J. Great Lakes Res. 21 (Supplement 1):233–245
Internat. Assoc. Great Lakes Res., 1995

Hatching, Dispersal, and Bathymetric Distribution of Age-0 Wild Lake Trout at the Gull Island Shoal Complex, Lake Superior

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ABSTRACT. *We studied age-0 lake trout* (Salvelinus namaycush) *associated with spawning and nursery areas of the Gull Island Shoal complex in western Lake Superior. Post-emergent age-0 lake trout were captured on rocky spawning substrate with a 3-m beam trawl and at the nursery area with a bottom trawl from June to September 1990 and June to August 1991. Catch data suggested that age-0 lake trout move distances of 7–11 km to the nursery area over a 3-month period. Water currents, measured at Gull Island Shoal, may be a part of the transport mechanism. Examination of daily-growth increments on the sagittae and back-calculation from the date of capture revealed that most fish hatched between 6 June and 19 July in 1990 and between 30 April and 30 May in 1991. The duration of the hatch was 100 days in 1990 and 120 days in 1991, and the estimated incubation period is about 7 months for lake trout eggs at this site. Similar hatch-date distributions of age-0 captured on different sampling dates suggested that natural mortality was low.*

INDEX WORDS: *Lake trout, hatching date, bathyretric distribution, seasonal distribution, early life history, Lake Superior.*

INTRODUCTION

Historically, the lake trout (*Salvelinus namaycush*) was one of the most important species in the commercial and sport fisheries of the Great Lakes (Smith 1972, Lawrie 1978). By 1960, predation by the parasitic sea lamprey (*Petromyzon marinus*), combined with overfishing in some areas, caused the extermination of lake trout from Lakes Michigan, Erie, and Ontario, and most populations in Lakes Superior and Huron (Smith 1968, 1972; Lawrie and Rahrer 1972; Christie 1974; Pycha and King 1975; Walters *et al.* 1980). With the advent of chemical control of larval sea lamprey (Smith *et al.* 1974), it became feasible to attempt to rebuild populations of adult lake trout by stocking large numbers of hatchery-reared fish. However, the development of self-reproducing stocks of lake trout has occurred only in Lake Superior, where some inshore stocks and most offshore stocks of lake trout survived sea lamprey predation (see Cornelius *et al.* 1995, Elrod *et al.* 1995, Eshenroder *et al.* 1995, Hansen *et al.* 1995, Holey *et al.* 1995). Lack of homing to appropriate spawning substrates, contaminants, and insufficient number of spawners have been proposed as reasons for the slow progress toward rehabilitation (Eshenroder *et al.* 1984), but fail to completely explain the limited success seen to date. It has been hypothesized that recruitment from hatchery-reared lake trout may be limited by poor survival between egg deposition and completion of the first year of life. Therefore, any knowledge of the reproduction and early life history of lake trout from a self-reproducing, wild population should be useful in determining the reasons for the limited success of hatchery-reared fish to produce offspring.

Since 1965, the U. S. Fish and Wildlife Service (most of the Research Branch is now the National Biological Service) has monitored the abundance of wild age-0 lake trout with bottom trawls each fall in a nursery area south of Michigan Island and approximately 11-km southwest of Gull Island Shoal, Lake Superior (Schram *et al.* 1995). These fish were presumed to be offspring of the Gull Island Shoal population, which is composed mostly the of progeny of native lake trout that survived the peak of sea lamprey predation (Dryer and King 1968, Swanson and Swedberg 1980). However, movement of fry from the spawning area to the nursery area had not been documented. In 1986-1989, the U. S. Fish and Wildlife Service did exploratory work with bottom trawls and a benthic sled (Reynolds and DeGraeve 1972) on a variety of dates and at locations in and adjacent to the nursery area and the spawning reef. Age-0 lake trout were captured at many locations around Michigan Island, but none were captured on or around Gull Island Shoal.

In 1990 a more systematic sampling design was implemented and detailed analyses of the specimens and data collected were begun. The objectives of this expanded study were to: 1) test the hypothesis that age-0 lake trout captured at the nursery area south of Michigan Island were from spawning at the Gull Island Shoal complex; 2) describe the bathymetric distribution of age-0 lake trout at the nursery area; 3) determine hatching dates and the duration of the hatching period by examination of sagittal microstructure; 4) examine environmental conditions on the reef as they may relate to the early life history of lake trout; and 5) determine extent and timing of natural mortality.

STUDY AREA

Gull Island Shoal (46°57′ N, 90°24′ W) and the nursery area at Michigan Island (46°52′ N, 90°28′ W) are located in western Lake Superior at the eastern edge of the Apostle Islands (Fig. 1). The geology of the area and surrounding islands is dominated by Precambrian sandstone bedrock deposited as sediment along a north-

