Diel Vertical and Horizontal Migration of Zooplankton Across a Gradient of Dissolved Organic Carbon

BIOS 35502: Practicum in Environmental Field Biology

Julia Hart

Advisor: Patrick Kelly

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Abstract

Increased browning of global freshwater ecosystems, a result of increased dissolved organic carbon (DOC), can significantly alter both the biotic and abiotic characteristics of aquatic systems. Most prominent among abiotic changes is a darkening, or browning, of the water color. Previous research has shown that diel migration patterns of freshwater zooplankton, an integral part of freshwater food webs and trophic interactions, stand to be affected by changes in water color. While much is known about the diel vertical migration (DVM) patterns of zooplankton, little research has been done about diel horizontal migration (DHM) in freshwater systems. This study asks how increased DOC affects both diel vertical and diel horizontal migration in north temperate lakes. As water color increased across three lakes, diel migration, both vertical and horizontal, generally decreased. With darker water color, zooplankton are provided refuge from visual predators, allowing them to remain in the food- and oxygen-rich epilimnion or distribute across the entire surface of the lake at any time of day.

Introduction

There has been a steady increase in the amount of dissolved organic carbon (DOC) in freshwater lakes over the last few decades (Monteith 2007). Potential drivers of this phenomenon include increased carbon dioxide emissions, increased nitrate deposition, decreased sulfur deposition, changing land use, and climate change (Monteith 2007). An increase in DOC in a freshwater lake can significantly darken the water color while also altering other physical and chemical properties of the lake (Houser 2006). For example, increased DOC attenuates UV radiation (Williamson, et al. 2001), impedes lake primary production, and decreases the depth of a stratified lake's thermocline, making the epilimnion both shallower and warmer (Sobek et al. 2007). Previous research has shown that the structure and functioning of lakes is tightly coupled to the terrestrial environment (Williamson et al. 2001) and that the exchange of materials between aquatic and terrestrial habitats is more ubiquitous than previously thought (Polis et al. 1997). Therefore, allochthonous carbon plays an important role in aquatic ecosystems.

Zooplankton are crucial to freshwater pelagic food webs and are thought to be good indicators of trophic state and ecological quality in lakes (Jeppesen et al. 2011). As primary consumers, zooplankton reside in the center of many freshwater food webs. While feeding on phytoplankton, zooplankton are commonly consumed by many planktivorous fish and invertebrate species (Lampert 1989). Previous research has shown that DOC explains more variance in zooplankton community structure than other variables such as changes in pH, the presence or absence of predators, or chlorophyll levels (Williamson et al. 2001). By attenuating light and darkening water color, DOC may provide zooplankton with a natural refuge from predators, especially visual predators like fish. Allochthonous resources like DOC can also provide an additional food resource for zooplankton, albeit not a preferable one (Brett et al. 2009).

During the day, zooplankton exhibit diel vertical migration (DVM) to avoid visual predation in the lighted epilimnion of lakes (Dodson 1988). Migrating to the colder and oxygen-depleted hypolimnion during the day, zooplankton will then return to the epilimnion at night to feed on phytoplankton under the cover of darkness (Lampert 1989). Recent research has shown that zooplankton are also capable of diel horizontal migration (DHM), migrating to the littoral zone during the day to avoid predators and returning to the pelagic epilimnion to feed at night. A study conducted by Burks et al. (2002) argues that

DHM should be favored when macrophyte abundance is high and planktivore abundance is low. Diel horizontal migration might allow zooplankton to make use of alternate littoral zone resources (Burks et al. 2002).

This study examines both diel vertical and horizontal migration of freshwater zooplankton across a gradient of dissolved organic carbon in lakes. I would like to determine how water clarity impacts zooplankton DVM and DHM. I hypothesize that as DOC concentrations increase, zooplankton will be less inclined to migrate from the pelagic epilimnion, and both vertical and horizontal migration will decrease as a result of decreased predation in the pelagic zone.

Methods and Materials

Study Sites

Lakes were chosen for study based on previously recorded DOC concentrations spanning a gradient of water color. Bay Lake, Long Lake, and Hummingbird Lake were chosen as low (approximately 6 mg/L), medium (approximately 8 mg/L), and high (approximately 23 mg/L) DOC lakes, respectively. All lakes are located at the University of Notre Dame Environmental Research Center (UNDERC) in Land O' Lakes, WI.

Sampling and Processing

Two horizontal transects were randomly chosen on each lake (Figures 1-3). Sampling took place along four locations at each transect: shore 1, open water 2, open water 3 (both evenly spaced along the transect), and shore 2 at all lakes except Hummingbird Lake. The second horizontal transect on Hummingbird Lake had only one open water stop due to the short diameter of the lake. At each shore, one sample was collected in the littoral zone of the lake. Along the open water stops, three samples were taken: a shallow (~3m), a medium (~5m), and a deep (~7m) sample, representative of the stratified layers of the lake. All samples were collected using a zooplankton tow net.

To account for any diel migration, samples were collected during the day and at night, approximately twelve hours apart. Day sampling began between 11 AM and 12 PM and night sampling between 11 PM and 12 AM. Each lake was sampled three times over a six-week period in June and July. Sampling start times were pushed back later in the summer to account for the later sunset. All samples were preserved in 70% ethanol upon collection and brought back to the lab for identification. Zooplankton were counted and identified to order in the case of copepods, and genus for *Daphnia, Holopedium,* and *Bosmina* spp..

