Transactions of the American Fisheries Society 135:680–694, 2006

DOI: 10.1577/T05-203.1

[Article]

Evaluation of Methods to Estimate Lake Herring Spawner Abundance in Lake Superior

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Abstract.—Historically, commercial fishers harvested Lake Superior lake herring *Coregonus artedi* for their flesh, but recently operators have targeted lake herring for roe. Because no surveys have estimated spawning female abundance, direct estimates of fishing mortality are lacking. The primary objective of this study was to determine the feasibility of using acoustic techniques in combination with midwater trawling to estimate spawning female lake herring densities in a Lake Superior statistical grid (i.e., a 10′ latitude × 10′ longitude area over which annual commercial harvest statistics are compiled). Midwater trawling showed that mature female lake herring were largely pelagic during the night in late November, accounting for 94.5% of all fish caught exceeding 250 mm total length. When calculating acoustic estimates of mature female lake herring, we excluded backscattering from smaller pelagic fishes like immature lake herring and rainbow smelt *Osmerus mordax* by applying an empirically derived threshold of −35.6 dB. We estimated the average density of mature females in statistical grid 1409 at 13.3 fish/ha and the total number of spawning females at 227,600 (95% confidence interval = 172,500–282,700). Using information on mature female densities, size structure, and fecundity, we estimate that females deposited 3.027 billion (10^9) eggs in grid 1409 (95% confidence interval = 2.356–3.778 billion). The relative estimation error of the mature female density estimate derived using a geostatistical model–based approach was low (12.3%), suggesting that the employed method was robust. Fishing mortality rates of all mature females and their eggs were estimated at 2.3% and 3.8%, respectively. The techniques described for enumerating spawning female lake herring could be used to develop a more accurate stock–recruitment model for Lake Superior lake herring.

Over the last century humans have harvested tens of thousands of metric tons of lake herring *Coregonus artedi* from Lake Superior. The commercial harvest of lake herring peaked in the 1940s when operators targeted flesh, that was obtained mostly during the lake herring reproductive period from October through early December (Selgeby 1982; MacCallum and Selgeby 1987). Through the 1960s harvest dropped dramatically as stocks plummeted (Selgeby 1982). Lawrie and Rahrer (1972) suggested the population decline likely resulted from successive overfishing as effort was first directed to spawning grounds near ports and then to more remote grounds. Selgeby (1982) later analyzed commercial catch data from Wisconsin waters and concurred with Lawrie and Rahrer's (1972) sequential overfishing hypothesis. Commercial fishing for lake herring has continued on Lake Superior to the present, but at a much reduced level. Operators now target lake herring for their roe using suspended gill nets that must be used at depths at least 3.7 m below the surface. The Wisconsin Department of Natural Resources (WIDNR) surveys commercial operators to estimate annual harvested biomass by statistical grid (10' latitude by 10' longitude areas). In recent years, annual harvest has been around 100 metric tons from Wisconsin waters of Lake Superior, which is roughly 5% of the annual harvest levels of the 1940s (WIDNR, unpublished data). Because no surveys exist to estimate spawning female abundance, direct estimates of fishing mortality are lacking. Development of techniques to assess lake herring abundance when the fish are spawning could be used to estimate fishing-induced mortality and facilitate understanding of harvest sustainability identified by the Lake Superior Technical Committee as a high research priority (M. P. Ebener, Chippewa Ottawa Resource Authority, unpublished data).

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Received August 5, 2005; accepted January 3, 2006
Published online May 30, 2006

Despite the reduction in commercial harvest, the lake herring population has apparently never fully recovered to historic levels (Bronte et al. 2003; Cox and Kitchell 2004). Since 1978, the first year that a fishery-independent trawl survey of prey fish species was initiated by the U.S. Geological Survey Lake Superior Biological Station (LSBS), lake herring year-class strength has been variable with most years having very low recruitment (Bronte et al. 2003; Hoff 2004). Bronte et al. (2003) showed that some of the weakest year classes were produced under the highest stock sizes suggesting some density-dependent compensation. However, annual recruitment indices in U.S. and Canadian waters have been correlated indicating some lakewide density-independent factors like weather and water temperature may also be important (Bronte et al. 2003; Hoff 2004).

Evidence suggests that mature female lake herring are largely pelagic and surface oriented during the spawning season, while male lake herring tend to be more bottom oriented. Recent monitoring of commercial gill net catches by the WIDNR has shown that females typically represent 75% of the annual catches in suspended nets (Table 1). Bottom gill nets, set overnight during November by the WIDNR having the same mesh (76 mm square measure) fished by commercial operators, have typically caught two times more males than females (Table 1). The pelagic nature of females, and an apparent spatial separation from male lake herring during November, could offer a excellent opportunity to develop an acoustic estimate of female abundance at a time when commercial operators target females for their roe.

TABLE 1.—Proportion of females caught in overnight bottom-set gill nets and suspended gill nets fished at least 3.7 m below the surface during the lake herring spawning seasons from 1998 to 2004. The bottom-set gill nets, fished by the Wisconsin Department of Natural Resources (WIDNR) were made of monofilament, while the suspended commercial gill nets were a mix of monofilament and multifilament. All nets had 76-mm-square measure. The WIDNR netting data were collected at a fixed site near Sand Island, Wisconsin. The commercial gill-net catches were monitored by the WIDNR and represent fish collected throughout the Apostle Islands region of Wisconsin during November and December of each year; *N* is the number of fish sexed by year.

	Bottom-set gill nets		Suspended gill nets	
Year	Proportion female	*N*	Proportion female	*N*
1998	0.40	124	0.72	208
1999	0.16	74	0.81	422
2000	0.29	77	0.84	160
2001	0.24	50	0.76	505
2002	0.39	46	0.78	417
2003	0.55	76	0.74	1,131
2004	0.19	120	0.76	645

Recently, a Ricker stock–recruitment model for Lake Superior lake herring was presented by Hoff (2004). In developing this model, Hoff (2004) used the density of lake herring greater than 200 mm total length (TL) captured during the annual LSBS spring daytime bottom trawl survey as a surrogate to adult stock density. Only data from Wisconsin waters from 1984 to 1998 were used to develop the model. Walters and Ludwig (1981) stated that stock–recruitment data should not be published unless accompanied by estimates of measurement error variance demonstrating that spawning stocks were measured precisely (i.e., relative standard error [RSE = SE/mean $\times$ 100] $\leq$ 30%). Hoff (2004) did not present the precision of adult density estimates so we used LSBS file data to determine that the average annual RSE equaled 53.5% (range = 41.0–82.2%) over the 14 years of data used for model development. Without precise estimates of fish densities, Walters and Ludwig (1981) stated that researchers may spend time explaining patterns that simply do not exist in the first place.

Rather than continue to measure adult lake herring densities with poor precision using the spring survey, we explored the feasibility of enumerating lake herring densities at the time of spawning. Rudstam et al. (1987) demonstrated that lake herring populations can be enumerated by acoustic techniques during nonspawning periods, but to our knowledge no study to assess spawning lake herring has been attempted. We also wanted to test the feasibility of estimating the number of eggs deposited using information on spawner densities, size structure, and the relationship of fecundity to size. All three estimates (mature female densities, size structure, and fecundity) would have inherent sampling variability. We hypothesized that uncertainty in the estimate of the number of eggs deposited would stem foremost from estimating spawning female densities. Because we were likely to estimate the size structure and fecundity of female lake herring with better precision, we predicted our estimate of deposited eggs would be less sensitive to these data inputs.

The objectives of this study were to (1) determine the feasibility of using acoustic techniques in combination with midwater trawling to estimate female numbers in Lake Superior statistical grid 1409; (2) if feasible, combine population estimates with size structure and fecundity information to estimate the numbers of eggs deposited in grid 1409; (3) conduct a sensitivity analysis to determine which data input contributed the greatest uncertainty to our estimate of deposited eggs; and (4) compare the female population estimate and egg deposition estimate to the commercial catch of females and roe to directly estimate fishing mortality on lake herring and their eggs in grid 1409. The sensitivity analysis will help identify how best to use available resources to improve the adult survey design in the future.

