Hydroacoustic Estimates of Abundance and Spatial Distribution of Pelagic Prey Fishes in Western Lake Superior

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ABSTRACT. *Lake herring* (Coregonus artedi) *and rainbow smelt* (Osmerus mordax) *are a valuable prey resource for the recovering lake trout* (Salvelinus namaycush) *in Lake Superior. However, prey biomass may be insufficient to support the current predator demand. In August 1997, we assessed the abundance and spatial distribution of pelagic coregonines and rainbow smelt in western Lake Superior by combining a 120 kHz split beam acoustics system with midwater trawls. Coregonines comprised the majority of the midwater trawl catches and the length distributions for trawl caught fish coincided with estimated sizes of acoustic targets. Overall mean pelagic prey fish biomass was 15.56 kg ha^{-1} with the greatest fish biomass occurring in the Apostle Islands region (27.98 kg ha^{-1}), followed by the Duluth Minnesota region (20.22 kg ha^{-1}), and with the lowest biomass occurring in the open waters of western Lake Superior (9.46 kg ha^{-1}). Biomass estimates from hydroacoustics were typically 2–134 times greater than estimates derived from spring bottom trawl surveys. Prey fish biomass for Lake Superior is about order of magnitude less than acoustic estimates for Lakes Michigan and Ontario. Discrepancies observed between bioenergetics-based estimates of predator consumption of coregonines and earlier coregonine biomass estimates may be accounted for by our hydroacoustic estimates.*

INDEX WORDS: *Hydroacoustics, Lake Superior, lake herring, rainbow smelt, coregonines.*

INTRODUCTION

Lake herring *Coregonus artedi* and rainbow smelt *Osmerus mordax* are an important resource for the recovering lake trout *Salvelinus namaycush* populations and also support a valuable commercial fishery in Lake Superior. Thus, lake trout and the commercial fishery represent a demand on the prey fish resource. A commonly used technique to determine if sufficient resources exist to support demand is demand-supply (D-S) analysis (Stewart *et al.* 1983, Ney 1990, Ney 1993, Stewart and Ibarra 1991, Rand and Stewart 1998, Baldwin *et al.* 2000, Johnson and Martinez 2000). D-S analysis combines estimates of prey abundance with predator consumption estimates from bioenergetics models to evaluate carrying capacity limitations (Ney 1990). Two relatively recent D-S analyses have suggested that demand by salmonine predators in Lake Superior exceeded prey supply (Negus 1995, Ebener 1995). Chinook salmon (*Oncorhynchus tshawytscha*) hatchery returns and harvest have declined steadily since the mid 1980s (Schreiner 1995, Bronte *et al.* 2003) suggesting a decrease in lake survival, which supports the imbalance suggested by the demand-supply analysis (Negus

1995). Moreover, salmonine growth rates and size at age have also declined (Johnson *et al.* 2001, M.T. Negus, Minnesota Department of Natural Resources, personal communication). Despite these apparent declines, Lake Superior now supports natural production of lake trout to the point where stocking was drastically reduced (Hansen *et al.* 1995) and wild populations have reached or exceeded historical levels in some locations (Wilberg *et al.* 2003). The success of lake trout restoration in Lake Superior contradicts the D-S discrepancy. The combination of the above evidence is thus inconclusive and suggests that a re-evaluation of the data used for the bioenergetics D-S analysis is necessary.

Required data for the bioenergetics D-S analysis includes predator mortality estimates, predator diet information, predator and prey energy content, and estimates of prey and predator fish biomass. State, tribal, and federal agencies have committed to increased sampling of salmonines for diet information in U.S. waters of Lake Superior and to increased efforts to estimate predator abundance, and we have sufficient information on predator and prey energy densities (Johnson *et al.* 1998, Johnson *et al.* 1999). Further understanding of dietary linkages has been

gained through stable isotope analysis of key fish species (Harvey *et al.* 2002, Harvey *et al.* 2003). However, accurate biomass estimates of the pelagic prey fish are still lacking. Thus, quantitative estimates of pelagic prey fish biomass are key to understanding the capacity of Lake Superior to support current and future populations of wild, naturalized, and hatchery produced predators.

The dominant salmonine predators in Lake Superior are the lean lake trout (*Salvelinus namaycush namaycush*) and siscowet lake trout (*Salvelinus namaycush siscowet*), while chinook salmon, coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) are also present but are far less abundant (Bronte *et al.* 2003). The primary prey items of the salmonine predators are lake herring and rainbow smelt (Dryer *et al.* 1965, Anderson and Smith 1971, Conner *et al.* 1993, Negus 1995, Ebener 1995). Currently, the United States Geological Survey (USGS) conducts population assessments of lake herring and rainbow smelt from spring bottom trawl surveys. These routine assessments provide a valuable "index of abundance" for a variety of pelagic and benthic fishes and information on trends, mortality, and size at age, but may not provide accurate estimates of absolute abundance for pelagic species. The lack of quantitative biomass estimates of prey fish can impede prudent management (e.g., stocking and catch limit decisions) for Lake Superior, and our understanding of predator prey interactions.

