DIEL DISTRIBUTION OF ZOOPLANKTON IN THE SKY LAKES

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Abstract. Zooplankton play an important role as primary consumers in freshwater ecosystems. Many exhibit diel (daily) vertical migration behavior in response to environmental stressors including predation, UV radiation, and anoxia. Horizontal migration, while less thoroughly studied, has been suggested to explain differences between zooplankton density in the water column in the pelagic zone (open water) from day to night. To examine this three-dimensional view of zooplankton migration, we measured both zooplankton and phytoplankton distribution in two lakes in consecutive day/night cycles. These lakes are presumed to have similar levels of zooplanktivory. We did this by sampling both shallow and deep sites and comparing the distributions of primary producers and consumers in different lake zones. We found diel differences in zooplankton density and biomass, as well as a mismatch between zooplankton distribution and phytoplankton distribution, suggesting zooplankton movement is controlled by factors other than proximity to food. We also found differing composition from day to night and by location, consistent with theories of interspecific competition and visual predation. Overall, our results indicate the presence of taxa-specific vertical and horizontal movement, which will directly affect the role of zooplankton connecting trophic levels in freshwater lake food webs.

INTRODUCTION

In most freshwater aquatic ecosystems, zooplankton function as primary consumers in their food webs. The functionality of these food webs influences key ecosystem goods and services such as drinking water supply and nutrient cycling, as well as recreational and commercial fishing (Strayer and Dudgeon 2010). Changes in zooplankton dynamics directly impact phenomena such as algal blooms/water clarity through release from top-down control (Richardson et al. 2016), therefore a better understanding of their movement patterns is needed.

Zooplankton in both saltwater and freshwater participate in daily vertical migration (DVM) behavior, where they change their vertical distribution in the water column based on the daylight cycle (Berge et al. 2008, Zaret and Suffern 1976, Doubek et al. 2018). During the day, high concentrations of zooplankton are found in the hypolimnion, which is the cold, dark strata at the bottom of temperate freshwater lakes, while at night, they are found in higher abundance in the epilimnion, the surface layer where their primary producer food source is most dense (Lampert 1989). Reasons proposed for this behavior include the key balance between being where food is most abundant and responding to harm or fear of harm from predation (Zaret and Suffern 1976, De Stasio 1993), avoidance of damage from UV radiation (Leech and Williamson 2001), and dissolved oxygen (DO) levels (Doubek et al. 2018).

In addition to DVM, zooplankton could also be moving horizontally (see Fig. 1). There is evidence for this (De Stasio 1993, Kvam and Kleiven 1995, Burks et al. 2002, Doubek et al. 2018); however, more work is needed. One proposed driver of this behavior is increased hypolimnetic anoxia and hypoxia as a result of climate change, because it compresses available habitat and limits DVM (Doubek et al. 2018). There is limited evidence of a deficit between day and night organismal density found in the pelagic water column, or a “diurnal deficit” (De Stasio 1993), but the cause of this is largely unknown. Predator presence could be the primary driving factor for movement, as it was found that distribution changed from day to night, with movement increasing in the presence of predators (De Stasio 1993).

Zooplankton make up a wide variety of differently sized taxa, and body size is an important functional trait with far-reaching implications in food web dynamics (Woodward et al. 2005). Larger taxa such as *Daphnia* are thought to be more susceptible to predation than smaller taxa (Kvam and Kleiven 1995, Burks et al. 2002, Nevalainen et al. 2014). Therefore, it is likely that both vertical and horizontal migration are exhibited differently by different taxa (Jung et al. 2004), and it is important to consider composition when examining movement patterns.

Our objective was to examine zooplankton vertical and horizontal distribution and identity in two freshwater lakes and compare this information with phytoplankton distribution under consecutive day and night conditions. We predicted that we would 1) observe a diurnal difference in zooplankton in the pelagic zone, and 2) observe a mismatch between phytoplankton distribution and zooplankton distribution, which will correlate with possible driving factors of migration behavior. This work functions as a first step in understanding zooplankton movement and migration patterns in our lakes and driving factors for these behaviors.

