Abundance and spatial distribution of *Mysis diluviana* in Lake Ontario in 2008 estimated with 120 kHz hydroacoustic surveys and net tows

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Mysids are an important component of Great Lakes foodwebs, both as a prey for fish and as a predator on zooplankton. We monitored mysid abundance in Lake Ontario using lake-wide hydroacoustics data and vertical net hauls collected 1–5 August 2008 during the Ontario Ministry of Natural Resources and New York State Department of Conservation forage fish survey. Acoustic volume backscattering strength was highly correlated with both density and biomass of mysids although the correlation with biomass was stronger. The slopes of these relationships were not significantly different from theory (0.10) indicating a linear relationship between abundance and backscattering strength. Size structure significantly affected the relationship between backscattering strength and density but not between backscattering strength and biomass. Average target strength for areas with small mysids was −91.9 dB per mysid, and in areas with both small and large mysids it was −88.2 dB per animal. Acoustic estimates for Lake Ontario calculated with these regressions provided a lake-wide estimate weighted by lake area within depth intervals, of 228 mysids m^{-2} (CV 17.6%) and 0.93 g dw m^{-2} (CV 12.9%). Density and biomass in 14 net hauls averaged 316 mysids m^{-2} (range 0 to 1113) and 1.35 g dw m^{-2} (range 0 to 3.89). Mysid biomass was 33% of the biomass of other crustacean zooplankton in the summer of 2008. As in 2005, areas of low mysid abundance were detected in the middle of the transects and along the north shore. Lakewide mysid abundance in the summer of 2008 was higher than in a similar acoustic survey in the summer of 2005 and in whole-lake autumn 2000–2007 net surveys, suggesting that mysids are persisting in Lake Ontario and abundant relative to other Great Lakes.

Keywords: hydroacoustics, mysis, vertical migration, patchiness, invertebrate ecology

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Introduction

The Opossum Shrimps in the *Mysis relicta* species group are common invertebrates in deep northern lakes and a dominant component of both the pelagic and benthic foodwebs of the Great Lakes (Gamble et al., 2011; Isaac et al., 2012; Warner et al., 2010; Owens and Weber, 1995). In Lake Ontario, the biomass and rates of predation on zooplankton by *Mysis diluviana* (previously *Mysis relicta*, mysids hereafter) are similar to that of Alewife (*Alosa pseudoharengus*), the most abundant planktivorous fish in the lake (Johannsson et al., 2003; Gal et al., 2006; Stewart and Sprules, 2011). Mysids are consumed by a variety of fish, including Alewife, Rainbow Smelt (*Osmerus mordax*), Slimy Sculpin (*Cottus cognatus*) and various coregonids (Owens and Weber, 1995; Boscarino et al., 2010).

Several recent ecosystem shifts have heightened the importance of mysids within Great Lakes foodwebs and our need to monitor changes in mysid abundance and condition. The continued decline of the native benthic amphipod *Diporeia* in Lake Ontario (Watkins et al., 2007; Birkett et al., 2015) as well as Lakes Michigan and Huron (Nalepa et al., 2009) have raised concerns that predation by fish on mysids could increase and potentially result in declining mysid abundance over time. For example, long-term fluctuations of fish populations (e.g. *Coregonis hoyi* or Bloater) have had recognizable impacts on mysid populations in Lake Michigan (Pothoven et al., 2010). From a bottom-up perspective, the carrying capacity of forage fish and by extension salmonid predators in the Great Lakes has been a concern, particularly with sharp decreases in primary productivity indices around 2004 for lakes Michigan and Huron (Fahnenstiel et al., 2010; Barbiero et al., 2011). This setting of abrupt change requires managers to have up-to- date information on mysid abundance that represents lakewide conditions and employs comparable methods and temporal/spatial coverage across lakes.

As in most lakes, mysids in Lake Ontario migrate from deep waters where they reside during the day to the lower metalimnion at night (Beeton and Bowers, 1982). The nighttime distribution is largely predictable from the animal's temperature and light preferences (Gal et al., 2004; Boscarino et al., 2007, 2009). Although there is a well-defined depth layer of mysids at night during the summer, there is considerable variation in their horizontal spatial distribution (Johannsson et al., 2003; Rudstam et al., 2008b). Much of that variance has been attributed to depth although variance within depths is also high; mysid abundance increases with bottom depth from shallow waters to a bottom depth of 100–150 m (Johannsson, 1995; Johannsson et al., 2003; Rudstam et al., 2008b). Higher abundances offshore have also been observed in Lake Michigan (Lehman et al., 1990; Pothoven et al., 2004; Warner et al., 2010). Johannsson et al. (2003) attributed this decline of mysid abundance closer to shore as either a direct avoidance reaction of mysids to fish that are typically more abundant in that area of the lake, or as a result of higher predation rates on mysids by fish.

In addition to this pattern of decreased mysid abundance closer to shore, there is likely substantial variation in mysid abundance offshore. Large-scale sampling of mysids with nets across multiple sites is rare because net tows are time consuming to both collect and process (Carpenter et al., 1974; Lehman et al., 1990; Johannsson, 1995). Vertical net tows sample a small area (about 1 m^2) and variation between replicate tows can be in the order of a factor 2 to 5, variation that obscures spatial differences. For example, water column densities obtained in replicate net tows in Lake Ontario in July 2005 ranged from 16 to 97 m^{-2} at one station (5 tows) and from 375 to 751 m^{-2} at another (3 tows; Rudstam et al., 2008b). We therefore need to collect more samples to better detect large and mesoscale patterns in distributions. Such patterns could be related to fish abundance, zooplankton abundance, light fields (such as light from large cities), hydrodynamic flow regimes such as upwelling and gyres, and benthic substrates in daytime habitat. Separating the effect of these different mechanisms with traditional net tows is difficult because of the noted high intra-station variability and coarse horizontal resolution. Hydroacoustic sampling is an attractive alternative because it is continuous over long distances and at all depths simultaneously (at least down to the detection range for the animals of interest), providing detailed information on both vertical and horizontal distributions of zooplankton (Foote and Stanton, 2000). Hydroacoustics is used routinely to measure the distribution and abundance of marine krill (Hewitt et al., 2003), but has only rarely been used to obtain quantitative estimates of freshwater mysids (Gal et al., 2004; Rudstam et al., 2008a,b; Axenrot et al., 2009).