Hydroacoustic surveys offer an alternative method to bottom trawl surveys for determining pelagic fish abundance, and when properly calibrated, hydroacoustics can provide estimates of absolute abundance. Hydroacoustics has been effectively used in Lakes Michigan (Brandt 1980, Brandt *et al.* 1991, Argyle 1992), Ontario (Mason *et al.* 2001), and Superior (Heist and Swenson 1983) and is an established assessment tool used throughout the world (Thorne 1983, Baily and Simmonds 1990). Our objectives were to estimate pelagic fish biomass and spatial distribution using hydroacoustics, and to compare hydroacoustic estimates of pelagic fish abundance to estimates from bottom trawl surveys. Any inconsistencies in the biomass estimates of pelagic fish may explain the D-S discrepancy. To address these objectives, we used spatial data comprised of concurrent hydroacoustic and mid-water trawl information collected in 1997, as well as information from the bottom trawl surveys in the same year, to identify the level of agreement between the two methods and to esti-

mate the biomass of prey fishes for comparison to predator demand. Also, we compared hydroacoustic results from surveys conducted during the day and at night and offer recommendations for future surveys.

METHODS

General Sampling Design

Nighttime hydroacoustic and midwater trawl surveys of pelagic fishes were conducted in western Lake Superior during 13–22 August 1997 along transects that spanned three distinctive regions-Apostle Islands (complex bathymetry), open lake (deep, cold), and a region directly influenced by Duluth, MN and the influx of the St. Louis River (Fig. 1). The survey employed vessels working in tandem: one that deployed hydroacoustic equipment and another that followed with the mid-water trawl gear. Hydroacoustic sampling was accomplished from the Wisconsin Department of Natural Resources R/V *Hack Noyes* (13–14 August) and the United States Environmental Protection Agency vessel R/V *Lake Explorer* (15–22 August). Midwater trawl tows from the USGS R/V *Siscowet* were used to identify acoustic echoes to species and to compare fish size with acoustic estimates of fish size. We also collected water quality, zooplankton, and forage fish diet information (see Johnson *et al.* 2004). Sampling was done primarily at night; however we collected some daytime acoustics in the Apostle Islands to compare to night estimates of biomass.

Acoustic Sampling

We used a 120 kHz split-beam (15°) digital echosounder (HTI model 241) to measure the spatial distribution, density, and size of pelagic fishes during day and night with 200.8 dB Source Level (re μPa @ 1m), –154.3 dB 40LogR system gain (dB re V μPa @ 1m), –133.4 dB 20LogR system gain (dB re V μPa @ 1m), pulse width of 0.4 ms and at two pings per second. The acoustic transducer was mounted on a 2.5-m aluminum towbody and towed alongside the research vessel at a depth of about 1 m from the surface at speeds of 2.5–3.5 m s^{-1}. Equipment performance was monitored in the field using an oscilloscope. Signals were digitized and recorded on digital audiotapes for later post-processing and analyses in the laboratory. Routine calibration was performed using a tungsten carbide reference sphere (Foote *et al.* 1987, Foote 1990).
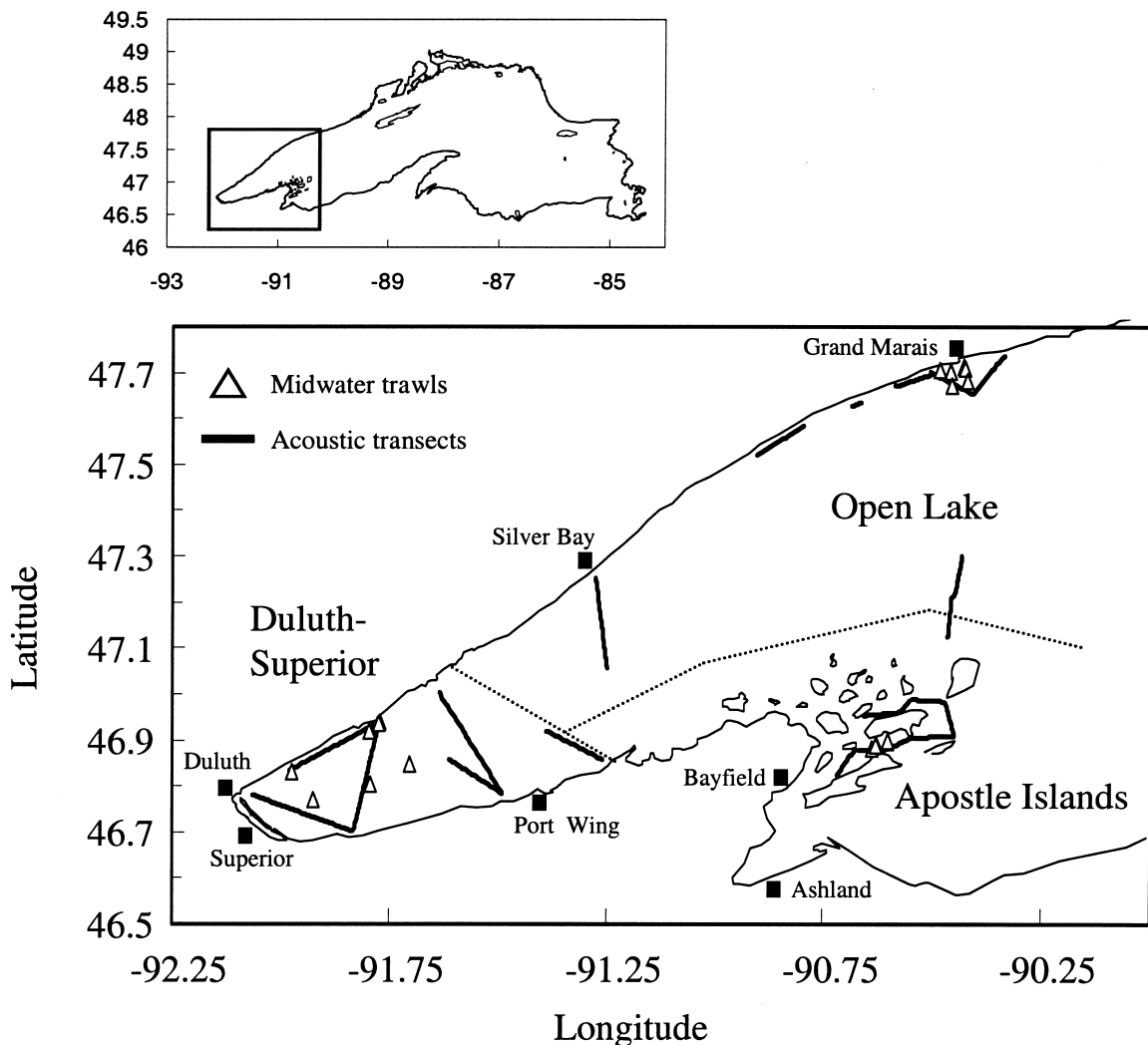
FIG. 1. *Map of Lake Superior with the locations of the hydroacoustics transects and midwater trawling sites. Dotted lines demark boundaries for the three zones identified in the text.*

