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Acoustic characterization of *Mysis relicta*

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Abstract

It is possible to increase the sampling resolution and the available information on zooplankton populations by applying acoustic sampling techniques. Knowledge of an organism's acoustic target strength (TS) is critical for translating acoustic data into meaningful biological information, such as numerical abundance. We have taken several approaches to evaluate the acoustic TS of *Mysis relicta,* a key benthic-pelagic invertebrate in the Laurentian Great Lakes. This included in situ TS measurements with a dual-beam 420-kHz system and comparison among net-based, optical plankton counter (OPC)-based, and acoustic-based estimates of numerical abundance of mysids. In addition, based on the in situ TS data, we modified a model previously applied primarily to marine zooplankton taxa. The resulting predicted TS was compared to other TS estimates. The estimated mean TSs from the in situ TS measurements and the OPC-acoustic comparison were within a narrow range (-76 to -74.8 dB). Analysis of the net-acoustic data comparison resulted in an estimated average TS of -73.1 dB. We suggest that the net-acoustic discrepancy relative to other methods is due to net avoidance and low filtering efficiency. The model predicted similar mean TSs for the size distribution present when R (reflectivity coefficient) was changed to 0.0675. We hypothesized that the modification of the model parameter values was necessary because of the differences in the medium surrounding marine vs. freshwater zooplankton.

The opossum shrimp, *M. relicta*, is a freshwater species in the mainly marine group of crustaceans belonging to the family Mysidaceae (Mauchline 1980). It is a benthic-pelagic invertebrate that inhabits offshore, hypolimnetic waters. Mysids avoid light, remaining in deep water during the day and moving up to the epilimnion at night (Beeton and Bowers 1982). The extent of vertical migration is primarily limited by light levels and temperature (Teraguchi et al. 1975; Moen and Langeland 1989; Rudstam et al. 1989). *M. relicta* is common in the Laurentian Great Lakes (North America), and its abundance typically increases with bottom depth (Reynolds and DeGraeve 1972; Carpenter et al. 1974; Johannsson 1992). Integrated abundance of >500 animals m^{-2} and biomass of >7 g wet weight (WW) m^{-2} have been observed in Lake Ontario and Lake Michigan (Grossnickle and Morgan 1979; Lehman et al. 1990; Johannsson 1992).

Because of their importance as prey for salmonids, mysids have been introduced to a number of North American and Scandinavian lakes to improve salmonid growth rates (Lasenby et al. 1986). However, these omnivorous animals are also important predators on zooplankton (Rybock 1978; Nero and Sprules 1986), and they therefore compete for food with the same fish. The interactions between fish and mysids are complex, and the results of mysid introductions into lakes have been dramatic and largely unexpected (Lasenby et al. 1986; Martinez and Bergersen 1988). A quantitative analysis of these interactions requires estimates of mysid production and consumption rates (e.g., Johannsson et al. 1994).

Accurate estimates of whole-lake production and consumption by mysids rely on quantitative assessments of mysid distribution and abundance. Mysid spatial distributions can be patchy (reported C.V. of up to 45%; Grossnickle and Morgan 1979), and this can affect the accuracy of abundance estimates obtained with traditional sampling gear. High-frequency acoustic methods can better resolve the patchy dis-

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Table 1. Acoustic systems: Configuration and setup.

System	ROV	DT-4000
Transducer beam angle (degree)	6°/15° (narrow/wide)	6°
Frequency (kHz)	420	420
Source level (re: 1 mPa @ 1 m)	221.3 dB	219.0
Receive sensitivity	Narrow: −160.6 dBv/uPa Wide: −167.4 dBv/uPa	−58.0 dB/uPa
Pulse length (ms)	0.33	0.40
TVG	40 log*R*	20 log*R*
Absorption coefficient (dB m^{-1})	Not applied	0.054
Ping rate (pings s^{-1})	5	1

tribution of mysids and allows sampling over broader ranges of temporal and spatial scales than are feasible with traditional sampling methods.

The use of acoustic methods to estimate the biomass of populations requires characterizing the acoustic properties of the target organism. The most important information required to convert acoustic data into numerical abundance data is the amount of sound backscattered from an individual (acoustic backscattering, cross-section—σ_{bs}, or in its logarithmic form—TS). Approaches used to estimate TS for marine zooplankton include modeling (e.g., Stanton 1989; Stanton et al. 1993), in situ TS measurements of single individuals (Greene et al. 1989), in situ TS estimates from ensembles of individuals (Foote et al. 1990), and TS measurements of tethered individuals within enclosures (Wiebe et al. 1990; Demer and Martin 1995). Work on the TS of freshwater zooplankton is rare (*but see* Rudstam et al. 1992; Melnik et al. 1993; Megard et al. 1997).

In this paper, we use several direct and indirect methods to determine mysid TS. We present in situ TS measurements of mysids at 420 kHz and estimates of TS derived from comparisons of 420-kHz acoustic data with data from net samples and data from OPC measurements. We also compare these results with predictions from a theoretical model (Stanton et al. 1993) and discuss differences between freshwater and marine applications of the model.

Methods

This study consists of several different approaches for estimating TSs. The first approach was to measure the in situ TS of mysids by using an acoustic system mounted on a remotely operated vehicle (ROV). The second approach was to compare high-frequency acoustic data with abundance estimates of mysids based on traditional net samples and data collected with an OPC (Herman 1992; Sprules et al. 1992). The final approach included a comparison of our empirical data with a theoretical model (Stanton et al. 1993) that has been previously applied to euphausiids.

Acoustic systems—Two different acoustic systems were used over the course of this study. The first system, a 420-kHz dual-beam analog echosounder (Table 1) custom built by BioSonics for deployment on an ROV (Greene et al. 1991), was used during the in situ TS portion of the study. This dual-beam system transmits sound with a narrow-beam transducer element and receives echoes on both narrow- and wide-beam transducer elements (Greene et al. 1989). Voltage differences between the echos received on the two beams provide information on the position of a target relative to the main axis of the acoustic beam. This information can then be used to estimate the equivalent on-axis voltage, thus allowing accurate estimation of TS. A precruise calibration was performed by the manufacturer. During the study, all data were recorded on digital audiotape cassettes and analyzed later in the laboratory. The transducer was oriented downward, and thus, we assumed a near dorsal aspect for the estimated TS values.

