

Densities and diel vertical migration of *Mysis relicta* in Lake Superior: a comparison of optical plankton counter and net-based approaches

Olaf P. Jensen, Peder M. Yurista, Thomas R. Hrabik, and Jason D. Stockwell

Introduction

The opossum shrimp, *Mysis relicta*, is an important prey item for benthic (e.g., deepwater sculpin, *Myoxocephalus thompsoni*) and pelagic (e.g., kiyi, *Coregonus kiyi*, bloater, *Coregonus hoyi*, and rainbow smelt, *Osmerus mordax*) fishes in Lake Superior (ANDERSON & SMITH 1971, SELGEBY 1988, JOHNSON et al. 2004). It is also an important consumer of zooplankton and phytoplankton (BOWERS & GROSSNICKLE 1978, JOHANNSSON et al. 1994, GAL et al. 2006). *Mysis* is known to exhibit classic diel vertical migration (DVM; HUTCHINSON 1967) in Lake Superior (BOWERS 1988) and other lakes (BEETON 1960, BEETON & BOWERS 1982), with the majority of the population located high in the water column at night and in deep water, near or on the bottom during the day. The DVM of *Mysis* appears to be an important, but not exclusive, driver of DVM patterns in coregonids (ESHENRODER & BURNHAM-CURTIS 1999, HRABIK et al. 2006, JENSEN et al. 2006). Despite the ecological importance of *Mysis*, the last published estimate of their densities and vertical distribution in Lake Superior was based on vertical net tows conducted at a single location in 1986 (BOWERS 1988).

Optical plankton counters (OPCs) use a beam of light to count and measure particles passing through an aperture (HERMAN 1992). They have been used to estimate *Mysis* density in Lake Ontario (GAL et al. 1999a, SPRULES 2000) and zooplankton biomass and size spectra in several of the Great Lakes (STOCKWELL & SPRULES 1995, STOCKWELL et al. 2002, YURISTA et al. 2005, 2006). The newer laser OPC (LOPC) uses a narrow laser beam that allows better performance in high particle densities and direct estimation of flow speed through the aperture by timing the passage of small particles (HERMAN et al. 2004). It is also capable of generating an image or “shape profile” of larger particles.

In this study, we used data from an OPC, an LOPC, and vertical net tows to estimate densities and describe the day/night vertical distribution of *Mysis* at a series of stations distributed throughout Lake Superior, and to evaluate the efficacy of using OPC and LOPC for examining DVM of *Mysis*.

Key words: diel vertical migration, Lake Superior, laser optical plankton counter, Laurentian Great Lakes, *Mysis relicta*

Materials and methods

We sampled *Mysis* during the thermally stratified period at 22 locations in oligotrophic Lake Superior using a combination of OPC, LOPC, and vertical net tows (Fig. 1). Lake Superior has a surface area of 82 000 km², mean and maximum depths of 146 and 406 m, respectively, and chlorophyll *a* concentrations around 1.0 mg m⁻³. Mean surface temperature has risen 2.5 °C over the last 29 years (AUSTIN & COLMAN 2007).

The OPC (OPC-1T, Focal Technologies Corp., Dartmouth, N.S., Canada) was deployed on a Triaxus tow body (MacArtney Offshore Inc., Houston, TX, USA) and the LOPC (Brooke Ocean Technology Ltd., Dartmouth, N.S., Canada) was deployed on a V-Fin 493 (YSI Marion, Massachusetts, USA). Stations in the western arm of Lake Superior were sampled in July 2005 and August 2006. The OPC was used at these stations, and the Triaxus was towed off the stern of the research vessel at a speed of 2–3 m s⁻¹ in a sinusoidal (tow-yo) pattern from 7 m to a maximum of 175–214 m. All other stations were sampled in July and August 2005 using the LOPC towed at a similar speed in a sinusoidal pattern from 3 to 100–150 m. Bottom depths varied between 100 and 340 m.