Acoustic data were processed using a threshold value of –60 dB for both the echo-squared integration and split-beam analyses. Echo-squared integration provides a relative measure of fish density that can be scaled to absolute fish density with system parameters obtained from equipment calibration and measures of the mean backscattering cross-section of the fish obtained from split-beam analyses (MacLennan and Simmonds 1992). Prior to processing, raw acoustic data were carefully inspected for noise and bottom intrusion; such were removed prior to processing. Acoustic signals were vertically binned beginning 2-m below the transducer (approximately 3-m below the surface) to 100 m at 1-m intervals and horizontally binned in intervals of 120 s, corresponding to a horizontal resolution of about 300–420 m. Sums of squared voltages were inspected for noise and bottom contamination before scaling to absolute estimates of abundance.

Split-beam analysis was used to determine the depth distribution of fish backscattering cross-section (σ_{bs}) and fish target strengths (TS, with $TS = LOG_{10}\ \sigma_{bs}$), i.e., fish acoustic size. Acoustic size is the fraction of incident sound energy that is reflected by a fish back toward the transducer and is related to size of the fish. Target strength values were converted to estimates of fish length and mass using an empirical relationship developed by Fleischer *et al.* (1997) for Great Lakes coregonine fishes:

$$Log_{10} W = 4.326 + 0.066 \ TS$$

$$Log_{10} L = 2.023 + 0.019 \ TS$$

where W is mass (g) and L is length (cm).

Fish biomass density (g m^{-2}) was determined by dividing the sums of squared voltages by the mean backscattering cross section ($\bar{\sigma}_{bs}$) and multiplying by the average mass (from TS-mass relationship) of an individual fish for each 1 m × 120 s cell. Mean backscattering cross-section ($\bar{\sigma}_{bs}$) was calculated for each 1 m vertical and 120 s horizontal distance, using only targets with multiple returns (two or more returns from a single target), to convert echo-squared integration into measures of fish density. When there were insufficient numbers of individual acoustic targets to estimate $\bar{\sigma}_{bs}$ within a cell, the mean $\bar{\sigma}_{bs}$ of horizontal neighboring cells were used. Cells were then summed vertically for each 120 sec segment and converted to kg ha^{-1}.

Biological Sampling

We used midwater trawls (N = 19 tows) to relate species identities and fish sizes to acoustic targets. The midwater trawl (14-m box design, 6-mm cod end mesh) was towed at about 4.8 km hr^{-1} for 45 min, filtering about 4,070 m^3 min^{-1} trawled. Midwater trawls were fished at discrete depths (headrope depth: 10 m, 20 m, 30 m, 40 m, or 50 m), and positions monitored using SCANMAR trawl mensuration gear. All fish captured were identified, counted, measured (± 1 mm), and weighed (± 1 g).

Abundance Estimates

We estimated pelagic fish biomass density (kg ha^{-1}) for the entire western basin and for each region (Fig. 1). To do this, we bootstrapped the nontransformed data (each 300–420 m segment) within and amongst regions 1,000 times using Splus® (Insightful Corp 2001) to estimate arithmetic mean and precision of biomass density.

In addition, we log$_{10}$ transformed the data and used Generalized Additive Models (GAMs) to determine the bathymetric depth-dependent biomass distribution of Lake Superior fishes. GAMs have additive terms like linear (regression) models, but the terms are obtained using nonparameteric scatterplot smoothers (here smoothing splines), which allow the data to suggest nonlinearities (Hastie 1992). Bathymetric depth and location, represented as a two-way interaction term between latitude and longitude, were used as predictors of fish biomass density. An iterative model search was conducted to identify the optimum smoothing parameter from a rich set of potential values for each of the additive terms, based on the Akaike Information Criterion (AIC; Akaike 1973). All GAMs reported here were fitted using Splus® 6.0 (Insightful Corp 2001).