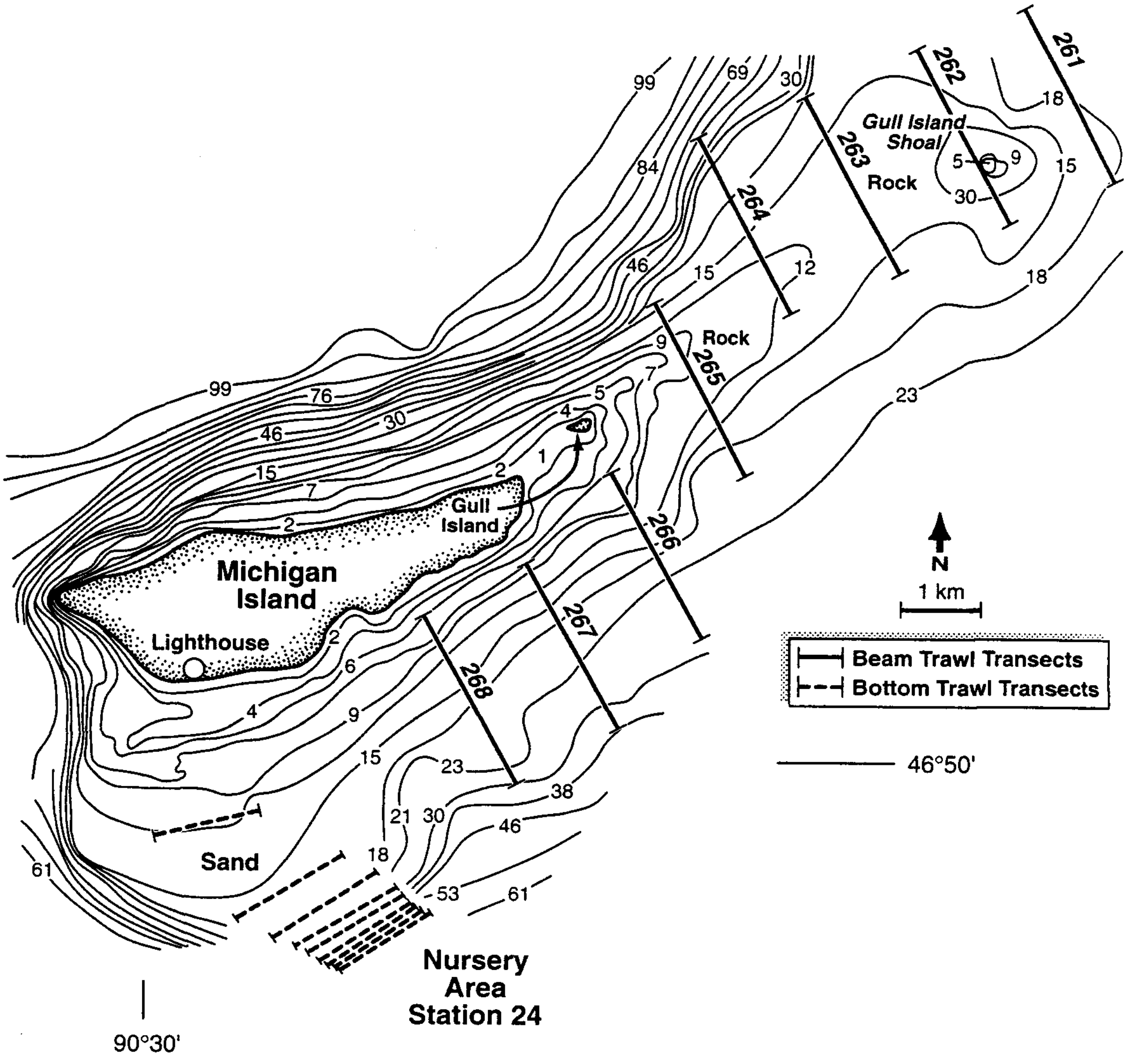

FIG. 1. Location of the Gull Island Shoal complex in Wisconsin waters of western Lake Superior and sampling locations on the spawning grounds (transects 261–268) and at the nursery area (station 24). Contour depths are in meters.

east-southwest axis. Stamm *et al.* (1981) provide details on substrate composition and bathymetry of the reef proper. Spawning habitat of varying quality extends intermittently from the apex of the reef southwest to the north end of Michigan Island and encompasses an area of about 3,100 ha. Lake trout in spawning condition can be captured in October throughout this area (S. Schram, Wisconsin Department of Natural Resources, Bayfield, WI, personal communication, December, 1993), but exact locations of egg deposition have not been found. The lake trout nursery area is located along the southeast shore of Michigan Island from the south end of the island northeast to almost the extreme north end and extends out into the lake from Michigan Island about 2.5 km. The distance between the nursery area and the apex of Gull Island Shoal is about 11 km. The depth profile of the nursery area along a 120° course from the Michigan Island lighthouse ranges from 10 m nearshore to 40 m about 1.9 km further out, where a steep bank descends to 70 m. The substrate is mostly current-rippled sand (J. P. Keillor, University of Wisconsin, Madison, WI, personal communication, December, 1993), and the coastal geomorphology of Michigan Island suggests that this sand is the product of long-term erosion and transport of littoral sediment from the northeast (Gull Island Shoal, Michigan Island, and Gull Island) to the southwest by currents associated with prevailing northeast winds during periods of lower lake levels (Curtis E. Larsen, U. S. Geological Survey, Reston, VA, personal communication, September, 1994).

METHODS

Wild age-0 lake trout were captured on Gull Island Shoal with a 3-m-wide beam trawl similar to the 1.2-m-wide trawl described by Stauffer (1981). The capture net (length 7.6 m, square width 3 m, cod-end width 0.3 m) was constructed of four panels of 6.35-mm bar-mesh nylon net, and the cod end (length 0.6 m) was made of 3.18-mm bar-mesh nylon net. Chafing gear, attached to the rear and bottom of the trawl frame, was made of a 9.1 m × 3.0 m heavy-vinyl, rip-stop tarpaulin and protected the net and cod end from tearing on rocks. The beam trawl was fished at about 1.6 km/hr off the port-side trawl winch of the 17-meter stern trawler-gill netter R/V *Siscowet*; faster speeds caused damage to the trawl frame. Just enough cable was deployed to place the trawl on bottom, and this length was determined by feeling for the intensity of vibrations transmitted up the cable from the trawl frame as it contacted rocks. We fished at eight transect stations (stations 261–268) evenly spaced along LORAN-C lines that ran perpendicular to the northeast-southwest axis of Gull Island Shoal (Fig. 1). Transects were about 2.1 km long and spaced about 1.4 km apart and ran across-contour in depths that ranged from 10 to 26 m.

We used a semi-balloon bottom trawl (11.9-m headrope, 15.6-m footrope, 12.7-mm stretched-mesh cod end) to sample age-0 lake trout at the nursery area south of Michigan Island (station 24). At the nursery area, one 15-minute tow at 4.3 km/hr was made within each of the following nine depth-contour intervals (m); 10–14, 15–19, 20–24, 25–29, 30–34, 35–39, 40–44, 45–49, and 50–54. Transect stations on Gull Island Shoal (n = 8) and depth contours (n = 9) at the Michigan Island nursery area were sampled five times in May-September, 1990, and five times in June-August, 1991. Additional catch data from the nursery area in July-October, 1965–1989, obtained by the same methods, were also analyzed to better determine seasonal bathymetric distribution of age-0 lake trout.

In 1990 and 1991, all age-0 lake trout captured were counted, measured to the nearest 1 mm, and preserved immediately in 95% ethanol or by freezing in water. All fish were alive at capture. Catches of age-0 lake trout were converted to number per hectare (density) based on the area swept by each sampling gear. Because the capture efficiencies of both trawls were unknown, we regard the calculated densities as minimum estimates. All sampling was done during the day because earlier comparisons between day and night sampling indicated that more lake trout were captured during the day (National Biological Service, Great Lakes Science Center, Ashland, WI, unpublished data).

In the laboratory, all, or subsamples of 5, preserved lake trout from each sampling site and date were measured to the nearest 0.1 mm and weighed to the nearest 0.001 g. Sagittal otoliths, used to determine daily ages, were extracted with microforceps under a dissecting microscope (8–40×). Tissue was removed from sagittae in a water-filled petri dish by twirling the sagittae in the bristles of a number-0, sable-hair artist brush. Sagittae were allowed to air dry and then were mounted sulcus-side up on a glass slide in a drop of Hillquest[1] (Hillquest, Seattle, WA) thin-section epoxy, placed into a 55°C oven for 10 minutes to remove air bubbles from the epoxy, and allowed to cure at room temperature for at least 24 hr.