Statistical Analysis

Data was analyzed according to the type of migration pattern: vertical or horizontal. To analyze diel vertical migration, samples at each open water location were pooled according to depth, resulting in a shallow, a medium, and a deep zooplankton abundance per transect per time of day. A one-way ANOVA, followed by a Tukey's Multiple Comparison Test (MCT) if significant, was used to determine if zooplankton abundance was significantly different at each depth. A repeated measures ANOVA was used to determine if the sampling point in the summer was a significant factor between the three sampling episodes.

To analyze diel horizontal migration, all shore and shallow samples for each transect were analyzed together. This provides the most accurate comparison for horizontal movement along the entire transect. Similar to the diel vertical migration analysis, a one way ANOVA with a subsequent Tukey's MCT was used to determine if zooplankton abundance differed across the surface of the lake. A repeated measures

ANOVA was used to determine if sampling time in the summer was a significant factor in zooplankton migration. All statistical analyses were performed with R statistical software (R Core Team 2012).

Results

Diel Vertical Migration

Zooplankton in Bay Lake, the lightest lake, exhibited standard diel vertical migration patterns. In both transects, zooplankton were most abundant in the hypolimnion, or the deep sample, during the day, and in the epilimnion, or the shallow sample, at night (Figure 4). There was no significant difference in the abundance of zooplankton at each depth on either transect at either time of day (p=0.221, p=0.504, p=0.246, and p=0,667). Repeated measures ANOVA was significant on both transects during the day (p=0.0026 and p=0.0113).

Zooplankton in Long Lake, the medium lake, showed little signs of any diel vertical migration. Regardless of the time of day, zooplankton across both transects were found mainly at the surface (Figure 5). There was no significant difference in the abundance of zooplankton at each depth on either transect at either time of day (p=0.462, p=0.149, p=0.265, and p=0.499). Repeated measures ANOVA revealed that sampling point in the summer was a significant factor during the day on transect 1 (p=0.0195).

Zooplankton in Hummingbird Lake, the darkest lake, also showed little evidence of diel vertical migration. Similar to Long Lake, the highest abundance of zooplankton, regardless of the time of day, was found in the epilimnion (Figure 6). A one-way ANOVA revealed that zooplankton abundance in the epilimnion was significantly higher than the hypolimnion on transect 1 at night (p=0.0499). There were no other significant differences in zooplankton abundance at each depth (p=0.739, p=0.975, and p=0.759). Sampling point in the summer was a significant factor for transect 1 during the day (p=0.0054) and transect 2 both day and night (p=0.0318 and p=0.0090, respectively).

Diel Horizontal Migration

Zooplankton abundance on the shores was low in Bay Lake during the day, but increased at night, suggesting some diel horizontal migration to the littoral zone of the lake (Figure 7). Zooplankton abundance was significantly greater in the shallow open water than shore 1 on transect 2 during the day (p=0.0337). All other abundances across the surface of the lake were not significantly different (p=0.0624, p=0.678, and p=0.481). Repeated measures ANOVA revealed that sampling point in the summer was only significant on transect 2 during the day (p=0.0395).

Zooplankton on Long Lake were fairly evenly distributed across the surface of the lake during the day on both transects (Figure 8). At night, more zooplankton were found in the littoral zone, evidence of diel horizontal migration. There was no significant difference in zooplankton abundance across the surface of the lake on either transect at either time of day (p=0.548, p=0.0856, p=0.362, and p=0.842). Sampling point in the summer was not significant for either transect at either time of day (p=0.1976, p=0.1767, p=0.486, and p=0.0602).

Similarly, zooplankton abundance on Hummingbird Lake were fairly evenly distributed across the surface during the day along both transects. Higher zooplankton abundance along the shores at night suggests diel horizontal migration (Figure 9). There was no significant difference in zooplankton abundance across the surface of the lake on either transect at either time of day (p=0.754, p=0.385, p=0.934, and p=0.72). Sampling point in the summer was a significant factor for migration pattern on transect 1 during the day (p=0.0353) and on transect 2 both day and night (p=0.0038 and p=0.0176, respectively).

Discussion

Diel vertical migration and diel horizontal migration patterns were reduced with increased DOC, supporting the hypothesis that as DOC concentrations increase, zooplankton will be less inclined to migrate from the pelagic epilimnion.

The DVM results in Bay Lake reflect standard migration patterns. Zooplankton migrate to the hypolimnion during the day to escape fish predation and return to the epilimnion at night to feed (Figure 4). The light color of this lake combined with a substantial fish population and predation pressure drives this process. The high DOC concentration of Hummingbird Lake, conversely, may provide a refuge for zooplankton in the epilimnion during the day. High zooplankton abundances are found at the surface during the day because it is not necessary for zooplankton to migrate during the day to avoid visual predators (Figure 6). Diel vertical migration in Long Lake appears most similar to that of Hummingbird Lake. Water color provides zooplankton with enough cover that migration from the surface during the day is not necessary. Low fish populations in Long Lake could also be contributing to this phenomenon; risk of predation is lower in this lake to begin with. Overall, there was a decrease in DVM as DOC concentrations increased. Zooplankton are less likely to migrate from the food- and oxygen-rich epilimnion in darker lakes.