METHODS

Study sites

Fieldwork was conducted at two of five glacial lakes known as the "Sky Lakes" in southeastern New York, USA: Lake Mohonk (41.766,-74.158) and Lake Minnewaska (41.726,-74.235). The lakes lie along the Shawangunk Ridge, which has bedrock composed primarily of quartz conglomerate (Epstein 1993). Both are rain-fed, with small watersheds. Although close in proximity to one another, the lakes have differently structured ecosystems. Mohonk, which has a shale inlier that buffers its pH (Richardson et al. 2018), is a mesotrophic lake with a complex ecosystem of multiple trophic levels of fish including golden shiners, sunfish, largemouth bass, and rainbow trout (Smiley and Huth 1983). Minnewaska, on the other hand, only supports one species of fish: largemouth bass. Despite these differences, the primary reason for choosing these two lakes is their proposed similarity in levels of zooplanktivory. The dominant fish taxa in both lakes are primarily piscivorous or insectivorous, and may only eat zooplankton when they are young. The sampling sites at each lake used in this study were already in use for long-term lake monitoring efforts (Richardson et al. 2016).

We designed our sampling protocol based on De Stasio (1993), and adapted it using knowledge of the field and our study sites. To determine estimates of zooplankton and phytoplankton abundance and distribution during the day and at night, we took a total of 24 zooplankton samples and 16 samples for chlorophyll-*a* analysis at each lake, for a total of 48 zooplankton samples and 32 chlorophyll samples. We identified four "shallow" sites (depth of 1-3 m) in the littoral zone accurately to represent differences in environment around the edge of the lakes based on bathymetry data, and one site at the deepest part of the lake (15-23 m). Fortunately, both lakes are bathymetrically simple and relatively similar to one another. We took temperature and dissolved oxygen measurements along a vertical profile at deep sites to determine the physical environment.

Zooplankton

For day sampling: at deep sites, we took three replicate full-column net tows to a depth of 20m at Minnewaska and to a depth of 11m at Mohonk; this was done to determine the presence or absence of a diurnal deficit. We also took samples along a vertical profile at different depths (0 m or elbow depth, above the thermocline, below the thermocline, and as close as possible to the bottom). This was done for a more detailed understanding of vertical distribution. We used a 2.3 L Van Dorn bottle to sample a total of 8-10

L at each depth, then filtered using a 65-micron sieve down to <45 mL concentrated samples. We administered approximately ¼ of an original Alka-Seltzer tablet before fixing with 100% ethanol to 70% concentration. For chlorophyll samples, we pulled up an additional Van Dorn bottle at each depth to fill 1 L light-resistant amber bottles. At the shallow sites, we collected samples using 5 L bottles submerged to elbow depth for a total of 8-10 L per sample, then filtered and fixed zooplankton using the same procedure. At Minnewaska, we took shallow samples by boat, while at Mohonk we waded in to waist depth (about 1 m deep) and waited 5-10 minutes for sediment to clear before filling 5 L bottles. This process was repeated for night sampling.

To process zooplankton, we swirled each sample gently to distribute specimens throughout the sample and then pipetted 1.2 mL onto a Sedgewick-Rafter counting cell. Using a compound light microscope at 40 to 100x magnification, we identified each individual encountered down to the lowest possible taxonomic level until 100 individuals had been counted for that sample. We recorded identity, size, magnification, and total volume of the sample. From this information, we calculated density and biomass of zooplankton per liter of lakewater, and the size of each individual in millimeters. To gain more insight into community dynamics, we divided samples into three representative taxonomic groups: Rotifera (rotifers, 0.1 - 0.5 mm), Cladocera (water fleas, 0.5 - 6.0 mm), and Copepoda (copepods, 1.0 - 2.0 mm) and calculated percent composition in each sample.