In this article, we use hydroacoustic data collected for standard fisheries surveys (120 kHz) in Lake Ontario from 1–5 August 2008 by the Ontario Ministry of Natural Resources (OMNR) and New York State Department of Environmental Conservation (NYSDEC). We have three objectives in this article. First, we continue to develop the acoustics methods initiated in Rudstam et al. (2008b) on 2005 data using this additional data collected in 2008. This comparison is useful towards improving this monitoring tool so that it can be consistently employed across the Great Lakes. Additional matched acoustic/net measurements provide insight toward standardization of this tool. Second, we will describe the observed spatial patterns using an improved visualization of transect data toward understanding consistently occurring features in Lake Ontario. Third, we will update the status of mysid abundance in Lake Ontario relative to summer 2005 acoustic surveys (Rudstam et al., 2008b) and traditional autumn net surveys (Johannsson et al., 2011) that yielded comparable estimates in the early 2000s.

Methods

Field data collection

Lakewide acoustic data were collected as part of the annual OMNR-NYSDEC survey for forage fish (Alewife and Rainbow Smelt) in Lake Ontario from 1–5 August 2008 (Figure 1). Five cross-lake transects (approximately 50 km each for a total of 276 km) were conducted in the main lake, one each night, under low moonlight conditions (mostly at less than half moon illumination). Transects were generally conducted between 22:30 and 04:00 Eastern Daylight Time (EDT). Data were collected with a Biosonics DT-X, 120-kHz split beam echosounder (7.2° beam width, 0.4-ms pulse length, 1 pings s^{-1}) deployed on a pole mounted to the vessel with the transducer at 1.8 m depth. Survey speed varied from 5.5 to 7 knots, depending on conditions. This unit was calibrated with a standard −40.7 dB tungsten steel sphere, and no correction was necessary from factory calibrations. All data were collected with a lower squared S$_v$ threshold of –100 dB or less.

Nighttime vertical nets were collected at 14 sites along the hydroacoustic transects for abundance and size structure of *Mysis diluviana* (Figure 1). These were done at least one hour after sunset and one hour before sunrise with all deck lights turned off and only red lights used. The net used was 2.3 m long and had a 1 mm mesh and a 0.73 m diameter (0.42 m^2 mouth area). The net was lowered to a depth below the acoustically detected mysid layer and paused for 30 seconds before raising at a speed near 0.3 m sec^{-1}. Drift was common during retrieval and documented using a depth/temperature probe (Richard Brancker Research [RBR Ltd.], http://www.rbr-global.com/) and GPS positions. The volume of water sampled was calculated based on the geometrically calculated sampling path to account for drift. A depth recorder attached to the net measured maximum depth reached. Mysids were rinsed from the cod end into a sample jar and preserved with 8% buffered formalin.

Temperature profiles were collected at seven sites along each transect with the RBR depth/temperature probe. These profiles were important for evaluating and documenting mysid thermal habitat and evaluating potential physical mechanisms affecting mysid depth occurrence. Profiles collected along the Cobourg transect did not sample below the thermocline and thus were not used to infer mysis habitat. In addition, a HOBO light meter (Onset, http://www.onsetcomp.com) was deployed on the aft deck of the vessel to measure shipboard light levels (in lux) every 10 s in order to identify periods when deck lights were turned on.

Analysis

Analysis of acoustic data was done with Echo-View 4.9 (Myriax Inc., Hobart, Australia) using the method described by Rudstam et al. (2008b). Ambient noise varied somewhat but was typically around −125dB (S$_v$) at 1 m. For the mysid density estimates, the noise was removed by subtraction of the calculated noise level at each depth (Korneliussen, 2000) and with the noise removal tool of Echoview using a variable noise level based on DeRobertis and Higginbottom (2007).