Maximum sagittae length and width were measured (0.01 mm) with a filar ocular micrometer. Sagittae were hand ground to the mid-sagittal plane to expose the incremental microstructure by using 600-grit, silicon-carbide wet/dry sandpaper followed by 1,000-grit, silicon-carbide grinding abrasive on a plexiglass plate. During grinding, sagittae were periodically checked under a compound light microscope (200–400×) to gauge the progress of material removal and degree of exposure of the microstructure. Ground sagittae were polished with aluminum oxide polishing compound on a wet-felt lap mounted to a plexiglass plate. Acid etching was not required to enhance the microstructure detail.

Ages in days were assigned to subsamples of age-0 fish by counting the growth increments along the poste-

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[1] Mention of trade names or manufacturers does not imply U. S. government endorsement.

rior field of the sagittae under light microscopy (400–1,000×). Three counts were made for each sagitta, and the mean of these counts was assigned as the estimated age. Increments were assumed to be daily (Campana and Neilson 1985), and daily formation has been validated by Brothers (1990) for lake trout. Hatching marks were not evident on all sagittae so all increments interpreted to be daily rings were counted. Examination of sagittae from known-age larvae, incubated in Lake Superior water at ambient lake temperatures, revealed that some increments (< 8) are deposited before hatching (National Biological Service, Great Lakes Science Center, Ashland, WI, unpublished data). Back-calculated hatching-date distributions for all age-0 fish were obtained by linearly regressing age on total length for all aged fish each year, estimating ages of unaged fish from the regressions, and subtracting the estimated ages from the day of year captured.

Water temperature, current direction, and current velocity were measured on Gull Island Shoal with Smart Acoustic Current Meters[1] (Neil Brown Instrument Systems, Inc.—Cataumet, MA) between June 1990 and July 1992 (Table 1). Two moorings, each with one current meter located 1 m above bottom, were established for each summer and winter measurement season except during the summer of 1992 when only one current meter was available. Failure of lithium batteries, water leakage, and other electronic problems prevented collection of complete time series for some moorings. Using all available temperature data from moorings between 15 and 18 m (recording data between depths of 14 and 17 m), we constructed a continuous time series from 1 June 1990 to 20 September 1991. Data from these depths, where the best incubation habitat occurs on Gull Island Shoal (National Biological Service, Great Lakes Science Center, Ann Arbor, MI, unpublished data), were considered the most representative of the thermal environment experienced by lake trout eggs and young. From this time series, we calculated the daily temperature units (DTU) from 17 October 1990 (day 290), considered the peak of the spawning period, to the modal day of hatching for the 1991 year class. Mean daily water temperatures were estimated by linear interpolation for days when no data were available.

RESULTS

Densities and Mean Lengths

Catches of age-0 lake trout varied across sampling locations, dates, and years. No age-0 lake trout were captured on either the reef or the nursery area in May or June 1990 (Table 2). By 23–25 July 1990, age-0 lake trout were captured at all transect stations on the reef and at the nursery area, and all fish captured lacked yolk sacs and corresponded closely with Step $A^2 12$ in their embryological development (Balon 1980). Densities on this date ranged from 1.6 fish/ha at stations 261, 262, 263 at the reef summit to 10.9 fish/ha at station 267 located near Gull Island. The mean density of age-0 lake trout during 23–25 July 1990 was 4.1 fish/ha on the reef (stations 261–268, n = 8) and 3.7 fish/ha on the nursery area (station 24 all depths, n = 9), but this difference was not statistically significant ($\log_e$ x +1 transformation, P = 0.38; t = 0.90). During 13–16 August 1990, catches of age-0 fish were made only at stations 266 and 267 near the nursery area and at the nursery area, but the difference in mean density between the reef (1.0 fish/ha) and the nursery area (7.6 fish/ha) was not significant (P = 0.08; t = –1.87). By 20–26 September 1990, no age-0 fish were captured on the reef, but they were captured at the nursery area at a density greater (74.6 fish/ha) than that measured previously on any of the transects on the reef. Combined densities from all transect stations on the reef and all depth contours at the nursery area when age-0 lake trout were captured were not significantly different across sampling dates (P = 0.08; repeated measures ANOVA; F = 2.72).

Trends in catch data were similar both years, but age-0 lake trout were captured at both the reef and nursery area earlier in 1991 than in 1990 (Table 2). During 17-19 June 1991, age-0 lake trout were captured at all stations on the reef and at the nursery area, much as seen on 23-25 July 1990, but densities in 1991 were significantly higher at the reef than at the nursery area (P < 0.0001; t = 5.64). In July–August 1991, densities declined at stations on the reef and increased at the nursery area, but densities were not significantly different between the reef and nursery area on 9–11 July 1991 (P = 0.21; t = –1.32), 15–17 July 1991 (P = 0.23; t = –1.26), or 5–7 August 1991 (P = 0.22; t = –1.28). By 27–29 August 1991, age-0 lake trout were captured only at reef stations close to the nursery area and at significantly higher densities at the nursery area (P = 0.002; t = -3.68). As in 1990, combined densities from all transect stations on the reef and all depth contours at the nursery area were not significantly different across sampling dates in 1991 (P = 0.12; repeated measures ANOVA; F = 1.91). Analysis of combined 1990 and 1991 density data for the reef indicated that stations 266, 267, and 268 had significantly higher densities than stations further to the northeast (P < 0.0001; ANOVA; F = 6.00).

Total lengths of age-0 lake trout differed by date and location of capture (Table 2). In 1990, mean total length for all age-0 fish across stations increased from 35 mm on 23–25 July to 60 mm at the end of September. Differences in mean length among all sampling dates in 1990 were statistically significant (P < 0.0001; ANOVA; F = 405.6). In 1991, mean total length increased from 28 mm on 17–19 June to 53 mm on 27–29 August and differences among dates were significant (P < 0.0001; ANOVA; F = 432.7). Mean lengths of age-0 lake trout captured at the nursery area were significantly larger

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TABLE 1. Location, waters depths, and deployment and retrieval dates for temperature/current meter moorings on Gull Island Shoal, Lake Superior, 1990–1992. Devices measured conditions 1 m above the bottom.

Mooring	Location	Depth Depth (m)	Deployment	Retrieval	Number days with data
1	46°56′44″ 90°23′36″	7.0	31 May 90	07 May 91	126
2	46°55′40″ 90°24′26″	15.2	31 May 90	07 Nov 90	110
3	46°55′38″ 90°24′29″	16.0	07 Nov 90	07 May 91	102
4	46°56′26″ 90°23′10″	18.0	07 Nov 90	07 May 91	120
5	46°55′44″ 90°24′36″	14.9	07 May 91	07 Nov 91	139
6	46°56′41″ 90°23′32″	7.9	07 May 91	07 Nov 91	76
7	46°55′42″ 90°24′30″	15.4	11 Nov 91	25 Aug 92	0
8	46°57′01″ 90°23′22″	16.0	11 Nov 91	13 Jul 92	0
9	46°56′45″ 90°23′39″	8.5	13 Jul 92	25 Oct 92	104

TABLE 2. Estimated densities (number/ha) of age-0 wild lake trout at Gull Island Shoal and the Michigan Island nursery area by sampling period and location (see Fig. 1), 1990 and 1991. Mean lengths (mm) at capture are in parentheses.

