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Original Article

Zooplankton community structure and diel migration patterns vary over hours, days, and years in the pelagic and littoral zone of a eutrophic reservoir

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ABSTRACT

Zooplankton play an integral role as indicators of water quality in freshwater ecosystems, but exhibit substantial variability in their density and community composition over space and time. This variability in zooplankton community structure may be driven by multiple factors, including taxon-specific migration behavior in response to environmental conditions. Many studies have highlighted substantial variability in zooplankton communities across spatial and temporal scales, but the relative importance of space vs. time in structuring zooplankton community dynamics is less understood. In this study, we quantified spatial (a littoral vs. a pelagic site) and temporal (hours to years) variability in zooplankton community structure in a eutrophic reservoir in southwestern Virginia, USA. We found that zooplankton community structure was more variable among sampling dates over 3 years than among sites or hours of the day, which was associated with differences in water temperature, chlorophyll *a*, and nutrient concentrations. Additionally, we observed high variability in zooplankton migration behavior, though a slightly greater magnitude of DHM vs. DVM during each sampling date, likely due to changing environmental conditions. Ultimately, our work underscores the need to continually integrate spatial and temporal monitoring to understand patterns of zooplankton community structure and behavior in freshwater ecosystems.

KEYWORDS: community structure; crustaceans; horizontal migration; rotifers; vertical migration

INTRODUCTION

Zooplankton play essential roles as intermediate trophic levels in freshwater food webs, serving as both a food source for predators (e.g. fish) and grazers of phytoplankton (Downing and Rigler, 1984; Carpenter *et al.*, 1987). Because of their sensitivity to environmental change, zooplankton are useful indicators of lake and reservoir water quality (Gannon and Stemberger, 1978; Jeppesen *et al.*, 2011; Almeida *et al.*, 2020; Pinto *et al.*, 2023). However, the influence that zooplankton have on water quality depends on their community dynamics, and relatively small shifts in zooplankton community composition, density, and behavior can lead to pronounced water quality consequences (e.g. Gannon and Stemberger, 1978; Reichwaldt *et al.*, 2004). For example, diel changes in zooplankton density due to migration behavior can alter surface water quality, as zooplankton that migrate and remain at deeper depths during the day can only graze on surface-dwelling phytoplankton at night (Reichwaldt *et al.*, 2004). Conversely, zooplankton that remain in the surface waters during both day and night can graze more phytoplankton, resulting in lower phytoplankton biomass (Reichwaldt *et al.*, 2004). Consequently, changes in zooplankton density and community composition in response to variable environmental conditions may have ecosystem-level effects (e.g. Leech and Williamson, 2000; Roman *et al.*, 2019) that mediate water quality in freshwater lakes and reservoirs.

Previous work has shown that zooplankton community structure (e.g. density and composition) can vary substantially over space and time (e.g. Rusak *et al.*, 2002; Lévesque *et al.*, 2010; Aboul Ezz *et al.*, 2014; Yebra *et al.*, 2022). Spatial variability in community structure within a lake is often driven by taxon-specific habitat selection based on environmental conditions (e.g. food resources; Leibold, 1990) or avoidance of low-quality habitat (e.g. low dissolved oxygen concentrations or high predation; Burks *et al.*, 2002; Romare *et al.*, 2003). For example, greater densities of *Daphnia* in surface pelagic waters may be observed in response to increased food availability (Leibold, 1990), whereas greater densities of *Daphnia* in littoral habitats may be a response to a lack of a hypolimnetic refuge or greater predation pressure in the epilimnion (Burks *et al.*, 2002). Additionally, studies have found that *Bosmina* and *Daphnia* use littoral habitat with macrophytes as a refuge during the day when planktivore abundance is high (Romare and Hansson, 2003), whereas copepod distribution may be driven more by temperature gradients or macrophyte abundance (Romare *et al.*, 2003). Temporal variability in zooplankton community structure over scales ranging from weeks to years has been well

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documented by the Plankton Ecology Group (PEG; Sommer *et al.*, 1986; Sommer *et al.*, 2012) and is generally linked to food quantity and quality. Shorter-term temporal variation in zooplankton community structure (i.e. within 24-hours) is typically related to physical and biological processes that alter zooplankton distribution. Ultimately, spatial and temporal variation in environmental conditions can have important implications on zooplankton community structure.