Methods

Data for this study were collected at night on 30 November and 1 December 2004 aboard the U.S. Geological Survey (USGS) research vessel *Kiyi*. Sampling commenced 30 min after nautical twilight and ended by 0100 hours each night. We sampled in a systematic fashion conducting a series of parallel acoustic transects spaced at roughly 2.5 km intervals (Figure 1). Acoustic sampling occurred while traveling at speeds of 2.1–2.6 m/s. The depth distribution, acoustic size, and abundance of fish were estimated using a DT-X digital echosounder (BioSonics, Inc., Seattle, Washington) equipped with a 120 kHz split-beam transducer with a half-power beam width of 6.7°. The transducer was mounted on a 1.2-m-long towbody and was deployed 1 m below the surface. The transducer emitted 3 pings/s with the pulse duration set at 0.4 ms. A standard target calibration was performed on 30 November using a 33-mm tungsten carbide sphere (theoretical target strength [TS] of −41.2 dB). Mean TS of the sphere equaled −40.8 dB, within the measurement capabilities of the system (±0.4 dB) and the confidence limits around the theoretical TS value. Vessel position was measured with an Ashtech model BRG2 differentially corrected global positioning system (accurate to 1 m) and positional information was embedded in the acoustic data files. We also collected temperature profiles at four sites using a SEACAT model 19 Profiler (Sea-Bird Electronics, Inc., Bellevue, Washington).

Trawling.—We conducted a total of six midwater trawls and one bottom trawl to assess fish community composition (Figure 1). The midwater trawl (Gourock Trawls, Ferndale, Washington) had 15.2-m headrope and footrope lines, and 13.7-m breast lines. The nylon mesh graduated from 300 mm stretch measure at the mouth to 12 mm stretch measure at the cod end. Four of the midwater trawl tows were fished horizontally for 20 min with headrope depths of 8, 12, 20, and 24 m, respectively. Two midwater trawls were fished in a stepped-oblique fashion (Kirn and LaBar 1991) with the headrope located at 5 m and 18 m for 10 min each. During five of the six trawls the footrope was fished within 10 m of the bottom. Midwater trawl catches should reflect species composition throughout the

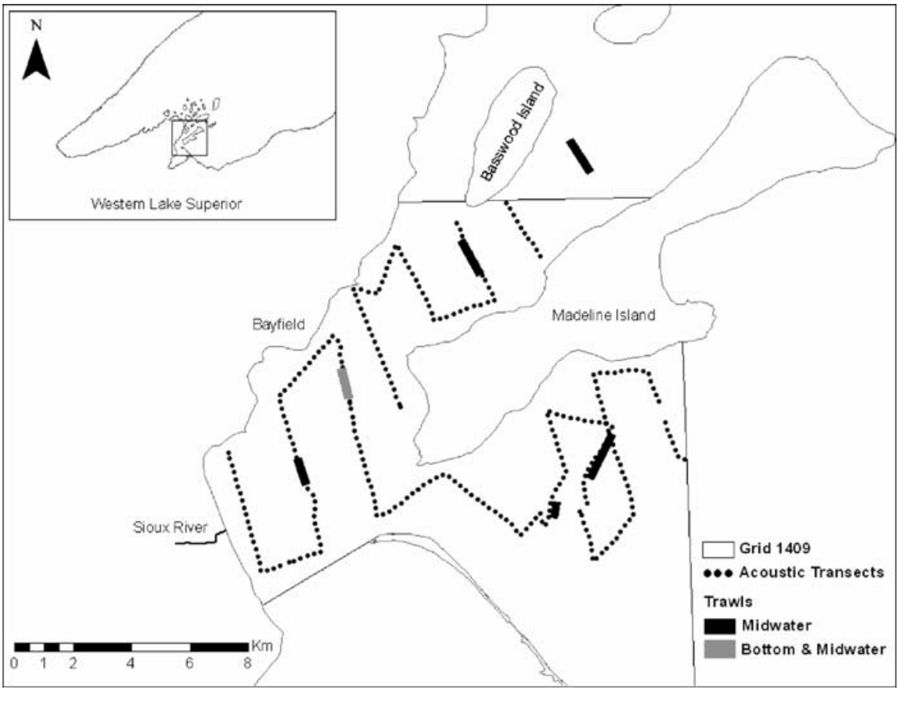

FIGURE 1.—Map of the acoustic transects and midwater trawl and bottom trawl stations sampled during the nights of 30 November and 1 December 2004.

water column from 5 m below the surface down to depths that the trawl could be safely fished.

The bottom trawl (3/4 Yankee trawl number 35) had 11.9-m headrope, 15.5-m footrope and 2.2-m wing lines with 89-mm stretch measure at the mouth, 64-mm stretch measure at the trammel, and 12-mm stretch measure at the cod end. We used NETMIND trawl mensuration sensors (Northstar Technical, Inc., St. John's, Newfoundland and Labrador) to record the midwater trawl headrope depth, headrope temperature, trawl mouth height, and trawl wingspread at roughly 10-s intervals during deployment. The midwater trawl mouth typically measured 10 m by 10 m when fishing. Only the wingspread sensors were deployed on the bottom trawl.

Fish processing.—Captured fish were kept on ice in the field and transported to LSBS in Ashland, Wisconsin, for processing the following morning. Each trawl catch was sorted to species, counted and weighed in aggregate to the nearest 0.0001 kg. All lake herring were measured to the nearest millimeter (total length). Small catches (<50 individuals) of other species were all measured. When catches of a single species were larger, a random subsample of 50 fish was measured, and the remaining fish were counted. In these cases, the length frequency by species was estimated for the entire catch based on the distribution of the measured individuals.

We used an ovary subsampling technique and linear regression to quantify the relationship between the fecundity and mass of mature female lake herring. A subsample of captured lake herring was sexed and their reproductive state assessed (unknown; immature males; mature males; immature females; green females; and recovering females). Green females had fully developed eggs, but had not yet spawned. Ovaries of green females were removed, placed in individually numbered plastic bags, and frozen. Ovaries were later thawed, placed in 100% glacial acetic acid for 30 min, rinsed with water, blotted for 1 min and weighed to the nearest 0.1 g. Five sections were removed (one near each end and three from the middle) from a single ovary per female and 100 eggs from each section were placed on a plastic weighing dish and weighed to the nearest 0.1 mg. The glacial acetic acid treatment made it easier to separate eggs during counting. The number of eggs per female was calculated by multiplying the total mass of the ovaries (after treatment with glacial acetic acid) by the estimated mass of individual eggs per female based on the five subsamples.

Acoustic data postprocessing.—Acoustic data files were processed with Echoview acoustic postprocessing software (version 3.10.132.06, SonarData, Ltd., Tasmania, Australia). Water temperature profiles showed isothermic conditions with an average temperature of 5°C. Therefore, we used an algorithm in Echoview to set the speed of sound at 1,422 m/s and the absorption coefficient at 0.005802 dB/m. A line 0.2 m above the lake bottom was defined on echograms using an Echoview algorithm. Bottom tracking anomalies were eliminated by visually inspecting echograms and manually redefining the bottom. Echograms were divided horizontally using three different bin lengths (250, 500, and 1,000 m) and fish densities were estimated in each bin from the surface to the bottom using 10 m high cells.

Echoview software measures fish backscattering on an area basis by calculating a nautical area backscattering coefficient (NASC), that is, NASC (m^2/nautical mile^2) $= 4\pi \times 1{,}852^2 \times 10^{(Sv/10)} \times T$, where Sv is the mean volume backscattering strength of the domain being integrated, 4π is the number of steradians in a sphere converting backscattering cross section to scattering cross section, 1,852 is the number of meters per nautical mile, and T is the mean thickness of the domain being integrated in meters.