RESULTS

Target Strength vs. Trawl Catch

Mean fish length was similar between TS- and midwater trawl-derived estimates (mean = 21.1 cm, Fig. 2). However, TS-derived estimates of fish length failed to capture the tri-modal length frequency distribution observed in the trawl catches. A comparison of mean mass between TS- and midwater trawl-derived estimates was less favorable (TS
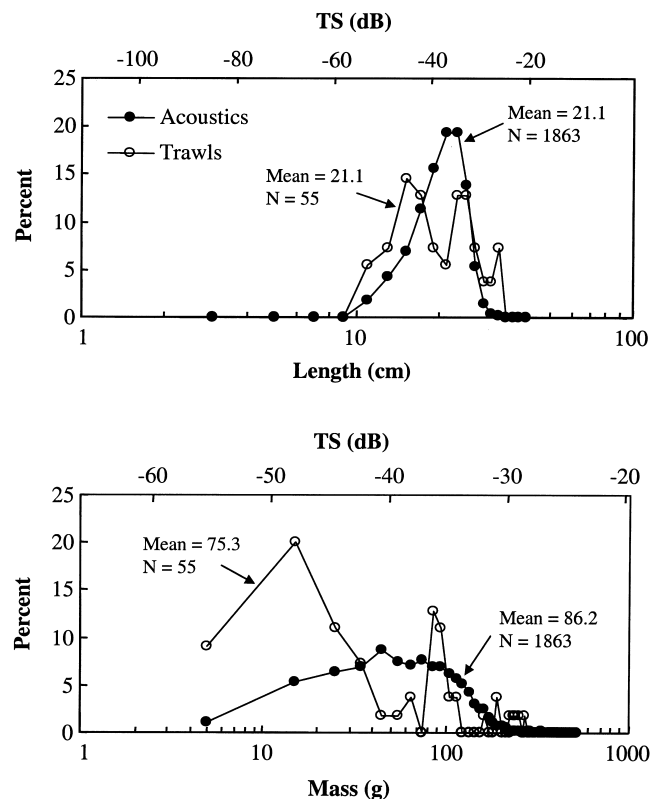

FIG. 2.   Comparison of trawl and hydroacoustic size estimates (i.e., target strength, TS). Lengths and mass of fish collected from trawls where converted to TS (dB), and TS values where converted from TS to length and mass units, using the equations found in Fleischer et al. (1997) for Lake Michigan fishes.

mean = 86.2 g, trawl mean = 75.3 g). Estimates of TS-derived mass failed to capture the modality of the field data, however the range in the data was similar.

Species Composition

We collected 137 fish representing five species—lake herring (N = 58), rainbow smelt (N = 45), bloater *Coregonus hoyi* (N = 18), kiyi *Coregonus kiyi* (N = 12), and lake trout (N = 1) with three unidentified coregonines. Due to the low catch rates we were unable to collect a sufficient number of fish in each region to construct realistic species compositions. For example, bloaters were absent from our midwater trawl tows in the Duluth and open water regions, despite their known occurrence in these regions. However, we did have relatively high catch rates in the Apostle Islands (total N = 55; bloaters N = 18)). From midwater trawls in the Apostle Islands, we discerned two nearly disjoint size classes representing two different groups of fish—coregonines and rainbow smelt (Fig. 3). We divided the two size groups at –40 dB, approximately 18.3 cm and 48.5 g (Fig. 3), and assigned the larger targets as coregonines (lake herring, bloater, kiyi) and the smaller fish as rainbow smelt. We then used this size criterion to estimate group composition and group specific biomass for all regions. Lack of significant recruitment of coregonines (few small individuals) and a size distribution skewed towards larger individuals (Bronte *et al.* 2003), supports our classification based on size threshold. For the Apostle Islands, our acoustical estimates of species composition on a mass basis were similar to that observed with the midwater trawl catches (Table 1). Our hydroacoustically derived species composition by biomass differed from species composition estimated from June bottom

TABLE 1. *Percent species compositions by biomass and number estimated from midwater trawls (N = 4) and acoustic target strength (TS) along a single transect in the Apostle Islands.*

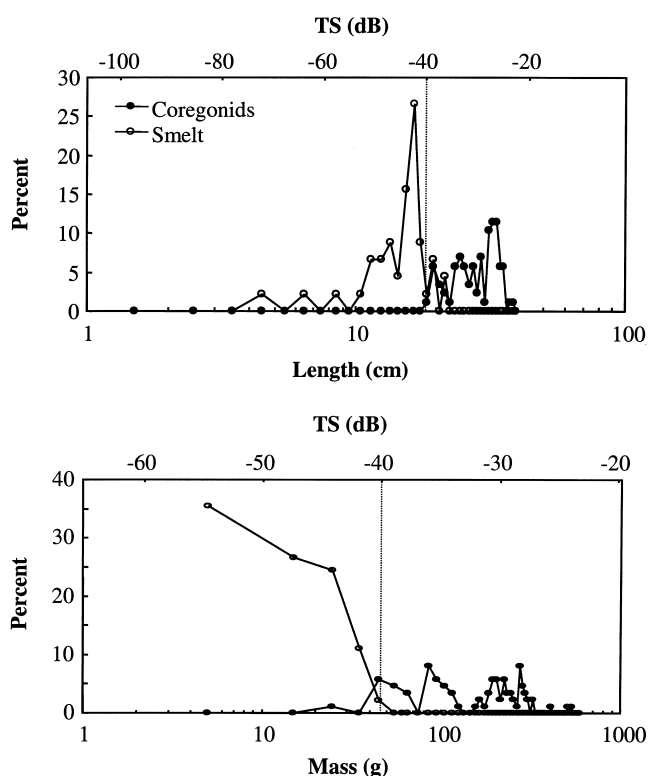|	Rainbow Smelt	Coregonines
Biomass		
Acoustics	8.5	91.5
Midwater trawl	11.5	88.5
Number		
Acoustics	23.5	76.5
Midwater trawl	46.3	53.7

FIG. 3. *Size distribution (length, mass, and target strength TS) of fish by group (rainbow smelt and coregonines) from midwater trawling in the Apostle Islands. Fish length and mass were converted to TS using the equations of Fleischer* **et al.** *(1997) for Lake Michigan fishes. Vertical dotted lines represents size cut for separating fish groups. See text for details.*

trawls (Table 2). For the Duluth-Superior region, hydroacoustic estimates of species composition tended to have lower percentage of rainbow smelt but higher percentage of coregonines when compared to the spring bottom trawl survey. However, hydroacoustics estimated a greater percentage of rainbow smelt and a lower percentage of coregonines in the open lake and Apostle Islands region.