Zooplankton in the darker lakes, Long Lake and Hummingbird Lake, did not show significant diel horizontal migration compared to those in the lighter lake. During the day, the shores at Bay Lake showed low zooplankton abundance, but high abundances at night (Figure 7). This suggests that only under the cover of darkness can the zooplankton take advantage of the food resources found in the littoral zone of this lake. During the day, there is little refuge from visual predators in this area. Contrastingly, during the day, zooplankton in Hummingbird Lake are just as likely to be found in the littoral zone as the epilimnion (Figure 9). The dark color of the water provides sufficient refuge across the entire surface of the lake. Across both transects, zooplankton abundance at the shores increased at night. Once again, migration in Long Lake most closely mirrored that of Hummingbird Lake. Though fairly evenly distributed across the surface during the day, there are much higher abundances found at the shores at night (Figure 8), even more so than Hummingbird Lake. This suggests that the water color of Long Lake does provide some refuge for zooplankton during the day, for the zooplankton are not afraid to simply sit at the surface or shores. But higher abundances at the shores at night suggests that fear of fish predation is still a possibility. Overall, DHM decreased across the three lakes; as DOC concentrations increased, zooplankton were less inclined to move to and from the littoral zone.

It is interesting to note that even where the water color provided a refuge from predation, abundance was greater at the shores at night (Figures 8-9). If the water color really does provide an ideal refuge, there should be no difference between the abundances in the littoral zone during the day and at night. My results, however, consistently show higher abundances at night, suggesting that zooplankton migrate to the shores at night only. It is difficult to conclude that purely horizontal migration is occurring at night, however. Zooplankton could be migrating from all points in the lake to the littoral zone.

Tracking these migrations patterns would be very difficult with such a small study organism.

These results are also the reverse of that suggested by previous research. Burks et al. (2002) predicted that if DHM was occurring, zooplankton abundance would be highest in the shores during the day. They hypothesized that the zooplankton would use the macrophyte vegetation in the littoral zone as shelter from predators during the day and return to the pelagic epilimnion to feed at night. This pattern was not observed on any of my study lakes. Instead, zooplankton migrated to the littoral zone at night, indicative of some desirable quality of the littoral zone. This trend could be explained by the highly variable macrophyte densities on each transect as well. Burks et al. suggest that food resources might differ in quality in the pelagic epilimnion versus the littoral zone. My results might indicate a higher quality of food resources in the littoral zone since zooplankton make a point to come to the shores at night, regardless of DOC concentration.

The use of a repeated measures ANOVA indicates when and where the sampling point in the summer was a significant factor in determining the differences between sampling episodes. Where this factor was significant, conditions in the lake were changing over the course of the summer such that zooplankton migration also changed. As a result, we can see temporal changes in diel vertical and horizontal migration of zooplankton. These changes could be due to any number of factors, biotic or abiotic. For example, lakes could be increasing in DOC concentration over the course of the season. Climatic events and watershed changes could influence how much terrestrial carbon leaches into an aquatic system, leading to a constant flux of dissolved organic carbon (Pace and Cole 2002).

Where the repeated measures ANOVA was not significant, the three sampling episodes could be used as replicates since conditions in the lake at those three times were not significantly different. Each sampling episode cannot be considered true replicates, however, since they did not happen concurrently. Regardless, averaging abundances together does provide a more complete look at the migration patterns along a specific transect. In most cases, however, transects were only significant at one time of day. To analyze diel migration patterns, both times of day would have to be significant to give an accurate representation of migration patterns.

The results from Long Lake can also be interpreted according to the whole-lake experiment currently in progress on this lake. The lake is divided by an impermeable curtain with the intent of observing natural changes in the lake's biotic and abiotic characteristics due to an increase in DOC in the east basin of the lake. A small inlet with considerable amounts of terrestrial carbon feeds this basin of Long Lake, thus leading to increased amounts of light-attenuating DOC. This experiment was previously completed in the early 1990's by Christensen et al. (1996), where they found that increased DOC altered the organic sediment depth, pH, conductivity, thermocline depth, and phytoplankton abundance in the eastern basin. The western basin remained relatively unchanged. In addition to abiotic changes, biotic communities are also affected by this whole-lake experiment. Carpenter et al. (2001) found that the zooplankton communities differed on either side of the curtain. The western basin was dominated by large-bodied grazers such as Daphnia and Holopedium while the eastern basin was dominated by rotifers and small-bodied crustaceans (Carpenter et al. 2001). The different physical profiles of the two halves of the lake led to different zooplankton community structures.

My results support these findings. Of the two transects located on Long Lake, one was located in the western basin and one in the eastern basin. Even after one year of division, the western basin was dominated by mostly large-bodied Daphnia while the eastern basin contained mostly small copepods and smaller Daphnia. While DVM profiles across the curtain were relatively similar (Figure 5), DHM in the eastern basin, the dark basin, more closely resembled the DHM in Hummingbird Lake (Figure 8-9). Distribution across the surface was fairly even during the day, but there was considerably higher zooplankton abundance at the shores at night, again even more so than Hummingbird at some points.

In addition to water color, food web structures can also have an effect on the diel migration patterns of zooplankton. A study conducted by Loose and Dawidowicz (1994) found that above a threshold concentration, zooplankton migration increased as fish kairomone levels also increased. The presence or absence of predators such as planktivorous fish or aquatic invertebrates like *Chaoborus spp.* can determine to what degree zooplankton migration occurs. *Chaoborus spp.,* more commonly known as the phantom midge larvae, live in the sediment of lakes and feed upon zooplankton. In this study, Bay Lake has high fish density, but low *Chaoborus* density. Long Lake has low planktivore density, but high *Chaoborus* density. Hummingbird Lake has high fish density and high *Chaoborus* density. Variation in predation pressure likely drives the direction and timing of migration (i.e. standard DVM, reverse DVM, or no DVM) rather than the magnitude of migration, which is predicted to be mediated more by water color.