Net sampling was conducted at night at 8 stations in August 2005 and 9 stations in October 2005. At each station, a 1 × 1 m opening rectangular net was used to sample *Mysis*. Mesh sizes tapered from 1000 μm to 250 μm, with 64-μm mesh in the cod end. The net was lowered to approximately 2 m off the bottom and retrieved at a speed of 0.3 m s⁻¹. Four replicate tows were conducted at each station. All *Mysis* in the samples were counted. If a sample contained more than 100 individuals, 100 individuals were randomly selected and measured to the nearest 0.1 mm (tip of rostrum to end of abdomen).

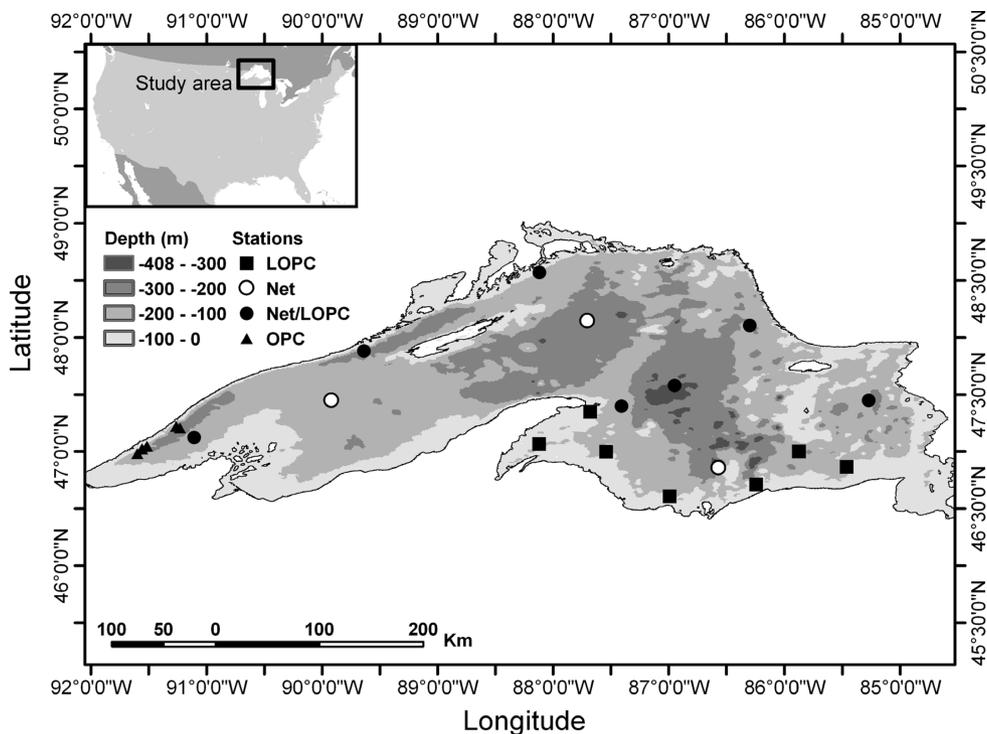


Fig. 1. Locations of optical plankton counter (OPC), laser optical plankton counter (LOPC) and vertical net tows (Net) in Lake Superior.

For analysis of density and vertical distribution of *Mysis* as measured by the OPC and LOPC, we used a size threshold of ≥ 4 mm equivalent spherical diameter (ESD). Assuming an ellipsoidal shape and a ratio of major to minor axis for an average zooplankton of 1.33 (SPRULES et al. 1998), this threshold results in an equivalent ellipsoid length (EEL; i.e., the length of an ellipse with the same area) of 4.6 mm. For *Mysis*, whose bodies are more elongated, a ratio of 4.5 is more appropriate (length-weight regression [K. Bowen, pers. comm.]) and assumption of 10% dry to wet weight ratio). The ≥ 4 mm ESD threshold is then equivalent to an EEL of 8.5 mm for *Mysis*. This threshold is larger than nearly all copepods or cladocerans found in the western arm of Lake Superior in July and August (JOHNSON et al. 2004). A previous analysis of *Mysis* abundance from OPC data (SPRULES 2000) used a threshold of 2.5 mm ESD. While the ≥ 4 mm ESD threshold that we used excludes many smaller *Mysis*, we found that lower thresholds showed evidence of contamination by particles other than *Mysis*.