The second system, which consisted of a 420-kHz single-beam digital echosounder (DT-4000), was also built by BioSonics (Table 1). A factory calibration was performed by the manufacturer during July 1995, and an in situ calibration with a standard target was performed during one of the surveys (August 1996). No corrections were needed to the configuration following the in situ calibration. Data were stored directly on the computer's hard disk and analyzed in the laboratory. This digital echosystem was used in the portion of the study comparing other abundance estimation techniques with acoustic estimates.

In situ estimates of TS—In situ TS measurements were conducted in Lake Ontario at a midlake station 28 km south of Cobourg, Ontario, Canada (Sta. 41, 130-m depth) between 23 and 25 May 1995. The data were analyzed by applying dual-beam analysis techniques (Greene et al. 1989). Post-cruise analysis of the data included partitioning the acoustic data into segments (''runs'') that each consisted of at least several hundred echoes and joint processing of the narrow- and wide-beam data to allow estimates of the in situ TSs. Only data collected between 2140 and 2155 h (runs 5 and 6), in which the transducer was within 10 m of the mysid scattering layer, are presented in this paper. The TS distribution was based on targets within 2–5 m of the transducer. Analysis of targets at greater ranges may lead to a bias against smaller targets and an increasing risk of including multiple targets. Data from within the mysid layer were not used for the analysis because at high densities, it is difficult to resolve the individual targets required for applying the dual-beam TS techniques.

Dual-beam analysis of TS requires comparison of the narrow- and wide-beam voltages. Use of the ROV acoustic system requires adjustment of gains for the narrow and wide beams to correct for losses in the long cable used (330 m). A problem in the receiver gain adjustment for the wide beam precluded correcting the wide-beam gain during the cruise. We adjusted the wide-beam voltages before the analysis by measuring differences in total voltage squared returned for both narrow and wide beams (accounting for differences in directivity and receiver sensitivity of the wide and narrow beams obtained from the manufacturer). Subsequent analysis of the acoustic data was carried out using the echo signal processing software (BioSonics).

In conjunction with the acoustic sampling, several vertical net samples were collected for comparison with the acoustic data. The net (a 1-m-diameter opening, 0.5-mm mesh) was lifted at a speed of 0.3 m s^{-1} (Nero and Davies 1982). Sampling was vertically stratified (30–0, 70–30, and 120–70 m) and replicated five times between 0145 and 0430 h (25 May). The size distributions from net samples corresponding to the mysid scattering layer (70–30 m) were used for comparison with the estimated TS distribution derived from the acoustic data. Although the acoustic-based distribution relies on targets just above the main mysid scattering layer, we assumed that the mysid size distribution in and above the layer was similar.

Estimates of TS based on comparisons of acoustic data with other sampling techniques—TSs can be obtained by comparing abundance estimates based on net sampling with echo integration (EI) values from the same location. To accomplish this, we sampled both acoustically and with nets at several locations in Cayuga Lake (New York, U.S.A.) and Lake Ontario. Acoustic sampling was conducted using the single-beam system.

Cayuga Lake—Several acoustic surveys of Cayuga Lake (42°41′30″N and 76°41′20″W; average depth = 54 m, maximum depth = 132 m) were conducted during August 1995 and August 1996 (day and night). One of two nets was used for net sampling to groundtruth the acoustic data: (1) an opening-closing net with a 1-m diameter and a 0.5-mm mesh (OC net), and (2) a 1-m-diameter, 1-mm mesh standard conical net (SC net). When sampling with the OC net, the sampling was stratified and targeted the water column above the scattering layer, the mysid layer itself, and the water column below the layer. During the day, the entire water column was sampled (down to a maximum of 100 m). When using the SC net, samples were collected from above the layer to the surface, from below the layer to the surface, and from the bottom of the lake (or to a maximum of 100 m) to the surface. On some occasions, samples were collected only from just below the strong scattering layer up to the surface. Net tows collected during 1995 were hauled manually, while 1996 samples were hauled by winch at ca. 0.3 m s^{-1}. Samples were preserved within minutes of collection in 70% ethanol.

Lake Ontario—During the summer and fall of 1995, several cruises aboard the RV *Seth Green* were conducted in the southeastern basin of Lake Ontario. Square grids consisting of four transects within 3.4 km^2 (1 nm^2) were conducted around a drogue drifter. All net samples were collected in close proximity to the drogue. Typically, acoustic data were obtained along the transects, either immediately before or after completing the net tows, or, in some cases, they were collected in conjunction with the net samples. In most cases, the net sampling was stratified using either the OC or SC net and followed the same stratified sampling conducted in Cayuga Lake. In contrast to Cayuga Lake sampling, maximum depth was limited to 90 m. Net samples were collected with the use of a winch at a speed of 0.3 m s^{-1}.

Mysids collected in the Lake Ontario and Cayuga Lake samples were later enumerated, sexed, and measured (tip of the rostrum to base of telson) to the closest millimeter. Lengths and densities were converted to dry weights (DWs) based on the relationship ln(weight) = $-12.27 + 2.72 \times$ ln(length) (Johannsson 1995), where lengths were in millimeters and DWs in grams.

Analysis technique—Sections of the acoustic data that were collected in proximity to the net samples were selected for comparisons with net samples. This was done by visually inspecting the echogram and selecting segments characterized by low noise levels and the absence of large targets (presumably fish) in the upper water column above the mysid scattering layer. The sections were 50–200 pings long, corresponding to a horizontal extent of approximately 50–200 m. We then measured volume backscattering (s_v, m^2 m^{-3}), which is the ratio of the sound intensity backscattered by a unit volume to the sound intensity of the incident sound wave. Measurements of s_v were made from the depth strata corresponding to that sampled by the nets, thereby providing EI values that could be compared to net estimates of mysid abundance. In some cases, it was not possible to find segments without large fish echoes above the mysid layer. In such cases, we used only acoustic data from the mysid layer and assumed all mysids sampled in the net were confined to the mysid scattering layer. In cases for which two or more acoustic sections were analyzed for comparison with a net sample, the EI results of the sections were averaged to obtain a single value. The s_v values were converted to the logarithmic form—S_v—as defined below:

$$S_v = 10 \log(s_v) \tag{1}$$

$$\overline{S_v} = 10 \log\left(\frac{\sum s_v}{n}\right) \tag{2}$$

where n is the number of acoustic samples averaged. We examined the relationship between logarithmic-transformed net sampled densities (and biomass) and S_v using functional regression techniques (Ricker 1973) and the following relationships:

$$\overline{TS} = 10 \log \bar{\sigma}_{bs} = 10 \log\left(\frac{\overline{s_v}}{N}\right) \tag{3}$$

where N is numerical density. Confidence intervals for all regression-based estimates of TS were calculated using Bartlett's method (Bartlett 1949; Simpson et al. 1960). We had relatively few data points of low mysid density, which thereby increased their proportional impact on the regression in

Table 2. Parameter values used for modeling mysid TS. All parameter values used to calculate A_{ij} with the exception of s_θ were taken directly from Stanton et al. (1993).