Most studies of freshwater zooplankton migration focus on a strictly vertical profile of a lake by sampling at one part of the lake and identifying the zooplankton at various depths. Few studies have been specifically designed with the intent of sampling the horizontal distribution of zooplankton. Combining both vertical and horizontal distribution profiles might provide the most accurate profile of a lake's zooplankton population.

In summary, diel vertical migration decreased as DOC concentrations increased across three lakes: Bay Lake, Long Lake, and Hummingbird Lake. While zooplankton in the light lake exhibited normal DVM, those in the dark lakes rarely migrated from the surface. Diel horizontal migration also decreased as DOC increased. Bay Lake, the light lake, had low zooplankton abundance at the shores during the day, but higher abundances at night. Long Lake, the medium lake, and Hummingbird Lake, the dark lake, had relatively high zooplankton abundance in the littoral zone both day and night. My results indicate that there is something to be gained from sampling zooplankton across the entire lake.

In the future, it would be interesting to replicate this experiment across a much larger gradient of dissolved organic carbon. Future studies could also isolate the drivers of these migration patterns. Perhaps food resources such as pelagic phytoplankton versus littoral phytoplankton are nutritionally different, providing more of an incentive for zooplankton to migrate to the shores. Variance in macrophyte abundance along the shores could also influence these migration patterns. Repeating this experiment *in situ*, controlling for planktivore densities, could also improve the interpretation of these results.

Finally, as global browning of freshwater ecosystems continues to rise, these migration patterns stand to change. The more that is understood about diel migration of zooplankton now, the better we will understand the changes this phenomenon might inflict upon zooplankton migration in the future.

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Figures

Figure 1. Bay Lake, University of Notre Dame Environmental Research Center. Arrows represent two randomly selected horizontal transects. DOC is approximately 6 mg/L.

Figure 2. Long Lake, University of Notre Dame Environmental Research Center. Arrows represent two randomly selected horizontal transects. Black line represents the curtain dividing the lake into two separate basins. DOC is approximately 8 mg/L.

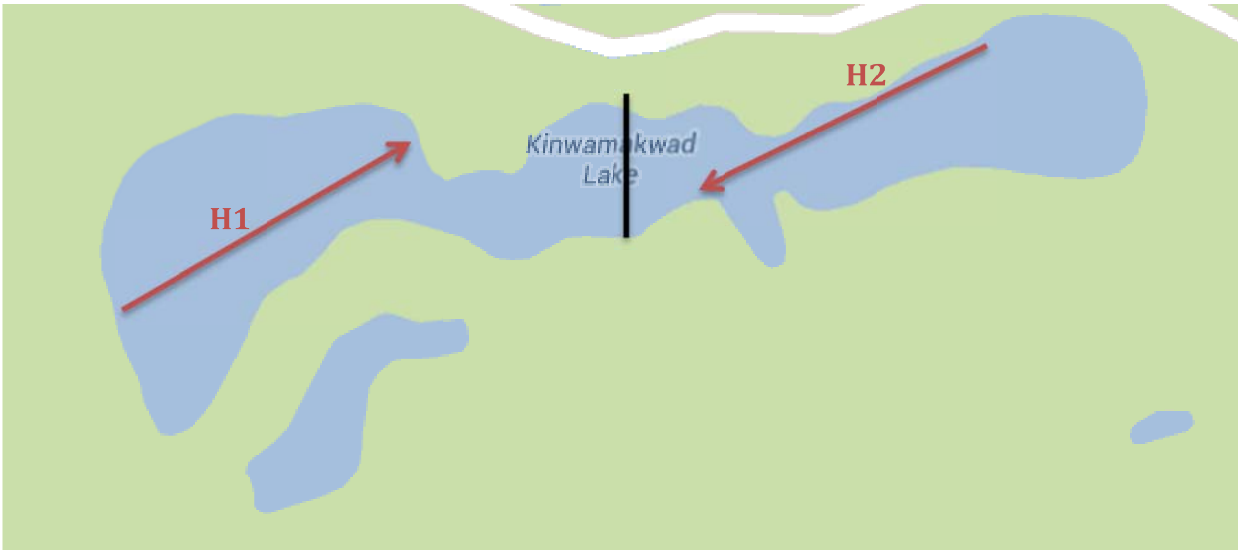

Figure 3. Hummingbird Lake, University of Notre Dame Environmental Research Center. Arrows represent two randomly selected horizontal transects. DOC is approximately 23 mg/L.

Figure 4. Diel Vertical Migration in Bay Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were taken at three depths to sample the epilimnion (S=shallow), the metalimnion (M=metalimnion), and the hypolimnion (D=deep). Zooplankton abundance was not significantly different at any depth on either transect at either time of day ($p=0.221$, $p=0.504$, $p=0.246$, and $p=0.667$). Sampling point in the summer was significant for H1 and H2 during the day ($p=0.0026$ and $p=0.0113$, respectively).