Data from the top 5 m of the water column were removed prior to analysis to reduce the potential for targets resulting from bubbles or positively buoyant debris. Areal densities from the LOPC were calculated by summing volumetric densities calculated over 2 m depth intervals. Both the OPC and the LOPC were used to estimate vertical distribution of zooplankton, but only the LOPC was used to estimate density because it is capable of estimating speed through the aperture. Precise boat speed information, which would have allowed calculation of absolute densities from the OPC, was

not available for many of the OPC tows. Densities were estimated only from stations with tow depths ≥ 100 m.

Results

A clear DVM was only apparent in the OPC data collected in July 2005 (Fig. 2A). In that sample, during the day, no targets (i.e., particles ≥ 4 mm ESD) were found shallower than 150 m, and the peak density occurred near 200 m. The night pattern was reversed, with a peak density found near 50 m and a smaller peak around 200 m. In the August 2006 OPC samples, the night peak at around 50 m was again apparent, but no targets were found during the day (Fig. 2B). However, in August 2006 only a limited volume (4.2 m^3) was sampled below 180 m, where the majority of targets were found in the July 2005 OPC sample. In the LOPC samples, peak densities were found in the 10–30 m range during day and night (Fig. 2C). It is important to note that daytime LOPC sampling did not extend below 120 m.

The *Mysis* length frequency histogram constructed from the net samples showed 2 distinct size classes: one from approximately 4–10 mm and another from 11–17 mm (Fig. 3A). The length frequency histograms from the OPC (Fig. 3B) and LOPC (Fig. 3C) showed a slight shift toward larger sizes at night, but little evidence of 2 dis-

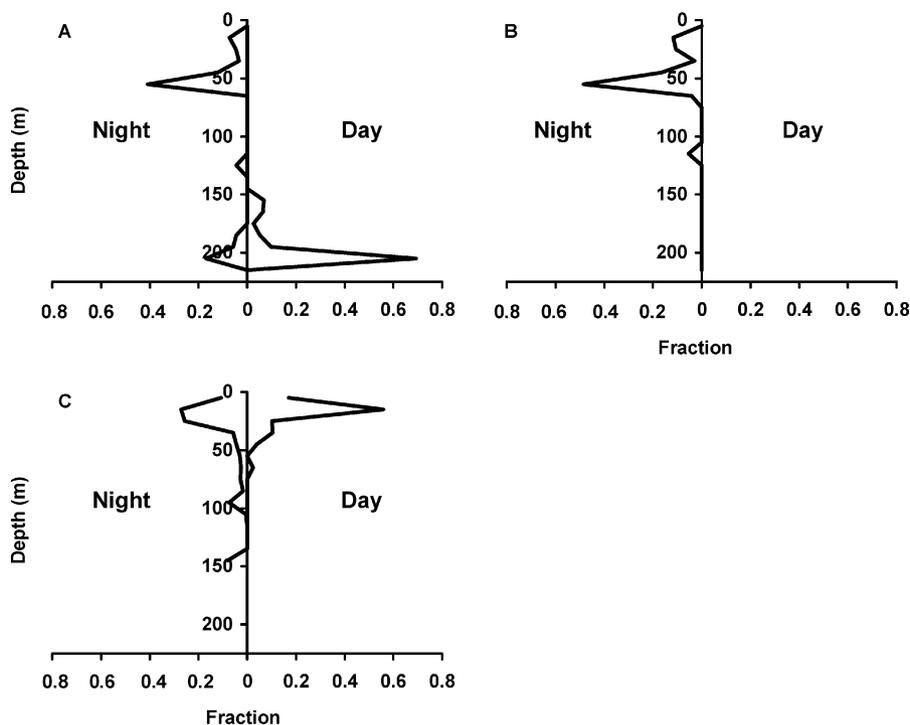


Fig. 2. Relative density at depth for particles ≥ 4 mm ESD from night (left) and day (right) tows of an optical plankton counter (OPC) in (A) July 2005 and (B) August 2006 and (C) laser optical plankton counter (LOPC) tows in July and August 2005.

tinct size classes. The LOPC showed a substantially higher frequency of large targets than the OPC (except in the > 20 mm category), though both devices showed relatively fewer large targets than the net samples.