In order to estimate mysid density, we first removed the contribution from fish to volume backscattering strength (S$_v$) by a mask that excluded an area around each fish target. Fish targets were defined as all backscattering larger than −60dB (uncompensated "target strength," TSu). In a few areas, acoustic backscattering from dense
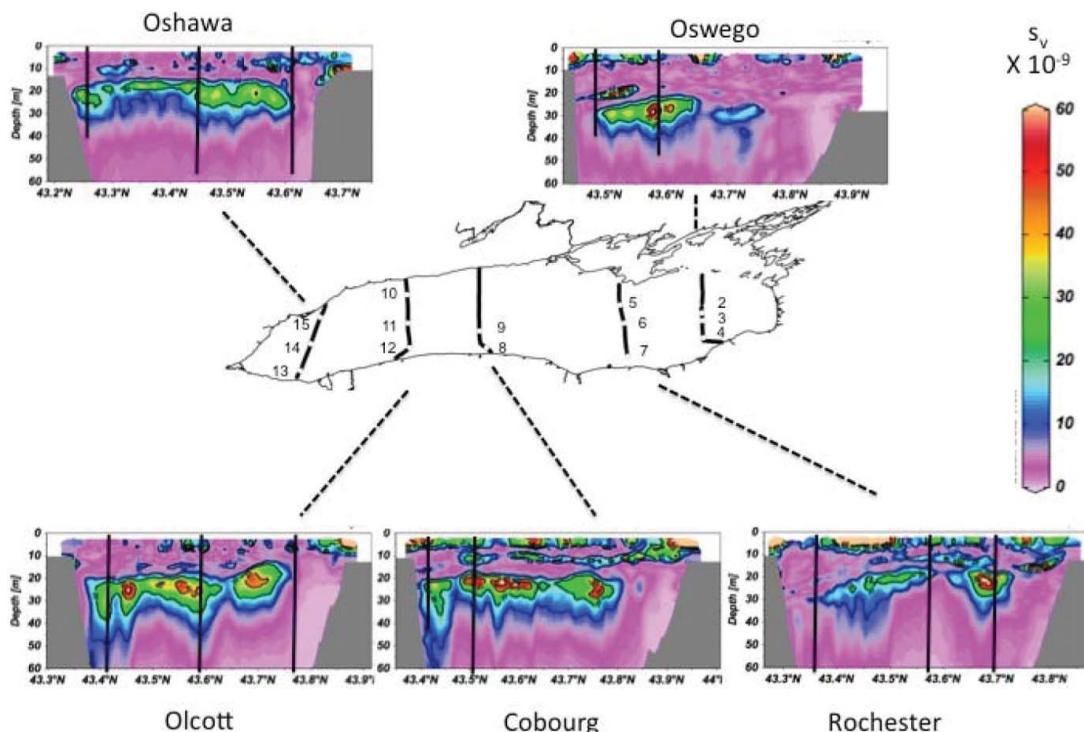
Figure 1. Map of Lake Ontario indicating the location of 5 acoustic transects and fourteen mysid net tows sampled 1–5 August 2008. One transect each night was conducted from approximately 22:30 to 04:00 local time. Scale is volume backscatter (s_v X 10^{-9}) from the surface to 60 m depth with contribution from fish removed (see methods). Vertical lines on sections and open circles on map represent locations of vertical net tows. Mysid layer is apparent at depths from 20 to 30 m as high backscatter.

mysids layers was also removed by this threshold and we therefore used a threshold of −55 dB in those areas. The mysid scattering layer was identified from the appearance on the echograms, from the location of the layer relative to the temperature profiles, and from the behavior of the scattering layer in response to shipboard light (Rudstam et al., 2008b). When the ship lights are on, mysid backscattering at 120 kHz decreases dramatically. This is due to the avoidance reaction of mysids that changes the orientation of the mysids relative to the sound beam (Gal et al., 1999; Rudstam et al., 2008b). Only the region from the top of the mysid layer to 2 m above the bottom or a maximum of 60 m depth was used, as 60 m represents a reasonable estimate of the detection limit for mysids in Lake Ontario given the noise level and acoustic frequency of the echosounder (Rudstam et al., 2008a,b). Depths close to the bottom were excluded because fish densities were sometimes high close to the bottom. We also excluded regions where the shipboard light was turned on. In most cases, the mysid scattering layer decreased at 50–

60 m depth indicating that most of the mysids that migrated into the water column were included in our estimate.

For the net samples, the number of mysids per sample was converted into areal density (number m^{-2}) by dividing the number of mysids in the sample by 0.42 m^2 (area of mysid net) and accounting for the calculated length of the tow (accounting for drift, see above). Mysid lengths were measured from the tip of rostrum to the cleft of the telson. Biomass was calculated using the equation Ln (W, dry wt, g) = −12.55 + 2.72 Ln (L, mm) from Johannsson et al. (1995) modified by Rudstam et al. (2008b) for this length measurement.

Acoustic data from the mysid layer were exported in 500 m horizontal intervals after removing noise and contributions from fish. We exported the volume backscatter coefficient s_v using a 1 m vertical resolution, latitude, longitude, and bottom depth for each 500-m interval into the software Ocean Data View (Schlitzer, 2011; Arthur Wegener Institute for Polar and Marine Research) for visualization within north-south

transects and comparisons with temperature profiles. Mysid density and biomass were calculated for each interval from the measured volume backscattering strength and the relationship between S_v and density and biomass. These relationships were derived from the comparisons with net tows (assuming all mysids were caught in the top 60 m of water) and acoustic backscattering (for the depth interval from the top of the mysid layer to the depth of the tow or 60 m) at the 13 sites. We also compared these empirical values with the data obtained in 2005 (Rudstam et al., 2008b) and with a backscattering model predicting mysid TS as a function of mysid size at different frequencies (Rudstam et al., 2008a). This backscattering model is based on the fluid-filled cylinder model presented in Stanton and Chu (2000) and adjusted for freshwater mysids (Rudstam et al., 2008a).

Areal density (# m^{-2}) is a common mysid abundance unit for monitoring programs. However, when relating the nets to acoustics, the volume backscatter strength S_v can only be directly compared with volumetric density of mysids (# m^{-3}). We use the derived relationship to estimate volumetric density, but then convert that to the more commonly used areal density by multiplying by the depth interval used in the analysis. This depth interval is defined as the top of the identified mysid layer (using backscattering and thermal info) to our acoustic limit (60 m) or the maximum depth of the plankton tow.

The calculation of lakewide mysid abundance requires weighting the estimates for different depth intervals by the proportion of the lake area these depths are represented. There are different approaches with Johannsson et al. (2011) using 50 m intervals and Rudstam et al. (2008b) and this study using the depth intervals 0–30 m, 30–50 m, 50–75 m, 75–100 m, and >100 m. Mysids are rare in nets collected in shallow habitats (0–50 m or 0–30 m) so the density of this depth interval is set to zero.

Results

For all five cross-lake transects in August 2008, a layer identified as mysids at depths from 20 to 30 m (25 to 35 m for Oswego) was characterized by a high volume backscattering coefficient (s_v) at 120 kHz up to 60×10^{-9} ($S_v = -72$dB, Figure 1). Shallower secondary backscattering layers observed

at 10 m depth along the Cobourg and Rochester transects and 20 m depth at the Oswego transects were not considered to be composed of mysids because of water temperatures that exceed thermal tolerances of mysids and the behavior of similar layers with ship lights turned on (see later discussion). The mysid layer was particularly prominent throughout the Olcott and Cobourg transects in the west central part of the lake. The layer was also apparent throughout the far western Oshawa transect but with somewhat lower backscatter (s_v up to 40×10^{-9}, $S_v = -74$dB). In the eastern part of the lake, the layer was apparent either on the north end (Rochester) or south end (Oswego) at high levels near s_v of 60×10^{-9} ($S_v = -72$ dB).