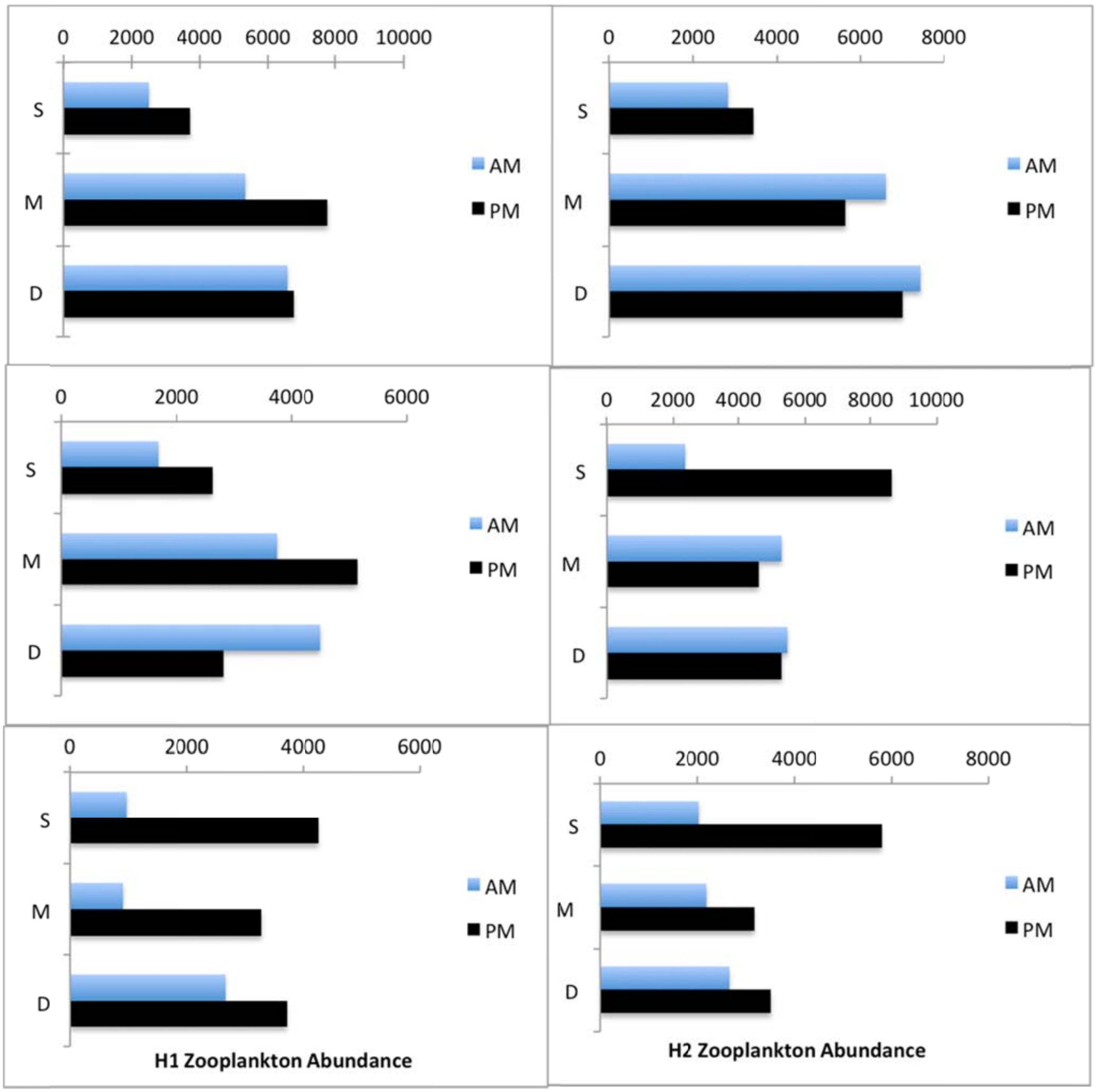

Figure 5. Diel Vertical Migration in Long Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were taken at three depths to sample the epilimnion (S=shallow), the metalimnion (M=metalimnion), and the hypolimnion (D=deep). Zooplankton abundance was not significantly different at any depth on either transect at either time of day (p=0.462, p=0.149, p=0.265, and p=0.499). Sampling point in the summer was significant for H1 during the day (p=0.0195).