Mean areal densities of targets ≥ 4 mm ESD from the LOPC was 332 ± 231 m^{-2} (SD, $N = 10$ stations) at night and 239 ± 223 m^{-2} (SD, $N = 3$ stations) during the day. In comparison, *Mysis* densities from the nighttime vertical net tows averaged 190 ± 86 m^{-2} (SD, $N = 17$ stations/seasons) with no significant difference between summer and fall densities ($p = 0.185$, ANOVA, Matlab v7.4, anovan function). Analysis of covariance (ANCOVA, Matlab v7.4, glmfit function) showed a significant ($p < 0.001$, $R^2 = 0.40$) positive relationship between *Mysis* density in vertical net tows and station depth (Fig. 4), with no significant difference in the densities at depth between 1971 (CARPENTER et al. 1974) and 2005 ($p = 0.128$) and no interaction between year and depth ($p = 0.661$).

Discussion

The DVM pattern of *Mysis*-sized targets inferred from OPC and LOPC data was not consistent among samples and only OPC samples from the western arm of Lake Superior in July 2005 matched the expected pattern.

Comparison of this sample with the others suggests that the failure to observe clear DVM of larger targets at other times/locations may be the result of insufficient sampling at depths > 150 m during the day and contamination by particles other than *Mysis*. The LOPC tows were part of a general zooplankton survey and were not optimized to sample *Mysis*. Analysis of staged vertical net tow data from a 280 m deep station in Lake Superior showed that the majority of *Mysis* in the water column were found below 200 m during the day (BOWERS 1988). The OPC data from July 2005 showed modest densities of large targets around 200 m at night. This result matches BOWERS' (1988) observations of a nocturnal deepwater fraction of the *Mysis* population. Horizontal patchiness (apparent from the high among-station variability in net and LOPC density estimates) may also have obscured DVM patterns. Staged net tows represent the vertical distribution of an organism at a single location and are thus less influenced by horizontal patchiness compared to data collected from towed nets or instruments.

No evidence of DVM was apparent in the day versus night comparison of the LOPC data. Relatively high densities of targets were consistently found above 50 m during the day. These high densities at shallow depths during the day are a strong contrast to most previous results on *Mysis* DVM in Lake Superior (BOWERS 1988) and Lake