The mysid layer was primarily an offshore feature, fading out at the north end of each transect when bottom depth became shallower than 70 to 90 m (Figure 1). On the steeper southern slope the layer developed in water as shallow as 40–50 m for the western transects (Oshawa, Olcott, and Cobourg). Strong spatial variability in backscatter (and presumably mysid density) was present along all transects offshore; the average area backscattering (s_a) attributed to mysids ranged over more than a factor of 10 even over bottom depths >100 m corresponding to less than 100 to over 1000 mysids m^{-2}. A common feature for the three central transects (Olcott, Cobourg, and Rochester) was a midbasin region of low backscatter at 43.6–43.7 degrees latitude. The mysid layer was generally 10–15 m thick. The vertical position of the layer from the surface was generally consistent along each transect but varied along the Olcott and Rochester transects. We later use the concurrently collected temperature profiles to interpret potential physical mechanisms structuring mysid distribution patterns.

Mysid abundance in fourteen vertical net tows ranged from 0 to 1113 mysids m^{-2} (average of 316 m^{-2}, 1 standard error (SE) 84, SE/mean = 26.6%). The three tows with mysid densities >500 m^{-2} were collected in the southern portion of the Olcott and Cobourg transects. Two size cohorts were present—approximately 10 mm (juveniles) and 15–25 mm (adults). These two size classes were equally represented at most sites but at five locations the population was predominately juvenile (Figure 2). These include midbasin sites within all transects except for the western Oshawa transect.

One tow from the Oswego transect was only to 38 m depth and did not catch mysids. This outlier
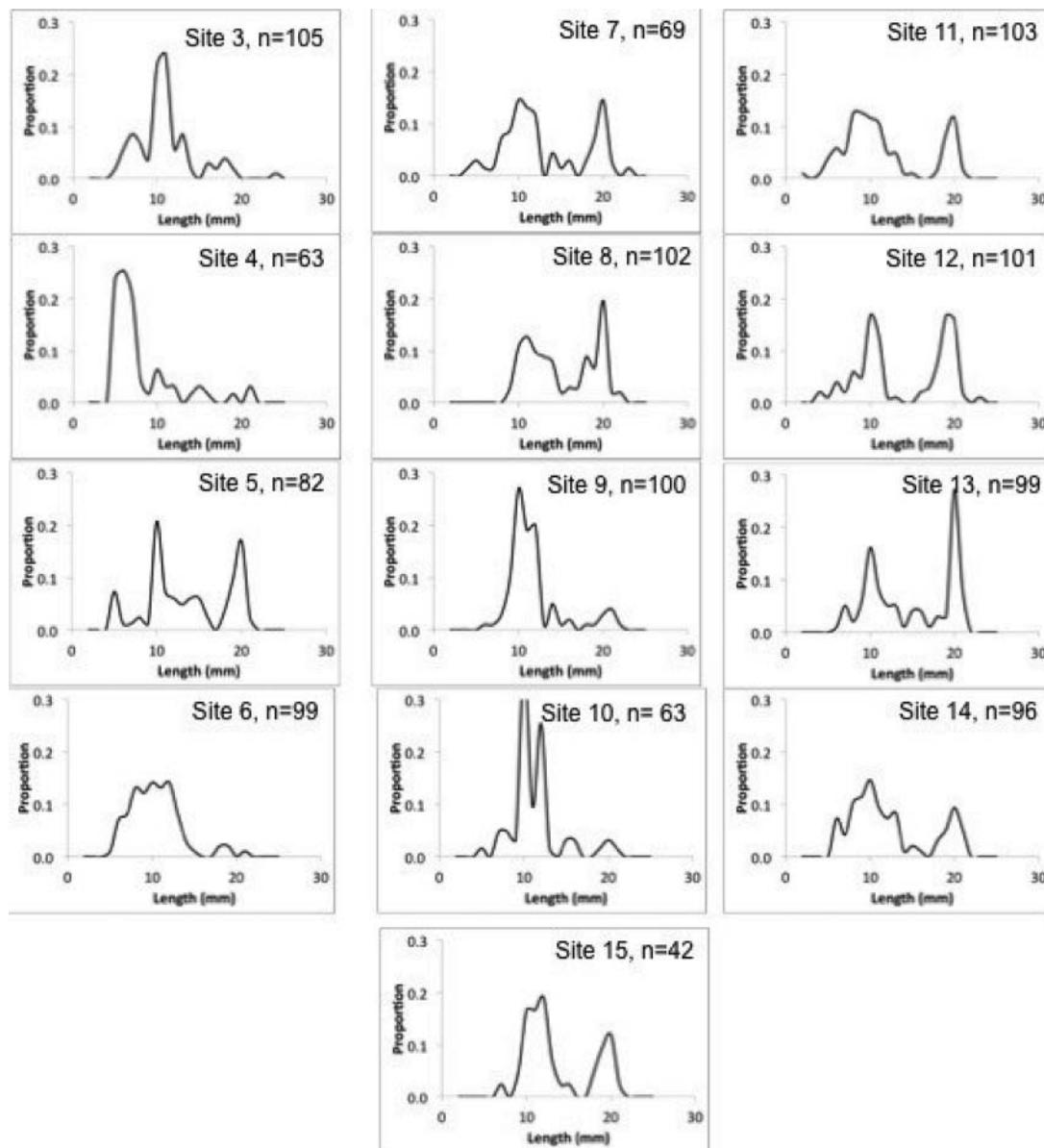
Figure 2. Size distribution histograms of mysids labeled by tow site (see map in Figure 1). Number of individuals measured is noted.