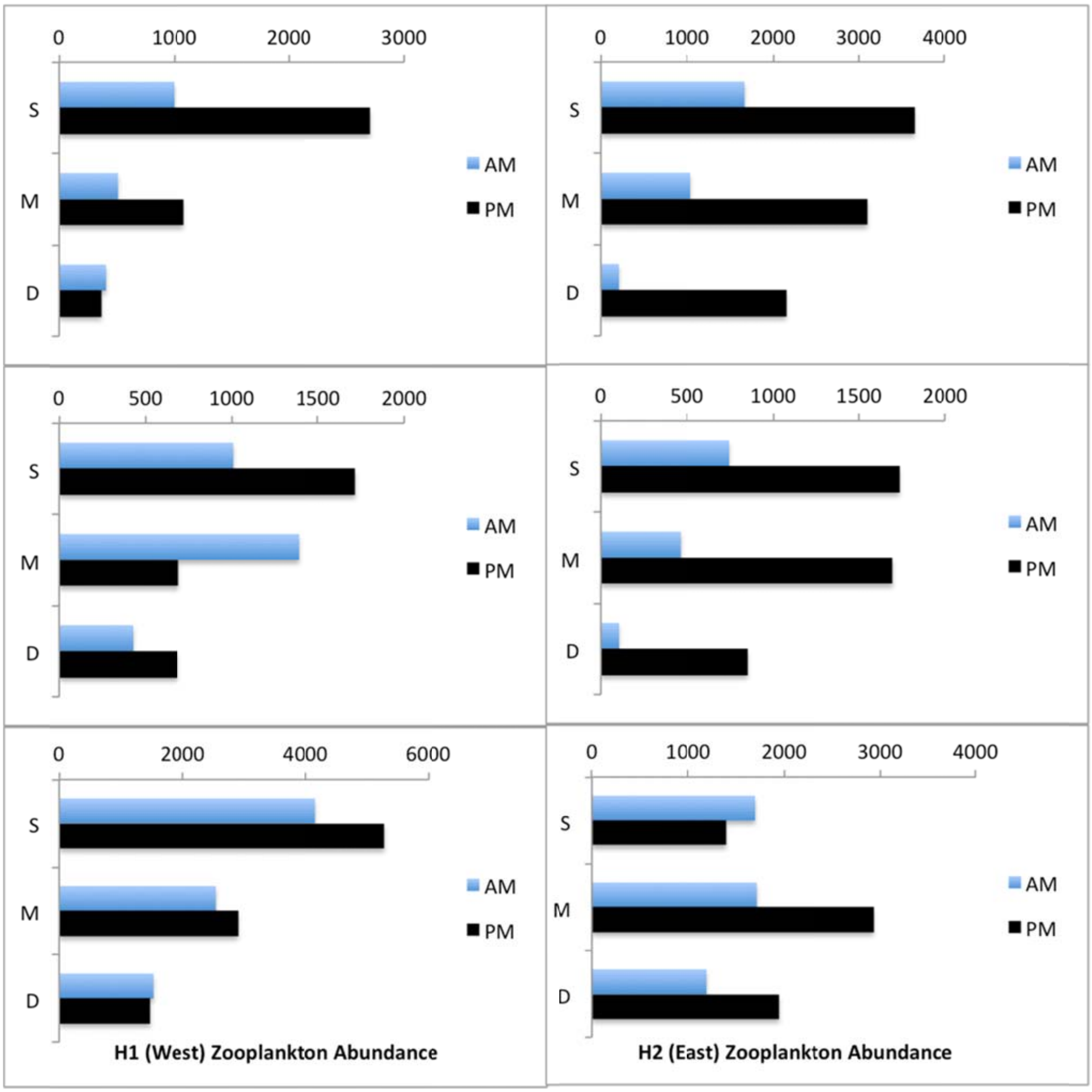

Figure 6. Diel Vertical Migration in Hummingbird Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were taken at three depths to sample the epilimnion (S=shallow), the metalimnion (M=metalimnion), and the hypolimnion (D=deep). Zooplankton abundance was significantly higher at night in the epilimnion (S) than in the hypolimnion (D) on transect 1 (p=0.0499). Zooplankton abundance was not significantly different at any other depth on either transect (p=0.739, p=0.975, and p=0.759). Sampling point in the summer was significant on H1 during the day (p=0.0054) and on H2 both day and night (p=0.0318 and p=0.0090, respectively).