Chlorophyll-a

At both deep and shallow sites, we submerged and filled amber bottles for chlorophyll-*a* at elbow depth. For processing, we strained the contents of the light-resistant amber bottles onto filters, which were then frozen for 24 hours. We then placed the filters into 90% ethanol and left them at 120 degrees C for 10 minutes to extract pigment. Finally, we ran samples through a UV-vis spectrophotometer to determine the concentration of chlorophyll-*a* via absorbance. This was used to estimate phytoplankton density and biomass in each sample.

Temperature and Dissolved Oxygen (DO) concentration were measured using a DO sensor every meter down to 12m at Mohonk, and every meter down to 10m then every two meters down to 20m at Minnewaska. Data were analyzed and visualized in Excel and RStudio.

RESULTS

Temperature and dissolved oxygen

Both lakes were similar in terms of temperature and dissolved oxygen concentrations as well as water clarity on the dates sampled. Both showed similar patterns of thermal stratification with thermoclines at 5 m and had similar estimates of water clarity via Secchi disk depth of 4.9 m and 5.1 m respectively (Fig. 2A). Dissolved Oxygen (DO) concentration peaks in the photic zone at the top of the thermocline (Fig. 2B), which coincides with Secchi depth.

Zooplankton movement patterns

At both Minnewaska and Mohonk, we found that zooplankton density increased from day to night in full water column net tow samples (Fig. 3A, 3B) and surface samples at all sites by approximately twofold (Fig. 4A, 4B). In Minnewaska, there was a significant interaction between timing (day/night) and location (littoral/pelagic sites) in terms of size ($F_{1,383} = 52$, $P = 0.02$, Fig. 4E). Zooplankton size was not significantly different between day and night in the littoral site, but was found to be significantly higher at night compared to day in the pelagic site. We performed a post hoc Tukey test, which confirmed that this difference is highly significant in the context of all other pairwise comparisons ($P \ll 0.001$). However, in

Mohonk, there was no significant interaction between timing and location and no location main effect (Fig. 4F). Individuals were significantly larger at night than they were during the day across both Minnewaska ($F_{1,385}$= 11, $P = 0.001$, Fig. 3D) and Mohonk ($F_{1,278}$= 12, $P = 0.0005$, Fig. 4F). Chlorophyll-*a* concentration decreased from day to night in all cases except the Mohonk deep site (Fig. 4C-D, indicating an inverse correlation with zooplankton density. Differences in biomass concentration followed a similar pattern as density, with larger concentrations present at night than were present during the day. Maximum biomass concentrations ranged from 225 µg/L at night in the full column tows at Mohonk to 350 µg/L at night in the shallow surface sample at Mohonk, while concentrations reached 2000 µg/L at night in the deep surface sample at Minnewaska.

Taxa

Examining composition, in the full tows we found that rotifers made up about 60% of the samples during the day and at night at Minnewaska (Fig. 6A, 6C, 6E), and 25-30% of samples during the day and night at Mohonk Fig. 6B, 6D, 6F). There were few rotifers present at the shallow sites in both lakes, but notably they dropped from ~10% during the day to ~2% at night at Minnewaska (Fig. 6C), and ~20% during the day to ~1% at night at Mohonk (Fig. 6D). In the deep surface samples, rotifers made up about 60% of composition during the day at both lakes, and this dropped to 10-20% at night (Fig. 6E, 6F). Cladocera and copepods, the larger taxa, were present in higher abundance at night compared to daytime in all cases except the Minnewaska shallow site; they exhibited an opposite pattern to the rotifers.

DISCUSSION

More zooplankton being present at night versus during the day at deep sites in both Minnewaska and Mohonk confirms the presence of horizontal migration out of the pelagic zone from day to night and aligns with results found by De Stasio (1993). Interestingly, however, that pattern also applies to shallow sites. This could indicate the presence of vertical migration even within shallow sites, as we only sampled at the surface in those locations, which were between 1 and 3 m deep.