Symbol	Definition	Value	Source
g	Density contrast between animal and water	1.036	Foote (1990)
		1.060	Stanton et al. (1993)
		1.070	This study
h	Speed contrast between animal and water	1.028	Foote (1990)
		1.060	Stanton et al. (1993)
		1.070	This Study
R	Reflection coefficient	0.0313	Foote (1990)
		0.0582	Stanton et al. (1993)
		0.0675	This Study
A_{ij}	Shape and orientation impact	$A_{ij} = \frac{T_B^2\, C_B^2\, J_\theta}{16\sqrt{\alpha_B s_\theta}} = 0.1 \times (s_\theta)^{-½}$	Stanton et al. (1993)
s_L	Standard deviation of the length	0.10	Stanton et al. (1993)
		0.36	This Study
T_B	Correction factor to account for tapering of cylinders	1	Stanton et al. (1993)
C_B	numerically determined coefficient	1.2	Stanton et al. (1993)
J_θ	Multiplication factor due to Gaussian distributed angle of orientation	1	Stanton et al. (1993)
α_B	numerically determined coefficient	0.8	Stanton et al. (1993)
s_θ	standard deviation of the angle of distribution*	30°	Kristensen and Dalen (1986)
		20°	Miyashita, et al. (1996)
		20–60°	Stanton et al. (1993)

* The angle of distribution is defined by the angle between the axis of the acoustic beam and the organisms' anterior-posterior axis.

relation to the large number of points of high mysid density. Hence, we used the mean TS calculated from Eq. 3 for our comparisons of net and acoustic samples.

A total of 42 samples were compared, 30 from Cayuga Lake and 12 from Lake Ontario. These samples conformed to the following criteria: (1) acoustic data were available for analysis within an acceptable time frame (within 15 min before the start or 15 min after the end of tow) of sample collection, and (2) collection was completed prior to the onset or after the completion of mysid diel vertical migration as observed acoustically.

An additional comparison was performed between EI data collected with the acoustic system and data collected with an OPC (Herman 1992). During a Lake Ontario cruise (15–16 June 1997), three nighttime (2303–0445-h local time) transects were conducted. During the first two transects (western basin of the lake, south of Toronto, Canada; bottom depth = 135–137 m), the acoustic system was towed at the surface, while the OPC was undulated between 20- and 60-m depths for the first transect and between 20- and 55-m depths for the second transect. The third transect involved an initial segment, during which the OPC was towed at 45-m depth, and a second segment, during which it was towed at 39.5-m depth. Towing speed was approximately 4 knots. Only targets that satisfied criteria set for mysid identification (primarily by size; Sprules pers. comm.) were considered a valid target. Three net samples were collected, one at the start of each transect, to determine the mysid size distribution. The samples were collected from 55 m to surface with a square-opening net having a 1-m^2 surface area.

Acoustic data were analyzed based on the OPC sampling depths; the horizontal resolutions were similar for all transects—~35 pings (ca. 70 m) per report. The vertical resolution for the first two transects was 2 m (over the entire portion of the water column sampled by the OPC) and 0.5 m for the third transect. Volume backscattering values were calculated for the water column between 20 and 60 m along the first transect and between 20 and 55 m for the second transect. Average backscattering (s_v) values were then calculated over the entire transect for the given depth range. For the third transect, an average s_v value was calculated for the corresponding depth bin along the transect. Data cells that were observed to include scattering from large targets (>-60 dB) were excluded from the averaging process.

Model estimates of TS—Theoretically derived estimates of individual TSs are commonly employed when direct measurements are not available. The weakly scattering, fluidlike, bent-cylinder model (Stanton et al. 1993) was adopted to estimate the TS of an individual mysid. This ray-based scattering model (Eq. 4) applies to elongated, bent organisms with sound-scattering characteristics that deviate only slightly from their environment and that exhibit a narrow Gaussian distribution of orientations. The model is described by the following expression (Stanton et al. 1993; *see Table 2*):

$$\langle \sigma_{bs} \rangle_{\theta,L} / \overline{L}^2 = A_{ij} R^2 |I_0|^2 \beta^{-1} \qquad (4)$$

where $|I_0^2|$ is defined as follows:

$$\langle |I_0^2| \rangle_L = 2\{1 - \exp[-8(k\overline{a}\, s_L)^2]\cos(4k\overline{a} + \mu_{p=2})\} \qquad (5)$$

I_0 describes the interference between echoes from the front and back interfaces of the cylinder (with $\theta = 0$), and for a given frequency, it is dependent on the organism's dimensions (a). k is the wave number ($=2\pi/\lambda$), a is the radius of the cylinder cross-section, and s_L is the standard deviation of the length. The cylindrical cross-section, a, was determined assuming a DW to WW ratio of 0.15 (Johannsson et al. 1994); volume was defined as $V = WW \times 10^{-6}$, and $a = (V/\pi L)^{0.5}$, where weights are in grams and lengths in meters (Demer and Martin 1995). $\mu_{P=2}$ was defined as $-(\pi/2)ka/(ka + 0.4)$. R is the reflection coefficient that depends on the material properties of the organism ($R = (gh - 1) \times (gh + 1)^{-1}$; g is the mass density of the body relative to that of the surrounding water, and h is the sound speed within the body relative to water); β is the length to radius ratio (L/a) of the animal. Parameters for which we had no prior information were based on published values for euphausiids (Foote 1990; Stanton et al. 1993). The s_L value was defined by Stanton at al. (1993) as the relative standard deviation of the length or a measure of tapering of the body of the elongated organism (Stanton pers. comm.). It can be measured from the ratio of standard deviation of the radius of the body to the mean radius of the body (std r/mean r). Three live mysids (lengths = 11.5, 13.49, and 17.25 mm) were digitized, and their radii were measured at equally spaced points along their bodies. The calculated ratios (std r/mean r) were 0.356, 0.359, and 0.357, respectively. This suggests that there is a near constant value for medium- to large-sized mysids. The value of 0.36 was used for s_L to model the TS. This value is used for all further estimates unless otherwise specified.