Fish density estimates were obtained by scaling cell NASC values by the mean backscattering cross section of individual fish (i.e., σ_{bs}) in each cell, calculated from the mean target strength (TS). By convention, $\sigma_{bs} = 10^{(TS/10)}$. We used the following algorithm presented in MacLennan and Simmonds (1992) to estimate fish density on a per area basis (FD_A):

$$FD_A\ (\text{fish/ha}) = \text{NASC}/(4\pi \times \sigma_{bs} \times 343),$$

where 343 is the number of hectares in a square nautical mile.

When estimating total fish densities per cell, we applied a −60 dB backscattering volume strength (Sv) threshold. To estimate σ_{bs} we used the single target detection criteria (split beam method 1) available in Echoview. The single target detection parameters we used are presented in Table 2. Only single echoes exceeding −55 dB were used to calculate σ_{bs}. Application of these thresholds helped ensure that fish density estimates were not biased by the inclusion of backscattering from invertebrates like *Mysis relicta*.

Acoustic densities versus trawl densities.—To estimate the densities of mature lake herring from acoustic data, we first conducted an analysis to determine the appropriate TS cutoff to separate mature lake herring (>250 mm TL) from smaller pelagic fish like rainbow smelt *Osmerus mordax* and juvenile lake herring. In addition to the six midwater tows conducted during the spawning season, we compiled catches from 13 midwater trawls collected from the eastern end of Lake Superior during August 2004 where large lake herring represented 100% of the catch of fish

TABLE 2.—Echoview software single-target detection parameters used during this study.

Parameter	Value
Target strength threshold (dB)	−55.00
Pulse length determination level (dB)	6.0
Minimum normalized pulse length	0.8
Maximum normalized pulse length	1.5
Beam compensation model	BioSonics
Maximum beam compensation (dB)	6.0
Maximum SD of minor-axis angles (degrees)	1.5
Maximum SD of major-axis angles (degrees)	1.5

exceeding 250 mm. We estimated densities of lake herring exceeding 250 mm (fish/m^3) in each trawl by dividing the numbers caught by the volume of water sampled by the trawl. The paths of midwater trawls were overlayed on echograms using trawl mensuration data and an Echoview parallelogram drawing tool (both the echogram and trawl mensuration data were time tagged). Acoustic density estimates in the trawl path were calculated on a per volume basis (FD_V) so that acoustic density estimates could be compared with trawl density estimates using the same units. The following formula was used:

$$FD_V(\text{fish/m}^3) = 10^{Sv/10}/\sigma_{bs}.$$

We developed frequency distributions of echoes meeting the single target detection criteria within each trawl path using 1-dB-wide bins from −55 to −20 dB. We calculated what proportion of the total targets in each trawl path exceeded −42 dB, −41 dB, −40 dB, and so forth up to −32 dB and multiplied the total FD_V in each trawl path by each proportion. Linear regression was used to measure the correlation coefficient (r) between the trawl density of large herring and the density derived from the eleven 1-dB cutoffs using each trawl tow as a sample unit. We then developed a bivariate plot with correlation coefficient values on the y-axis and target strength cutoffs on the x-axis and fit a third-order polynomial line to the plot. We used this polynomial model to predict at what TS value the correlation coefficient was maximized. When estimating densities of mature female lake herring (>250 mm) during the spawning survey we multiplied the total fish density in each cell by the proportion of fish exceeding the TS cutoff with the maximum correlation coefficient. We compared our empirically derived TS cutoff value to an equation predicting lake herring lengths from TS developed by Rudstam et al. (1987).

Estimating mean densities and mapping fish distributions.—Because fish aggregate to spawn, we expected acoustic density data to be spatially autocorrelated within the statistical grid. Owing to logistical constraints, acoustic surveys are typically conducted by sampling continuously along a regular grid; thus, samples lack true independence and violate the assumptions of classical variance estimators and random sampling theory (Petitgas 1993; Williamson and Traynor 1996). Several studies (Petitgas 1993; Maravelias et al. 1996; Páramo and Roa 2003; Mello and Rose 2005) have used model-based approaches instead of design-based approaches (e.g., stratified or random transects) to estimate fish abundance from acoustic survey data. Model-based approaches offer substantial advantages because they require less emphasis on survey design. Moreover, design-based approaches can prove less effective when fish distributions are patchy and survey results include a small number of extremely high values (Petitgas 1993; Maravelias et al. 1996; Páramo and Roa 2003). Geostatistical algorithms to calculate estimation variance from acoustic data are now available in the user-friendly computer software EVA2 created by Petitgas and Lafont (1997).

Our geostatistical analysis consisted of constructing empirical variograms, fitting theoretical variogram models, evaluating the assumption of stationarity, and calculating the estimation variances of the total fish densities and densities of mature female lake herring using EVA2. Before importing density estimates into EVA2, latitudes and longitudes of bin midpoints were converted from decimal degrees to Universal Transverse Mercator coordinates. When calculating the empirical variograms we used a maximum lag distance of 10,000 m, which was about half the length of the longest axis of the study area recommended by Petitgas (1993). Spherical or exponential models were fit to empirical variograms with emphasis placed on fitting the first few lags (e.g., 3–6) as closely as possible (Williamson and Traynor 1996). The theoretical variogram model nugget is the pure random component of the spatial structure representing white noise or microstructures, or both, at scales less than the bin length (Petitgas 1993). The ratio of the theoretical variogram model nugget to the sill is a measure of the total variation explained by spatial structuring. We followed the recommended approach of Rivoirard et al. (2000) to explore if the ratio of the nugget to sill could be minimized by using different bin lengths and lag distances. Three bin lengths (250, 500, and 1,000 m) and three lag distances (500, 1,000, and 2,000 m) were investigated. Theoretical variogram models were used to calculate estimation variance using the intrinsic two-dimensional method (scheme E) available in EVA2.

Under this intrinsic method fish populations are conceptualized as spatially stochastic processes, fish density varying randomly at any given location. It is assumed that the sampling produced just one realization of the stochastic process (Petitgas 1993; Páramo and Roa 2003). The intrinsic method also assumes stationarity, which is a process with a constant mean with the variance defined only as a function of distance and not location (Cressie 1993). We evaluated our data to determine whether it met the assumption of stationarity using mapping features in EVA2, where density values are scaled from the minimum to the maximum value using graduated circles and displayed within the study area polygon. Bivariate plots of density versus latitude, and density versus longitude, where also examined for trends. Mean densities were estimated using the arithmetic mean of the sample values within the study area polygon (Petitgas 1993).

To map the densities of mature female lake herring, we used ordinary kriging available in the Geostatistical Analyst Extension of ArcMap version 9.1 (ESRI, Redlands, CA). Densities at unsampled locations were estimated based on the theoretical variogram model that minimized the ratio of nugget to sill. The interpolated values were calculated using a minimum of two and a maximum of five neighboring density values.

Estimating eggs deposited in and harvested from statistical grid 1409.—We estimated the total number of eggs deposited by females in statistical grid 1409 using the following approach: The acoustic estimate of mature lake herring in grid 1409 was apportioned to 25 mm length bins based on the frequency distribution of female lake herring caught by midwater trawling. The mean mass of female lake herring at each bin midpoint was calculated using a length–mass equation derived from lake herring captured during this survey. We estimated the average fecundity of females at each bin midpoint using the fecundity-versus-mass equation we developed. Numbers of females in each length bin were multiplied by the average fecundity for that length bin to estimate the numbers of eggs per bin, and then summed across all bins to estimate total eggs deposited in grid 1409.

To estimate what proportion of eggs carried by spawning lake herring were harvested, we combined information on the biomass of lake herring harvested, the size structure of harvested fish, and the relationship of fecundity to female mass that we developed. The biomass of harvested lake herring was estimated by combining WIDNR and Red Cliff Band of Lake Superior Chippewa annual catch statistics. We assumed that females represented 76% of the total harvested biomass during 2004 (Table 1). We developed a length-frequency distribution of harvested females based on individual measurements of green females caught by commercial operators during late October to mid-November 2004. The estimated average mass at each bin midpoint was calculated using our lake herring length–mass equation. The count of fish in each 25-mm bin was multiplied by their predicted mean mass and all bins were summed to estimate the mass of the measured green females. We then determined what proportion of the total mass of the measured females was in each bin and used these values to apportion the total biomass of harvested lake herring to length bins. We then converted harvested biomass to harvested numbers in each length bin using our lake herring length–mass relationship. Finally, numbers of females in each length bin were multiplied by the average fecundity for that length bin to estimate the numbers of eggs per bin, which were then summed across all bins to estimate the total number of eggs harvested in grid 1409.