Despite the importance of both spatial (among and within lakes) and temporal (hours to years) variability, few studies consider the relative importance of both scales. Some studies have suggested that temporal variability in environmental conditions and biotic interactions over seasonal time scales dominates zooplankton community dynamics (e.g. Eloire *et al.*, 2010; Yebra *et al.*, 2022; Zhang *et al.*, 2022). In contrast, others have emphasized the importance of spatial processes, such as currents within a lake and latitudinal differences among lakes, for driving variability in zooplankton community structure (e.g. Molinero *et al.*, 2008; Schartau *et al.*, 2022). Of the studies that have compared the relative importance of spatial and temporal variability for zooplankton communities, most have focused on variability among different lakes rather than sites within the same waterbody (Kratz *et al.*, 1987; Seebens *et al.*, 2013). In particular, while monitoring programs in large lakes may sample multiple deep-water sites (e.g. Patalas and Salki, 1992; Pinel-Alloul *et al.*, 1999), rarely are pelagic vs. littoral habitats considered within the same waterbody. Alternatively, some studies focus on temporal variability from manually collected zooplankton data, but only at scales longer than 24-hours (e.g. Klais *et al.*, 2016), neglecting the critical diel scale at which zooplankton migration typically occurs. While increased attention on day vs. night sampling for understanding zooplankton community dynamics suggests that there is high variability over 24-hours (e.g. Doubek *et al.*, 2020), the relative importance of different temporal scales is not fully understood. Given the high environmental variability that exists across sites, sampling dates, hours of the day, and years within a single waterbody, understanding how these different scales contribute to variability in zooplankton community structure and migration behavior is integral as climate change continues to modify freshwater ecosystem functioning.

Importantly, both spatial and temporal variability in zooplankton community structure within a single waterbody are likely shaped by diel migration behavior. Two of the most common migration behaviors, Diel Vertical Migration (DVM) and Diel Horizontal Migration (DHM), are avoidance behaviors that allow zooplankton to experience lower predation pressure and avoid damaging ultraviolet (UV) radiation in pelagic surface waters during the day by using the hypolimnion (DVM) or littoral habitats (DHM) as refugia (de Paggi, 1995; Burks *et al.*, 2002; Hays, 2003; Jensen *et al.*, 2010; Dawidowicz and Pijanowska, 2018). During the night, migrating zooplankton return back to the pelagic surface waters to feed on phytoplankton. Two other migration behaviors, reverse DVM and reverse DHM, have also been observed as a way for zooplankton to avoid invertebrate predators that are in the hypolimnion or near-shore macrophytes during the day, resulting in opposite migration patterns to the “typical” DVM and DHM, though these are less well-studied (e.g. Meerhoff *et al.*, 2007; Jensen *et al.*, 2010).

The relative influence of vertical and horizontal migration behaviors play an important role in mediating spatial and temporal variability of zooplankton within a lake. While numerous studies on zooplankton vertical and horizontal migration have been conducted, little is known about the prevalence of both migration behaviors among different taxa across multiple years in the same ecosystem. For example, migration studies often focus on DHM in shallow lakes that lack a hypolimnetic refuge or DVM in deeper lakes, rather than both migration patterns concurrently (e.g. Burks *et al.*, 2002; Meerhoff *et al.*, 2007). While some studies have observed both DVM and DHM in the same waterbody (e.g. DeStasio, 1993; Masson *et al.*, 2001; Meerhoff *et al.*, 2007; Jensen *et al.*, 2010), these studies typically only consider migration behavior for a single day, potentially missing changes in zooplankton migration over time in response to changing environmental conditions. To the best of our knowledge, no studies have compared migration behavior and its consequences for spatial and temporal variability on zooplankton community structure among > 3 days of manually collected, hour-resolution zooplankton data within a single waterbody.

Moreover, different zooplankton taxa may favor one migration pattern over the other, and taxon-specific determinations of DVM vs. DHM are rare, particularly when both migration behaviors are occurring simultaneously in the same ecosystem. In this case, zooplankton functional traits, such as body size or tolerance to environmental conditions, may be responsible for determining which migration behavior is most favorable for different zooplankton within an ecosystem (Ge *et al.*, 2022). For example, fish predation is typically considered to be the primary driver of zooplankton migration for large-bodied taxa, such as cladocerans and large copepods (Dodson, 1974; Lampert, 1993). However, if fish predation pressure is low, large-bodied zooplankton, which are more susceptible to predation due to their high visibility, may no longer need to migrate vertically (Gliwicz, 1986). Similarly, invertebrate predation is generally attributed to be driving the migration of smaller zooplankton, such as rotifers and smaller copepods (Vogt *et al.*, 2013). Interactive effects of environmental drivers (e.g. predation and UV radiation), as noted in the transparency-regulator hypothesis proposed by Williamson *et al.* (2011), may also mediate patterns of zooplankton migration behavior.

To quantify variability in zooplankton community structure (i.e. composition and density), as well as characterize zooplankton DVM and DHM among multiple zooplankton taxa, we conducted multiple intensive 24-hr sampling events over three summers. We used a multivariate approach to compare variability in zooplankton community structure across different spatial and temporal scales. Our research questions were: (i) How variable is zooplankton community structure across spatial scales (i.e. between sites within the same waterbody) and temporal scales (i.e. both among hours in a day and days across multiple years)? (ii) Which environmental drivers (e.g. water temperature, chlorophyll *a*, photosynthetically active radiation) best explain variability in zooplankton community structure? and (iii) How does zooplankton migration vary among taxa and over time (days)? We expected that zooplankton community structure would be more variable among hours within a 24-hour period rather than sites or years due to differences in diel migration behavior (Q1). Additionally, due to the importance of food availability and habitat selection, we expected that temperature and chlorophyll *a* would best explain variability in zooplankton community structure (Q2; Lampert *et al.*, 2003). Finally, we expected that the most common migration strategy would differ among zooplankton taxa and days due to differences in functional traits and environmental conditions, respectively (Q3).

