Trends in Partial Diel Vertical Migration of *Mysis diluviana* Along a Depth Gradient in Lake Ontario

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Abstract:

Mysis diluviana is a small shrimplike crustacean native to the Laurentian Great Lakes. They are vital to maintaining the ecosystem of the Great Lakes due to their mid-level trophic status and diel vertical migration behavior that links benthic and pelagic habitat. It has been assumed that the entire mysid population performs a complete diel vertical migration, but recent evidence has suggested that some mysid populations exhibit a partial diel vertical migration (PDVM). This consists of some mysids remaining in the benthos at night, and others in the water column during the day. This study examined whole water column mysid net tows along a depth gradient in Lake Ontario to compare daytime and nighttime catches in order to determine if mysids exhibit PDVM in Lake Ontario, and answer whether depth and life stage influence the extent of PDVM. Very few mysids were caught during the day below 175m, but at 175m and 200m, an average of 276 and 476 mysids were caught per net tow, respectively. At 200m this daytime catch represented 87.5% of the nighttime catch. In addition, the vast majority of those mysids caught during the day at each site were juveniles. However, at 200m, there was very little difference between mysid day and nighttime catches and length distributions. With these results, it can be concluded that mysids do exhibit PDVM in Lake Ontario by not fully retreating to the benthos during the day. Juvenile individuals are also more likely to exhibit PDVM than adults, and mysids in general are more likely to exhibit PDVM at deeper sites. There are many possible explanations for why juvenile mysids are more likely to exhibit PDVM, and it is likely that low light levels in the water column at deeper sites contributes to this behavior. More research on mysid PDVM is necessary to understand their nuanced behavior and gain insight into how traditional mysid sampling, which is currently only done in the water column at night, may be biased.

Introduction:

Mysis diluviana, commonly known as the “Opossum Shrimp” (hereafter referred to as mysids), are freshwater shrimp-like crustaceans native to deep oligotrophic lakes in the Northeastern United States and Southern Canada, including the Laurentian Great Lakes. In the Great Lakes, *Mysis diluviana* is known to be an opportunistic omnivore, and an important mid-level trophic species that both feeds on zooplankton, and is a high quality food source for many fish species. Mysid populations are regularly monitored because they are key in maintaining the offshore food web (Ball et al., 2015, Rudstam & Johannsson, 2009, Holda et al., 2023).

One well-known dimension of *Mysis* behavioral ecology is that they exhibit a diel vertical migration between benthic and pelagic environments each day, extensive relative to other zooplankton species (Jude et al., 2018, Hays, 2003). At night mysids often aggregate in a distinct layer near the thermocline, where they can prey on nutrient-rich zooplankton, suggesting some affinity to a preferred cooler water temperature than warmer surface waters (Beeton & Bowers, 1982). This distribution is why most historical mysid monitoring programs have sampled at night with vertical whole-water column plankton nets (Silver et al., 2016).

Mysids are very sensitive to light, and at sunrise they are generally thought to migrate to the lake bottom. This behavior is thought to have developed as a strategy for mysids to avoid predation by fish in the water column when the sun is out, and visibility is high, but still be able to feed on zooplankton at night, when there is less risk of predation (Gal et al., 1999, Boscarino et al., 2009). Their sensitivity to temperature and light essentially restricts this organism to deep (>40 m) stratified lakes, and also leads them to favor offshore habitats in deep lakes (Wang et al.

2012). Their extensive migration highlights the important role of mysids in coupling benthic and pelagic habitats in these ecosystems.

However, recent research indicates that mysid migration behavior is more nuanced than previously thought. One study conducted on the Baltic mysid, *Mysis salemaai*, concluded that stable isotope ratios between benthic and pelagic caught *Mysis* were significantly different, with pelagic individuals having a more stable and carnivorous diet (Ogonowski et al., 2013). This suggests that some *Mysis salemaai* only utilize benthic habitat, and do not migrate upward to feed on zooplankton. This affinity for benthos has also been suggested in observations of populations of *Mysis diluviana*. Instead of a total migration of all individuals between the benthic and pelagic environments, some mysids remain in the water column during the day, and some remain in the benthic layer at night (Euclide et al., 2017). This behavior has been referred to as partial diel vertical migration (PDVM) (Chapman et al., 2011).