Initially, model predictions with R values derived from the literature were compared to empirical results from the in situ TS measurement portion of this study. We then adjusted the value of R to provide a better overlap between the predicted and observed in situ TS values. Once we were satisfied with the value of R, we compared the theoretically calculated values using the adjusted model with the mean TS values estimated from the acoustic-net and acoustic-OPC portions of the study. Finally, the adjusted model was employed to calculate theoretical TSs for mysids ranging from 3 to 20 mm.

Results

In situ estimates of TS—A total of 1,073 targets were identified and accepted during the two runs analyzed. Both runs displayed a near normal distribution of TS, with a slight tail toward the lower TS range. There was no significant difference between the two runs (K-S two-sample test; $P > 0.5$), so results were pooled (Fig. 1A). The calculated mean TS was −76.0 dB (−79.0 to −74.3 dB, 95% CI). Analysis of σ_{bs} as a function of distance from the transducer for runs 5 and 6 (linear regression: slope was not significantly different from 0, $P > 0.36$ and 0.39, respectively, and $P > 0.34$ for the combined runs) demonstrated there was no relationship between range and σ_{bs} up to a distance of 5 m.

There was no significant difference between the size distributions of the five net samples from the 70- to 30-m strata (Kolmogorov-Smirnov two-sample test; $P > 0.26$); therefore, these samples were combined (Fig. 1B). The total number of mysids was 209 (average length = 13.7 mm; range = 3.3–19.8 mm), with a bimodal distribution.

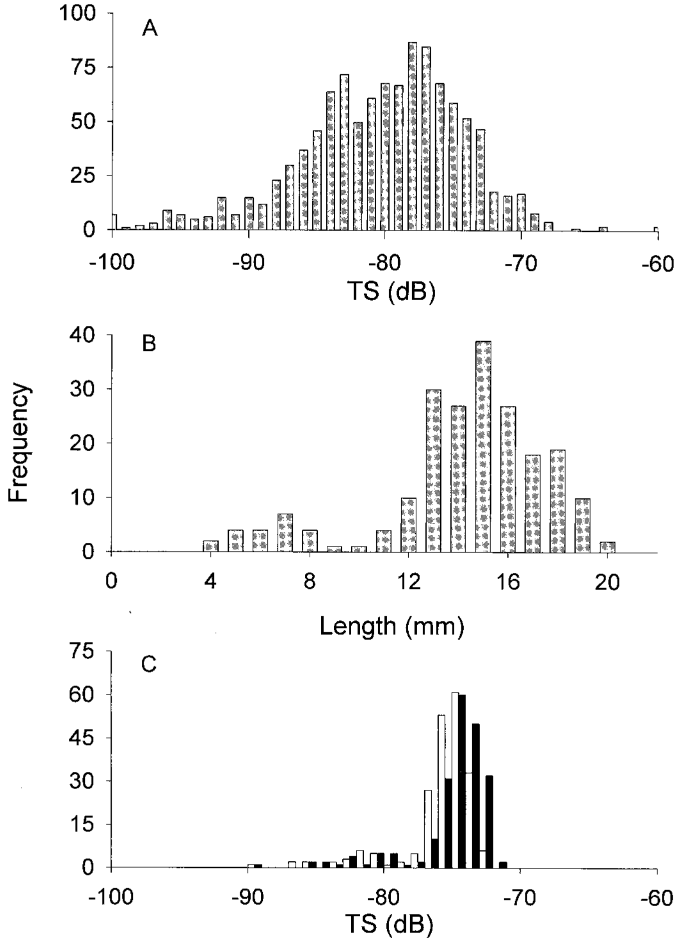

Fig. 1. In situ TS measurement study. (A) TS distribution summary of acoustic targets based on dual-beam analysis. Total number of targets was 1,073. (B) The combined size distribution frequency of five net samples. The data presented are from the 70- to 30-m strata. (C) Predicted mysid TS distribution. Size distribution information was derived from the net sample data (B above) and transformed to an estimated TS distribution based on the ray model (Stanton et al. 1993) for a frequency of 420 kHz, $R = 0.0675$, $s_L = 0.36$, and two values of s_θ: dark bars—$s_\theta = 20°$ and hollow bars—$s_\theta = 30°$.

Estimates of TS based on comparisons of acoustic data with other sampling techniques—There was a significant relationship between the logarithmic-transformed net estimated abundances and the corresponding S_v values (Fig. 2; $S_v = -71.6 + 6.71 \log_{10}$ density; $r^2 = 0.58$, $P < 0.001$). The relationship between the logarithmic-transformed net biomass (DW) and the S_v values was tighter (Fig. 3; $S_v = -54.01 + 6.18 \log_{10}$ DW; $r^2 = 0.66$, $P < 0.001$). TS estimated from the mean density and s_v values (Eq. 3) yields a mean TS of −73.1 dB (−73.3 to −71.9 dB, 95% CI), where the mean density and s_v values were 8.43 ind. m^{-3} and $4.16 \times 10^{-7} m^2 \, m^{-3}$, respectively.