Our prediction that we would find a mismatch between zooplankton and phytoplankton distribution was confirmed. This suggests that proximity to food is unlikely to be the primary driving factor behind zooplankton movement. Rather, migration is likely being driven by other factors such as predation pressure (Zaret and Suffern 1976, De Stasio 1993) and UV radiation (Leech and Williamson 2001). Our results for both zooplankton density and biomass support this conclusion, with both being higher overall at night than they were during the day, while chlorophyll-*a* concentration exhibited an opposing trend.

In terms of composition, the fact that we found more rotifers present during the day than were present at night, but more Cladocera and copepods present at night than were present during the day in the majority of sites lends insight into some interesting community dynamics. Some possible causes of this behavior include interspecific competition (DeMott 1989) and niche partitioning (Ye et al. 2013). In addition, the prediction that larger species may be more likely to participate in migration behavior because of increased risk of visual predation (Kvam and Kleiven 1995, Burks et al. 2002, Nevalainen et al. 2014) was supported by the percentages of larger taxa present at the surface at night versus during the day.

We suspect that we did not find explicit evidence of horizontal migration between the pelagic and littoral zones because we sampled relatively early in the season, and there was no hypolimnetic hypoxia present in either lake. If we returned to sample later in the summer, when hypoxia is present at least in Mohonk, we might see more pronounced horizontal migration because of vertical habitat compression (Doubek et al. 2018). We did see horizontal migration out of both pelagic and littoral zones from day to night, however, which confirms that our sampling methods and procedures were sound. This work is an important step to understanding zooplankton movement patterns and drivers in Lake Minnewaska and Mohonk Lake, and from that, to gain more detailed knowledge of trophic function and important freshwater food web dynamics.

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LITERATURE CITED

Berge, J., F. Cottier, K. S. Last, Ø. Varpe, E. Leu, J. Søreide, K. Eiane, et al. 2008. Diel vertical migration of Arctic zooplankton during the polar night. Biology Letters **5**:69-72. doi.org/10.1098/rsbl.2008.0484

Burks, R. L., D. M. Lodge, E. Jeppesen, and T. L. Lauridsen. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. Freshwater Biology **47**:343-365.

Charifson, D. M., P. C. Huth, J. E. Thompson, R. K. Angyal, M. J. Flaherty, and D. C. Richardson. 2015. History of fish presence and absence following lake acidification and recovery in Lake Minnewaska, Shawangunk Ridge, NY. Northeastern Naturalist **22**:762-781.

DeMott, W. R. 1989. The role of competition in zooplankton succession. In: Sommer, U. (ed.). Plankton Ecology. Brock/Springer Series in Contemporary Bioscience. Springer, Berlin, Heidelberg.

De Stasio, B., Jr. 1993. Diel vertical and horizontal migration by zooplankton: population budgets and the diurnal deficit. Bulletin of Marine Science **53**:44-64.

Doubek, J. P., K. L. Campbell, K. M. Doubek, K. D. Hamre, M. E. Lofton, R. P. McClure, N. K. Ward, and C. C. Carey. 2018. The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. Ecosphere **9**:e02332.

Jung, J. et al. 2004. Diel vertical migration of zooplankton in Lake Baikal and its relationship to body size. In Smirnov, A. I., Izmest'eva, L. R. (eds.). Ecosystems and Natural Resources of Mountain Regions. Proceedings of the first international symposium on Lake Baikal: The current state of the surface and underground hydrosphere in mountainous areas (pp. 131-140). Nauka, Novosibirsk.

Kvam, O. V. and Kleiven, O. T. 1995. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. Hydrobiologia **307**:177-184.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Functional Ecology **3**:21-27.

Leech, D. M., and Williamson, C. E. 2001. In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. Limnology and Oceanography **46**:416-420.

Nevalainen, L. et al. 2014. Zooplankton (Cladocera) species turnover and long-term decline of *Daphnia* in two high mountain lakes in the Austrian Alps. Hydrobiologia **722**:75-91.