To generate confidence intervals for the number of eggs deposited in statistical grid 1409, we used a bootstrap approach that incorporated uncertainty in each of the following three estimates used to calculate the numbers of egg deposited: the density of mature female lake herring; the size structure of spawning females; and the mass–fecundity relationship. We believed the length–mass relationship would contribute very little to uncertainty in our egg deposition estimates, so we held this relationship constant. First, we randomly selected density estimates (based on 75 1-km cells in grid 1409) with replacement and calculated a mean density. Next, we randomly selected five midwater trawls with replacement and calculated the mean percent contribution of each length-bin class (midpoints at 263, 288, 313, 338, 363, 388, and 413 mm) to the total catch of spawning-size female lake herring. Because one of the six midwater trawls did not capture mature lake herring, we used only five midwater trawls to measure uncertainty in size structure. We then apportioned the mean bootstrap density estimate to length bins based on the bootstrapped mean percent of total catch for each length bin. Third, we assumed the length–mass relationship was constant, and assigned a mean mass for all fish assigned to each length bin. Fourth, for the mass–fecundity relationship, we randomly selected 22 pairs of observations (mass, number of eggs) with replacement, calculated the slope and intercept from this regression, and applied this regression to the average mass for each length bin to calculate the average number of eggs per female in each length bin. We then multiplied the number of females in each length bin by their corresponding estimated number of eggs per female to generate the number of eggs per hectare. Finally, we summed across length bins and multiplied by the surface area of grid 1409 (17,133 ha) to estimate the number of eggs deposited in the statistical grid. This process was repeated 1,000 times to generate a distribution of the number of eggs deposited. We used the bias-corrected percentile method to calculate 95% confidence intervals (Manly 1997).

To examine how sensitive our estimates were to each component, we held two of the three observed values (density of mature lake herring, size structure, and fecundity) constant (observed values) and varied the other component to estimate the numbers of eggs deposited. This was done for each of the three components. Comparing the variability around the mean estimates for each of the 1,000 simulations for each of these scenarios would illustrate where our greatest uncertainty was and indicate where future sampling effort should be concentrated.

Results

A total of 3,027 fish were caught in the six midwater trawls. Rainbow smelt were predominant (79.8%), followed in decreasing order by lake herring (18.8%), bloater *C. hoyi* (0.9%), spoonhead sculpin *Cottus ricei* (0.4%) and ninespine stickleback *Pungitius pungitius* (<0.1%). There was minimal overlap in length distributions of rainbow smelt and lake herring captured in the midwater trawl (Figure 2). Rainbow smelt were generally small with a modal length of 63 mm (Figure 2A), while the length distribution of captured lake herring (Figure 2B) was bimodal (modes at 188 and 338 mm). We determined the sex of 209 lake herring caught by midwater trawl (Figure 2C). Of the 154 fish less than 250 mm long, 47% were female and 53% were male. Of the 55 fish exceeding 250 mm, 52 (94.5%) were female and three (5.5%) were male. Females smaller than 250 mm were immature and females greater than 250 mm were mature (Figure 2D). Of the 52 captured females exceeding 250 mm, 22 were green and 30 were recovering.

We measured the fecundity of the 22 green females. The model predicting fecundity from mass was as follows:

$$\text{Fecundity (number of eggs)} \\ = -86.5 + 46.5 \times \text{mass(g)},$$

with $R^2 = 0.880$, $N = 22$, $P < 0.0001$, and range = 126.6–567.5 g.

Not all fish were weighed so we developed the following mass-versus-length equation from 138 lake herring (both sexes) that had been weighed:

$$\log_e[\text{mass(g)}] = -12.7 + 3.16 \times \log_e[\text{length(mm)}],$$

with $R^2 = 0.99$, $N = 138$, $P < 0.0001$, and range = 141–422 mm.

A total of 779 fish from 10 species were caught in the single bottom trawl sample. Rainbow smelt and other small demersal species like trout-perch *Percopsis omiscomaycus*, spoonhead sculpin, slimy sculpin *Cottus cognatus*, deepwater sculpin *Myoxocephalus thompsoni* and ninespine sticklebacks dominated the catch (Figure 3A); these species rarely exceed 175 mm. Of the 82 fish exceeding 175 mm (Figure 3B), 65 (79.3%) were lake whitefish *C. clupeaformis*, 10 (12.2%) were lake herring and 7 (8.5%) were other species. We sexed the 10 lake herring caught in the bottom trawl and found seven males and three females. Because lake whitefish were the predominant large-bodied species caught in the bottom trawl, we excluded fish targets within 2 m of the bottom when estimating mature female lake herring densities. Trawling results were consistent with November and December gill net data (Table 1), with mature female lake herring exhibiting a pelagic existence, and male lake herring being more bottom-oriented.

Estimating Mean Densities and Estimation Variance and Mapping Fish Distributions

The correlation coefficients from regressing midwater trawl densities of lake herring exceeding 250 mm against acoustic density estimates derived using the eleven 1-dB cutoffs ranged from 0.24 to 0.58. Based on the third-order polynomial line fit, we determined that the correlation coefficient was maximized at a TS cutoff of –35.6 dB. When estimating densities of mature females we multiplied the total fish density in each cell by the proportion of fish with TS exceeding –35.6 dB. This cutoff value is consistent with the predicted TS of a 250-mm lake herring (–36.6 dB) using the Rudstam et al. (1987) equation.

Our geostatistical analysis showed that the density data exhibited a high degree of spatial structuring for total fish densities and moderate spatial structuring for the densities of mature female lake herring. For total fish densities, the ratio of the nugget to the sill was minimized (0.13) using 250-m bins and 500-m lags (Table 3). Most of the variability in total fish densities (87%) was explained by spatial structuring, and the pure random component of the spatial structure was small (13%).

The minimum ratio of nugget to sill for mature female lake herring densities (0.35) was realized using 1,000-m bins and a lag distance of 2,000 m (Table 3). The model nugget was important and represented 35% of the data variance. The amount of variation in mature female densities explained by spatial structuring did not increase using smaller bin lengths (Table 3).

The frequency distributions of mature female lake herring density samples from the three investigated bin