For the acoustic-OPC comparison, a total of 59.2, 58.3, and 28.2 m^3 was filtered by the OPC during transects 1, 2, and 3, respectively. The OPC registered 160 mysids on the first transect, 144 mysids on the second, and 129 mysids on the final transect. The number of mysids identified corresponded to density estimates of 2.7, 2.5, and 4.6 ind. m^{-3} for transects 1, 2, and 3, respectively. The mysid size dis-

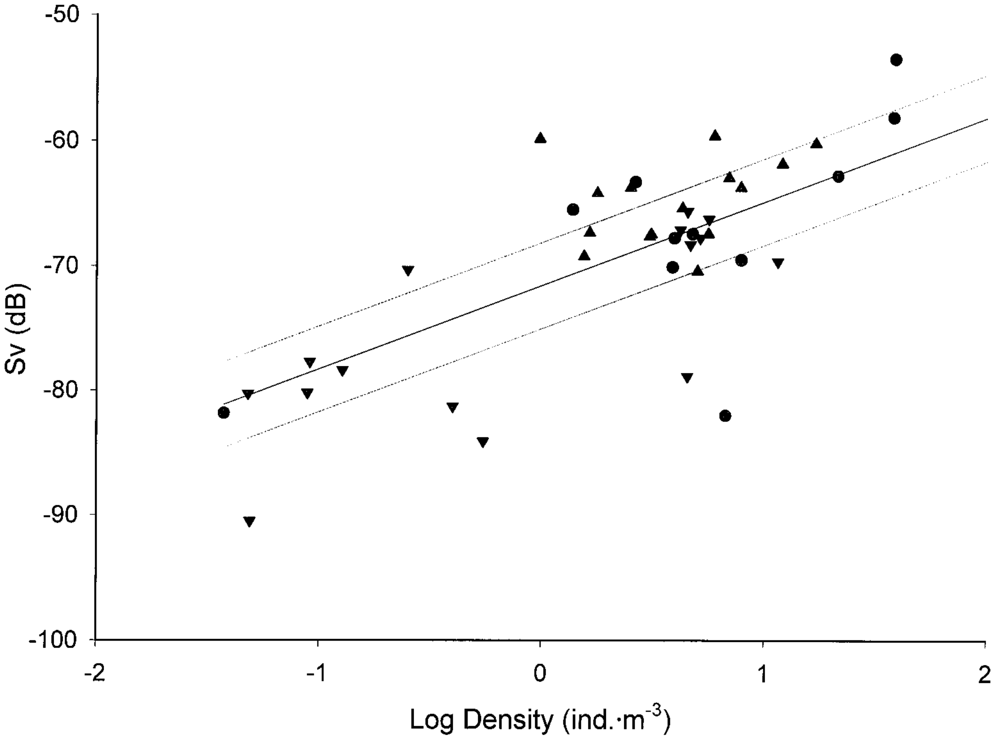

Fig. 2. Functional regression (solid line) and 95% CI (dashed lines) of logarithmic-transformed net estimated density values and EI values. The density estimates were based on net samples collected during the net-acoustic comparison study. Circles represent data collected from Lake Ontario; upward triangles and downward triangles represent data collected in Cayuga Lake in 1995 and 1996, respectively.

tribution was determined for the net samples collected prior to each OPC-acoustic transect. There were no significant differences between the size distributions for the three transects (*t*-tests, all $P > 0.4$; $n_1 = 152$ mysids, $n_2 = 68$, $n_3 = 290$), and therefore, these were pooled. The overall mean length was 12.8 mm, with a range of 2.3–26.3 mm. The acoustic backscattering values were relatively consistent for the first two transects; mean S_v values were −72.8 dB for the first transect and −72.5 dB for the second. During the third transect, the average S_v was −66.7 dB. Since an increase of 3 dB is equivalent to a twofold increase in abundance, this result suggests a fourfold increase in abundance between the first two transects and the final one. The estimated average TS for the combined transects calculated from the acoustic backscattering values and the OPC density estimates was −74.8 dB (range = −77.1 to −73.3 dB).

Model estimates of TS—The calculated TS values for the unadjusted model with $R = 0.0582$ (Table 3) ranged between −88.2 dB and −74.6 dB for mysids between 3 and 20 mm long, with a standard deviation of orientation, s_θ, of 30°. Applying a smaller standard deviation of orientation, $s_\theta = 20°$, the minimum- and maximum-predicted TS values were −86.5 dB and −72.9 dB, respectively, suggesting that the range of orientation angles that the animals display in nature has, as expected, an impact on the measured TS. Changing the R value to 0.0313, with $s_\theta = 20°$, resulted in lower TS values (Table 3). Thus, alteration of R also had a very significant effect on TS. It was evident from a comparison between the modeled values ($R = 0.0582$ and 0.0313) and the field data that adjustment of R was necessary. The R value that visually provided the best fit to the in situ TS estimate data was 0.0675. As a consequence, g and h required alteration and were both set to equal 1.07 for lack of additional information.

Adjusted model results obtained using $R = 0.0675$ and $s_\theta = 20°$ produced TS values higher (Table 3) than those estimated above. Furthermore, modal oscillations were reduced as a result of the increase in the value of s_L (Fig. 4).

The size distribution of the combined net samples from the in situ TS measurement portion of the study was converted to two expected TS distributions using the ray model and two cases of s_θ, 20 and 30°. These TS distributions were then compared to the directly measured TS distribution (Fig. 1A,C). The predicted mean TS values were −74.4 dB ($s_\theta = 20°$, −74.7 to −74.2 dB, 95% CI) and −76.2 dB ($s_\theta = 30°$, −76.4 to −75.9 dB), compared to the directly measured mean TS value of −76.0 dB (−79.0 to −74.3 dB).

The same comparison was performed for the size distributions from the net samples collected during the acoustic-net sampling comparison. The size distributions for all net samples were transformed to TS values based on the ray model, resulting in predicted mean TSs of −77.8 dB ($s_\theta = 20°$, −77.8 to −77.6 dB) and −79.6 ($s_\theta = 30°$, −79.7 to −79.4 dB), compared to a mean TS of −73.1 (−73.3 to −71.9 dB, 95% CI) as computed with Eq. 3.