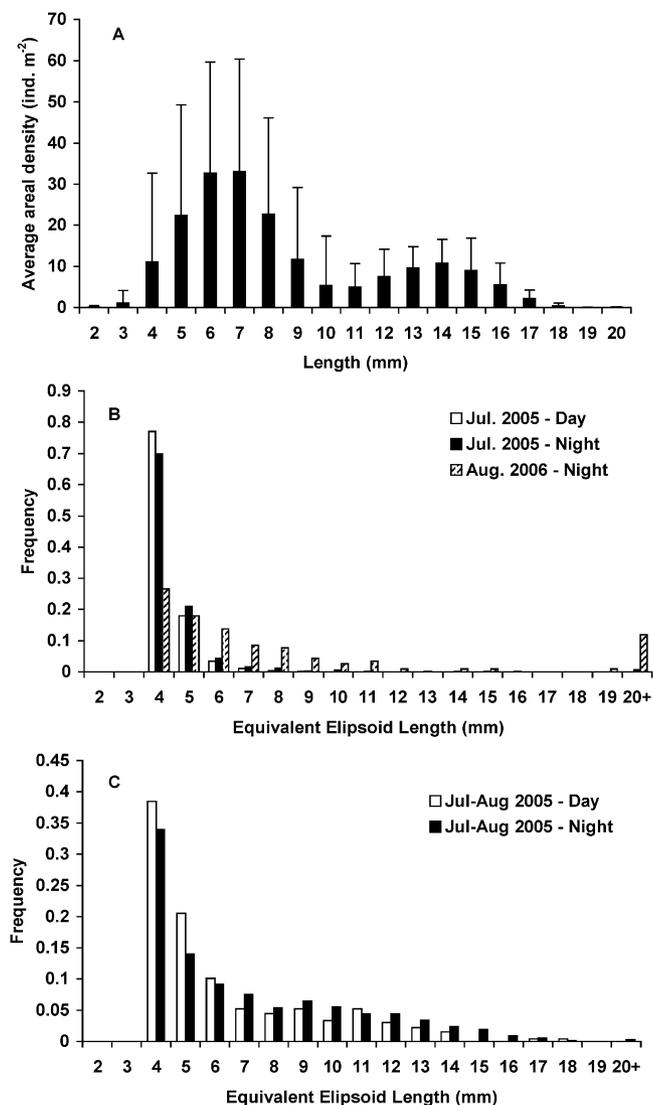


Fig. 3. (A) Areal densities (individuals m⁻²) by length (mm) for *Mysis* captured in vertical net tows and length frequency histograms for targets ≥ 4 mm equivalent ellipsoid length (EEL, assuming a ratio of major to minor axis of 4.5) from day (open bars) and night (shaded bars) tows of (B) an optical plankton counter (OPC), and (C) a laser optical plankton counter (LOPC).

Ontario (GAL et al. 1999b, 2004) and suggest that large epipelagic plankton other than *Mysis* are being counted. These high abundances of targets at shallow depth were found even when the threshold was raised as high as 5 mm ESD. Although *Mysis* are found in shallow (0–50 m) net tows during the day, their densities are low, and they are typically smaller individuals (BOWERS 1988). In the absence of supporting evidence from net tows, the most plausible explanation for the high densities of shallow daytime targets seen in the LOPC data

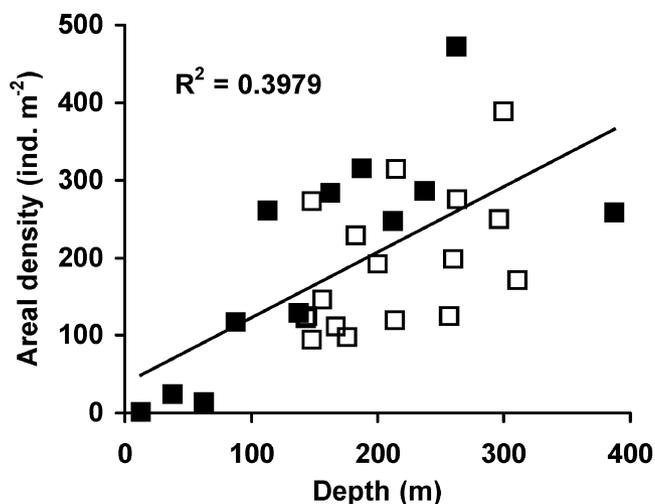


Fig. 4. Areal density (individuals m⁻²) vs. depth and linear regression line for *Mysis* sampled with vertical net tows in this study (open squares) and from CARPENTER et al. (1974, filled squares). Regression line is for both years because no significant year effect was found.

must be that these targets are something other than *Mysis*.

The length frequency histograms from the OPC and LOPC were clearly shifted toward smaller sizes relative to the net samples. Higher OPC:net biomass ratios for larger plankton have been reported elsewhere (NOGUEIRA et al. 2004). This is likely due to a combination of several factors. First, zooplankton pass through the beam of the OPC or LOPC in many different orientations. The EEL is calculated based on the assumption that a zooplankton passes through perpendicular to the beam. Therefore, a 4 mm *Mysis*, for example, will result in a range of EELs, with a maximum of 4 mm. For zooplankton with relatively elongated body patterns, like *Mysis*, this can result in a substantial number of individuals whose lengths are underestimated (SPRULES et al. 1998). FINLAY et al. (2007) found that the LOPC underestimated the size of large *Daphnia* spp. by 25%, suggesting that similar or larger biases may occur with the more elongated *Mysis*.

The second explanation for the high abundance of small targets is that other zooplankton overlap with the *Mysis* length distribution. The OPC and LOPC record sizes of targets but do not identify them. Although *Mysis* are larger on average than other zooplankton in Lake Superior, they do overlap in size with some other species, including the invasive spiny water flea (*B. longimanus*). Densities of *B. longimanus* as high as 3 ind. m⁻³ (i.e., 300 ind. m⁻² in 100 m depth) have been reported from 100-m vertical net tows in 2001 in the western arm of Lake

Superior (BROWN & BRANSTRATOR 2004), where large (3-spine) individuals attained an average body length of 3.2 mm. Still, individuals of this size are unlikely to be counted using a size threshold of ≥ 4 mm ESD. The transparent gelatinous coating of *Holopedium gibberum* is often large enough that, if sufficiently opaque to block the light beam, may be recorded as ≥ 4 mm ESD. *Holopedium* is one of the most abundant cladocerans in Lake Superior (BARBIERO et al. 2001) and were found in many of the net tows. There is, unfortunately, no information on the length-ESD relationship of *Holopedium*. Bubbles and other nonzooplankton particles can also be recorded by the OPC and LOPC (HERMAN 1992). We removed the top 5 m from the analysis to limit this problem, but bubbles or particles were possibly still present at greater depths.