was not included in the density and biomass equations. Log-transformed mysid biomass was strongly correlated with S_v for the remaining thirteen tows (Figure 3). The resulting equation for biomass was:

$$\text{Log}_{10} \text{ (Biomass in g dw m}^{-3}) = 0.09 \text{ (S}_v \text{ in dB)} + 5.70, \text{ r}^2 = 0.80$$

and for density:

$$\text{Log}_{10} \text{ (Density in \# m}^{-3}) = 0.07 \text{ (S}_v \text{ in dB)} + 6.56, \text{ r}^2 = 0.49$$

Because neither of these slopes were significantly different from the theoretical expectation of 0.10, we re-ran the two regressions forcing the slope to be 0.10:

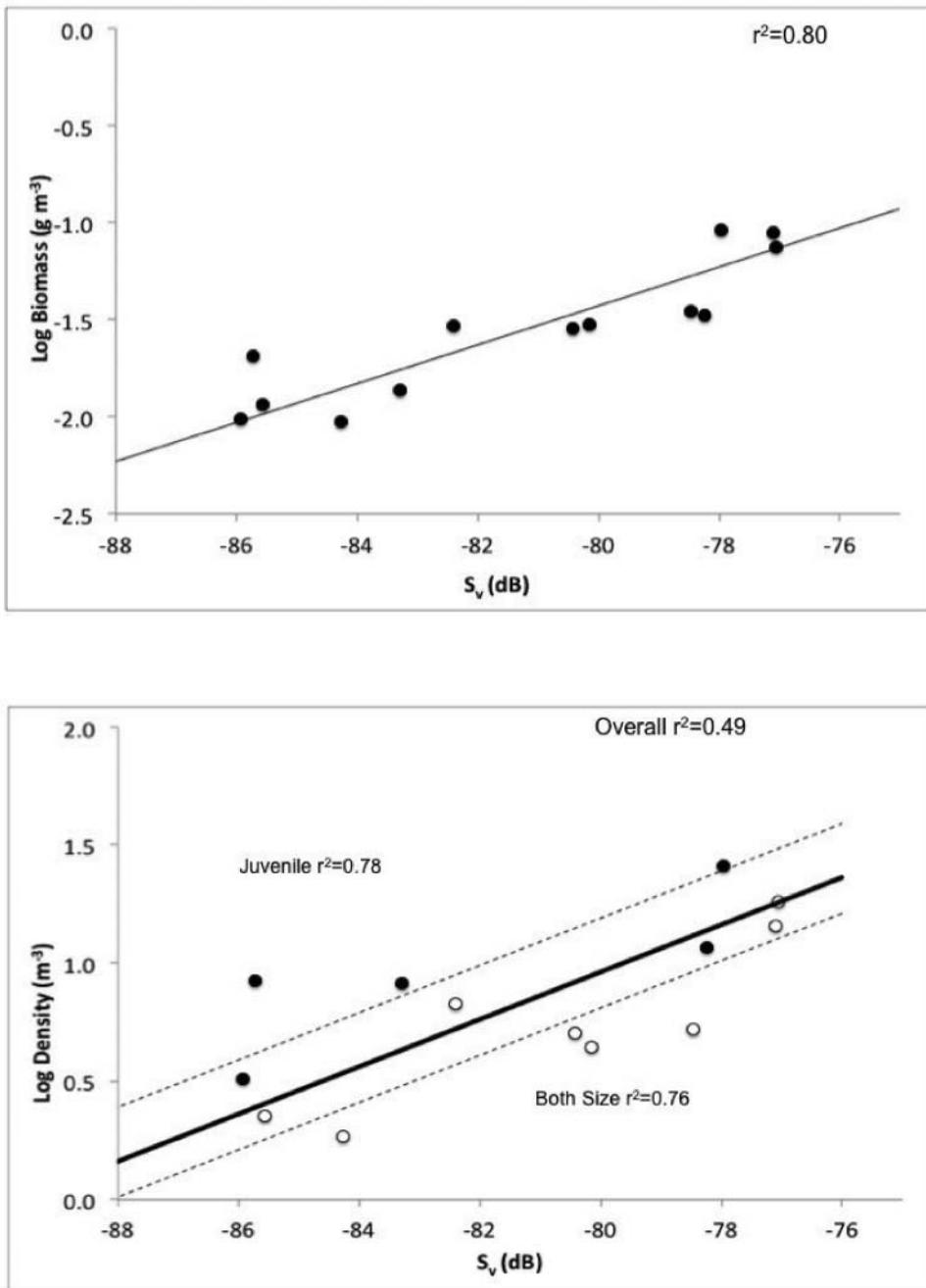$$\text{Log}_{10} \text{ (Biomass in g dw m}^{-3}) = 0.10 \text{ (S}_v \text{ in dB)} + 6.57$$

Figure 3. Relationship of log transformed biomass (g m^{-3}) and mysid density (# m^{-3}) to volume backscatter S$_v$ (dB). Solid lines represent lines with theoretically expected slope of 0.10 for all sites. Size was not significant (p = 0.55) in the relationship of S$_v$ and biomass. S$_v$ per gram biomass was -65.7 dB. For density, size was a significant factor (p = 0.0099). Sites with only small mysids (filled circles, upper dashed line) had a smaller S$_v$ per mysid (-91.9 dB) than sites with both small and large mysids (open circles, lower dashed line, -88.2 dB) using the theoretical slope. For all sites (used for transect density calculation) the value of Sv per mysid was -89.6 dB. Mysid abundance data are from net tows and are directly compared to volume backscatter from the mysid layer for that horizontal interval.

and for density:

$$\text{Log}_{10} \text{(Density in \# m}^{-3}) = 0.10 \text{ (S}_v \text{ in dB)} + 8.96$$

With this formulation, the target strength of one mysid can be calculated to be -89.6 dB and the target strength of 1 g dw to be -65.7 dB. The coefficient of variation (CV) in the estimated backscattering cross sections ($\sigma_{bs;}$ TS $= \log_{10}(\sigma_{bs})$) based on these net hauls was 15.2% for individual mysid σ_{bs} and 9.3% for the biomass based σ_{bs}. These estimates of error were included in the overall variance for the whole lake mysid estimates for density and biomass using standard error propagation assuming the errors in the equation and the errors associated with spatial variability were independent (Mood et al., 1974).