The *Mysis diluviana* population in Lake Champlain is the most well studied when it comes to PDVM behavior. It has not only been found that this mysid population exhibits PDVM, but also that the proportion of the population remaining in the water column during the day was much higher at a deep site (100m) than a shallower one (60m). In one observation at 100 m depth, the number of pelagic mysids at night was not different from the number pelagic during the day. In addition, smaller mysids were more likely to be found in the water column during the day at both deep and shallow sites (O'Malley et al., 2018). This suggests that both bottom depth and life stage influence whether individuals fully migrate or not.

This pattern is also supported by research conducted before PDVM was a known behavior in mysids. One study found that life stage influences the rate and timing of vertical migration in mysids (Teraguchi, 1969). A laboratory study found that juvenile mysids can tolerate higher light levels and temperatures than adults, which may explain why juvenile mysids are more likely to remain in the water column during the day (Boscarino et al., 2010).

This confirmed phenomenon of PDVM in mysids raises many questions about why the behavior takes place. There are multiple contending hypotheses for why the size difference between benthic and pelagic mysids is observed. The hunger-satiation hypothesis states that mysids migrate only when their stomachs are empty and they need to prey on zooplankton. A recent field study suggests that this is likely not a plausible explanation for PDVM, as mysids eat continuously when in the benthic environment, mostly on detritus (O'Malley & Stockwell, 2019). Another example is the size-predation hypothesis, tested in different partially migrating aquatic organisms, which theorizes that larger individuals may be less likely to migrate and remain in the benthos because they have a greater risk of predation in the water column than smaller individuals (Skov et al., 2010).

PDVM exposes a potential limitation in current mysid monitoring because the standard sampling protocol only utilizes pelagic nighttime net tows, which means that the non-migrating subset of a *Mysis* population is missed. This biases overall Great Lakes ecosystem understanding, because mysid monitoring data is used in models that inform decisions regarding how the ecosystem should be managed, such as mass-balance food web models (Stockwell et al., 2020).

Research on PDVM can therefore provide more accurate estimates of Great Lakes *Mysis* population sizes and demographics, which are essential details that fisheries and other Great Lakes managers make decisions such as what fish to stock and how many, which greatly impact those who are affected by the economically important Great Lakes ecosystem. Also, although Great Lakes mysid populations did not decline significantly between 2006 and 2016, they have fallen from historical highs seen in the 1960s-1990s, so having accurate information on these populations is essential in terms of deciding how to conserve them and predicting their response to external drivers such as new invasive species, as well as the entire ecosystem's response (Jude et al., 2018). The latest data also suggests that mysids in Lake Michigan have recently sharply decreased from 2016-2019 (Holda et al. 2023).

Objectives and Hypothesis

If, and to what extent, partial diel vertical migration (PDVM) occurs in mysid populations at different depth sites in Lake Ontario is the question explored in this study. A transect along an increasing depth gradient has never been sampled for mysids during both day and nighttime hours. This sampling allows for a direct comparison of daytime and nighttime individuals in the water column that reveal what component of the Lake Ontario mysid population remains pelagic during daylight hours at various depths.

For nighttime net hauls, I expected to see an increase in mysid net catches with depth, given their preference for deep habitat. These tows represent an important baseline for evaluating daytime catches, because the entire population is supposed to be represented under the assumption of complete diel vertical migration. For daytime hauls, I expected few if any mysids in the water column, but potentially some net catches at deeper sites. This prediction derives from the idea that mysids likely exhibit downward migration to avoid light, and deeper sites have more deep pelagic habitat that light cannot reach during the day, and therefore meet this preference for darkness.

Another prediction is that the mysids in the water column during the day are primarily juvenile. This prediction stems from the ideas that juvenile mysids are less sensitive to light than adult mysids, and follows the pattern observed in the Lake Champlain population.