	1990					1991				
Station Number	May 30– June 1	June 25–27	July 23–25	August 13–16	September 20–26	June 17–19	July 9–11	July 15–17	August 5–7	August 27–29
261	0.0	0.0	1.6 (28)	0.0	0.0	1.6 (28)	0.0	0.0	0.0	0.0
262	0.0	0.0	1.6 (25)	0.0	0.0	1.6 (28)	0.0	0.0	0.0	0.0
263	0.0	0.0	1.6 (26)	0.0	0.0	3.1 (31)	0.0	0.0	0.0	0.0
264	0.0	0.0	3.1 (26)	0.0	0.0	4.7 (27)	1.6 (33)	1.6 (35)	0.0	0.0
265	0.0	0.0	1.6 (36)	0.0	0.0	1.6 (31)	0.0	0.0	0.0	0.0
266	0.0	0.0	3.1 (35)	6.2 (46)	0.0	9.3 (29)	1.6 (32)	1.6 (36)	15.5 (41)	0.0
267	0.0	0.0	10.9 (32)	1.6 (43)	0.0	14.0 (28)	68.3 (33)	43.5 (34)	41.9 (40)	14.0 (46)
268	0.0	0.0	9.3 (33)	0.0	0.0	10.9 (27)	26.4 (32)	18.6 (34)	9.3 (38)	6.2 (44)
24	0.0	0.0	3.7 (39)	7.6 (50)	74.6 (60)	0.2 (27)	11.3 (36)	11.9 (37)	12.8 (46)	25.4 (54)

than those captured on the reef in 1990 (P < 0.0001; t = –15.3) and in 1991 (P < 0.0001; t = –14.5).

Bathymetric Distribution

We examined the bathymetric distribution of age-0 lake trout at the nursery area across sampling dates in 1990 and 1991 and from the catches of age-0 fish at this area during 1965–91. On 23–25 July 1990, the bathymetric distribution of age-0 lake trout was bimodal with higher densities at the 15- to 19-m and the 35- to 39-m depth intervals than at other depths (Fig. 2). On 13–16 August 1990, total densities had increased more than two-fold from July, and most fish were captured at 15–19 m. By 20–26 September 1990, densities were about 10 times greater than in August, and most fish were found at 30–44 m. A similar trend in bathymetric distribution was seen in 1991. In June, all fish were captured in less than 20 m of water, and, as the season progressed and total densities increased, more fish were captured at deeper depths. Analysis of the combined length-frequency data from 1990 and 1991 indicated that fish length increased significantly with depth of capture (P < 0.0001; ANOVA; F = 25.60) (Fig. 3) .

The bathymetric distribution of 10,402 age-0 lake trout caught in 707 bottom trawl tows in 1965–1991 at the nursery area shows conclusively that age-0 lake trout move from depths less than 20 m in late July to depths greater than 40 m in early October (Fig. 4). Temperature

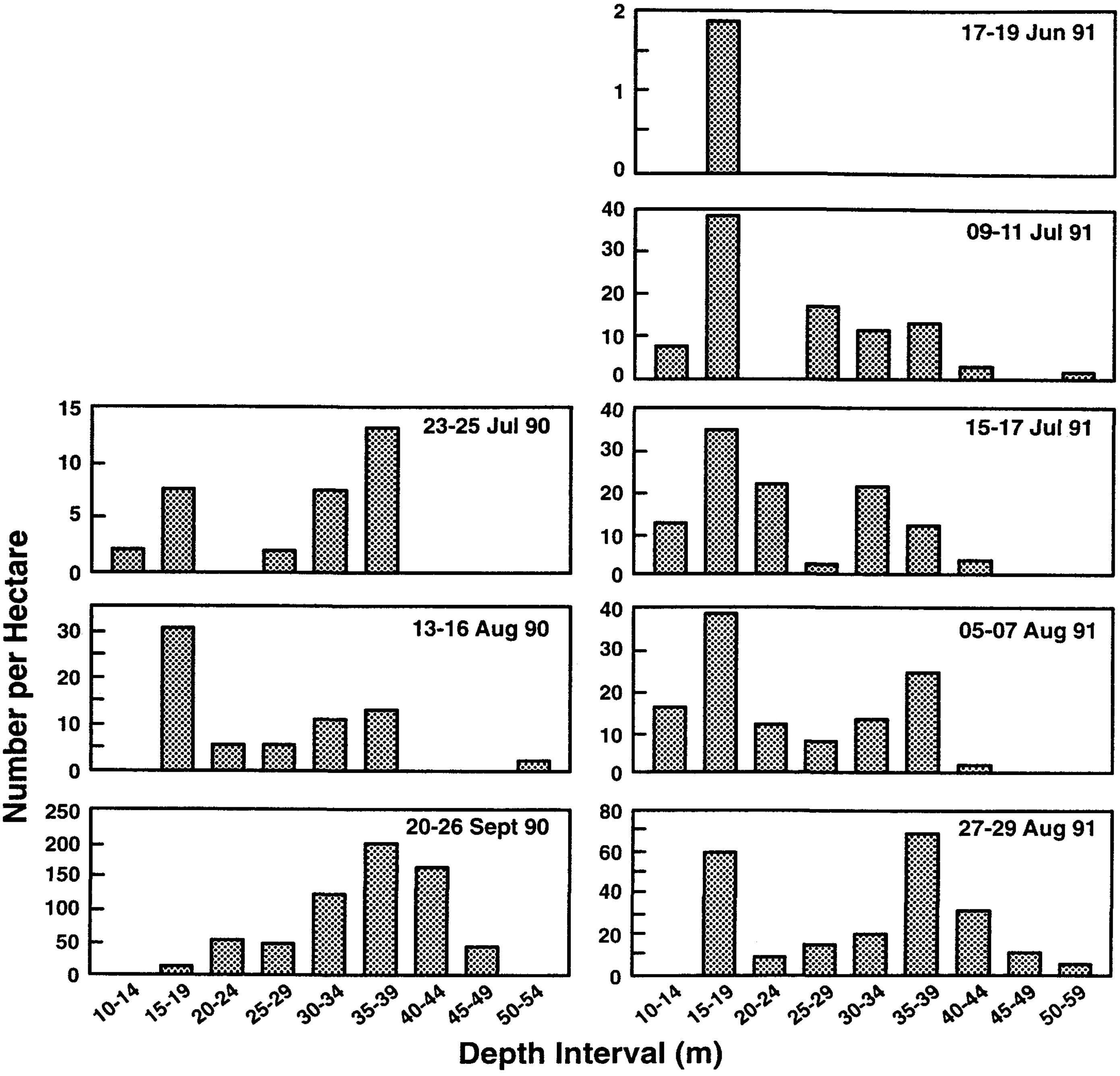

FIG. 2. Bathymetric distribution of age-0 lake trout by date of capture at the Michigan Island nursery area in 1990 and 1991.