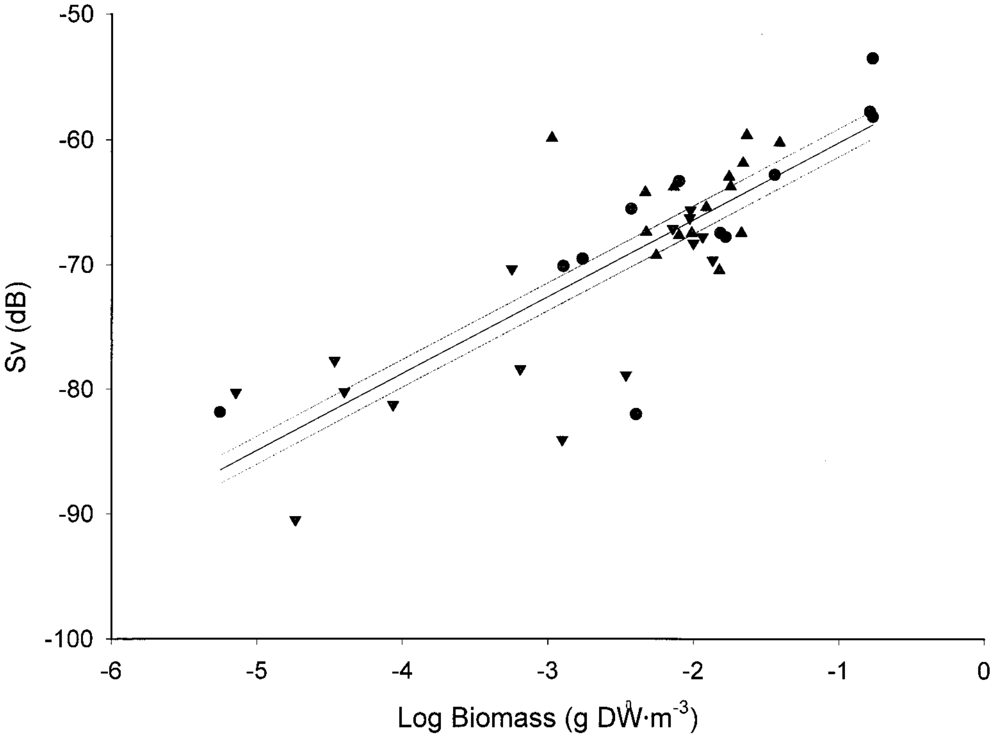

Fig. 3. Functional regression (solid line) and 95% CI (dashed lines) of logarithmic-transformed net estimated biomass values and EI values. The biomass estimates were based on net samples collected during the net-acoustic comparison study. Symbols are as in Fig. 2.

The mysid size distribution determined from the net samples collected during the acoustic-OPC study was converted to a TS distribution based on the model. The TS distribution produced estimated mean TSs of −74.7 dB (s_θ = 20°, −75 to −74.4 dB, 95% CI) and −76.4 dB (s_θ = 30°, −76.7 to −76.1 dB, 95% CI).

Discussion

Knowledge of the acoustical properties of animals is a prerequisite for accurate, acoustic-based studies of their population ecology. Knowledge of such properties allows the transformation of acoustic data into meaningful biological variables such as numerical abundance and biomass. TS estimates of *M. relicta* at 420 kHz were within a narrow range when a variety of approaches were compared (Fig. 5). Results of the direct measurement of mysid TS (in situ portion of study) provided a mean TS of −76.0 dB. The average length of the mysid population was 13.7 mm. The net data-acoustic data comparison resulted in an estimated average TS of −73.1 dB for a mean size of 8.6 mm. The OPC-acoustic comparisons yielded an estimated TS range of −74.8 dB for a mean length of 12.8 mm. Our comparison of directly measured vs. modeled estimates of mysid TS provides some validation for a model that has been widely used for marine zooplankton. The calculated theoretical values for mysids of 8.6 and 12.8 mm were −77.7 (s_θ = 30°, −79.4) and −75.5 dB (−77.2), respectively (Fig. 5). While there was a discrepancy between the predicted and estimated TSs for the acoustic-net sample comparison data, the adjusted model was successful in predicting the TS of a sampled population in our acoustic-OPC portion of the study.

Table 3. Model predictions of mysid TS.

Lengths (mm)	*R*	Source	s_θ	TS range (dB)
3–20	0.0582	Stanton et al. (1993)	30°	−88.2 to −74.6
3–20	0.0582	Stanton et al. (1993)	20°	−86.5 to −72.9
3–20	0.0313	Foote (1990)	20°	−91.9 to −78.3
3–20	0.0675	This study	20°	−85.2 to −71.6
13.7	0.0675	This study	20°	−74.4
13.7	0.0675	This study	30°	−76.2

The estimated mean TS from the acoustic-net data comparison was higher than the estimated TS values derived from the other techniques and higher than the predicted theoretical values. Reported measurements of TS of euphausiids and marine species of mysids are also lower. Wiebe et al. (1990) measured mean TS values ranging from −80.9 to −72.6 dB for marine mysids (*Neomysis rayii*) 12–31 mm in length and a mean TS range of −77.9 to −77.1 dB for the euphausiid, *Euphausia pacifica* (21 mm). The measurements were conducted at a frequency of 420 kHz. Demer and Martin (1995) presented 420-kHz data for two species, *Neomysis kadiakensis* and *Hetacarpus stylus*, which had TSs of −79.4 to −77.2 (18–25 mm) and −82.9 to −73.1 dB (14.6–37.6

