td>3</td>
<td>407</td>
<td>F19</td>
<td>–</td>
<td>0.0 (0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>6</td>
<td>428</td>
<td>F19</td>
<td>–</td>
<td>0.3 (0.21)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>7</td>
<td>434</td>
<td>F19</td>
<td>–</td>
<td>0.0 (0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>8</td>
<td>441</td>
<td>F19</td>
<td>–</td>
<td>0.2 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>9</td>
<td>449</td>
<td>F19</td>
<td>–</td>
<td>0.0 (0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>10</td>
<td>458</td>
<td>F19</td>
<td>–</td>
<td>0.7 (0.49)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>13</td>
<td>483</td>
<td>F19</td>
<td>–</td>
<td>0.8 (0.31)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>14</td>
<td>492</td>
<td>advanced F19</td>
<td>–</td>
<td>1.0 (0.52)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>15</td>
<td>500</td>
<td>advanced F19</td>
<td>–</td>
<td>0.2 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>17</td>
<td>518</td>
<td>early F210</td>
<td>–</td>
<td>0.8 (0.65)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>21</td>
<td>554</td>
<td>F210</td>
<td>–</td>
<td>2.5 (0.76)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>22</td>
<td>563</td>
<td>F210</td>
<td>–</td>
<td>5.2 (0.95)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>23</td>
<td>572</td>
<td>F210</td>
<td>–</td>
<td>8.0 (2.02)</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>27</td>
<td>609</td>
<td>Advanced F210</td>
<td>4% (50)</td>
<td>31.7 (4.98)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly</td>
<td>28</td>
<td>619</td>
<td>Advanced F210</td>
<td>57% (92)</td>
<td>50.0 (6.23)</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Daily</td>
<td>32</td>
<td>658</td>
<td>A111</td>
<td>100% (25)</td>
<td>48.7 (2.78)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

advanced developmentally, and peaked in association with swimbladder filling (A111 stage; Table 1). The fewest fry caught were the early life stages (F19 and early F210 stages). As fry neared emergence (mid to late F210), the mean number of fry captured over a 24 hour period per tank increased about ten times from 6.0 to 65.8 fry in the first trial (day 17 to 30) and from 5.2 to 48.7 fry in the second trial (day 22 to 32). Large increases in fry catch began in the advanced F210 stage, after day 24 in both trials.

Diel Pattern

More fry were captured at night than during daylight hours in both trials (each trial P < 0.001; Fig. 1). This pattern occurred from the mid sac fry stage (mid F210) through swimbladder filling. Peak catch periods tended to be three to five hours after sunset. Mean catch rates (± SE) per tank for the first trial were 0.09 (± 0.036) fry/h during the day and 1.24 (± 0.28) fry/h at night. Similarly, in the second trial catch rates were 0.01 (± 0.0063) fry/h during the day and 3.1 (± 1.03) fry/h at night.
Vertical Distance Above the Substrate

The three trap heights caught different numbers of sac fry with unfilled swimbladders in the first and second trials (each trial \( P < 0.001 \)). The traps nearest the bottom caught the most fry, and the traps closest to the surface caught the least (Table 2). A similar pattern of capture occurred among the three heights for alevins with filled swimbladders in the first trial \( (P < 0.001) \), but not the second trial \( (P = 0.30) \). Even though each of the upper two trap heights caught fewer sac fry than the bottom traps, sac fry of the earliest life stages used in this study were captured in the middle (37 cm vertical distance) and high (57 cm) traps in both trials. For example, on the first day of trapping in the first trial (day 3), only one fry was caught, but it was caught in a high trap. On day 8 when three fry were caught, two fry were caught in high traps, and one was taken in a bottom trap. In the second trial, the first fry to be caught in either a middle or high trap was on day 8, with one fry in a middle trap. On day 13, one fry was caught in a middle trap and one in a high trap. As the fry developed, catches increased at all three trap heights.

No difference was found between the number of fry captured by the inner (close to center of tank) versus outer (close to tank walls) trap positions in both trials (first trial \( P > 0.3 \); second trial \( P > 0.5 \)).