Richardson, D. C., et al. 2016. Reconstructing a trophic cascade following unintentional introduction of golden shiner to Lake Minnewaska, New York, USA. Inland Waters **1**:29-33.

Richardson, D. C., et al. 2018. Watershed management and underlying geology in three lakes control divergent responses to decreasing acid precipitation. Inland Waters **8**:70-81.

Smiley, D. and Huth, P. C. 1983. Fish disappearance in the northern Shawangunks between 1862 and 1982. Research report for Mohonk Preserve, Inc.

Strayer, D. and Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society **29**:344-358.

Woodward, G. et al. 2005. Body size in ecological networks. Trends in Ecology and Evolution **20**:402-409.

Ye, L. et al. 2013. Increasing zooplankton size diversity increases the strength of top-down control on phytoplankton through diet niche partitioning. Journal of Animal Ecology **82**: 1052-1061.

Zaret, T. M. and Suffern, J. S. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnology and Oceanography **21**:804-813.

APPENDIX

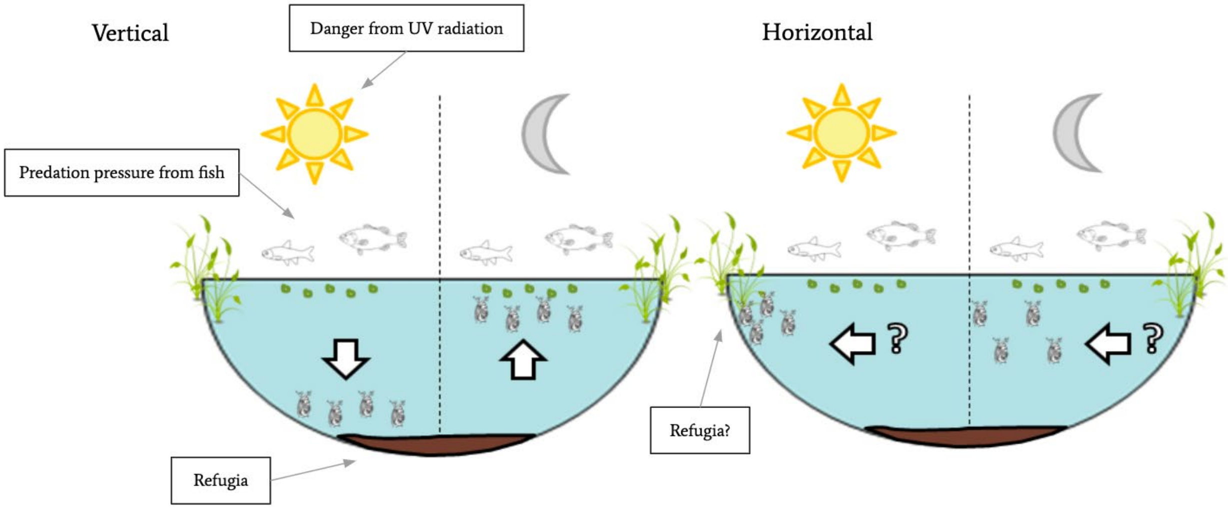

FIGURE 1. Conceptual diagram depicting two types of diel zooplankton migration: (A) vertical and (B) horizontal. In both diagrams, the sun represents day and the moon represents night. The green dots at the surface represent phytoplankton; driving behavioral factors (predation pressure from fish and danger from UV radiation) indicated with corresponding arrows. Question marks in horizontal model indicate uncertainty about the presence of horizontal migration and usage of the littoral zone as refugia. Animals not to scale.