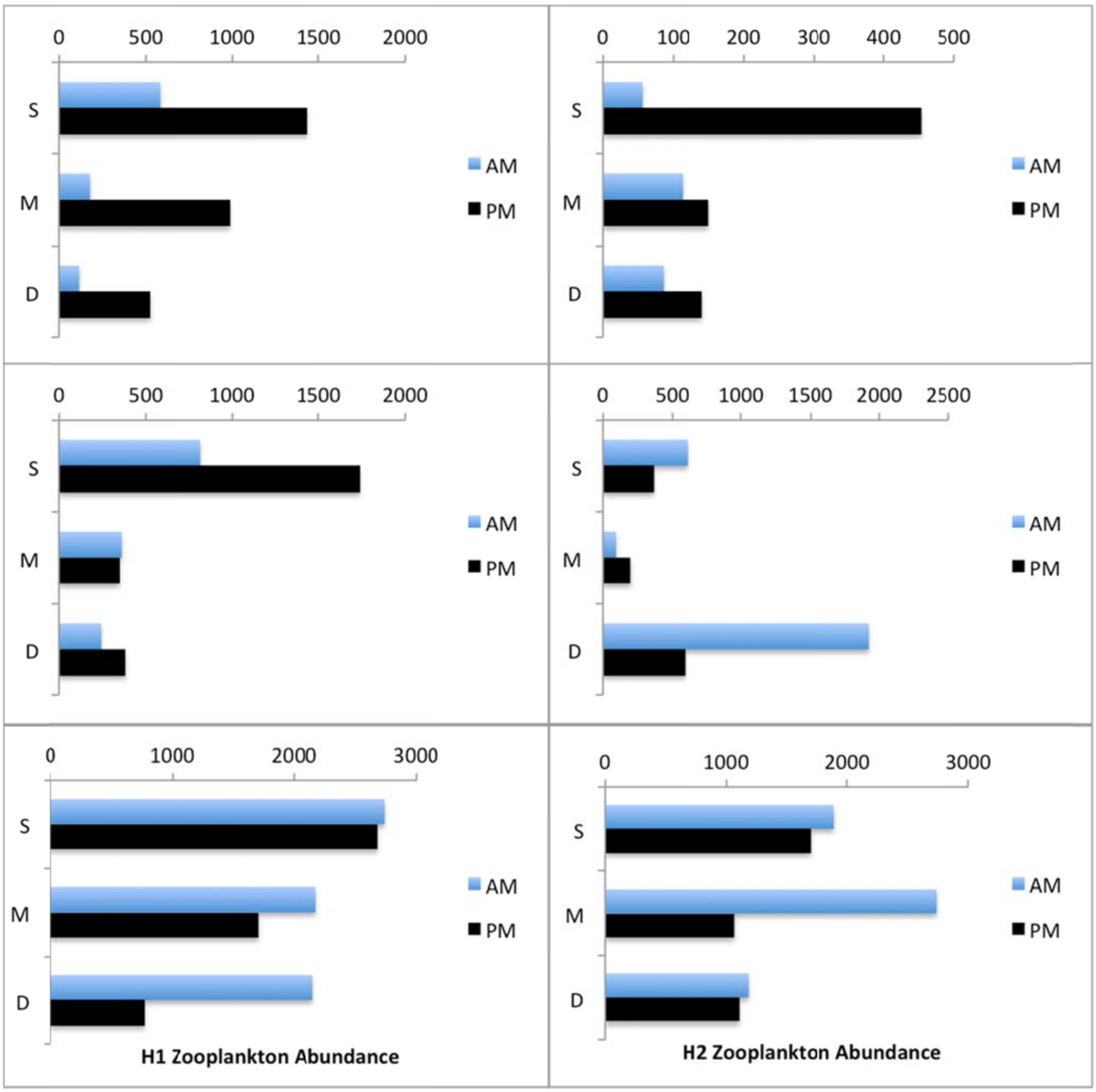

Figure 7. Diel Horizontal Migration in Bay Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were collected at the shores on both ends of each transect as well as at two open water locations, S2 and S3, both collected from the epilimnion. Zooplankton abundance was significantly higher at the second open water site (S3) than shore 1 on transect 2 during the day (p=0.033). Zooplankton abundance was not significantly different at any other location on either transect (p=0.0624, p=0.678, and p=0.481). Sampling point in the summer was significant on H2 at night (p=0.0395).