DISCUSSION

Lake trout sac fry in laboratory tanks moved out of the substrate and up into the water column at night prior to swimbladder filling. While only a few fry per day moved immediately after hatching, movement out of the substrate increased before any swimbladder filling occurred. The youngest sac fry used in this study moved as much as 57 cm off the bottom. The consistent pattern of movement indicates a behavior that would explain their vulnerability to traps set on a spawning area in Lake Ontario (Krueger et al. 1995). Fry moved throughout their development, not just at swimbladder filling, and this behavior will increase fry vulnerability to predation.

The mean number of fry caught per tank per day may be biased high for periods when hourly samples were collected as compared to days when daily collections were made (Table 1). Individual fry could have been captured multiple times in one sample day when the traps were checked multiple times during the night because the fry were released back into the tanks. In contrast, when traps were checked at 12 or 24 h intervals the fry captured were not available for capture until after the 12 or 24 h period. Thus, direct comparisons among the number of fry captured each sampling day should only be made within a sample type (hourly or daily). Regardless of these differences, the overall pattern of increasing movement as swimbladder filling approached was consistent between sample types.

The percent of the fry population in a tank moving in a trapping day was estimated by expanding the number of fry captured by the twenty traps to the area not covered by the traps to account for the area not trapped. The twenty traps in an experimental tank covered 51.3\% (0.60 m\(^2\) of 1.17 m\(^2\)) of the area of tanks. Thus, to estimate the percent of the total number of fry moving out of the substrate, the percent captured of 153 (the total number of fry in the tanks) was multiplied by 1.949 (1 ÷ 0.513, the portion of a tank covered by the traps). However, this calculation did not account for fry that were caught multiple times on intensive sampling days (traps checked every 2 hours at night), which would bias this estimate high in comparison to when traps were only checked at 12 to 24 hour intervals and only during daytime. This calculation also did not account for mortality (total fry alive in the tanks was < 153) which would bias estimates low. Despite these problems with this calculation, an estimate of the percent of the population moving may be obtained for particular time periods. The estimated total percent of fry moving over a 24 h period was low during the F19 to mid F210 stages (from near zero up to 3\%), then increased to up to a maximum of 84\% on day 30 of the first trial, and 64\% on day 28 of the second trial. At swimbladder filling all fry need to access the surface to gulp air, so a large percentage of the population would be expected to be moving off the bottom then. However, a number of fry moved when few had filled their swimbladders. Thirty percent of the population was estimated to move out of the substrate on day 24 of the first trial, one day before the first neutrally buoyant fry were observed, and 41\% of the fry were estimated to move on day 27 of the second trial when only 4\% of the captured fry had filled their swimbladders. From 16 to 21\% of the population in the first trial and from 3 to 10\% in the second trial moved in each 24 h sample 3 to 6 days before the first swimbladder filling was observed.

Because fry were returned to the tanks following capture, the movement pattern reported here could be argued to have been due to a relatively small number of fry that moved in each tank and were...
FIG. 1. Diel catch of fry during hourly sampling days in mean number of fry captured per tank for each sampling interval. The three trap heights are combined. Down arrows indicate time of sunset, up arrows sunrise. Graphs from both trials are arranged developmentally by Balon (1980) stage, with the earliest life stage in the upper left and the most advanced fry in the lower right and follow the order of letters in the upper left of each graph. Traps were set in the tanks at the first time period, checked at each time shown, and removed at the last time indicated on the x-axis. Error bars are plus and minus one standard error.
captured multiple times. However, the number of fry captured increased by such a large amount over each trial that multiple captures of the same fry could have not possibly been important in the reported pattern of fry activity over their development. Repeated captures of the same fry may have had a greater influence on the hourly samples, but the pattern of primarily nocturnal fry activity would not be changed by multiple captures of the same fry. Further research into lake trout sac fry movements should examine individual variation in vertical movements. For example, do fry make multiple trips out of the substrate before and during swimbladder filling, and do some individual sac fry move more than others?