Materials and Methods:

Field Sampling

Mysis field samples were collected on 6/14/2022 along a transect in Lake Ontario starting from the USGS Lake Ontario Biological Station (USGS LOBS) in Oswego, NY and heading Northwest into the Rochester Basin. Lake Ontario was chosen as the study area because the mysid population in Lake Ontario is known to be healthy and abundant, and therefore highly likely that many mysids could be caught per tow. Oswego has deepwater access to the Rochester Basin relatively close to shore, ensuring that a complete transect could be traversed in a single day and night cycle. Six sites were selected along the 17 km transect both during the day and at night, at depths of 60m, 110m, 137m, 150m, 175m, and 200m. At each of these stations, two replicate net tows of the entire water column were taken using a *Mysis* net (1 m diameter, 250 um mesh, 0.7854 m^2 area), following standard collection procedures outlined by the EPA (EPA, 2015). The transect was sampled two times on 6/14/23 - once during daylight hours, and once at night. All daytime samples were taken at least 2 hours and 45 minutes before sunset, and nighttime samples started just after sunset, concluding before midnight. 6/14/23 was also a full moon. Samples were then preserved in ethanol for preservation.

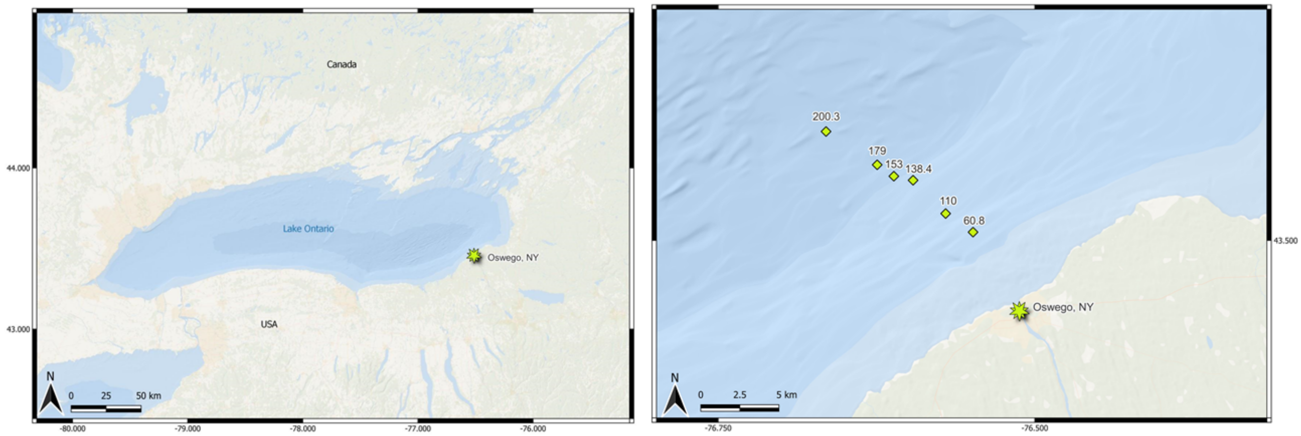


Figure 1 - Map of the launch point in Oswego, NY, and the transect sampled with bottom depth (m) for each

Laboratory Analysis

Analysis of each sample began with conducting a count of all mysids in each replicate tow for a measure of total abundance. Then, sex and life-stage demographic information was determined for a randomly chosen subset of up to 200 individual mysids from each tow using a dissecting microscope. Mysids under 10mm in length were classified as juveniles. These mysids were then photographed and each individually measured for body length using the software ImageJ from the rostrum to the base of the abdomen in mm. Laboratory analysis followed the procedure outlined in the EPA standard operating procedure manual (EPA, 2019). In total, one day of sampling the transect yielded sixteen net hauls with mysids present for a catch of 3,813 total mysids. 2,417 of these were selected for measurement and sex/life stage determination.

Figure 2 - Mysids organized by sex and life stage (adult males, females, gravid females)

Results:

As predicted initially, at night, which is the time mysids are typically monitored, net catch increases almost linearly with depth (Figure 3). This ranged from no mysids caught at the 60m site, day or night, to over 500 mysids caught on average during nighttime hours at the 200m site. Mysids were caught in the water column during daylight hours at some sites. For sites shallower than 175m, the number of mysids caught during the day was very small compared to the number caught at night, suggesting that most individuals perform complete diel vertical migration to the benthos. However, at 175m, a threshold was crossed, and many more mysids were caught during the day until at 200m, the average total abundances of the replicate net tows for day and night could not be considered different, based on overlapping error bars. At 175m, there is no point of direct comparison between day and night catches, because no night catch was attempted at this site, due to difficulties in the field. This day sample still provides an important sampling of daytime abundance at this depth.