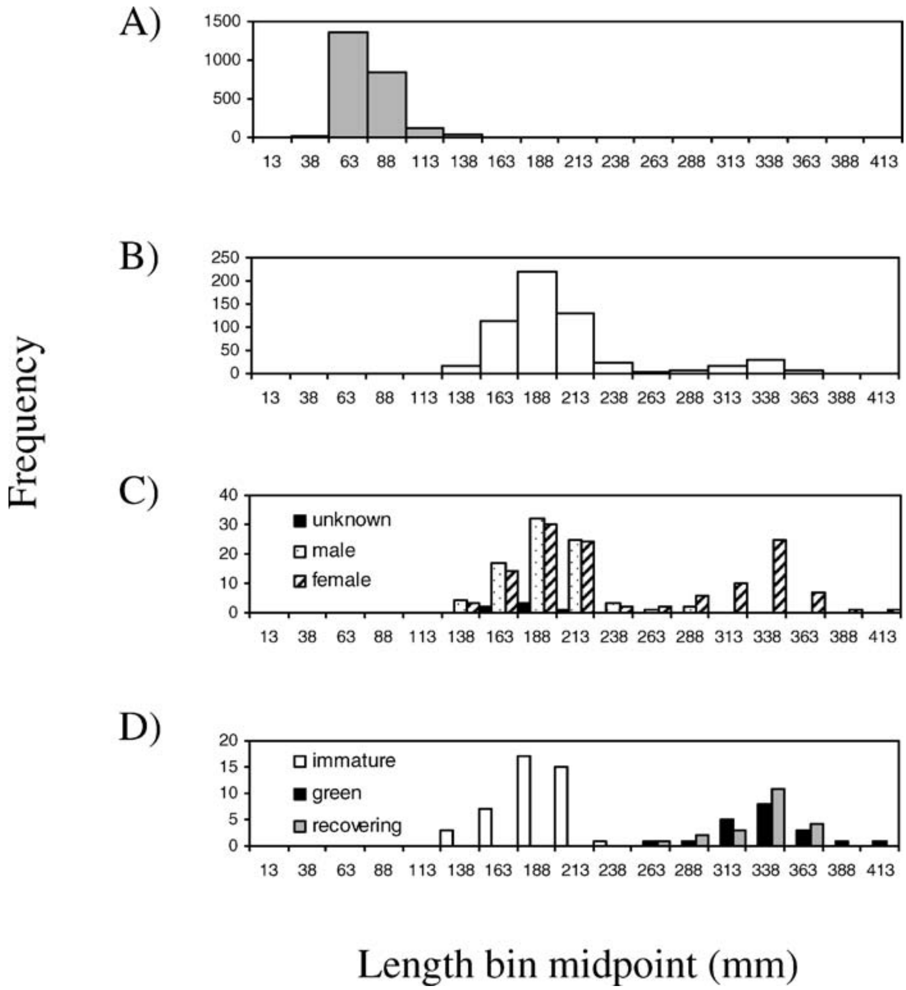

FIGURE 2.—Length-frequency distributions of **(A)** rainbow smelt and **(B)** lake herring caught in six night midwater trawls during 30 November and 1 December 2004; **(C)** length-frequency distributions of female and male lake herring captured in midwater trawls; and **(D)** reproductive state of females captured in midwater trawls (green females had fully developed eggs but had not yet spawned). Note that the scale of the *y*-axis is different for each graph.

lengths (Figure 4) showed a higher percentage of zero values using 250-m bins (35%) than using 500-m (20%) and 1,000-m (13%) bins. Moreover, the 250-m bin frequency distribution had a much higher percentage of extreme density values (>40/ha, 7%) than the 500-m (3%) and 1,000-m bins (3%). Thus, the estimation variance was minimized using 1,000-m bins (Table 3).

Examination of density data using graduated circles did not indicate large-scale "trends" for either the total fish density or mature female lake herring density data sets, so raw density data were used for variogram analysis and kriging. There was no indication of anisotropy after examination of graduated plots so isotropic models (with nugget effects) were used (Figure 5). The first three lags of the empirical variogram for the mature female lake herring density data (Figure 5A) were best fit with a spherical model: $\gamma(h) = \text{nugget}\ (58) + \text{spherical}\ (\text{sill} = 107, \text{range} = 3{,}200$ m). Mello and Rose (2005) computed variograms under different scenarios of random and gregarious fish density distributions, and our theoretical variogram for total fish densities most closely approximates their scenario of moderately variable fish density samples within dense aggregations. The first six lags of the total fish density empirical variogram (Figure 5B) were best fit with an exponential model: $\gamma(h) = \text{nugget}\ (2.0 \times 10^5) + \text{exponential}\ (\text{sill} = 1.3 \times 10^6, \text{range} = 3{,}000$ m). The

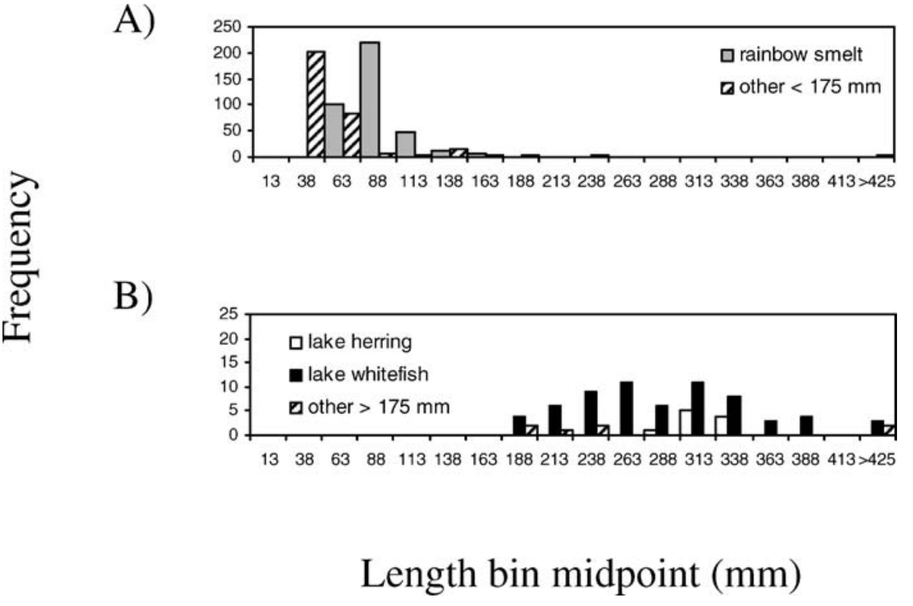

FIGURE 3.—Length-frequency distributions of **(A)** rainbow smelt and other species smaller than 175 mm caught in one night bottom trawl on 1 December 2004 and **(B)** lake herring, lake whitefish, and other species exceeding 175 mm caught in the bottom trawl. Other species include bloater, deepwater sculpin, lake trout *Salvelinus namaycush*, ninespine stickleback, slimy sculpin, spoonhead sculpin, and trout-perch. Note that the scale of the *y*-axis is different for each graph.

mature female lake herring theoretical variogram (Figure 5B) is consistent with uniformly low sample values distributed within aggregations (Mello and Rose 2005). The theoretical variogram models were used to calculate estimation variances using EVA2 and to map density distributions.

The arithmetic mean fish density of all fish in grid 1409 was 1,036 fish/ha ($N = 292$ cells; Table 3), while the mean density of mature female lake herring in grid 1409 was 13.3 fish/ha ($N = 75$ cells; Table 3). The estimation variance ($\sigma_E{}^2$) of the total fish density estimate was 17,500 and the estimation variance of mature female lake herring density was 2.7 (Table 3). The relative estimation errors (i.e., σ_E/arithmetic mean $\times$ 100) for the total fish and mature female lake herring density estimates equaled 12.8% and 12.3%, respectively. Assuming errors were distributed normally, the 95% confidence interval (CI) can be calculated by the mean $\pm$ $1.96\sigma_E$. The 95% CI surrounding the density of all fish was 777–1,295 fish/ha, while the 95% CI

TABLE 3.—Theoretical variogram models of mature female lake herring densities and total fish densities. Three bin lengths (250, 500, and 1,000 m) and three lag distances (500, 1,000, and 2,000 m) were evaluated. The maximum range used to develop each empirical variogram was set at 10,000 m for all cases. The mean densities (fish/ha) and estimation variances (σ_E2) for mature female lake herring densities and total fish densities reported in the text were based on the theoretical variogram models that minimized the ratio of nugget to silk (bold italics). The number of cells in statistical grid 1409 used to calculate mean density is *N*.