Spatial Distribution

Distinct diel vertical migration of fishes occurred in the Apostle Islands region (Fig. 4). During the day, peak concentrations of fish biomass (from hydroacoustics) occurred near the bottom in shallower areas, with lower concentration of fish found over deeper water. At night, fish dispersed and migrated toward the surface. Daylight estimate of arithmetic mean fish biomass density was 20.80 kg ha^{-1},

TABLE 2. *Percent group compositions by mass as estimated from acoustics and from the USGS bottom trawl assessment in June.*

Region	Rainbow Smelt	Coregonines
Acoustics		
Duluth-Superior	11.5	88.5
Open Lake	16.9	83.1
Apostle Islands	12.9	87.1
Bottom Trawl		
Duluth-Superior	39.5	60.5
Open Lake	9.8	90.2
Apostle Islands	3.3	96.7

which was 78% of the estimated night fish biomass density.

Fish biomass density also varied with respect to bathymetric depth (Fig. 5). Maximum fish biomass density peaked between the bathymetric depth contours of about 55–100 m. For the Duluth and the Apostle Islands regions, peak in biomass density was spread out across these depths. For the open lake region, peak biomass density occurred between about 75–100 m bathymetric depths. Biomass density across all regions dropped rapidly as bathymetric depths approached 100 m. As a result of this observation, we also estimated fish biomass for bathymetric depths less than and greater than 100 m.

Biomass Estimates

Biomass differed among regions (Table 3) with highest biomass measured in the Apostle Islands (27.98 kg ha^{-1}), followed by Duluth-Superior (20.22 kg ha^{-1}), and then the open lake region (9.46 kg ha^{-1}). Highest biomass occurred within the 100-m bathymetric contour where biomass was 4–24 times greater than offshore waters (Table 3). On a group-specific basis, coregonine overall biomass density was highest in the Apostle Islands (24.37 kg ha^{-1}) and lowest in the open lake region (7.86 kg ha^{-1}) (Fig. 6). For rainbow smelt, greatest overall biomass density occurred in the Apostle Islands (3.61 kg ha^{-1}) and was lowest in the open lake region (1.60 kg ha^{-1}) (Fig. 6).

Comparison with Traditional Bottom Trawl Assessment

The principal motivation for this study was to identify whether discrepancies between prey fish abundance and predator demand could be explained by bias in prey fish biomass estimated using the area-swept method from bottom trawls. The discrepancy between demand and supply identified by Negus (1995) used USGS bottom trawl data. We compared hydroacoustics estimates of fish biomass to estimates from the USGS trawl surveys. USGS bottom trawl surveys use the area-swept method and integrate across the bathymetric depths 15 to about 75 m with a maximum depth of 100 m. Sampling is conducted during the daylight hours when fish are typically associated with the bottom. The range in trawling depths is consistent with our observations that much of the fish biomass is inshore of the 100-m bathymetric contour (Table 3, Fig. 5).

Our hydroacoustic estimates of mean total fish biomass inshore of the 100-m bathymetric contour were consistently higher than the bottom trawl estimates from June of the same year (Fig. 7). Hydroacoustics estimates of mean biomass were on average greater by a factor of about fifty, but the magnitude of the difference was dependent upon region. By regions, hydroacoustics estimates were 2.0, 14.4, and 134.1 times higher for Apostle Islands, Duluth-Superior, and open lake regions, respectively (Fig. 7). Our estimates of coregonine biomass were 1.8, 21.1, and 1,141.0 times higher than for bottom trawl estimates for the Apostle Islands, Duluth, and open lake regions, respectively (Fig. 8). For rainbow smelt, acoustic biomass estimates were 7.7, 4.2, and 25.1 times that of the trawl estimates for Apostle Islands, Duluth, and open lake regions, respectively.