Coincidence (i.e., 2 or more plankton overlapping as they pass through the beam) can result in an upward bias in ESD; however, the densities of plankton in open water regions of Lake Superior are lower than those at which coincidence typically becomes a serious concern (SPRULES et al. 1998), particularly for the LOPC, which is less sensitive to this problem (HERMAN et al. 2004). Thus, we do not believe that coincidental counts strongly influenced the patterns in our data.

Finally, large *Mysis* may have been better able to avoid the OPC and LOPC than small *Mysis*. The OPC has an aperture height of only 2 cm (width is 25 cm), and a relatively small vertical movement would be required for a large *Mysis* to avoid entering the aperture. The LOPC has a higher square aperture (7×7 cm) that may make it better able to capture large zooplankton. The higher frequency of large targets in the LOPC data supports this idea.

Despite the fact that the LOPC sampled a smaller portion of the water column than the net tows, areal densities estimated from the LOPC were substantially higher. The net tow densities in this study were similar to the average density at depth found in Lake Superior in 1971 (CARPENTER et al. 1974) and lower than the average density found at a single 280 m location in 1986 (695 and 790 ind m^{-2} for day and night samples, respectively; BOWERS 1988). Nets may underestimate *Mysis* densities due to net avoidance and pressure waves. The LOPC likely reduces this problem because it is mounted on a hydrodynamically streamlined towbody with nothing behind the aperture to create backpressure. However, the LOPC may overestimate densities due to counting of particles other than *Mysis*. Vertical net tows, the OPC, the LOPC, and hydroacoustics are all poorly adapted to estimating the abundance of *Mysis* slightly above, on, or buried in the sediment. BOWERS (1988) found high densities of *Mysis*

(62 ind. m^{-3} day, 28 ind. m^{-3} night) at 2 m above the bottom using a submersible equipped with net pumps and reported observations of *Mysis* emerging from unconsolidated sediments during electrofishing. Accurate estimation of *Mysis* densities for the whole water column may require a combination of benthic (e.g., benthic sled) and pelagic sampling.

Mysis are an important component of the Lake Superior food web. Understanding their DVM patterns and accurately estimating their abundance have ecological (e.g., benthic-pelagic coupling and DVM of *Mysis* predators) and fishery management implications (e.g., potential food limitation of *Mysis* predators, including commercially valuable coregonids). The apparent presence of particles other than *Mysis* in the OPC and LOPC data severely limits the usefulness of this technology for understanding DVM patterns in Lake Superior. Future studies should investigate the possibility of using shape information from the LOPC to classify targets taxonomically. The distinct differences in body shape of *Mysis* from other relatively large invertebrates (*B. longimanus*, *Limnocalanus macroides*, *Senecella calanoides*, and *H. Gibberum*) suggest that this approach is the necessary next step. Tows designed to estimate *Mysis* abundance and DVM patterns should include adequate day and night representation of all depths, including near-bottom layers.

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Authors' addresses: O.P. Jensen, Center for Limnology, University of Wisconsin-Madison, 680 North Park Street, Madison, WI 53706, USA. Current address: School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA. E-mail: ojensen@u.washington.edu

P.M. Yurista, U.S. Environmental Protection Agency, 6201 Congdon Boulevard, Duluth, MN 55804, USA.

T.R. Hrabik, University of Minnesota-Duluth, 207 Swenson Science Building, 1035 Kirby Drive, Duluth, MN 55812, USA.

J.D. Stockwell, U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station, 2800 Lakeshore Drive, Ashland, WI 54806, USA. Current address: Gulf of Maine Research Institute, 350 Commercial St., Portland, ME 04101.