Bin length (m)	Lags	Lag distance (m)	Pairs in first lag	Model type	Range	Nugget	Sill	Nugget–sill ratio	*N*	σ_E^2
				Mature female lake herring densities						
250	10	1,000	516	Spherical	4,000	172	145	0.54	12.6 (292)	3.4
	20	500	178	Spherical	3,200	152	153	0.50	12.6 (292)	2.8
500	5	2,000	294	Spherical	3,000	82	123	0.40	12.9 (148)	2.9
	10	1,000	94	Spherical	3,800	97	127	0.43	12.9 (148)	3.1
1,000	***5***	***2,000***	***59***	***Spherical***	***3,200***	***58***	***107***	***0.35***	***13.3 (75)***	***2.7***
				Total fish densities						
250	10	1,000	516	Exponential	3,700	3.0 × 105	1.2 × 106	0.20	1,036 (292)	18,700
	20	***500***	***178***	***Exponential***	***3,000***	***2.0 × 105***	***1.3 × 106***	***0.13***	***1,036 (292)***	***17,500***
500	5	2,000	294	Exponential	5,000	4.0 × 105	9.0 × 105	0.31	1,030 (148)	18,600
	10	1,000	94	Exponential	4,500	2.0 ×105	1.1 × 106	0.15	1,030 (148)	20,000
1,000	5	2,000	59	Exponential	5,000	2.0 × 105	1.1 × 106	0.15	987 (75)	25,100

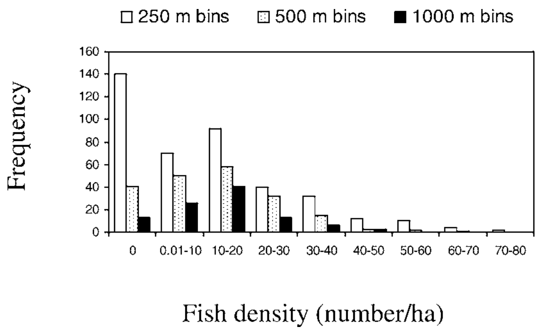

FIGURE 4.—Frequency distributions of density estimates of mature female lake herring in statistical grid 1409 using three horizontal bin lengths.

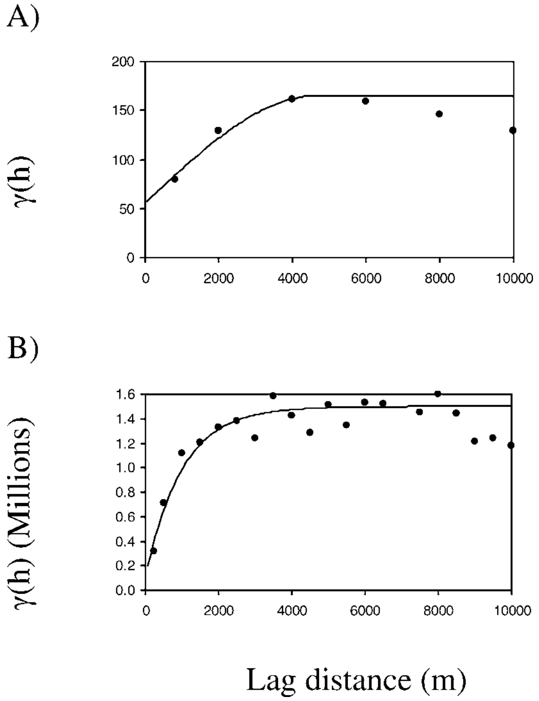

FIGURE 5.—Empirical and theoretical variogram models for **(A)** mature female lake herring densities and **(B)** total fish densities. The mature female lake herring density isotropic model is $\gamma(h)$ = nugget (58) + spherical (sill = 107, range = 3,200 m). The total fish density isotropic model is $\gamma(h)$ = nugget (2.0×10^5) + exponential (sill = 1.3×10^6, range = 3,000 m).

surrounding the density estimate of mature female lake herring was 10.1–16.5 fish/ha. Using a surface area of 17,113 ha, we estimated the total pelagic fish numbers in statistical grid 1409 at 17.7 million (95% CI = 13.3–22.2 million). The total number of lake herring >250 mm was 227,600 (95% CI = 172,500–282,700).

Total fish densities were highest (>3,500 fish/ha) southeast of Madeline Island and southeast of the town of Bayfield (Figure 6A). Densities of mature female lake herring were highest (25–30 fish/ha) southwest of Madeline Island (Figure 6B), with moderate densities also found southeast of Madeline Island, and between Madeline Island and Basswood Island. The concentration of large fish southwest of Madeline Island was suspended within 20 m of the surface over a generally soft bottom where bottom depths ranged from 15 to 35 m.

Frequency distributions of targets meeting the single-target classification criteria grouped by 10-m depth strata (Figure 7) suggest that spawning lake herring distributions were also vertically structured. The percentage of targets exceeding −35.6 dB by strata was highest between 40 and 50 m deep (2.4%) and 10 and 20 m deep (2.3%). In general, small acoustic targets (less than −45 dB), probably rainbow smelt, made up the largest proportion of the targets detected below 20 m.

Estimating Eggs Cast in a Statistical Grid and Sensitivity Analysis

We estimate the number of eggs cast by female lake herring in statistical grid 1409 at 3.027 billion (10^9) eggs (Figure 8). Based on our bootstrapping approach, the lower and upper 95% confidence intervals were 2.356 and 3.778 billion eggs, respectively. Incorporating uncertainty in the acoustic estimate of spawning female density, size structure, and fecundity, one at a time, revealed that density of spawning females contributed the greatest variability to estimating the numbers of eggs cast (Figure 8), followed by uncertainties in size structure. Uncertainty in the mass–fecundity relationship contributed very little to the overall variability when isolated from the other two factors. These results suggest that focusing efforts to improve precision of mature female density estimates will result in better precision of estimates of the numbers of eggs deposited.

The biomass of lake herring caught by commercial operators (WIDNR, file data) and tribal gill-net fishers (Red Cliff Band of Lake Superior Chippewa, file data) equaled 3,291 kg in grid 1409 (females = 2,501 kg) during the 2004 spawning season. The length-frequency distribution of a sample of 72 harvested green females showed that fish smaller than 325 mm were too small to be caught by gill nets. We estimate that 5,300 female lake herring carrying 116 million eggs were harvested from statistical grid 1409 during 2004. We estimate the fishing mortality of mature female lake herring and their eggs in statistical grid 1409 at 2.3% and 3.8%, respectively. The upper 95% confidence interval for the exploitation rates for adult females and eggs was estimated to be 3.1% (5,300 harvested/172,500 females in grid 1409) and 4.9% (116 million