DISCUSSION

Evaluation of the D-S Paradox

Negus (1995) suggested that the demand-supply discrepency for the Minnesota waters of Lake Superior may partly be due to the biases associated with using bottom trawls to estimate pelagic prey fish biomass. The discrepancy was substantial and indicated that lake trout eat about 21.4 times more rainbow smelt and 7.6 times more coregonines than were available, as estimated from the trawl surveys. Our hydroacoustic estimates of rainbow smelt abundance were greater than estimates from bottom trawls by a factor of 4.1 in the Duluth-Superior region and a factor of 25.0 in the open lake region (Fig. 8), suggesting that there may be about 17.3 times (weighted for area less than 100-m bathymetric contour) more biomass of rainbow smelt than estimated from the bottom trawls. The biomass estimates of coregonines from hydroacoustics were
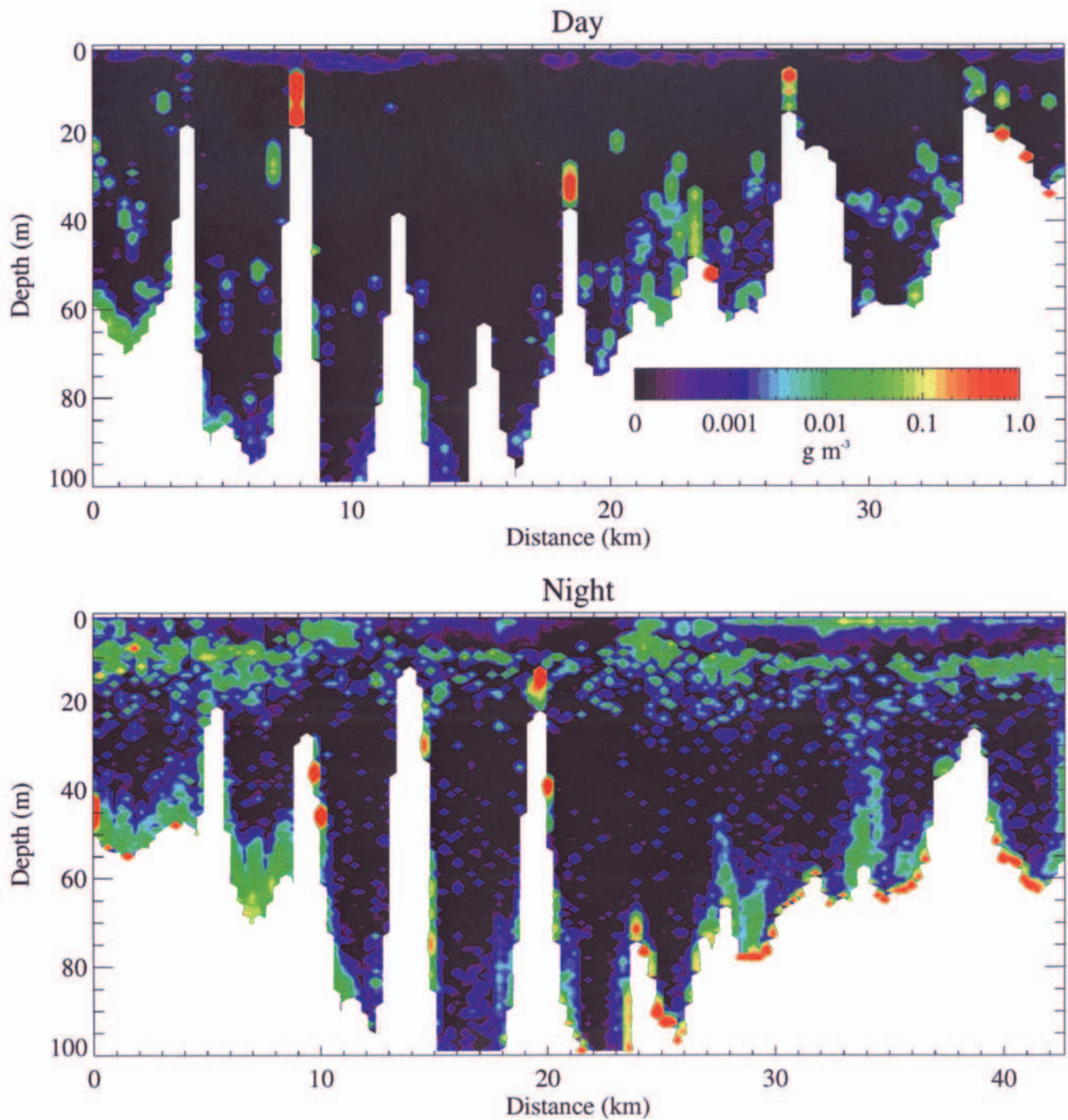
FIG. 4. *Two-dimensional visualization of acoustic estimates of prey fish biomass density (g m⁻³) for daylight and night in the Apostle Islands region. White region in graphic represents bottom, with the peaks (shallow bottom) occurring when ship approached and then steamed away from an island. Note that bottom echoes where removed from the analysis by careful inspection of the data before processing. Color legend is log_{10} scaled, but forced to zero (black) where no fish were measured.*
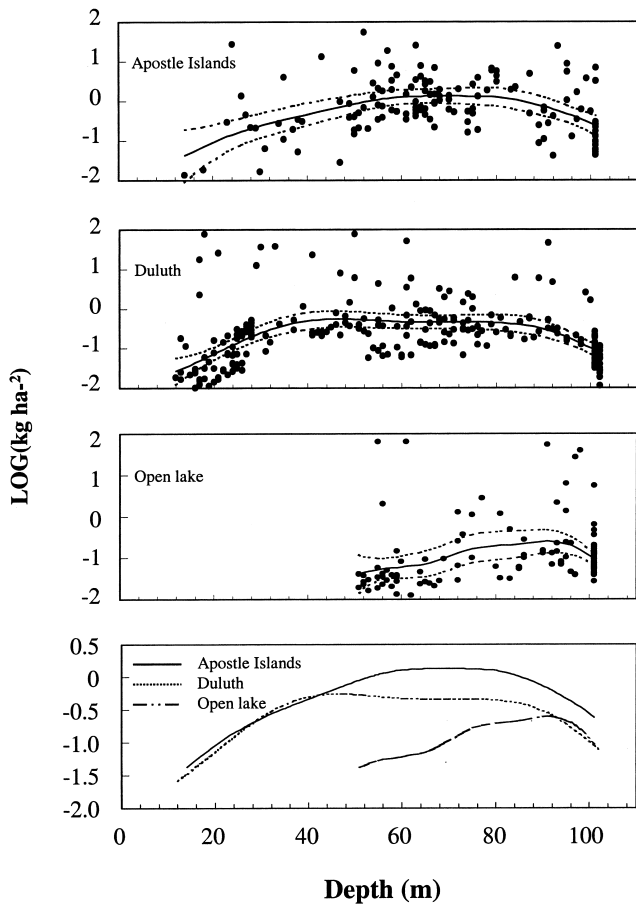
FIG. 5. *Results of General Additive Model (GAM) with respect to bathymetric depth for each region and combined for the western basin of Lake Superior. High density of points occurring at the 100-m bathymetric contour represents estimates of fish density for the upper 100 m of the water column for fish offshore of the 100-m contour.*