These equations were used to track north-south trends of mysid density for each transect (Figure 4). Highest mysid density (averaging >300 m^{-2}) occurred as strong peaks within the central Olcott and Cobourg transects and decreased toward the east. The overall lakewide average (weighted by area of lake within depth intervals) was 228 mysids m^{-2} (CV 17.6%) and a biomass of 0.93 g dw m^{-2} (CV 12.9%, Table 1).

The position of the mysid layer was generally at the base of the thermocline, between 5 and 10°C (Figure 5). The thermocline deepened from the western transects (Oshawa and Olcott) to the east (Rochester and Oswego). The eastern Oswego transect with the deepest thermocline also had the deepest mysid layer at 25 to 35 m. Subtle (0–5 m) changes in the vertical position of the mysid layer closely followed sloping isotherms for the Rochester and Olcott transects. Thermal habitats of the layers were generally consistent for individual transects, i.e. warmest along the Rochester transect at 8–12°C and cooler for the Olcott and Oswego transects at 5–8°C. In contrast, the layer crossed isotherms for the western Oshawa transect with a thermal habitat of 6–8°C in the south and 5–6°C to the north.

To further explore the acoustic–net data comparisons, we tested if dominance of juvenile mysids in 5 of the net hauls affected the intercept using a t-test assuming unequal variance (and assuming a slope of 0.10). The intercept for density was significantly higher for the juvenile net hauls than for the net hauls with both age groups (Figure 3). The TS calculated for these groups separately revealed a TS for the juvenile mysids of -91.9 dB and for the mixed age groups of -88.2 dB. There were no significant differences in intercepts for the biomass relationships.

Log Density (in # m^{-3}) $= 0.10(S_v) + 9.19$ (predominantly young mysids present, n = 5)

Log Density (in # m^{-3}) $= 0.10(S_v) + 8.82$ (both size classes present, n = 8)

Discussion

Hydroacoustics has the potential of being an effective method for estimating mysid biomass in the Great Lakes. Although mysid distributions have been investigated with acoustics for four decades (Teraguchi et al., 1975; Rudstam et al., 1989; Levy, 1991), quantitative estimates of mysid abundance have only rarely been attempted. This is in contrast to marine acoustics where biomass of krill is routinely estimated in the South Seas by the Conservation of Antarctic Marine Living Resources (Hewitt et al., 2003; Demer and Conti, 2005). A major problem in the Great Lakes is to remove the contribution from fish to acoustic backscattering. We followed the method described by Rudstam et al. (2008b) for fish removal. The resulting relationship between acoustic backscattering and net estimates of mysid abundance is linear and the slope (0.10) as expected if the contribution of individual mysids to the backscattering is additive (Rudstam et al., 2008b). This should be the case unless the densities are substantially higher than observed here (Foote, 1983; Foote and Stanton, 2000). Any significant inclusion of fish backscattering would distort this relationship.

The relationship between net tows and backscattering resulted in a smaller TS for an individual mysid in 2008 than in 2005 (-89.6 dB in 2008 compared to -86.3 dB in 2005). The TS of mysids obtained from the areas with predominately small mysids was smaller (-91.9 dB) than obtained in areas with both size groups (-88.2 dB). Rudstam et al. (2008a) application of a theoretical model for mysid TS at 120 kHz predicts an average TS for the small mysid size distribution to be -87.2 dB (85.8–89.0 dB) and for the size distributions with both size classes to be -83.3 dB (-84.6 to -82.2 dB). These values are also higher than the observed values for 2008, but the differences between the two size
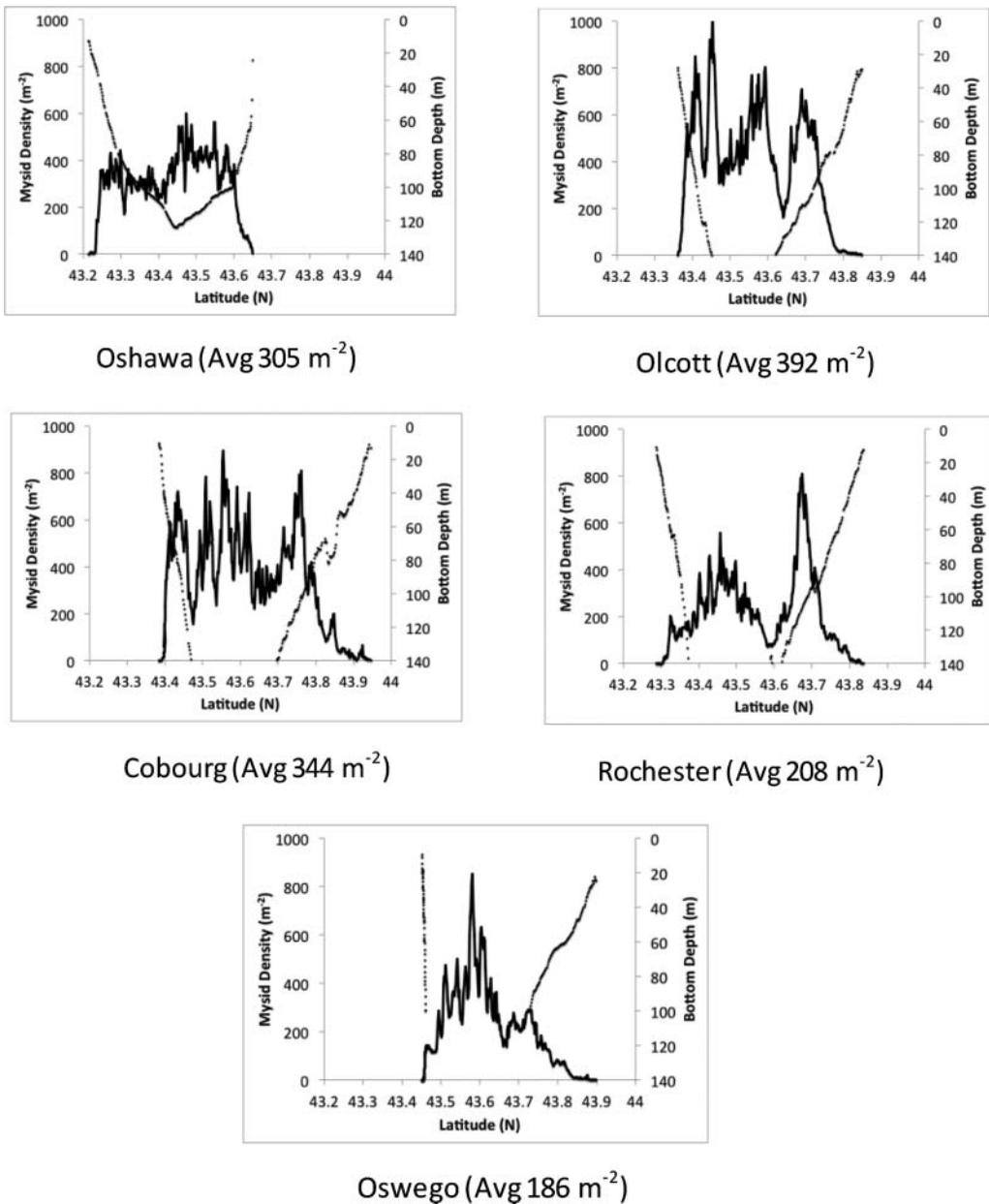
Oshawa (Avg 305 m⁻²)