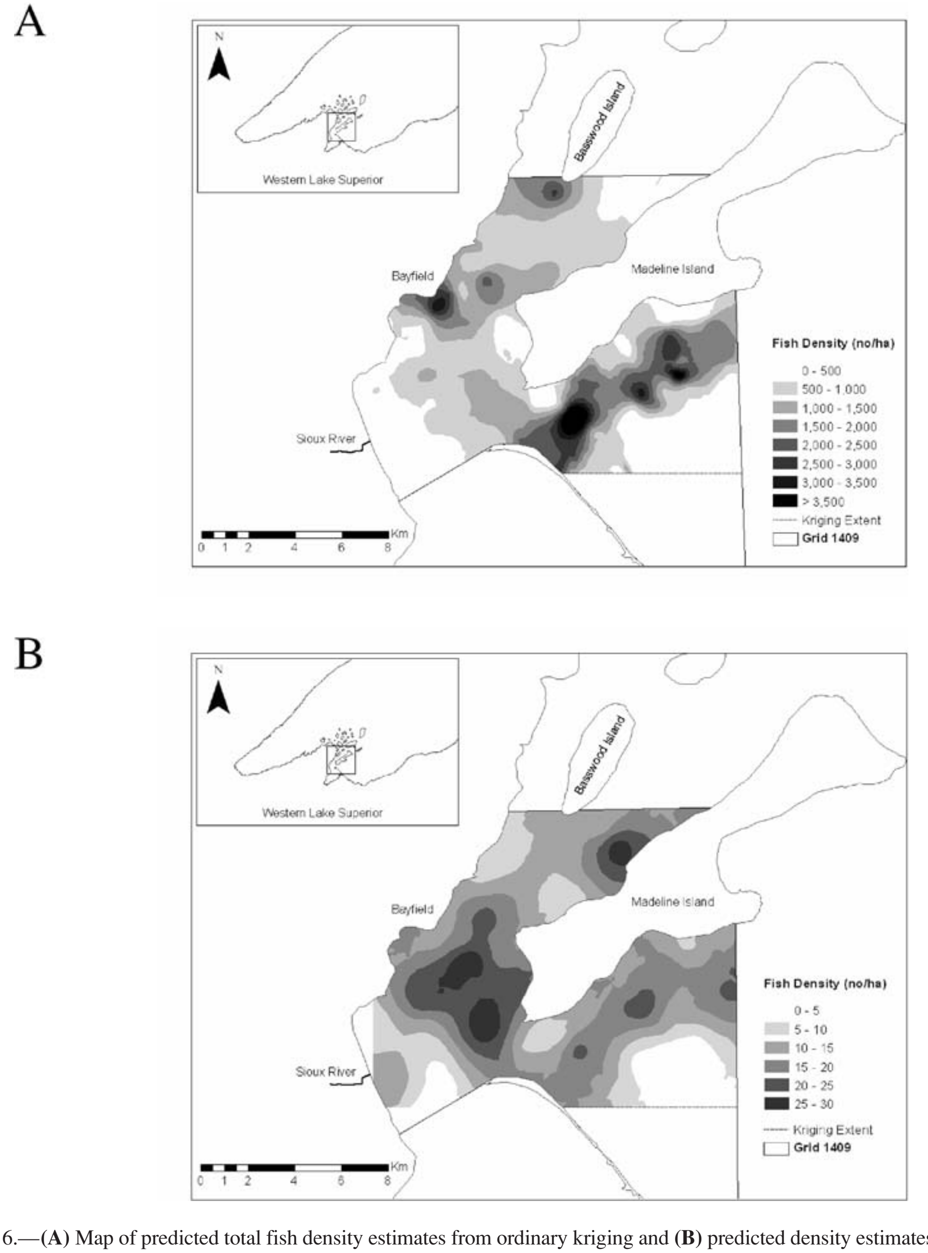

FIGURE 6.—**(A)** Map of predicted total fish density estimates from ordinary kriging and **(B)** predicted density estimates of large lake herring for the 30 November–1 December 2004 survey of statistical grid 1409.

eggs/2.356 billion eggs cast), respectively. These high-end estimates do not account for uncertainty in the harvest estimates, so it is possible that actual exploitation rates could be higher.

When calculating exploitation rates we assumed that mature lake herring densities in statistical grid 1409 measured over the 2 nights of sampling were representative of the entire fishing season. If female lake herring move rapidly away from spawning grounds after they spawn, or if "waves" of spawning herring come and go over the fishing season, then mortality estimates would be lower. When apportioning acoustic backscatter to species we assumed that midwater and bottom trawl catches were not biased, meaning all species, sizes and sexes were equally vulnerable to both gears. This assumption, although widely used, is difficult to validate (McClatchie et al. 2000).

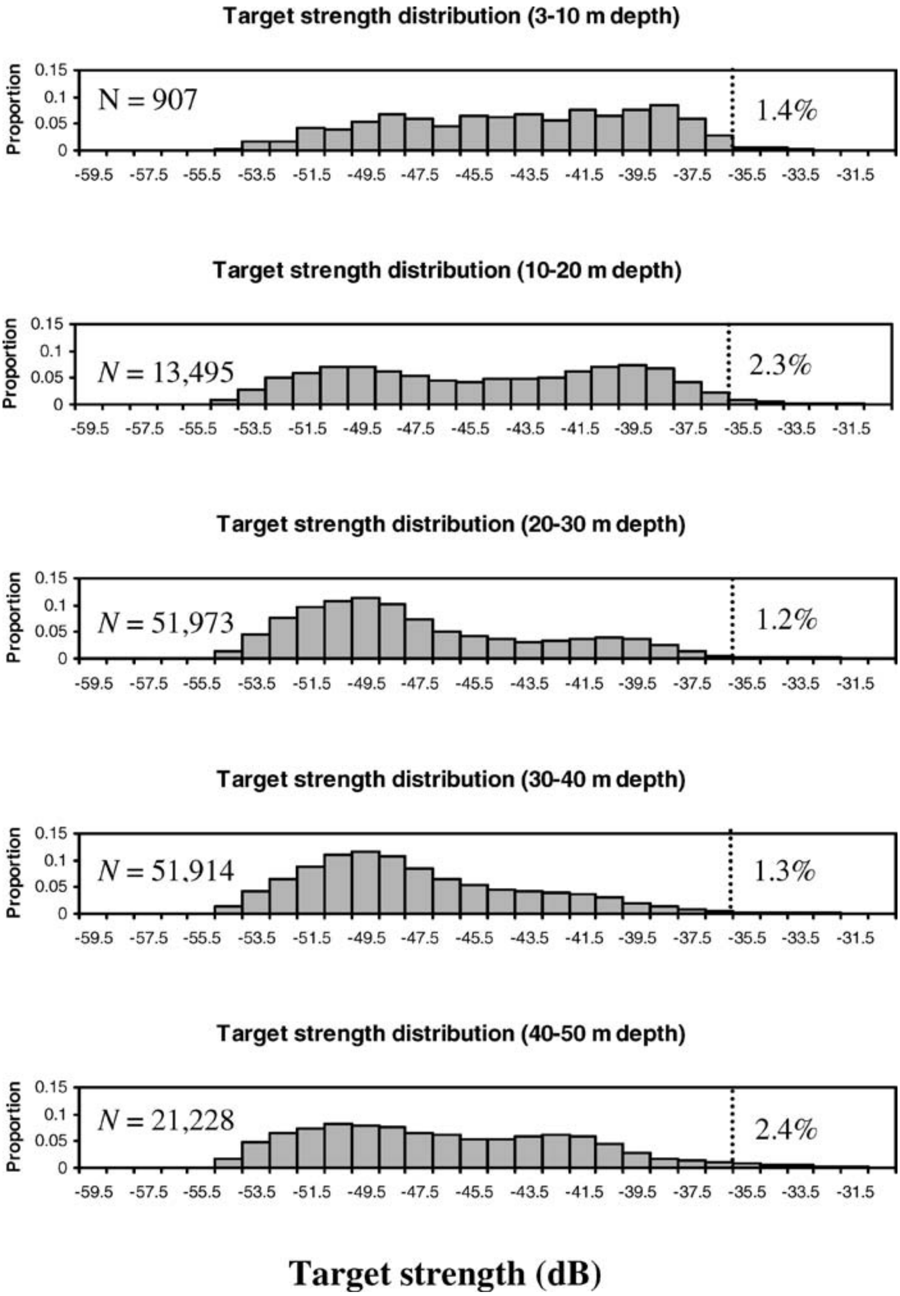

FIGURE 7.—Target strength frequency distributions of all targets meeting the single-fish classification criteria grouped by 10-m depth strata. The dashed line at −35.6 dB shows the cutoff used to estimate the densities of mature female lake herring exceeding 250 mm. The percentage of targets exceeding −35.6 dB in each stratum is also presented.

Discussion

This study demonstrates that the number of spawning lake herring females and the eggs they deposit in a statistical grid can be estimated with reasonable precision. Our sensitivity analysis showed that variability in the estimate of spawning female densities contributed the most uncertainty to the estimate of lake herring eggs deposited. However, the relative estimation error (i.e., [σ_E/arithmetic mean] $\times$ 100) of the mature female lake herring density estimate in grid

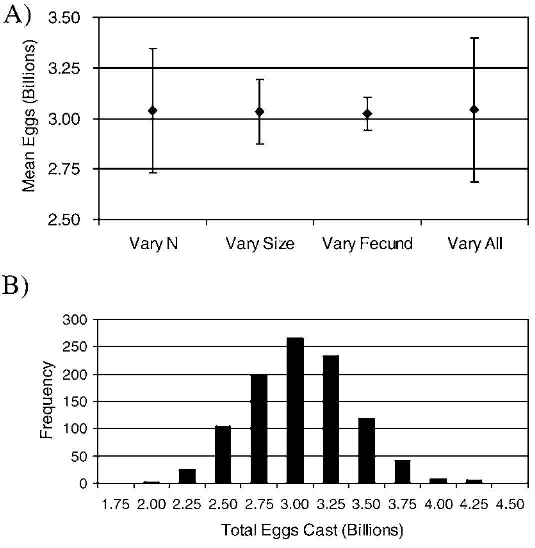

FIGURE 8.—Panel **(A)** shows the mean ± SD number of eggs cast by lake herring in statistical grid 1409 from 1,000 simulations varying female density (*N*), size structure, and fecundity one at a time as well as all three at once. Panel **(B)** shows the frequency distribution of the number of eggs cast by lake herring in statistical grid 1409 from 1,000 bootstrap simulations concurrently incorporating uncertainty in the estimates of spawning female density, the size structure of trawl catches, and the relationship between fecundity and mass. The relationship between the length and the mass of fish was held constant. The upper and lower 95% confidence limits were 2.356 and 3.778 billion (10^9) eggs, respectively (see Methods section for details).