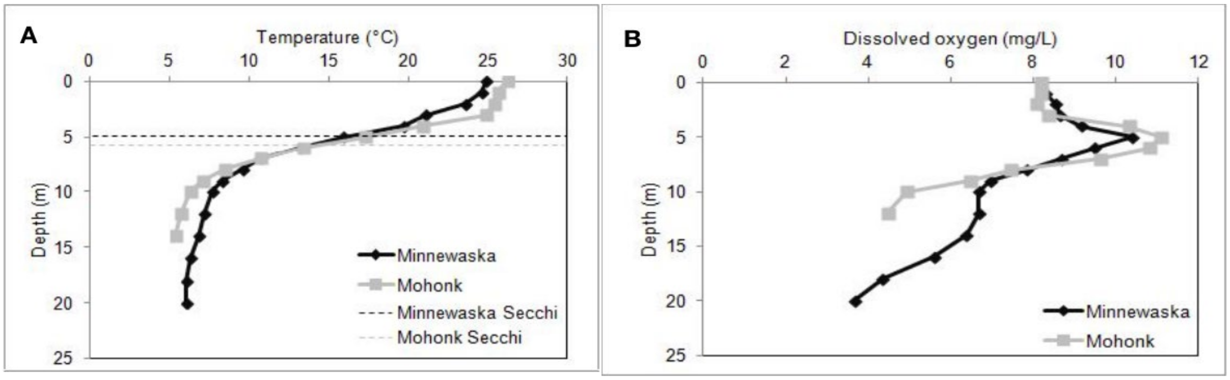

FIGURE 2. Abiotic framework in terms of depth in both lakes at the time of data collection: (A) temperature in °C and Secchi depth, and (B) dissolved oxygen (DO) in mg/L. Stratification is visible in both the decreasing temperature gradient in (A) and decreasing DO profile in (B). Of note is the peak in DO at ~5 m, indicating photosynthetically active zone. Mohonk and Minnewaska Lakes, NY, Jun-Jul 2019.

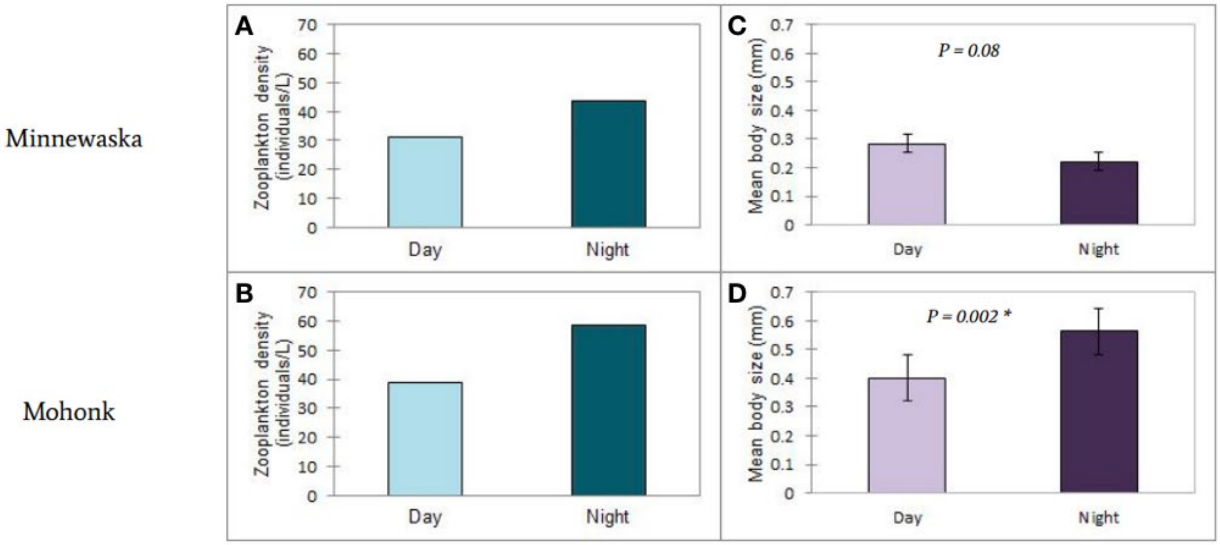

FIGURE 3. Zooplankton density in pelagic zone full water column net tows in (A) Minnewaska and (B) Mohonk, and mean body size in (C) Minnewaska and (D) Mohonk. Lighter shades indicate day and darker shades indicate night. In both (A) and (B) an increase in density from day to night is visible. The only significant difference from day to night in mean body size is in (D) ($P = 0.002$). Mohonk and Minnewaska Lakes, NY, Jun-Jul 2019.