FIG. 6. *Comparison of mean fish biomass (± 95% CI) estimated using hydroacoustics and bottom trawls, inshore of the 100-m bathymetric contour.*

greater than bottom trawl estimates by a factor of 21.1 to 1,141 (Fig. 8). The magnitude of the difference in the biomass estimates between our 1997 hydroacoustics and 1997 USGS bottom trawls for rainbow smelt does not appear sufficient to account for the differences between demand and prey bio-
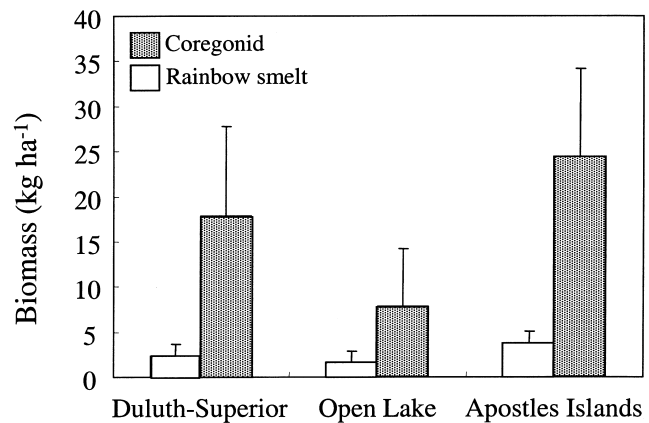
mass. However, estimates of coregonine biomass using hydroacoustics suggest that there are sufficient coregonine prey resources to support predator and fishery demand. Differences in biomass estimates of coregonines between the two approaches may be attributable to diel vertical migration that takes fish deeper than 100 m during daylight hours.

A second D-S exercise expanded the spatial coverage of the analysis to include the entire western basin of Lake Superior (Ebener 1995). Ebener (1995) found that there should be 1.25 times more rainbow smelt than estimated by bottom trawls and that there was sufficient coregonine biomass. Our hydroacoustic estimates of rainbow smelt biomass, when averaged over the three stratified regions inshore of the 100-m bathymetric contour, was about 11 times greater than that estimated with bottom trawls. If differences between acoustics and trawl estimates were consistent between years, it would appear that there were sufficient rainbow smelt resources to balance estimated predator consumption and observed fish removals.

The discrepancy observed between predator consumption of coregonines and coregonine biomass

TABLE 3. *Arithmetic mean biomass densities (kg ha⁻¹), with lower and upper 95% confidence limits in parentheses, for each region of the western basin (Fig. 1) and for the entire western basin of Lake Superior. Mean biomass is based on bootstrapping of acoustics segments.*

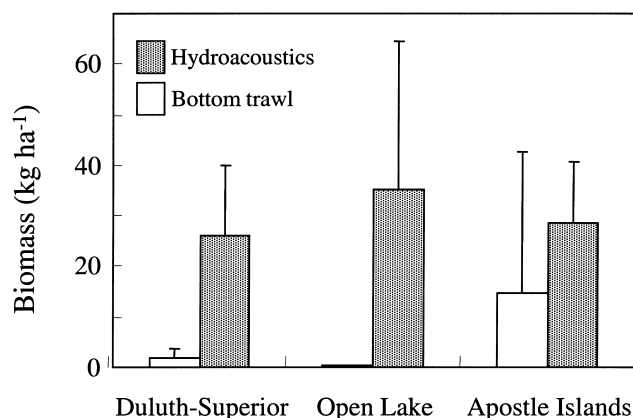|	Duluth-Superior	Open Lake	Apostle Islands	Western Basin
Wt. Mean	20.22 (9.12, 31.33)	9.46 (1.78, 17.13)	27.98 (16.75, 39.22)	15.56 (10.95, 20.95)
< 100 m	26.35 (11.86, 40.84)	35.70 (6.51, 64.89)	28.99 (17.58, 40.40)	28.49 (19.01, 37.97)
≥ 100 m	1.11 (0.56, 1.66)	1.70 (0.39, 3.01)	6.67 (−0.86, 14.20)	2.04 (0.94, 3.14)

FIG. 7. *Comparison of mean hydroacoustics biomass density estimates (± 95% CI) for coregonids and rainbow smelt amongst sampling regions in western Lake Superior.*

may be accounted for by using hydroacoustics for biomass estimates. While the D-S paradox for rainbow smelt biomass estimates is not yet totally resolved, hydroacoustics appears to hold promise. Rainbow smelt biomass derived from hydroacoustics surveys over larger spatial regions estimated sufficient rainbow smelt resources, while estimates on a small spatial region still provide inconclusive results. Such contrasting results across spatial scale may suggest that salmonine growth and foraging is not confined to the Minnesota waters of Lake Superior (Negus 1995), but rather occurs over a much larger spatial arena. For example, pacific salmonines in the Great Lakes show little site affinity during the year (Keller *et al.* 1990, Peck *et al.* 1999) making population estimates and spatial estimates of consumption difficult. Alternatively, pelagic prey fishes may undergo seasonal lake wide movements, periodically enhancing local prey abundance sufficient to support predator demand. Such seasonal patterns in prey fish spatial distributions have been observed for rainbow smelt and alewife (*Alosa pseudoharengus*) in Lake Michigan (Brandt *et al.* 1991) and may contribute to the discrepancies observed in western Lake Superior.