1409 was quite low (12.3%). Additional acoustic data might improve the precision of density estimates, but at a cost of less spatial coverage of other statistical grids. Uncertainty in the numbers of eggs deposited in grid 1409 was also caused by our inability to precisely characterize spawning female size structure from only six midwater trawl samples. Because acoustic data can be collected concurrent with midwater trawling, more trawls (e.g., 2–3 more per grid) could be conducted without devoting a great deal of additional vessel time.

Our acoustic estimates of mature female lake herring densities were predicated on defining a threshold value where the correlation of trawl catches of lake herring exceeding 250 mm and acoustic density estimates was maximized. The correlation, however, was not high with an estimated maximum R^2 of 0.34 using the −35.6 TS threshold cutoff. Parkinson et al. (1994) compared acoustic densities and midwater trawl densities of age-1–3 kokanee *Oncorhynchus nerka* (105–245 mm) in an Idaho lake and reported similar results with a correlation coefficient of 0.5 ($R^2 = 0.25$). Our empirically derived cutoff value did compare favorably (within 1 dB) to the TS value predicted by the Rudstam et al. (1987) equation for a 250-mm lake herring (−36.6 dB). We conclude that our density estimates of mature female lake herring are reasonable. Our analysis to define a TS cutoff threshold for calculating mature female densities from acoustic data could have benefited from a larger data set, the collection of which will be important to future studies.

A wide range of techniques have been used to apportion acoustic data to species when stocks are mixed, but to our knowledge no other study has reported an estimate of only females. Because fish species have different temperature preferences, acoustic targets collected from thermally stratified lakes have been assigned to species based upon depth. Lake Superior was isothermic during our survey, thus pelagic species were not thermally segregated. In the present study we found mature male lake herring near the lake bottom, while mature female lake herring, immature male and female lake herring, and rainbow smelt were largely pelagic. By combining available technology (our ability to use a TS threshold to exclude small fish) with biology (mature females occupying different habitat than mature males and other large species) we were able to enumerate densities of mature female lake herring. It is important to note that a study of spawning lake herring near Bayfield, Wisconsin, showed that the percentage of females caught in overnight bottom-set gill nets, retrieved daily, increased gradually from 44% on 20 November to 84% on 6 December 1961 (Dryer and Beil 1964). The Dryer and Beil (1964) study suggests that females likely become less pelagic as the spawning season progresses and become more difficult to assess using acoustic techniques.

Previous studies of Lake Superior lake herring have used eggs per gram of female body mass as a means to compare fecundity over time. Dryer and Beil (1964) reported a mean fecundity of 29.7 eggs/g for 30 lake herring collected at Keweenaw Bay and Marquette during 1950–1954 before the collapse of lake herring populations in Lake Superior (Selgeby 1982). No measure of precision surrounding this estimate was presented. Bowen et al. (1991) reported an average fecundity of 50.2 eggs/g body mass (SD = 8.1) for 25 lake herring from Keweenaw waters collected during 1983 and concluded that the fecundity of female lake herring in Lake Superior was much higher at lower population levels. In the present study, 22 lake herring captured near Madeline Island had a mean fecundity of 46.5 eggs/g (SD = 5.9). We performed a one-tailed *t*-test comparing the mean fecundity reported by Bowen et al. (1991) and our mean and found no significant difference (*t*-value = 1.901, $P = 0.97$, df = 43). We conclude that lake herring fecundity in Lake Superior remains unconstrained by density-dependent growth. Any contemporary studies involving lake herring fecundity should not rely on the extensive information published in Dryer and Beil (1964).

Total exploitation of mature female lake herring from grid 1409 is probably low compared with historic peak levels. By comparing acoustic density estimates of mature lake herring females to commercial catch statistics, we estimate the conditional fishing mortality rate of female herring, or m (Ricker 1975), in grid 1409 during 2004 at 0.023. Selgeby (1982) shows the location of six major spawning areas used historically by lake herring, including a site southwest of Madeline Island (Bayfield fishing grounds) that we also identified in the present study (Figure 6B). Selgeby (1982) reported that instantaneous rates of fishing mortality (F) of lake herring from the Bayfield fishing grounds between 1936 and 1950, when annual exploitation was the highest on record, ranged from 0.18 to 0.67. By convention $m = 1 - e^{-F}$, such that conditional fishing mortality rates between 1936 and 1950 ranged from 0.17 to 0.49 annually. Based on these results, we conclude that current exploitation levels of all mature female lake herring at the Bayfield fishing grounds is low compared with historic levels. Because commercial gill nets typically catch lake herring greater than 325 mm, it is likely that the exploitation rate of the very largest of females (e.g., 400 mm) exceeds 0.023. Before exploitation rates of the largest female lake herring can be calculated we must determine if these individuals are in fact rare as our midwater trawl catches suggest, or if larger fish are better at evading trawl capture. All sizes of female lake herring were likely equally vulnerable to acoustic detection, so our estimates of lake herring females exceeding 250 mm were probably sound.

We recommend that the stock–recruitment model for Lake Superior lake herring developed by Hoff (2004) be used with caution. After compiling the density estimates that Hoff (2004) used in model development, we found the estimates had rather poor precision (mean RSE equaled 53.5%; range, 41.0%–82.2%). Estimates of adult densities gathered by daytime bottom trawling during spring are probably biased downward. For example, using the same stations from Wisconsin waters used by Hoff (2004), we calculated the mean density of lake herring exceeding 250 mm during the spring of 2004 was 3.1/ha (both sexes), which was only 23% of the mean density of mature females (13.3/ha) found during our winter 2004 survey. Furthermore, during the spring 2004 bottom trawl survey we gathered acoustic data while trawling and encountered huge schools in the pelagic zone above the bottom trawl path at some stations. Milne et al. (2005) reported that lake herring schooled in open water of Lake Opeongo, Ontario, during daylight so it is possible the schooling fish we encountered in Lake Superior were also lake herring. Given daytime bottom trawling likely provides erroneous estimates of adult densities, we believe stock–recruitment models developed from these data are also suspect.

Given the success of this initial research, we plan to enumerate spawning adults in more Lake Superior statistical grids in upcoming years. Clearly, replicate surveys spanning the entire spawning season are needed to understand the repeatability of results. Additional surveys to assess swim-up larvae, age-0, and age-1 lake herring densities are also needed and are under development. With time, we hope that these surveys will result in more accurate data to develop a lake herring stock–recruitment model for Lake Superior. Restoration of lake herring and other native planktivores is a high priority for management agencies on the other four Great Lakes (DesJardine et al. 1995; Eshenroder et al. 1995; Stewart et al. 1999; Ryan et al. 2003). Results from this spawning lake herring survey could provide a foundation to monitor the recovery of lake herring in these lakes once restoration efforts are underway.

Acknowledgments

We thank the Captain and crew of the research vessel *Kiyi* for their assistance in the field. Ed Roseman, Jean Adams, David Warner, Jaci Savino, Patrick Sullivan, Scott Gangl, Christopher Taylor and one anonymous reviewer provided helpful comments on earlier versions of the manuscript. This article is Contribution 1350 of the USGS Great Lakes Science Center.

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