Olcott (Avg 392 m⁻²)

Cobourg (Avg 344 m⁻²)

Rochester (Avg 208 m⁻²)

Oswego (Avg 186 m⁻²)

Figure 4. Mysid density (# m^{-2}, derived from volume backscatter equation) along each transect from south to north. Dotted line is bottom depth (scale to 140 m). Overall transect average densities of mysids along each transect are noted.

groups are similar (3.7 dB in the observation, 3.9 dB in the theoretical model). The differences between the 2008 and 2005 data could be associated with net performance since nets of different mouth opening and length were used. Calculations for volume filtered included drift in 2008 but not in 2005. The transducer was mounted firmly on a pole attached in the same way on the

same vessel in each year, so it is unlikely that transducer angle contributed to the difference in TS between years. The potential sources of error in the acoustic data and mysid orientation is less important because our density estimates are based on the relationship between net data and acoustic backscattering from the survey in question. Differences in catches obtained by using

Table 1. Whole lake mysid abundance and biomass estimated with hydroacoustics 1–5 August 2008. Whole lake estimates are weighted by the proportion of different depth regions in the lake obtained from the bathymetric map of Virden et al. (2000). Densities are estimated from five transects. Whole lake CV also includes errors in TS estimates for both density and biomass obtained in this study. Densities in depths shallower than 30 m are set to 0.

Bottom depth	Average density, # m^{-2}	CV (%), N	Average biomass, g dw m^{-2}	CV (%), N	Proportion of lake
0–30 m	0		0		0.217
30–50 m	63	45%, 10	0.26	45%, 10	0.115
50–75 m	178	31%, 10	0.73	31%, 10	0.127
75–100 m	300	20%, 10	1.22	20%, 10	0.112
Over 100 m	384	11%, 5	1.52	11%, 5	0.429
Whole Lake	228	17.6%	0.93	12.9%	

different styles of nets remains an issue and will be directly related to our estimates. Clearly, we need a better understanding of the sources of error in mysid TS estimates including net performance. Uncertainty in mysid TS has been contributing significantly to the uncertainty in mysid abundance estimates from acoustics in Lake Ontario and the results presented here put these relationships on more solid ground. Interestingly, and maybe not surprisingly, the relationship with mysid biomass and acoustic backscattering was stronger ($r^2 = 0.80$) with no significant effect of mysid size structure differences.