Peak activity of fry before and after swimbladder filling was at night; few fry were captured during daylight periods. This nocturnal activity of fry confirms an earlier report based on limited aquaria observations that sac fry move primarily at night (Krueger et al. 1995). Movement out of the substrate appeared to be triggered by darkness, with movement increasing soon after sunset. Light intensity is diminished in deep water, so the nocturnal pattern of movement by lake trout sac fry may be less pronounced for the fry of deep-water spawning populations. Lake trout fry have been reported to be less photophobic immediately before emergence than other salmonids (Carey 1985). However, the observed pattern of movement suggests they were still photophobic at this life stage. In this study, fry just prior to emergence showed almost exclusively nocturnal movement (Fig. 1, E and F). Similar to the pattern reported here for lake trout, emergence patterns of other salmonid species typically show a diel pattern with a nocturnal movement peak most common (Hoar 1956, Godin 1981, Gustafson- Marjanen and Dowse 1983).

The consistent pattern of sac fry movement out of the substrate observed in these tank experiments and also reported from the field (Krueger et al. 1995) suggests that this behavior is typical for lake trout sac fry as they approach the emergent stage. In a laboratory study on lake trout fry movements, newly hatched lake trout sac fry were found to move out of simulated spawning substrate starting 1 week after hatching until 12 weeks after hatching with 50% of the fry moving as sac fry within 6 weeks of hatching (Stauffer 1978).

Several alternative explanations may explain the catch of sac fry from Lake Ontario, such as movement in response to stress from low dissolved O$_2$ in the substrate from organic decomposition (Sly 1988), fry seeking refuge in the traps as an alternative source of cover, or being washed into the traps by wave action. These alternatives do not explain the similar behavior observed here in both trials. Dissolved O$_2$ levels were unlikely to have been sufficiently low to cause stress as no organic material was placed in the tanks (except for the fry), and water exchange rates prevented stagnation. Also, a lack of stress could be indicated by the consistently high fry survival in every tank. The traps may not offer an important alternative source of cover, especially because high traps suspended in the center of the tank caught fry as well as traps near the tank walls. Fry had to swim through the water column to enter the high traps in the center. The tanks in this study also had no wave action to transport fry out of the substrate. Thus, this movement reflects typical nocturnal behavior for lake trout sac fry and should be detectable in other lake trout populations.

### TABLE 2. Total catch by trap height for sac fry (no gas present in swimbladder) and fry with filled swimbladders. Sac fry numbers were calculated by excluding the last sampling day from both trials (when most or all fry had filled their swimbladders) and by subtracting the fry with filled swimbladders on other days. Trap height is the vertical distance from the substrate to the uppermost part of the funnels inside the traps.

<table>
<thead>
<tr>
<th>Trap height</th>
<th>First trial Sac fry</th>
<th>First trial Filled swimbladders</th>
<th>Second trial Sac fry</th>
<th>Second trial Filled swimbladders</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (57 cm)</td>
<td>118</td>
<td>93</td>
<td>105</td>
<td>153</td>
</tr>
<tr>
<td>Mid (37 cm)</td>
<td>125</td>
<td>126</td>
<td>160</td>
<td>144</td>
</tr>
<tr>
<td>Low (17 cm)</td>
<td>184</td>
<td>176</td>
<td>167</td>
<td>171</td>
</tr>
</tbody>
</table>
Why do sac fry move off the bottom at night? First, fry may have an innate response to move off the bottom to avoid benthic fry predators such as sculpins and burbot. Second, sac fry may be beginning to feed, learning how to capture food while still obtaining nutrition from their yolk sac (Braum 1967). Whitefish (Coregonus spp.), for example, often start feeding within 2 weeks after hatching, before yolk sac absorption is complete (Freeberg et al. 1990, Karjalainen and Viljanen 1994, Savino and Hudson 1995). Lake trout fry (22 to 24 mm) captured in Lake Superior with large yolk sacs did not have food in their digestive tracts, while some 25 mm lake trout with prominent yolk sacs had ingested food (Swedberg and Peck 1984). Most 25 to 27 mm fry still had yolk left and about half had ingested food. Furthermore, these fry were collected by trawling over sand substrate in Presque Isle Harbor in Lake Superior (Swedberg and Peck 1984), so apparently these fry had left the spawning substrate interstices as sac fry. Feeding while yolk sac reserves are still available could be advantageous when fry are making the transition from endogenous to exogenous feeding. The yolk will still provide nutrition while the fry learn how to effectively capture food items. Third, sac fry may be moving off the bottom to improve swimming ability before they make the potentially long trip to the surface to fill their swimbladders. Short trips off the bottom could strengthen swimming muscles and efficiency so the fry are stronger swimmers when they move to the surface. Last, this movement could also aid fry in dispersing from spawning areas to juvenile rearing areas (DeRoche 1969, Bronte et al. 1995).