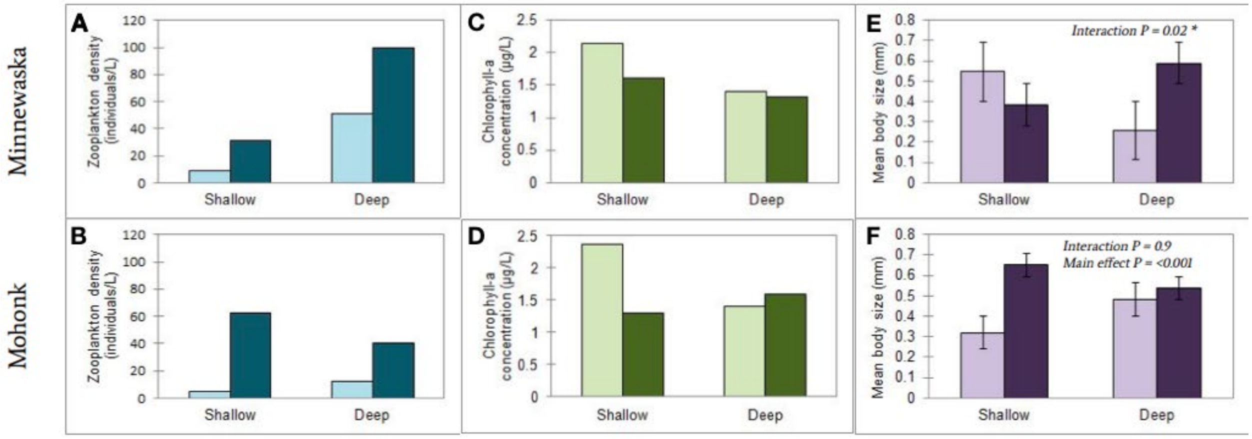

FIGURE 4. Zooplankton density (A, B), chlorophyll-a concentration (C, D), and mean body size (E, F) for surface samples in shallow and deep locations in both lakes. Density increases from day to night at all locations in both lakes. Chlorophyll concentration decreases from day to night at all locations except the Mohonk deep site. There is a significant interaction in mean body size between shallow/deep and day/night variables at Minnewaska ($P = 0.02$), while at Mohonk there is no significant interaction but there are significantly larger individuals present at night compared to day ($P < 0.001$). Mohonk and Minnewaska Lakes, NY, Jun-Jul 2019.