profiles measured at the time of sampling showed that age-0 lake trout were exposed to a wide range of water temperatures from mid-July to mid-October. In late July when most fish were concentrated in less than 20 m of water, mean bottom temperatures were about 14°C at the 0- to 9-m depth interval and about 8°C at 10–19 m (Fig. 4). In August and early September, mean bottom temperatures ranged from 13.0°C at 10–19 m to 3.1°C at 50–59 m, and age-0 lake trout were captured at all depths. In late September and early October most age-0 lake trout had descended to depths where temperatures were between 4.4 and 6.5°C.

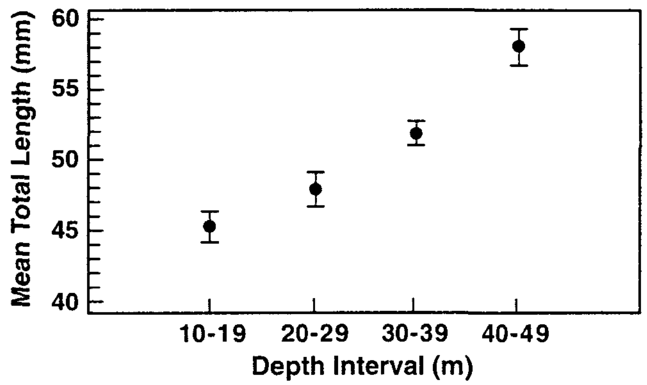

FIG. 3. Mean length (mm) and 95% confidence intervals for age-0 lake trout by 10-m depth intervals at the Michigan Island nursery area in 1990 and 1991.

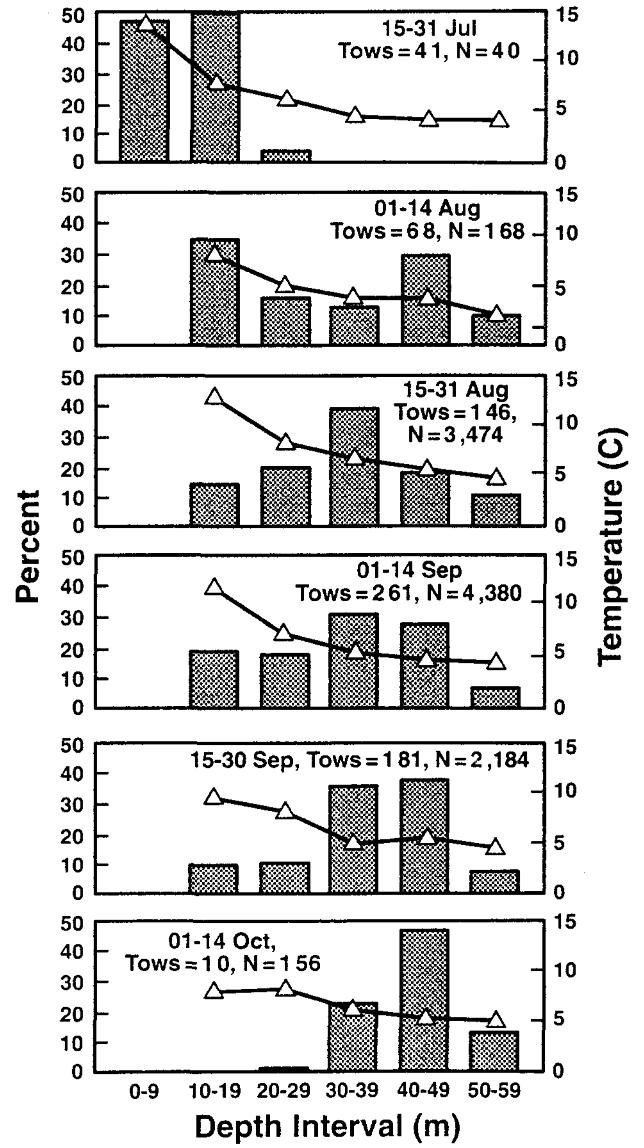

FIG. 4. Percent of age-0 lake trout captured and mean bottom temperatures (C) at various depth intervals for 2-week periods at the Michigan Island nursery area. Data from 707 on-contour trawl tows taken during 1965–1991 at station 24.

Ages and Hatching Dates

Sagitta length (SL) and width (SW) regressed separately against fish total length (TL) resulted in the following isometric relationships:

$$SL = 0.0806 + 0.0144\ (TL)$$
$$(n = 283,\ r^2 = 0.87,\ P < 0.0001)$$

and

$$SW = 0.0314 + 0.0112\ (TL)$$
$$(n = 283,\ r^2 = 0.91,\ P < 0.0001)$$

and indicated that sagittae size increased with total length. Linear functions best described the relationship between age in days and total length and resulted in the following year-specific relationships:

$$1990\ Age = -55.267 + 2.388\ (TL)$$
$$(n = 88,\ r^2 = 0.69,\ P < 0.0001)$$

and

$$1991\ Age = -67.903 + 3.361\ (TL)$$
$$(n = 200,\ r^2 = 0.59,\ P < 0.0001).$$

In 1990, modal ages of age-0 lake trout increased from 33 days on 23–35 July to 95 days on 20–26 September (Table 3). In 1991, modal ages increased from 28 days on 17–19 June to 110 days on 27–29 August. The difference in days elapsed and the difference in the modal ages were similar within all sampling periods in 1990 but only within sampling periods in June and July in 1991. Modal ages were slightly higher for fish captured on sampling dates in August 1991 compared to the number of days that elapsed between sampling periods.

Hatching-date frequency distributions differed between the 2 years (Fig. 5). In 1990 the modal hatching date was 14 June (day 165), and most hatching occurred between 6 June (day 157) and 19 July (day 200). Duration of the hatch was approximately 100 days. In 1991, hatching occurred earlier than in 1990, and most estimated hatching dates were between 30 April (day 120) and 30 May (day 160). The modal date was 28 May (day 148) and the duration of the hatch in 1991 was 120 days. Earlier hatching in 1991 corresponds well with the catch data. No fish were captured in June 1990, presumably because most had not emerged from the substrate, but in 1991 age-0 lake trout were captured at all locations on 17–19 June.