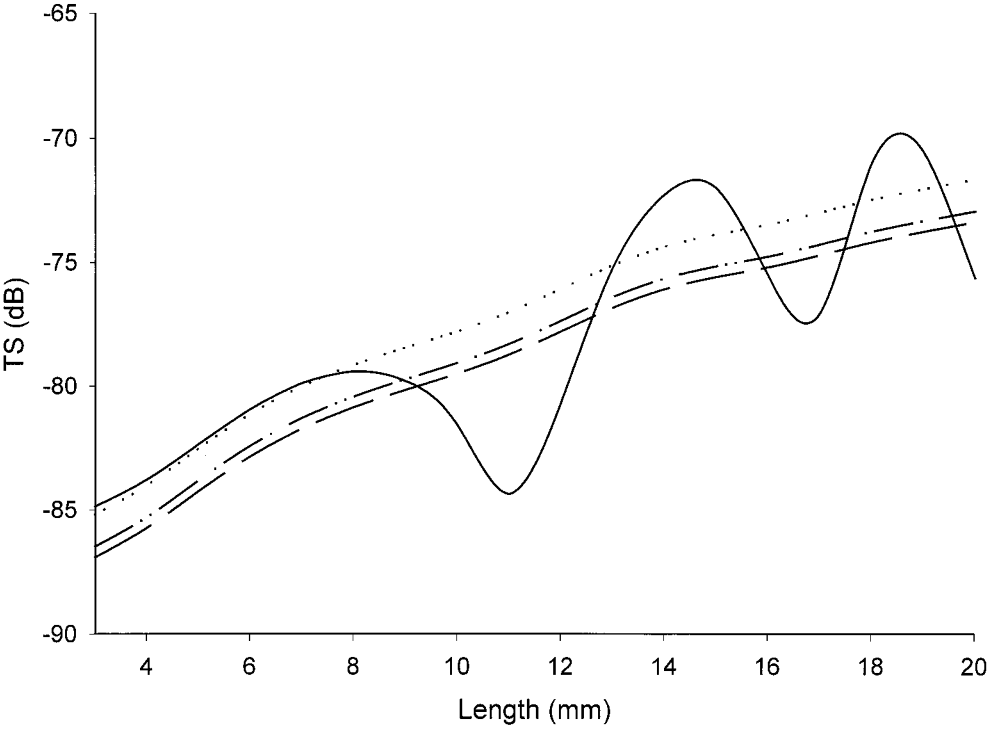

Fig. 4. Predicted TS values for mysids 3–20 mm long based on the ray model (Stanton et al. 1993). The predicted values are for a frequency of 420 kHz and varying values of *R*, s_θ, and s_L. (—): $S_L = 0.1$, $R = 0.0675$, $s_\theta = 20°$; (--): $S_L = 0.36$, $R = 0.0675$, $s_\theta = 20°$; (--): $S_L = 0.36$, $R = 0.0675$, $s_\theta = 30°$; (-··-): $S_L = 0.36$, $R = 0.0582$, $s_\theta = 20°$.

mm), respectively. These estimates are considerably lower than our measured values. Some of the inconsistencies may be driven by differences in the environment generating variations in *R* values (*see below*).

Net sampling of populations provides valuable biological information but may yield biased estimates of abundance because of animal avoidance of the net or uncertain filtering efficiency (Fraser 1968; Omori and Ikeda 1984). Sampling efficiency has been shown to depend on factors such as size of the net opening, mesh size, light intensity, population density, towing speed, tow angle, and reaction to hydrodynamic stimuli caused by the tow cable (e.g., Fleminger and Clutter 1965; Omori and Ikeda 1984; Hovekamp 1989). Nets may undersample certain size classes, thereby presenting a bias in the estimated mean length or size distribution of the population (e.g., Gehrke 1992; Tilney and Buxton 1994).

To minimize avoidance and maximize the filtering efficiency, we adopted the procedure suggested by Nero and Davies (1982) and used a wide-opening net. Nero and Sprules (1986) calculated a filtering efficiency of 87% for their 1-m^2 net. The net efficiency of our net (round 0.78-m^2 opening) was not measured, but efficiencies of 70–90% are common for similar setups (Omori and Ikeda 1984; Chipps and Bennett 1996). In addition, some avoidance may have taken place. We therefore recalculated the estimated abundances from the net samples assuming three different net sampling efficiencies of 90, 75, and 50%. Sampling efficiency differs from filtering efficiency in that it also includes possible net avoidance. Compensating for these sampling efficiencies, the predicted TSs from Eq. 3 would be −73.5, −74.3, and −76.1 for net sampling efficiencies of 90, 75, and 50%, respectively. Hence, net sampling efficiency may account for the discrepancy between the estimated mean TS (based on the acoustic-net sample comparison) and the predicted value (based on the model). No information is available on possible avoidance of the OPC by mysids. The OPC has a relatively narrow opening (~60 cm^2) that may lead to some avoidance by mysids, but this may be compensated for by the rapid towing speed (ca. 4 knots); we therefore assumed there was only little avoidance by the mysids during the OPC sampling.

Volume backscattering was a better predictor of biomass than of density, although the variance was relatively large. As discussed above, avoidance by mysids may explain some of the variance seen in the net sample–acoustic data relationship. Two additional sources of error may explain the observed deviation from the regressions in Figs. 2, 3. Although the acoustic sampling was conducted as close in time to the net samples as possible, in most cases, they were not conducted concurrently. Therefore, the net samples may represent a volume of water with higher or lower abundance than that sampled acoustically. There can be a factor of two difference in abundances between replicate net tows of mysids in Lake Ontario (Johannsson pers. comm.). We tried to minimize variance in the acoustic sampling by analyzing relatively large segments of acoustic data, thereby averaging over a large range of abundances. The second potential source of error is related to the acoustic sampling. Although