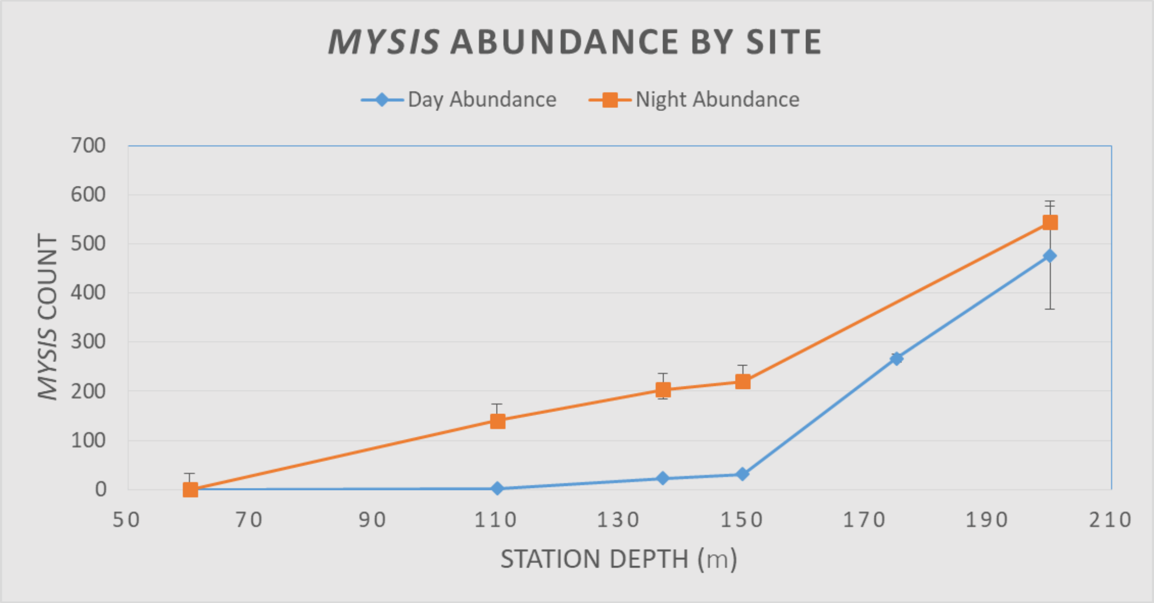


Figure 3 - Graph of the average Mysid abundance caught at each depth site for replicate net tows (error bars represent standard error between the two replicate tows)

Beyond overall abundance, size distributions at each site in the day and night help evaluate which components of the nighttime population remain present in the water column during the day. In length distributions, the average abundance of mysids per net tow is plotted against the body length of those mysids. Mysid body lengths were rounded to the nearest mm, so that they could be binned by 1 mm increments easily. For larger net tows that yielded more than 200 individuals, because some mysids were not measured, the length distribution was scaled up by the proportion of mysids not measured so that the distribution could be scaled up to the contents of the entire net tow.

At the 110m depth site, no mysids were collected during the day. The nighttime catch for this site showed a clear bimodal distribution, with the smaller peak (4-7 mm) representing the juvenile cohort of mysids, and the larger one (12-16 mm) representing the adult cohort. Each cohort was collected at almost equal abundance at 110m.