TABLE 3. Estimated modal ages in days, changes in modal age, and days elapsed between sampling periods for age-0 lake trout from the Gull Island Shoal and Michigan Island nursery area, 1990 and 1991.

Sampling Period	Number of fish	Modal Age in Days	Change in Age	Change in Days
23–25 Jul 90	38	33	—	—
13–16 Aug 90	40	54	21	21
20–26 Sep 90	251	95	41	40
17–19 Jun 91	36	28	—	—
9–11 Jul 91	114	47	19	22
15–17 Jul 91	97	52	5	6
5–7 Aug 91	102	78	26	17
27–29 Aug 91	130	110	33	22

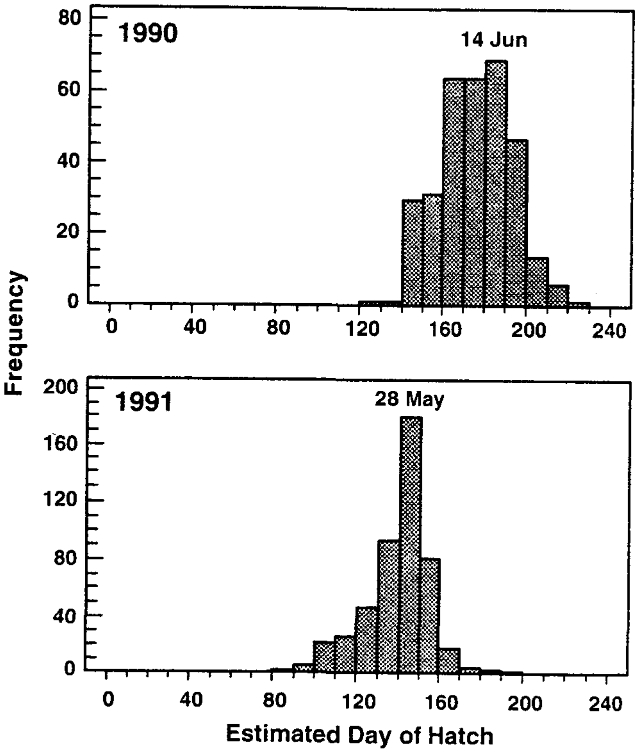

FIG. 5. Estimated hatching-date distributions of the 1990 and 1991 year classes of age-0 lake trout. Dates presented are modal hatching dates.

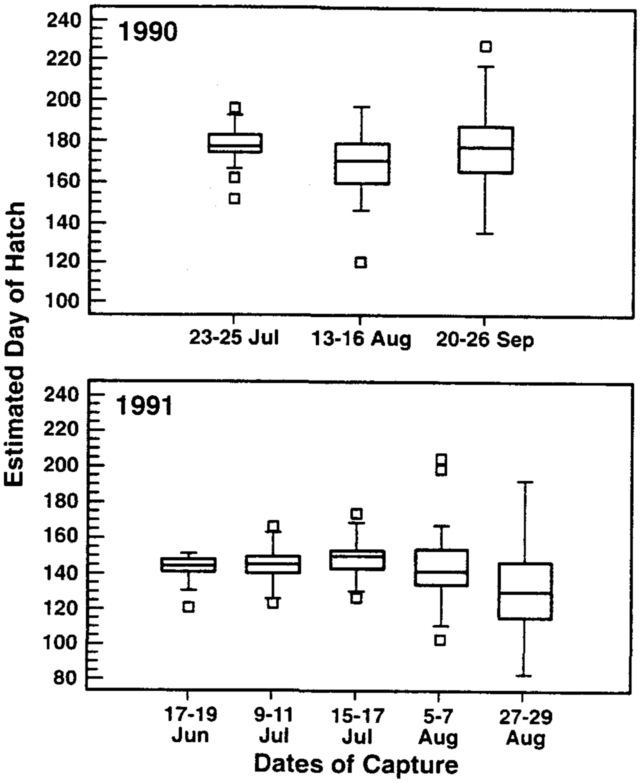

FIG. 6. Hatching-date distributions by sampling date for the 1990 and 1991 year classes of age-0 lake trout.

Mean estimated hatching dates varied with the day of capture in 1990 and 1991 (Fig. 6). In 1990, mean hatching dates of fish captured on 23–25 July (day 178) and 20–26 September (day 176) were significantly greater than for fish captured on 13–16 August (day 168) ($P < 0.03$; ANOVA; $F = 3.79$), but differences were small. In 1991, similar mean hatching dates were calculated across sampling dates. The mean hatching date was significantly less for fish captured on the last sampling period in August ($P < 0.0001$; ANOVA; $F = 22.42$), but differences among the remaining sampling dates were not significant.

Water Temperature and Currents

In 1990, mean daily water temperature increased from about 4.5°C on 31 May to a maximum of about 12°C at the beginning of August and oscillated around 10°C until September when the current meter malfunctioned (Fig. 7). From early November to the end of December 1990, water temperatures declined from about 7°C to about 1°C, and remained between 0 and 1°C until early March, 1991. No data were available from early March to early May, but we assumed that water temperatures began to rise from below 1°C in mid-February to about 10°C in late-July. The total of daily temperature units required for the incubation of the 1991 year class was about 520 (C). We could not estimate DTU for the 1990 year class because water temperature data were not available for the entire incubation period. The 1991 year class hatched when water temperatures were between 2 and 3°C.

Currents measured at 14 m on Gull Island Shoal varied by month and year during months when age-0 lake trout were sampled. In 1990, currents moved predominantly along a course of 235° (northeast to southwest) in June, 255° in July and August, and 275° in September. Composite current direction over the 4-month period was southwesterly (~ 255°) (Fig. 8). In 1991, current direction was 295° in May, 160° in June, 155° in July, 170° in August, and 190° in September. Composite current direction for the 5-month period was south-southeasterly (~ 165°) (Fig. 8).

DISCUSSION AND CONCLUSIONS

Catches from the beam-trawl on Gull Island Shoal and bottom trawls at the Michigan Island nursery area in 1990 and 1991 indicate that age-0 lake trout from the nursery area are the progeny of lake trout that spawned on or near Gull Island Shoal. From June through July to August through September, densities of age-0 lake trout decreased on the reef and increased at the nursery area. The linear distance moved by age-0 from spawning areas to the nursery grounds ranged between 7 and 11 km. Schram *et al.* (1995) found a positive and linear relationship between the relative abundance of wild female spawners at and near the shoal and the density of age-0 fish captured at the nursery area the following fall. We believe that these data are strong evidence that Gull Island Shoal spawners are the parents of young lake trout

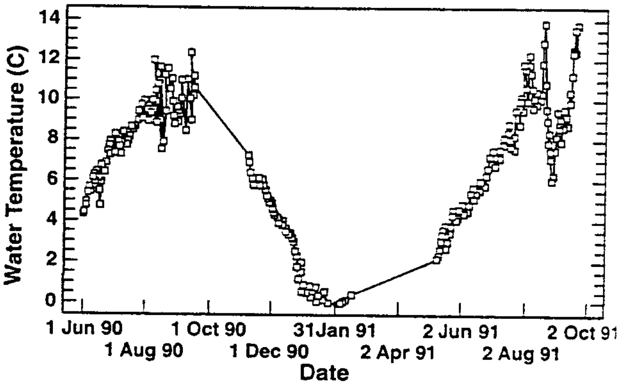

FIG. 7. Water temperatures at 15–18 m on Gull Island Shoal measured during June 1990–September 1991. Straight lines indicate periods when no data were collected.