Potential Biases in the D-S Analysis

While there are clear mechanisms for possible bias in bottom trawl surveys, there are also possible sources of errors in estimates produced using hydroacoustic analyses, such as the inclusion of noise, scattering from plankton, and second echoes or bottom intrusions. We have attempted to minimize
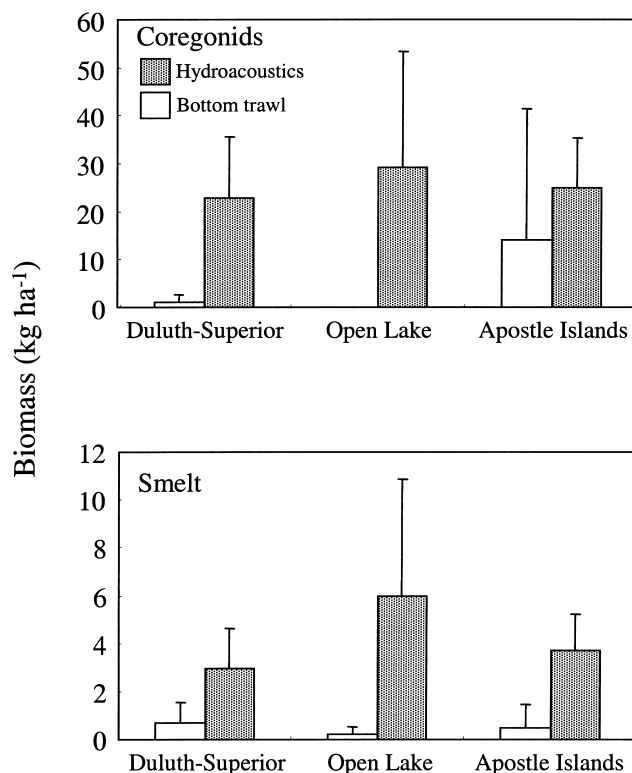

FIG. 8. *Comparison of group-specific mean biomass (± 95% CI) estimated using hydroacoustics and bottom trawls, inshore of the 100-m bathymetric contour.*

these errors by careful post processing of the data. In addition, the selection of target strength-length equations used also represents a possible source of error in computing biomass estimates. We selected the equations established by Fleischer *et al.* (1997). These relationships were established for species encountered that corresponded in size to those collected in our trawl samples. These equations tend to overestimate length of small targets and underestimate lengths of large targets (Rudstam *et al.* 2003). We recommend using alternative equations if the size range of fish being sampled falls outside the size range used to develop the relationship. For example, in years with a strong lake herring year class (i.e., many small fish), the Fleisher *et al.* equation may bias the results and lead to estimates that greatly exceed the actual biomass of fish in the survey area. Conversely, if large coregonids dominate the composition, the biomass estimated using the Fleischer equation will underestimate the biomass density of prey species.

Comparison with the Other
Laurentian Great Lakes

Hydroacoustic estimates of pelagic fish biomass density (area-weighted arithmetic estimates) in western Lake Superior are roughly an order of magnitude less than similar estimates of fish biomass from Lakes Michigan and Ontario. In Lake Michigan, Brandt *et al.* (1991) estimated pelagic fish biomass in late summer of 1987 to be 93.90 kg ha^{-1}. Similarly, Argyle *et al.* (1998) estimated pelagic fish biomass to range from 59.00–260.80 kg ha^{-1} (mean: 135.70 kg ha^{-1}) during early fall for the years 1991–96. For Lake Ontario, average lake-wide biomass density of pelagic fishes was 191.00 kg ha^{-1} in 1990 (Mason *et al.* 2001). The difference in pelagic fish biomass between Lake Superior and the other Great Lakes in not unexpected as Lake Superior is the coldest and most oligotrophic of all the Great Lakes.

Our results represent a significant first step for quantifying pelagic prey fish biomass using hydroacoustics, and for understanding the demand-supply relationships in Lake Superior. Comparison of day vs. night sampling indicates that night sampling offers the most effective means of estimating fish density. However, the equipment employed restricted meaningful analyses of fish targets to water column depths shallower than 100 m, and we had limited effort in the open lake region. It is possible that fish migrate below 100 m depth during the day and the presence of a vertical migration may offer a mechanism explaining the observed discrepancy. Increased efforts to quantify prey fish biomass in deeper areas and in the open water regions of the lake may provide insight into the existence of additional forage utilized by predators. Moreover, a more rigorous midwater trawling regime is necessary to determine fish species composition for calculating species-specific biomass estimates from acoustics, and for further testing the TS-length (and mass) relationship used here. Lastly, the comparison of hydroacoustics estimates of biomass to bottom trawl estimates should be continued to develop statistical models that may allow corrections to be applied to bottom trawl data for more accurate estimates of bottom trawl determined biomass. Bottom trawl surveys, while underestimating pelagic coregonine abundance, still are the only source for biomass and trend data for a variety of fishes (e.g., sculpins), which also serve as forage for salmonines, and are generally undetected by hydroacoustics.

There appears to be significantly more pelagic prey fish in Lake Superior than previously thought, and this will have a large impact on our understanding of predator-prey dynamics in the lake. However, Lake Superior appears to support a much lower pelagic prey fish biomass than the other Great Lakes. Our results suggest that there may be sufficient prey resources to support the current predator population. Further study into the spatial variability in prey distribution will continue to provide needed insight into demand-supply debate in Lake Superior.

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