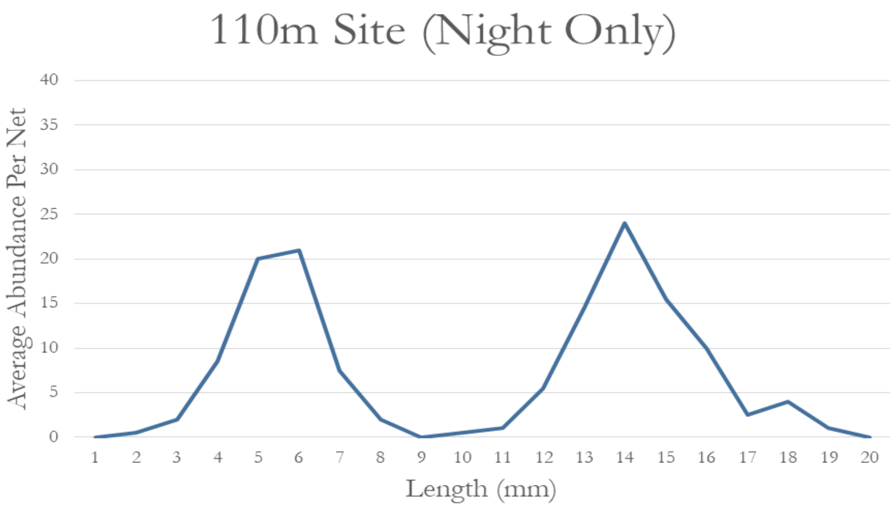
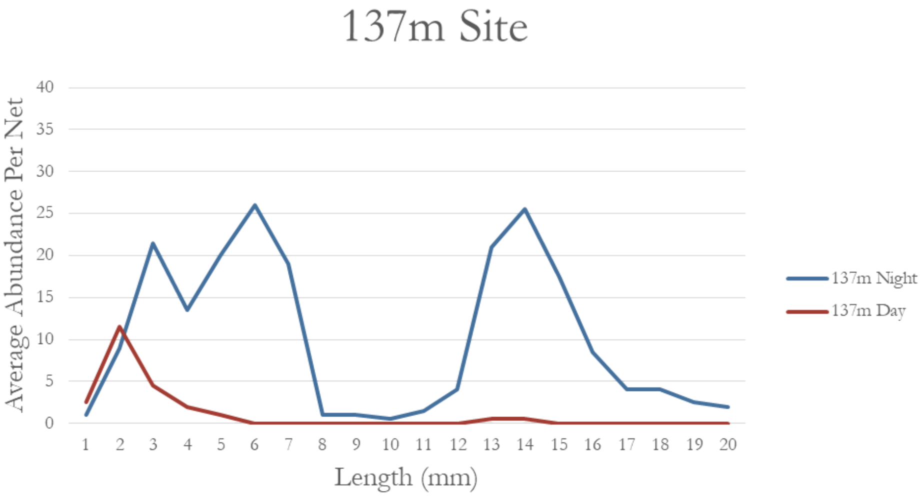
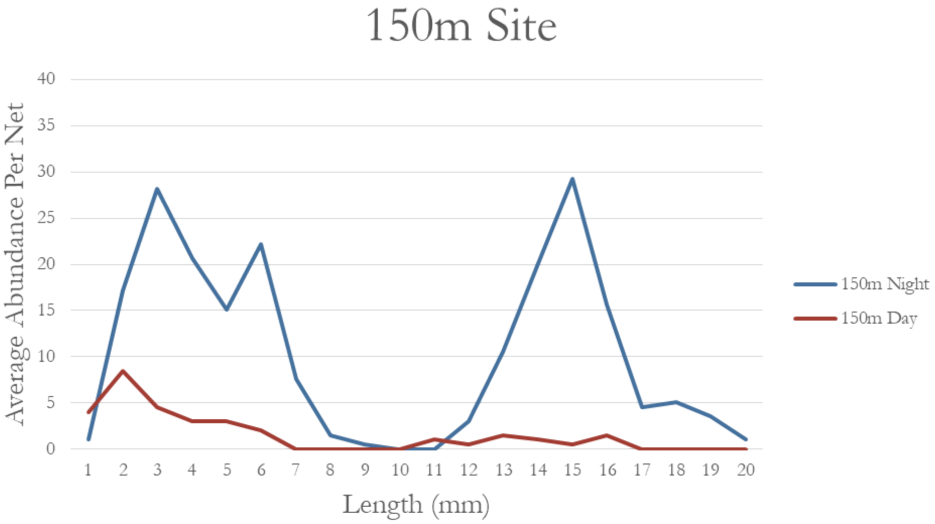


Figure 4 - Mysid length distribution graph for the 110m site during night. No mysids were caught at this site during the day.