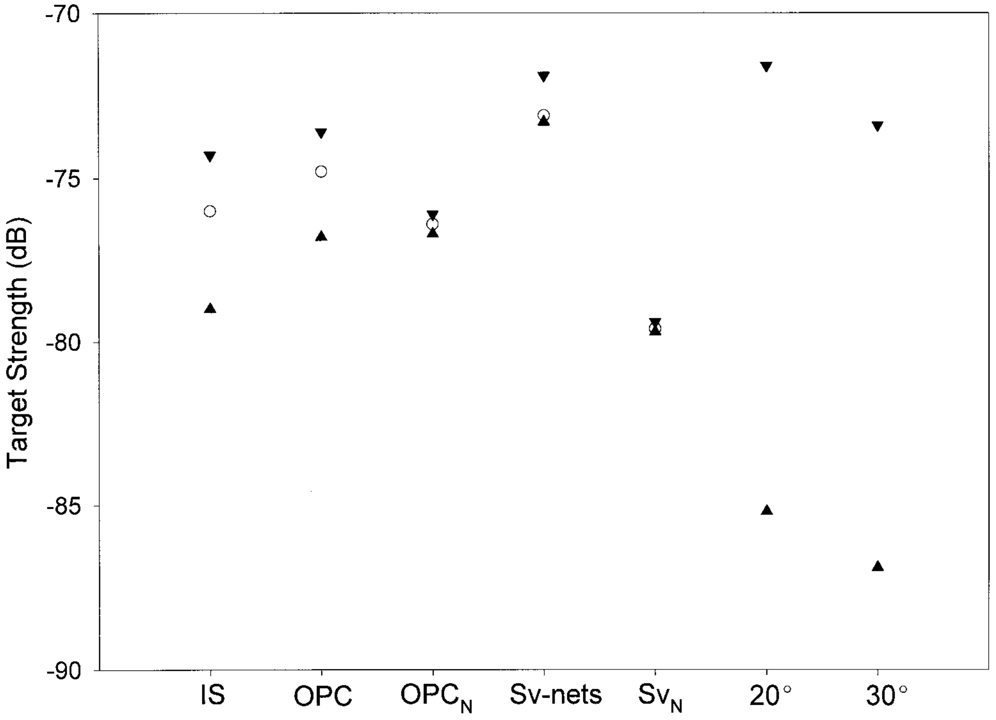

Fig. 5. Summary of TS estimates based on observations and model predictions. Circles represent the mean values, while down- and up-facing triangles represent the upper and lower 95% CI values, respectively. *IS*—derived from the dual-beam analysis; *OPC*—OPC-based estimates (mean value and range) determined by dividing measured *sv* by the OPC-estimated mysid density; *OPC$_N$*—mysid size distribution derived from net samples collected prior to and after the OPC transects converted to *sv* based on the ray model assuming $R = 0.0675$, $s_L = 0.36$, and $s_\theta = 30°$; *Sv-nets*—mean TS derived from Eq. 3 (*see text for further details*); *Sv$_N$*—net sample size distribution from the acoustic-net comparison portion of the study converted to *sv* values assuming $R = 0.0675$, $s_L = 0.36$, and $s_\theta = 30°$; *20°* and *30°*—upper and lower range of predicted TS for the ray model for mysids 3–20 mm in length, assuming $R = 0.0675$, $s_L = 0.36$, and s_θ values = 20 or 30°.

mysids are the most dominant zooplankton sound scatterer in the water column in the lakes we studied, this does not exclude a situation in which a portion of the sound returned from the water column (s_v values) may be due to other zooplankton species. Sound scattered by other zooplankton species that we did not account for would lead to acoustic overestimates of mysid density with respect to the number of mysids caught by our nets. The large mesh size used to sample mysids precluded any option of estimating zooplankton composition and abundance.

The TS of an organism is greatly influenced by its angle of orientation relative to the sound source (Sameoto 1980) and its physical properties (speed of sound and density). Modeled estimates of TS can vary significantly from observations when some fixed orientation is assumed, but they can be improved considerably when the organism's angle of orientation is considered (Sameoto 1980; Cochrane et al. 1991; Demer and Martin 1995). Little is known in general about the actual orientation of zooplankton in their natural environment. While it is reasonable to assume that large zooplankton taxa, such as mysids and euphausiids, display a dorsal orientation relative to the acoustic beam produced from a down-looking transducer, it is also reasonable to assume that they display some variation in that angle while present in a scattering layer during the night. The range of orientation angles has a major effect on potential TS values, as can be seen by comparing results of the ray model with different s_θ values (Table 3; Fig. 4). Few studies have addressed this issue. Kristensen and Dalen (1986) observed two euphausiid species in situ and found an average standard deviation in tilt angle of 34°, ranging between 25 and 45°. The observations included periods of vertical migration; therefore, they suggested a value of 30° as more appropriate for organisms that had completed their vertical migration. Miyashita et al. (1996) observed a range in the standard deviation of orientation angles from 12.4 to 33.4°; they suggested an appropriate standard deviation value of 20°. Bowers et al. (1990) described major differences in mysid orientation during periods of vertical migration vs. typical horizontal movement during the night. A comparison of measured TS values in this study and predicted values using the ray model (Fig. 1) suggests that an s_θ of 30° is appropriate for mysids residing in a nocturnal scattering layer.

In addition to orientation, the factors dominating differences in the amount of backscattering are physical characteristics of the organisms themselves. The R value combines many of the animal's physical characteristics into a single parameter. The higher the contrast between the physical properties (density contrast and speed of sound contrast) of the organism and its surroundings, the more efficient the scattering (Stanton et al. 1994) and the larger the value of *R*. Animals with material properties similar to the surrounding water will have low *R* values (e.g., salps). Animals with very different material properties will exhibit relatively large values of *R*. This can result in large differences in the acoustic backscattering from animals of comparable size (Stanton et al. 1994).

Differences in *R* values also might be expected when comparing two similar organisms living in different environments. While there are numerous similarities between *M. relicta* and marine euphausiids, they live in environments of different salinities. Most mysids, including *M. relicta*, reach an iso-osmotic point at salinities of 20–30‰ (Mauchline 1980 and references therein). Therefore, *M. relicta* is constantly hyperosmoregulating and has a higher salt concentration and, hence, a higher density than its surrounding environment. This is not the case for marine species. Increased salt concentration would also increase the speed of sound contrast between the animal and the surrounding water. The differences between the freshwater and marine environments support the use of higher *g* and *h* values as we have suggested in this paper. Although the *g* and *h* values used here were only slightly higher ($<1\%$) than those used by Stanton et al. (1993), the effect on predicted TSs is substantial and may explain the lower TSs observed for marine species at 420 kHz. Lower TS values (-82 dB for a 15-mm animal) have been observed for a pelagic freshwater amphipod species (Rudstam et al. 1992; Melnik et al. 1993), but this may be related to taxonomic and morphological differences between the organisms or to the lower acoustic frequency (200 kHz) used by those authors. Additional work is needed to address the issue of frequency dependence of invertebrate TSs.

The information presented in this study provides a foundation for detailed studies of mysid population ecology using acoustic methods. The mean TS value for mysids is higher than that observed for similar species in marine environments. This has consequences for scientists using acoustic systems to study the distribution of fish species in lakes in which *M. relicta* is abundant. For example, acoustic backscattering of -60 dB or higher (at 420 kHz) in freshwater lakes from a mysid layer is expected if the density of mysids is 30 ind. m^{-3}. Mysids reach such densities or higher (Moen and Langeland 1989; Lehman et al. 1990; Johannsson 1995). If this acoustic backscattering is assumed to be fish, fish abundances might be severely overestimated. For example, Rudstam et al. (in prep.) estimated the TS of a mixed age population of rainbow smelt, a common planktivore in Lake Ontario, at -50.6 dB. Smelt can be found as deep as mysids. If the mysid scattering layer was assumed to be smelt, it would result in a fish density of 0.1 ind. m^{-3}. Estimated summer density of rainbow smelt (young of the year and adult) in Lake Ontario is approximately lower by two orders of magnitude (Mills et al. 1995). Given the mean TSs presented here, we need to account for the possible ‘‘mysid effect’’ in acoustic estimates of fish populations and reconsider the use of high-frequency acoustic systems (e.g., 420 kHz) for fish surveys.

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