Fish in both trials filled their swimbladders at the end of the F210 stage and early in the A111 stage and remained photophobic for 1 to 2 days afterward. This differs considerably from the description of the early ontogeny of lake trout given by Balon (1980) who stated that strong photophobia terminates at the end of the F210 stage, and the swimbladder is filled after fat reserves in the yolk and body cavity are absorbed. Balon also noted that emergence from the substrate occurred at stage A111 but that the swimbladder was not filled until A212. Thus, swimbladder filling and emergence may not necessarily occur at the same developmental stage in all populations. Gametes used by Balon (1980) were taken from adults from Lake Opeongo, Algonquin Park, Ontario whereas the fish used in this study originated from Seneca Lake, New York. Differences in early development have been reported among lake trout populations, including emergence in relation to morphological development, and were attributed to genetic differences among populations (Horns 1985).

The difference in the number of degree days required to reach swimbladder filling between the two fry groups was likely because of the different temperatures at which each group was reared. The fry used in the first trial developed in relatively warm water (8.9°C) until after hatching, and then were held in cold water (often < 1.0°C) until the start of the trial. The second group was incubated at colder temperatures (2.7°C) until close to hatching, after which temperatures were warmer than for the first trial fish. The first group of fry required more degree days to develop to hatching (534 vs. 400) and swimbladder filling (804 vs. 658) than the second group, accumulating about 134 more degree days at hatching than the second group. Even with these different developmental conditions, similar behavior patterns were found with both groups of fish.

Movement out of the substrate prior to emergence would expose fry to predation by predators above rock substrate. Predators found within the substrate include crayfish (Orconectes spp.), sculpins, and mudpuppies (Hacker 1956, Stauffer and Wagner 1979, Horns and Magnuson 1981, Savino and Henry 1991, Savino and Miller 1991). Above the substrate, this behavior would expose fry to predation by native demersal or benthic fish such as round whitefish (Prosopium cylindraceum), burbot, and suckers (Catostomus spp.) (Stauffer and Wagner 1979). Potential pelagic predators include the exotic alewife and rainbow smelt (Osmerus mordax), although smelt may not be an important predator on lake trout fry (Jones et al. 1995). Alewives, in contrast to smelt, may be important predators of lake trout fry. Alewives congregate in large schools in near-shore areas of the Great Lakes in the spring (Janssen and Brandt 1980, O’Gorman et al. 1991) and move shoreward at night (Ross et al. 1993). This movement at night can occur over lake trout spawning areas at times when fry move out of the substrate (Krueger et al. 1995). Lake trout are adapted to conditions where few pelagic predators are present on spawning areas at the time fry are emerging from the substrate. Thus, in the absence of such predators, moving out of the substrate as sac fry may not increase predation risk, but could be a maladaptation when non-native predators such as alewife are abundant. Based on this study, sac fry would be vulnerable to predation above the substrate before swimbladder filling, especially from the mid F210 stage on. While sac fry
movement prior to swimbladder filling is probably not to the surface, the fry have left the protection of the substrate interstices and become vulnerable to pelagic and epibenthic predators. This vulnerability of sac fry is in addition to the time period when alevins go to the surface to fill their swimbladders. After fry fill their swimbladders, fry may be better able to avoid predators.

Models of lake trout egg and fry mortality caused by predators (Jones et al. 1995, Savino et al. 1999) required relatively high rates of fry predation (at least 4 to 6 fry/m²/d) to greatly reduce abundance. The results of this study show that fry from a single fertilization day are vulnerable to pelagic and epibenthic predators for about 2 weeks before and during swimbladder filling. With spawning lasting about 30 days in the Great Lakes, fry with unfilled swimbladders may be present above the substrate for at least 45 days, during which time the predation rate may be great given the relatively poor swimming ability of sac fry. This extended period of vulnerability in the presence of non-native predators could reduce the potential for successful reproduction and rehabilitation of lake trout in the Great Lakes.

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