At 137m and 150m, two distinct cohorts are seen again at night, with slightly more total mysids caught at each subsequent depth (Figures 5 and 6). The cohorts again appear at similar abundances to each other. However, there is some daytime catch at these sites. It was rare to see any adults in the water column during the day. The majority of this daytime catch consisted of juvenile mysids, and small juvenile mysids specifically (between 1 mm - 5 mm). Overall, there was a large difference in average mysids caught per net at these sites during the day vs. at night (difference of 181 individuals and 188.5 individuals for 137m and 150m, respectively).





Figures 5 and 6 - Mysid length distribution graphs for the 137m and 150m sites for day and night.

175m was the first depth sampled that showed two distinct cohorts of mysids in the water column during the day (Figure 7). The cohorts do not, however, appear at similar abundances to each other, even though both cohorts appear at greater abundances than the shallower sites. At this site, there are about four times as many juveniles present than adults during the day. As mentioned there was no corresponding night tow set for this depth

Figure 7 - Mysid length distribution graph for the 175m site during the day. No mysid tows were conducted at night.

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Finally, at 200m, two cohorts were found in both daytime and nighttime samples (Figure 8). At this depth, day and night catch abundances and length distributions mirrored each other closely. There was an overall 68 mysid difference between average daytime and nighttime net tows, with this difference in abundance coming mostly from an increase in adults at night. Interestingly, both daytime and nighttime length distributions at 200 m revealed a much larger juvenile cohort than the adult cohort.

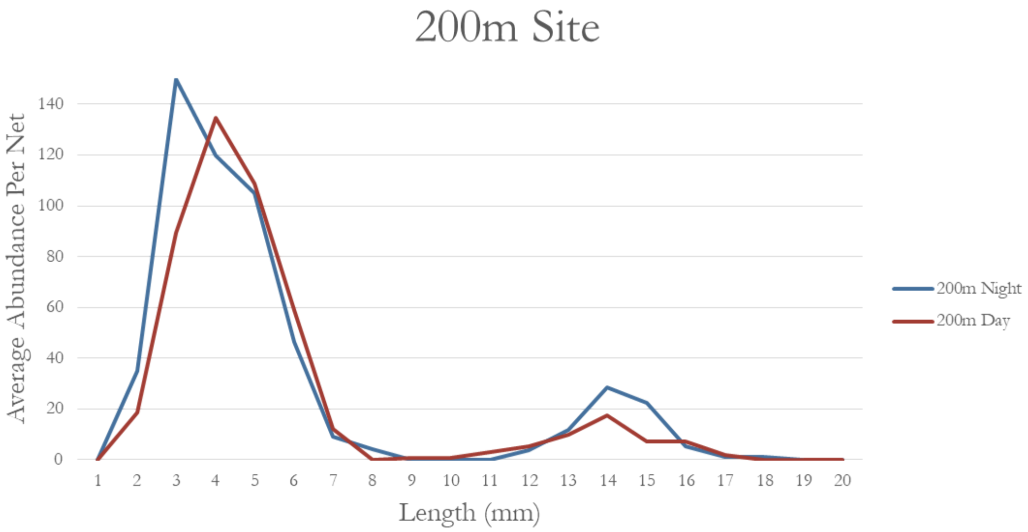
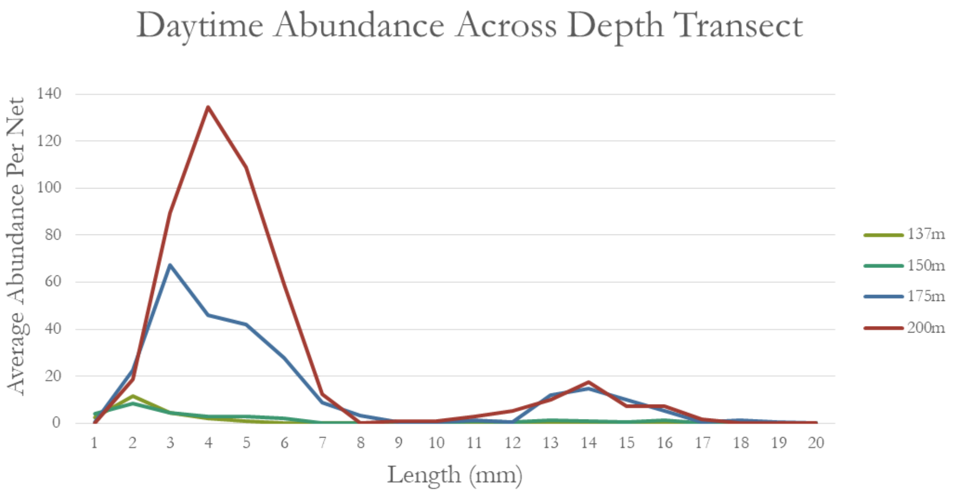
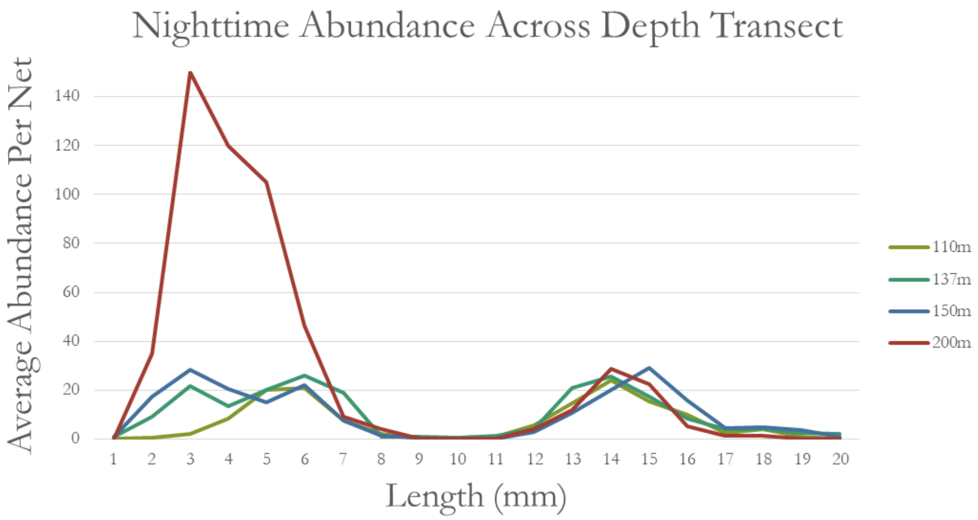