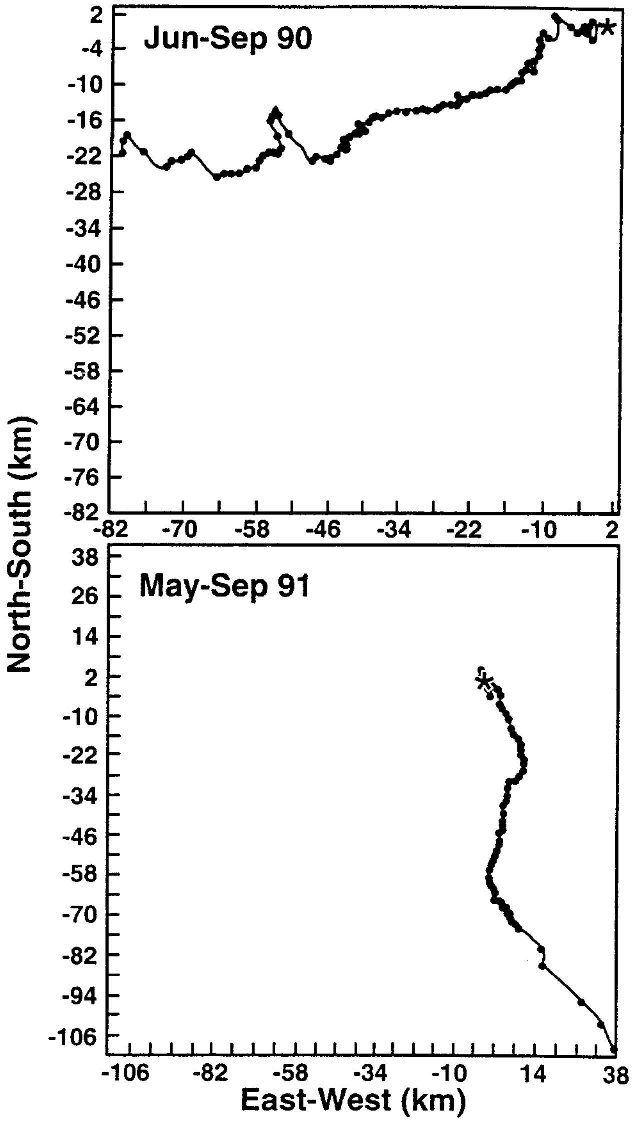

FIG. 8. Composite progressive vector plots of currents at 14 m on Gull Island Shoal in June–September 1990 and May–September 1991.

captured on the Michigan Island nursery area. Recruitment from other shoals in the region is very unlikely because they are all separated from the nursery area by deep channels.

Our catch data indicate that Gull Island Shoal proper (stations 261–265) may not be the major source of recruitment. Densities of age-0 lake trout were consistently higher from stations adjacent to Gull Island and the northeast tip of Michigan Island (266–268) than on the shoal, which suggests that the main egg deposition may be nearer to Michigan Island. However, egg traps that were fished in this area in October 1991 captured no lake trout eggs (Schreiner *et al.* 1995). In addition, the substrate relief is much lower at this end of the reef than further to the northeast. Therefore it is possible that the catch data may be biased by varying catchability of lake trout among stations. Hudson *et al.* (1995), examined stomachs of slimy sculpins (*Cottus cognatus*) collected in beam-trawl catches from this study and found six lake trout eggs, all from sculpins captured on stations 263 and 264 in November 1991. These contradictory data make a determination of the importance of specific areas for egg deposition inconclusive.

Our results on age-0 lake trout habitat use, other research, and *Mysis* biology suggest that sand substrate is important to age-0 lake trout. The nursery area at Michigan Island is composed mostly of sand substrate. Peck (1982) showed movements of age-0 lake trout from an artificial spawning area to sand substrate as the season progressed from May to August. Similarly, Eschmeyer (1955) captured lake trout fry at a sandy area adjacent to spawning grounds in central Lake Superior, and he suggested that these fish had not moved far from their hatching site. *Mysis* are an important food of young lake trout (Eschmeyer 1955, Swedberg and Peck 1984, Hudson *et al.* 1995). Sandy substrates, such as where age-0 lake trout are found, are a source of the foods of *Mysis* which are known to utilize macrobenthos and benthic detritus (Grossnickle 1982, Beeton and Gannon 1991). Juday and Birge (1927) noted that *Mysis* were most abundant where the bottom consisted mostly of sand in Green Lake, Wisconsin. We commonly captured *Mysis* as by-catch at beam trawl stations near the nursery area and in bottom trawls at the nursery area were the substrate was mostly sand. Divers have observed *Mysis* near the bottom over sand at densities of about 200/m^2 in this same area during August 1980 (J. P. Keillor, University of Wisconsin, Madison, WI, personal communication, December, 1993).

Water currents may be important in the transport of emergent lake trout from the spawning area to the nursery area. Predominant current directions were westerly in 1990 and southerly in 1991 during the months when age-0 lake trout were captured. The Michigan Island nursery area is located southwest of the spawning area and midway between the predominant current vectors measured in June-September 1990 and May-September 1991. While this does not clearly demonstrate that currents are a major component of a transport mechanism, currents in 1990 and 1991 could have transported fish from the area of incubation and hatching southwest toward the nursery area. Densities of age-0 lake trout declined on the reef and increased at the nursery area during months when the seasonal current vectors were focused in directions toward the nursery area (NOAA, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, unpublished data). Due to mass conservation, currents must follow the bathymetric contours of Gull Island Shoal which run northeast to southwest, and therefore could transport age-0 lake trout from the reef southwest to the nursery area. Sand ripples, which are formed perpendicular to the current, were oriented southeast to northwest and east to west at the north tip of Michigan Island on 18 October 1989 and suggest that water currents may be moving southwesterly (or northeasterly). Waves and currents driven by northeasterly winds are responsible for the long-term transport of sand and finer particles eroded from the reef and islands to the nursery area (Curtis E. Larsen, U. S. Geological Survey, Reston, VA, personal communication, September, 1994). The apex of the reef is composed of large boulders that give way to rubble and cobble substrate to the southwest and to fine sand on the southeast side of Michigan Island (Stamm *et al.* 1981). Therefore the forces that created the nursery habitat may also be responsible for moving young lake trout to it.