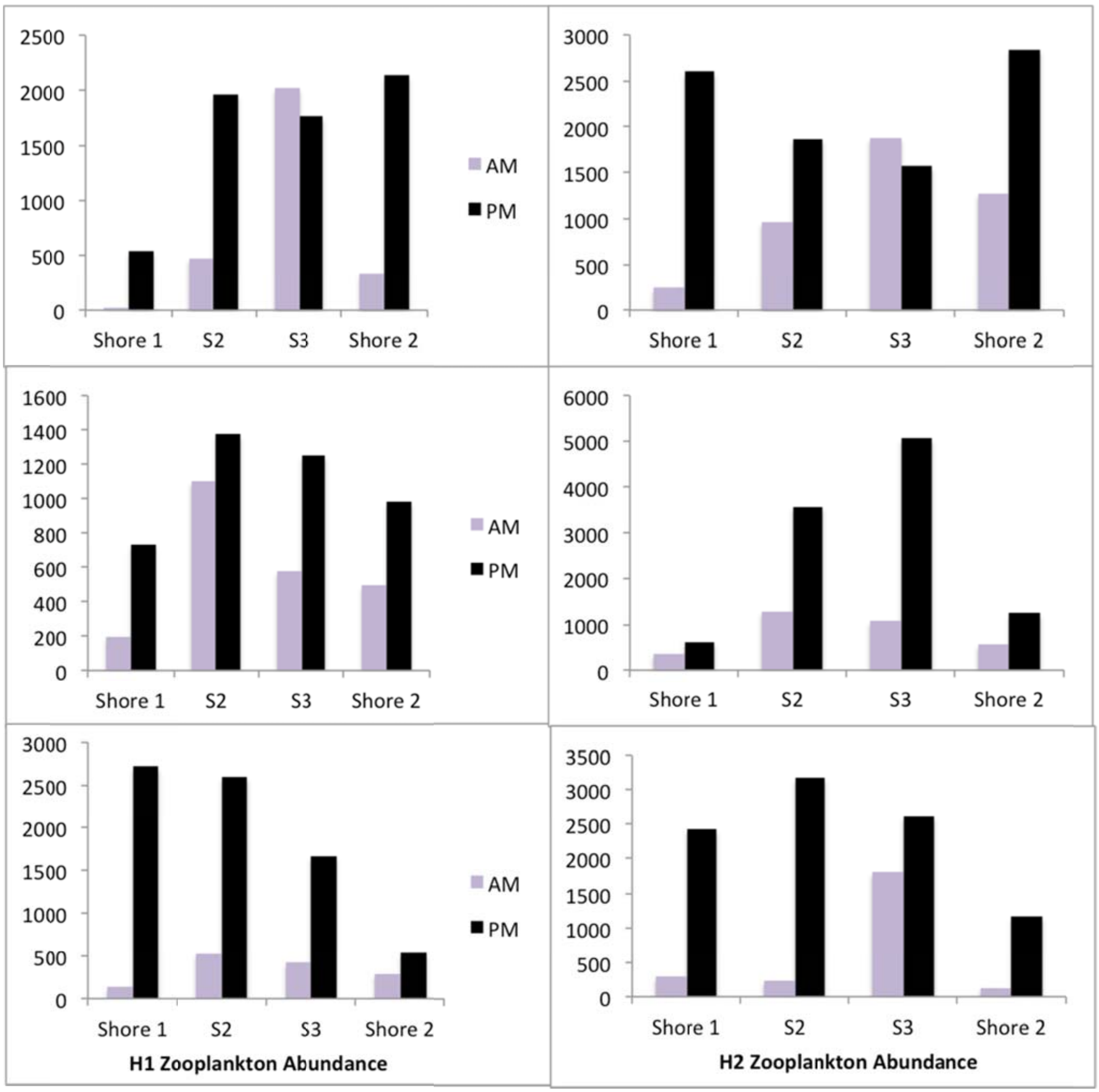

Figure 8. Diel Horizontal Migration in Long Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were collected at the shores on both ends of each transect as well as at two open water locations, S2 and S3, both collected from the epilimnion. There was no significant difference in zooplankton abundance at any location on either transect, day or night (p=0.548, p=0.0856, p=0.362, and p=0.842). Sampling point in the summer was not significant for either transect both day and night.

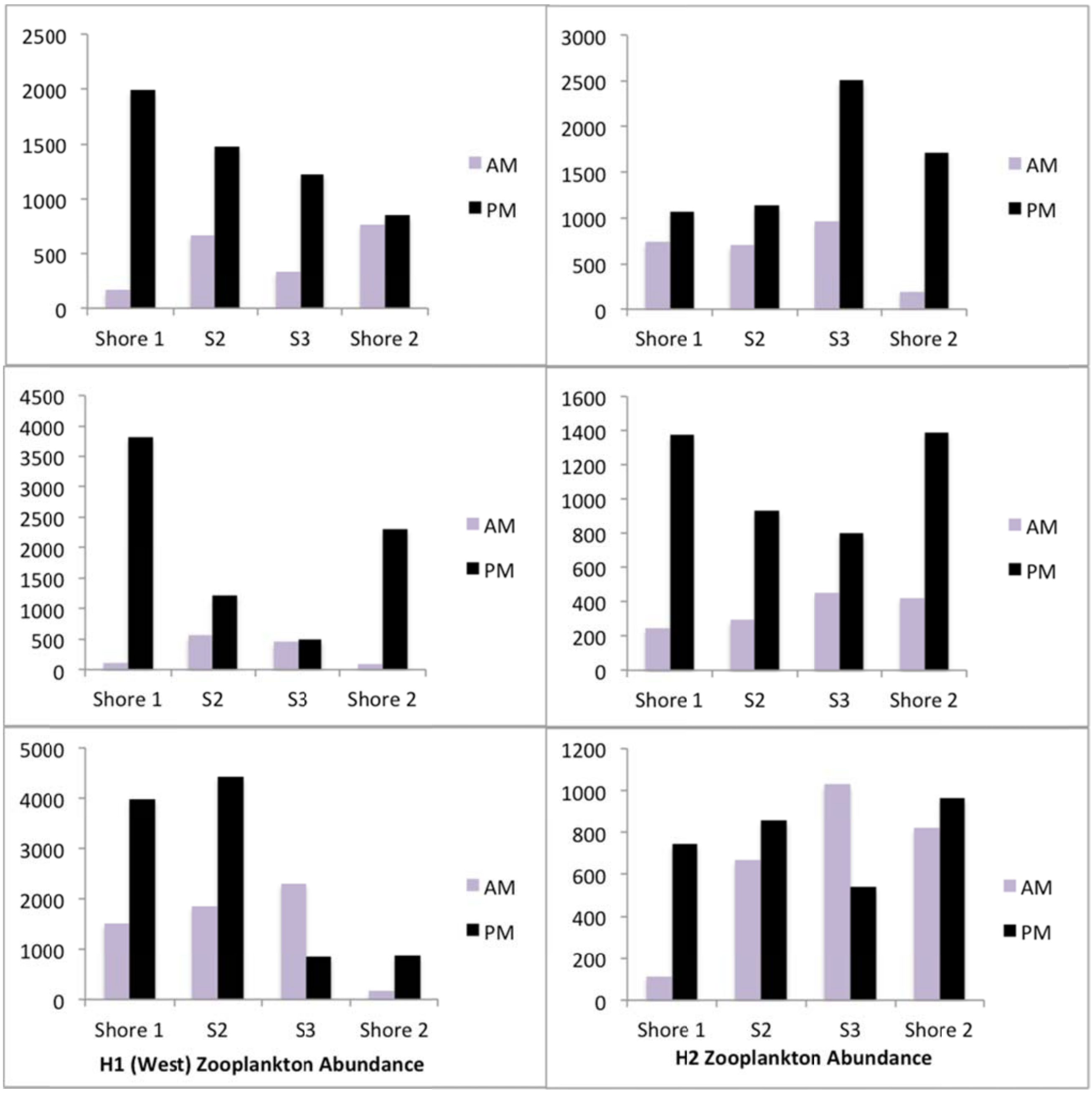

Figure 9. Diel Horizontal Migration in Hummingbird Lake. Samples were collected along two randomly selected horizontal transects, H1 and H2, at three points throughout the summer. Samples were collected at the shores on both ends of each transect as well as at two open water locations, S2 and S3, both collected from the epilimnion. There was no significant difference in zooplankton abundance at any location on either transect, day or night ($p=0.754$, $p=0.385$, $p=0.934$, and $p=0.72$). Sampling point in the summer was significant on H1 (West) during the day ($p=0.0353$) and on H2 (East) both day and night ($p=0.0038$ and $p=0.0176$, respectively).