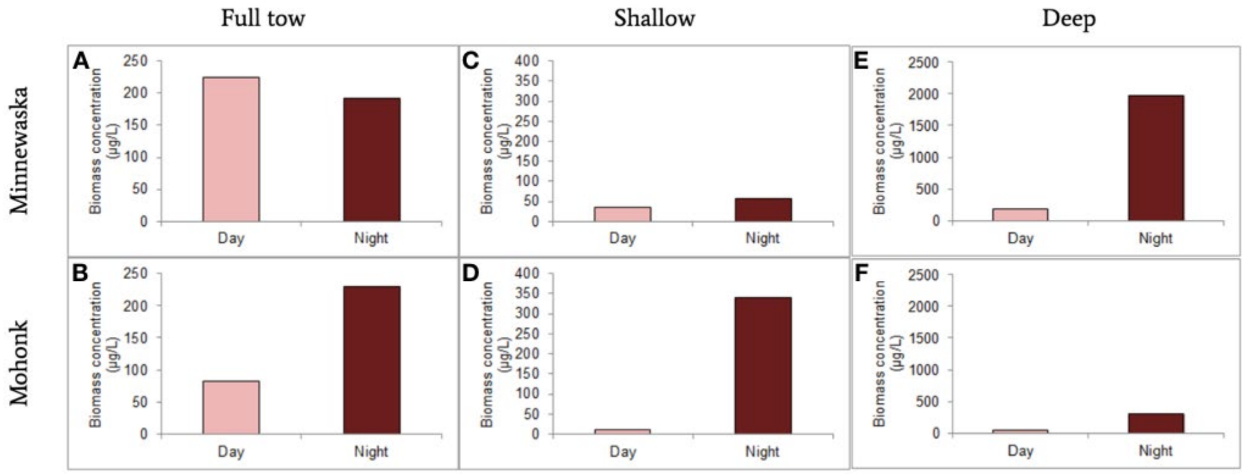

FIGURE 5. Differences in biomass concentration (ug/L) from day to night in full water column net tow (A, B) and surface samples (C, F). Biomass concentration is higher at night than during the day in all comparisons except the Minnewaska full tow. Note the differences in scale on the y-axis. Mohonk and Minnewaska Lakes, NY, Jun-Jul 2019.

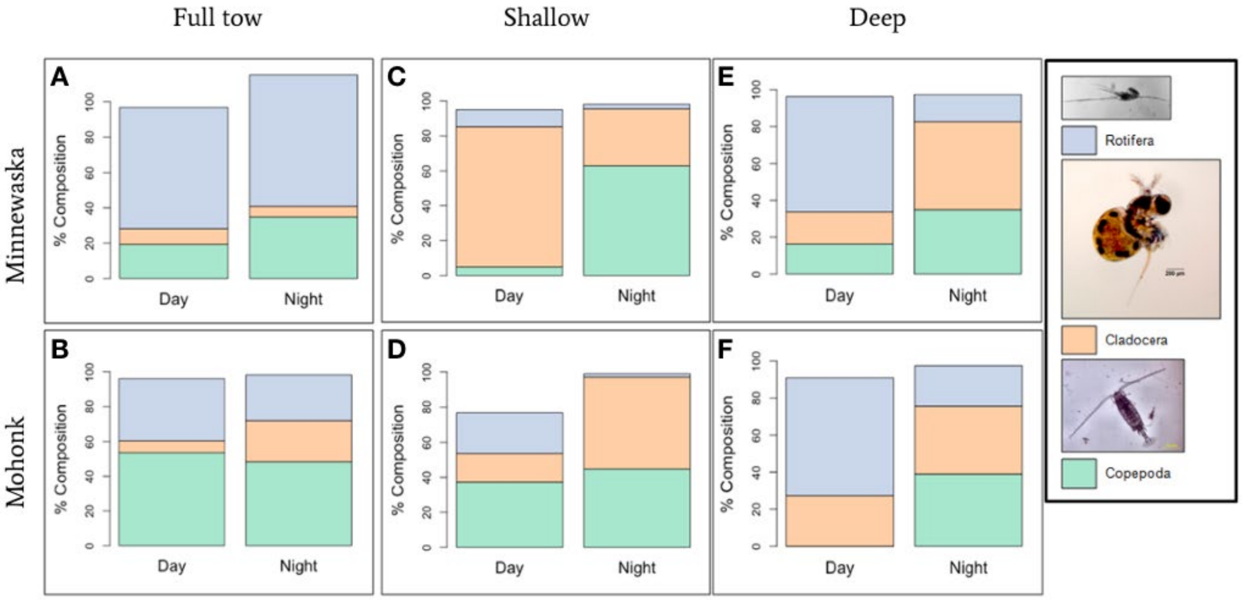

FIGURE 6. Percent composition from day to night in full water column net tow (A, B) and surface samples (C, F). Taxa considered are rotifers, Cladocera, and copepods. Rotifers maintain similar percent composition in full tow samples, but are more abundant at night in surface samples; the opposite is true for Cladocera and copepods. Mohonk and Minnewaska Lakes, NY, Jun-Jul 2019.