Figure 8 - Mysid length distribution graph for the 175m sites. No mysids were caught at this site during the day.

Comparing all daytime length distributions across the sites sampled, the mysids caught at the shallower sites are almost exclusively small juvenile individuals. Between 150m and 175m, as well as between 175m and 200m, there is a sharp increase in the number of juvenile mysids present in the water column during the day, and adult mysids are present in the water column during the day only at the deeper sites of 175m and 200m depths.

For the nighttime length distributions, shallower sites have similarly sized cohorts of juveniles and adults, but there is also a similar sharp increase in juveniles between the 150m and 200m sites as seen during the day (175m was not sampled at night). The overall number of adult mysids at all depths remains relatively consistent. This suggests that the observed increase in mysid abundance with depth is driven by increased abundance of the juvenile cohort. Between daytime and nighttime distributions, many more juvenile and adult mysids were found in the water column during the night at shallower depths (150m and below). However for the deepest site, distribution was relatively consistent between daytime and nighttime catches.





Figures 9 and 10 - Mysid length distributions for each depth sampled for both daytime and nighttime catches, respectively.

Discussion:

Extent of PDVM along transect

Based on results shown, a large number of mysids in Lake Ontario exhibit partial migration behavior of not reaching the benthos during the day, confirmed by the net catches during the day. The extent of partial migration is strongly influenced by depth. The proportion of mysids partially migrating by remaining pelagic during the day is fairly small at shallow sites (below 175m), given that many more mysids can be caught at night than during the day. This suggests that most mysids at these shallower sites perform a full diel vertical migration. However, this trend changes at sites deeper than 175m, as many more mysids can be found to remain in the water column during the day. By 200m, there is actually very little difference between the total abundance of mysids caught during the day vs. at night, and the difference is mostly attributed to an increase in adult mysids at night. These findings are consistent with the idea that light level is an important parameter to consider when predicting mysid behavior. There likely is a light level threshold between 150m and 175m in Lake Ontario at which the mysids are comfortable being in. This depth threshold was different from that found in the Lake Champlain mysid population. In that study, similar mysid abundances for day and night pelagic tows were found at a 100m depth site, which was considered a deep site for that lake (O'Malley et al., 2018). Based on Secchi depth, Lake Ontario has higher water clarity than Lake Champlain, which is a mesotrophic lake, likely explaining why this mysid threshold light level is at a much deeper depth in Lake Ontario (O'Malley et al., 2018). This difference highlights why context, specifically light penetration and site depth, are such important factors when evaluating the extent of PDVM in mysid populations.

Prevalence of different life stages on PDVM

Another major finding of this study, also confirming results from work on the Lake Chaplain mysid population, is that life stage also influences the extent of PDVM behavior in mysids (O'Malley et al., 2018). Specifically, juvenile mysids are much more likely to remain pelagic during the day than adults. This is a trend displayed at all depth sites with any evidence of partial migration. At shallower sites (below 175m) the daytime pelagic catch suggested that almost exclusively juvenile mysids partially migrate, while the remainder of the population emerges from the benthic layer at night. At deep sites, many more juveniles also exhibit PDVM, and a fairly large number of adults do as well. The most extreme case is at 200m, where day and nighttime length distributions mirror each other, except for an increase in adult mysids migrating from the benthos at night. This result suggests that almost the entire juvenile cohort avoids migrating all the way down to the benthos, and rather prefers to stay pelagic during the day.

This finding can be plausibly driven by many of the contending theories for why PDVM behavior occurs, including the size-predation hypothesis. Another explanation that fits with the higher propensity for juvenile mysids to partially migrate is that there is a tradeoff between avoiding predation and obtaining energy. Because juvenile mysids must focus on gaining energy reserves to support growth, they may use benthic habitat less at deeper, darker sites (Chess & Stanford, 1998). In addition, mysids are known to cannibalize each other, which could also partially explain why juvenile mysids avoid the benthos, where more adults are present, as long as light conditions are favorable at deeper sites (Chipps et al., 2022).

Another interesting finding is that the nearly linear increase in mysid abundance with depth was driven mostly by increases in the juvenile cohort. This suggests that juvenile mysids show more of a preference for deeper habitat than adult mysids do. They also show a higher rate of partial migration at these deeper sites. It seems plausible that there may be a relationship between depth and life stage when considering PDVM behavior. Perhaps the reason why juvenile mysids prefer deeper sites is because they have the ability to partially migrate there. If this were true, it would suggest that partial migration may be an evolutionarily effective strategy for juvenile mysids, and help illuminate the reason for PDVM behavior in juveniles. More research investigating this preference for deep habitat and the increase in PDVM at deep habitat is recommended to help find out why PDVM occurs.

Future Research

Now knowing that PDVM behavior is present in Great Lakes mysids, more research on the reasons for and ecological ramifications of this behavior is recommended. Specifically, studies on the non-migrating benthic mysids would be very helpful, as this study did not sample the benthic component of the mysid population. Sampling transects like the one in this study, with the coupling of pelagic net tows with benthic sled tows during both daytime and nighttime hours would be especially useful. This addition could help determine how many mysids are missed by the current monitoring paradigm by remaining in the benthos at night. It would also be useful to know the length distributions for this subset of the mysid population, which is predicted to be adults. Further studies of pelagic or benthic mysids could also include food web markers which would confirm the use of specific food resources in each of these habitats.

Conclusion:

Results from this study indicate that PDVM is a behavior exhibited by mysids in Lake Ontario. This partial migration behavior is found to be both depth and life stage dependent, with juveniles remaining in the water column during the day. As depth increases older mysids also remain in the water column until at 200m, relatively few appear to migrate all the way to the benthos. These conclusions offer additional support to other studies on mysid PDVM, and help cement the importance of this behavior in understanding mysid behavior. It is the hope that these results will serve as a gateway to more research on *Mysis* PDVM and an overall improved understanding of Great Lakes ecology.

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