Using the relationship between S_v and net abundance obtained in 2008 resulted in a lake-wide mysid density of 228 mysids m^{-2} (CV 17.6%) and biomass of 0.93 g dw m^{-2} (CV 12.9%). These results indicate that mysid density has increased relative to 2005 (acoustic estimates of 118 m^{-2}, net estimates of 93 m^{-2}; Rudstam et al., 2008b). Net monitoring time series showed that lake-wide mysid density declined from values around 300 m^{-2} in 1988–1994 to values varying between 60 and 250 m^{-2} without a time trend from 2001 to 2007 (Johannsson et al., 2011) at depths deeper than 50 m. Our estimate for the summer of 2008 in depths deeper than 50 m is higher: around 331 m^{-2} (Table 1). These levels indicate that the mysids in Lake Ontario are abundant and higher than estimates from Lake Michigan (112 to
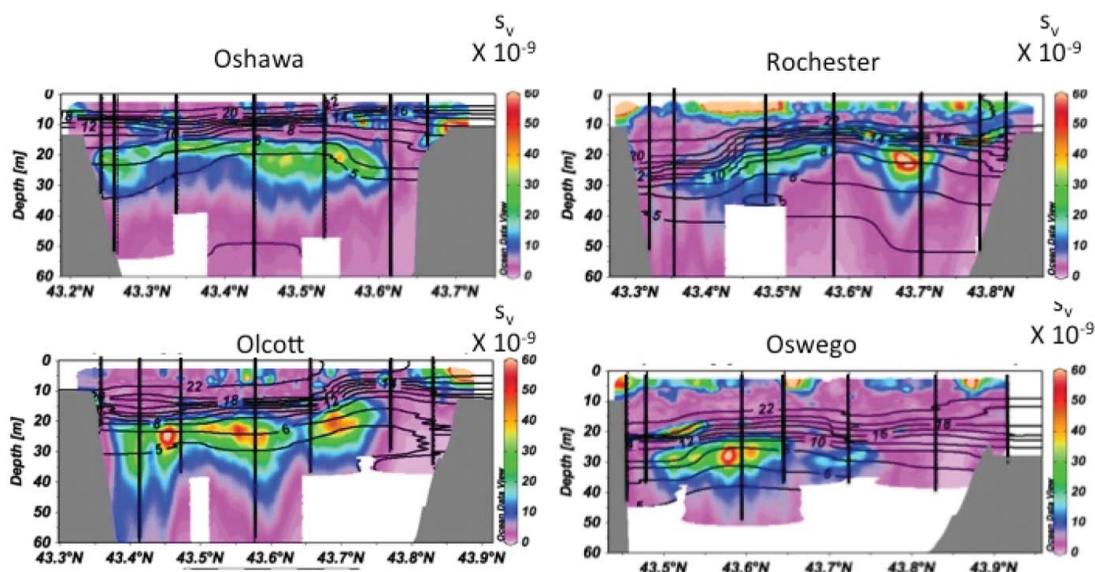

Figure 5. Relationship of temperature (°C) and the mysid layer. Up to seven temperature profiles (vertical lines) were used to construct the temperature contours for each transect.

185 m^{-2} for 2005 to 2009; Warner et al., 2010). Mysids are persisting and may even be increasing in Lake Ontario despite losses of other native organisms such as the amphipod *Diporeia.*

Mysid biomass is also high relative to other components of the foodweb. The biomass of other crustacean zooplankton was estimated to be 2.84 g dw m^{-2} in the offshore of Lake Ontario in 2008 (Rudstam et al., 2015). Mysid biomass is therefore almost 33% of all other zooplankton in the lake. Average 1989–2005 Alewife biomass was estimated to be 8.9 g ww m^{-2} (Murry et al., 2010) that corresponds to 2.2 g dw m^{-2} (assuming a dry/wet weight ratio of 0.25; Rudstam et al., 2011). This is only 2.4 times higher than the mysid biomass. Since mysids and Alewife consume similar proportions of their body weight per day, mysids are almost at par with Alewife as zooplankton predators in Lake Ontario (as suggested by Gal et al., 2006). Mysids may benefit from the vertical restructuring towards more deep production in Lake Ontario (Twiss et al., 2012; Watkins et al., 2015). This has important implications for both native and introduced fish populations that both rely on mysids as a nutritious food source and compete with mysids for zooplankton prey. Mysids were also more common in Alewife diets in the 2000s than in the 1990s (Stewart et al., 2009).

These analyses also demonstrate the utility of the hydroacoustic survey in documenting both vertical and horizontal variability in the mysid layer and its association with physical gradients. The annual survey is generally done at peak summer stratification close to the time of the new moon. Mysid migration is limited to below the thermocline in cool water yet low light conditions during the new moon enable peak migration. The August 2008 transect data delineate a maximum in offshore mysid abundance within the west-central portion of the lake (Olcott and Cobourg transects). A common pattern for these transects was a consistent decrease in mysid abundance at 43.6–43.7° Latitude. A similar gap was found in 2005 (Rudstam et al., 2008b). The consistency of the location of the gap in both years suggests that some large-scale recurrent mechanism is the cause, but it is unclear whether this offshore abundance minimum was associated with current boundaries or other physical gradients. The most likely explanation points to the prevailing counter-clockwise circulation gyre in the eastern basin (Pickett, 1976;

Beletsky et al., 1999). The immediate effect of these large-scale circulation features on mysids is unclear but may create local, unfavorable conditions leading to the observed, relatively low biomass. A clear advantage of continuous acoustic profiling (in this case more than 250 km) over net tows is the ability to detect the high horizontal variability in the mysid layer.

Mysids were often distinctly layered by depth, primarily below the thermocline. Boscarino et al. (2010) found good agreement between laboratory derived preferred temperatures (6–7°C) and preferred light levels (10^{-4} lux) and mysid distributions in the field using data from the region around Oswego. In 2008, we also found that the mysid vertical distributions followed the 5–8°C isotherms across transects although there were some regions with mysid backscattering in warmer waters. Most of the survey was conducted close to the new moon, making light less of a factor in the vertical distribution of mysids in this survey.

Mysid size structure clearly showed 2 cohorts, representing juvenile and adults in Lake Ontario (Johannsson et al., 2003). Interestingly, some samples were dominated by juveniles whereas others had approximately the same number of juveniles and adults. This indicates some patchiness in size structure across the lake. Similarly, in other samples from July 2008, size distributions were consistently different at two stations sampled with multiple hauls (Rudstam et al., 2012). In addition, TS estimates were affected by the size structure as expected. These differences in the distribution of the two cohorts will affect the acoustic backscattering strength relationship to mysid density in ways that require further analyses. It is because of these size structure differences across the lake that biomass estimates are more precise than density estimates.

Conclusions

The 2008 acoustic survey for forage fish abundance also allowed us to estimate mysid density and biomass on a whole lake basis as well as elucidating some of the spatial patterns inherent in the distribution of this species in Lake Ontario. Mysid density was relatively high in 2008 compared to results from previous years in the 2000s. Clearly, this species remains one of the most important

predators on zooplankton and potential prey for forage fish in Lake Ontario.

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