Our data indicate that until the end of July most age-0 lake trout can be found in less than 20 m of water for at least 2 months. Stauffer (1981), Wagner (1981), and Peck (1982) suggested an even shallower (< 10 m) distribution at other locations in Lake Superior. Jude *et al.* (1981) captured age-0 lake trout from April to August at depths of 6–15 m in Lake Michigan. These data from the Great Lakes are in marked contrast to observations from small inland lakes where lake trout move from the spawning beds to deeper water soon after emergence (Royce 1951, Martin 1957, DeRoche 1969). Our data show that age-0 lake trout move to depths greater than 30 m in late August and early September and are found mostly between 30 and 60 m by early October. Rising water temperatures do not appear to be responsible for this migration. In late July (Fig. 5), many age-0 lake trout were found in less than 10 m of water where mean water temperatures were about 12°C. In general, there was no inverse relation between catches at any depth and water temperature, probably because water temperatures at this location rarely exceed 15°C, the apparent upper avoidance temperature for young lake trout based on laboratory (McCauley and Tait 1970) and field (Jude *et al.* 1981, Peck 1982) observations. In this study, most age-0 lake trout were captured at temperatures that ranged from 4 to 8°C.

Hatching dates for lake trout from the Gull Island Shoal complex are later than those reported for most populations. In inland lakes, hatching times occur in late November (Loftus 1958) and December (Paterson 1968) in the same year of egg deposition, January (Royce 1951), February (Martin 1957), March (Martin 1957, DeRoche 1969), April (Greeley 1936, Royce 1951), and May (Hacker 1957). Eschmeyer (1955) reported collecting one egg and two sac-fry in March 1953 at a depth of 18 m near Laughing Fish Point in south central Lake Superior. On 22–23 June 1953 he collected 29 fry, 22–30 mm long, many of which still had remnants of yolk, at a sandy area adjacent to spawning grounds near Laughing Fish Point. From these observations we infer that duration of hatching spanned at least 80 days, similar to our findings at Gull Island Shoal. Peck (1982) reported capturing emergent lake trout throughout May in Presque Isle Harbor, Lake Superior, which suggested that most hatching occurred sometime in April. In Lake Michigan, fry collected near Port Sheldon in April and June were presumed to have hatched in late February and in March (Jude *et al.* 1981). At both Presque Isle Harbor and Port Sheldon, lake trout eggs were deposited by hatchery-reared lake trout on man-made substrates placed over power-plant intake and discharge pipes located nearshore. Perkins and Krueger (1995) reported that most lake trout eggs hatched in early April on Stony Island Reef in eastern Lake Ontario. At all these locations water temperatures during incubation, especially at the time of egg deposition, were much higher than at our study site and almost certainly led to earlier hatching. In this study the later hatching time in 1990 compared to 1991 was almost certainly due to cooler water during the early stages of incubation. Most DTU are accumulated early in the incubation period when water temperatures are the highest (Casselman 1995). Although we did not measure water temperatures for the 1989–1990 incubation period, water temperatures were almost certainly much cooler in the fall and early winter in 1989 than in 1990. Air temperatures in December, 1989, the second month of incubation at this site, were far below normal (Assel and Norton 1990). We assume, therefore, that water temperatures were cooler and led to the slower rate of DTU accumulation and later hatching in spring of 1990.

The incubation period for Gull Island Shoal lake trout appears to be much longer than for other populations. The peak of lake trout spawning activity at this site is nearly always in the brief period, 17–20 October (S. Schram, Wisconsin Department of Natural Resources, Bayfield, WI, personal communication, October, 1993). The incubation period for lake trout eggs, therefore, based on the estimated modal hatching dates in 1990 and 1991, was about 7 months. This incubation period exceeds all other times reported or implied for this species (2 months—Loftus 1958; 4 months—Paterson 1968, Greeley 1936, Royce 1951, Martin 1957, DeRoche 1969, Jude *et al.* 1981; 5 months—Perkins and Krueger 1995; 6 months—Hacker 1957, Peck 1986), but may be typical for offshore spawning sites in the Great Lakes where water temperatures are cooler at the beginning of incubation and are near 0°C for longer periods.

Post-emergent natural mortality appears to be low throughout the first 4 months of life for age-0 lake trout at the Gull Island Shoal complex. We were not able to calculate a natural mortality rate from density estimates because of continual recruitment of fish at the nursery area. However, some of our results suggest low mortality. First, analysis of variance showed no significant differences in the mean densities calculated from all sampling locations across sampling dates in both years. Second, mean hatch dates differed little from fish captured during the first and last sampling periods in 1990 and 1991. Back-calculated hatch-date distributions are based on the age of survivors captured well after the actual time of hatching. These distributions are inherently negatively skewed compared to the actual hatch-date distributions because fish that hatch earlier suffer greater cumulative mortality than those that hatch later (Campana and Jones 1992). If natural mortality were high, modal back-calculated hatching dates should become progressively later the further in time the fish are sampled from the actual hatching dates. Therefore the small differences in the mean day of hatching across sampling dates shown in this study should be indicative of low mortality.

Both estimated hatching dates and the incubation period are based solely on our interpretation of the microstructure of sagittae. Errors associated with failure to discriminate daily increments from sub-daily increments, including increments deposited prior to hatch, can cause daily ages to be overestimated (Campana 1992, Neilson 1992). Relations between age and total length were linear and significant, but coefficients of determination did not exceed 69%, which suggests we assigned some ages incorrectly. Also, expected ages were higher for the last sampling period in August 1991, which suggests that some fish ages were overestimated. Correction of these errors would make true ages younger, the modal hatching period later in the year, and the estimated incubation period longer than reported here. These results would only reinforce the uniqueness of the hatching time (late) and incubation period (long) associated with lake trout at Gull Island Shoal. In general, differences in the estimated modal ages between sampling periods and the number of days that elapsed between sampling periods were similar, which suggests that sagittal increments were formed at approximately daily intervals.

ACKNOWLEDGMENTS

We thank Charles Bowen for instruction on sagittae preparation, Angela Cornwell, Seth Moore, Chris Pyhel, and Scott Sapper for processing and ageing the sagittae, and Captain Elmer Hendrickson of the R/V *Siscowet* for the construction of the beam trawl. Reviews by Edward Brown, Randy Eshenroder, Michael Hansen, James

Peck, Charles Olver, Jacqueline Savino, and an anonymous reviewer greatly improved the manuscript. This is contribution 898 of the National Biological Service, Great Lakes Science Center, Ann Arbor, Michigan 48105.

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