METHODS

Site description

We conducted our study in Beaverdam Reservoir (BVR; 37.313° N, 79.816° W; Fig. 1), a eutrophic reservoir located in Vinton, Virginia, USA ($Z_{max} = 11$ m, surface area $= 0.28$ km^2, catchment area $= 3.69$ km^2, residence time $= 1\ 300 \pm 335$ (1 S.E.) days; Doubek *et al.*, 2019; Hamre *et al.*, 2018; Woelmer *et al.*, 2023). The reservoir is located in a completely deciduous forested catchment (Carey *et al.*, 2022). BVR is owned and operated by the Western Virginia Water Authority as a secondary drinking water reservoir and exhibits hypolimnetic anoxia during the summer, with dissolved oxygen (DO) concentrations < 1 mg/L (Hamre *et al.*, 2018). Dominant crustacean zooplankton taxa in BVR during the summer stratified period include cyclopoid copepods and *Daphnia* (Doubek *et al.*, 2019; see Table S1 for list of all zooplankton taxa). BVR also has both planktivorous and piscivorous fish present (Doubek *et al.*, 2019). Routine water quality monitoring has occurred approximately weekly during the summer stratified period and fortnightly to monthly throughout the rest of the year since 2014 (Carey, Breef-Pilz, *et al.*, 2023; Carey, Lewis, and Breef-Pilz, 2023; Carey, Wander, *et al.*, 2023).

Field sampling

Across the summers of 2019, 2020 and 2021, we conducted five 24-hour sampling campaigns to quantify variability in zooplankton community structure across space and time among different taxonomic groups. In 2019, sampling occurred on 10–11 July and 24–25 July; in 2020, sampling occurred on 12–13 August; and in 2021, sampling occurred on 16–17 June and 7–8 July. We chose these dates spanning from early to late summer to capture differences in anoxic depth and volume. We collected zooplankton using vertical net tows with an 80-μm Wisconsin-style zooplankton net (diameter $= 0.3$ m, length $= 0.95$ m; Wildlife Supply Company, Yulee, Florida, USA) at a pelagic site ($Z_{max} = 11$ m) where long-term monitoring occurs and a littoral site (mean Z_{max} during the study $= 3.5$ m) located ~6 m from the macrophyte-covered shore and 38 m from the pelagic site (Fig. 1). The water column at the littoral site was fully mixed and representative of the epilimnion, as determined at the pelagic site. At the littoral site, we collected tows from 2 m depth, which was chosen to avoid net interference with the sediments. At the pelagic site, we collected full water column tows (10 m) that integrated both epilimnetic and hypolimnetic layers and epilimnetic tows from 4 m depth on all sampling dates, based on data from previous years suggesting that zooplankton exhibit surface avoidance of up to 2 m in the pelagic zone (Carey *et al.*, 2018; Doubek *et al.*, 2018). The paired epilimnetic tows at the pelagic and littoral site were collected at all sampling times (see below) within the 24-hour monitoring periods, while the full-water column tows at the pelagic site were only collected at noon and midnight. We collected $n = 2$ tows at all sites and times to serve as replicates. All samples were immediately preserved in 70% ethanol in the field and brought back to the lab to be processed.

Within each 24-hour sampling date, we collected zooplankton at multiple times and two sites (pelagic and littoral) to capture spatial and diel variability in their community structure. Sampling occurred at 11 different times within each 24-hour period at both littoral and pelagic sites: we sampled once at approximately noon, four times around sunset (within the two hours before and one hour after sunset), once at midnight, four times around sunrise (within the two hours before and one hour after sunrise), and once at noon the following day. These sampling times were chosen based on previous work that found that zooplankton migration is most likely to occur around sunrise and sunset (Ringelberg, 1999).

We collected a variety of environmental variables at the pelagic site during each sampling date to better understand drivers of zooplankton community structure variability. We used a Conductivity, Temperature, and Depth profiler (CTD; SeaBird Electronics, Bellevue, Washington, USA) to collect water temperature, dissolved oxygen, specific conductance, chlorophyll *a*, and photosynthetically active radiation (PAR; Carey, Lewis, and Breef-Pilz, 2023). We collected CTD data during all sampling dates except on the last sampling date in 2021, for which we used data from a CTD profile that occurred 4 days after that sampling date. During each sampling date, we also measured Secchi depth as a metric of water clarity and collected unfiltered water samples from 0.1 m depth to analyze total nitrogen (TN) and total phosphorus (TP) concentrations (Carey, Wander, *et al.*, 2023). All nutrient samples were collected in acid-washed bottles and frozen in the laboratory until analysis. Wind speed and air temperature data were obtained from a nearby meteorological station located at a downstream reservoir located 3 km away from BVR (Carey and Breef-Pilz, 2023).

Lab processing

Zooplankton were enumerated and measured to determine density and biomass with a Meiji RZ dissecting microscope (Meiji Techno, San Jose, California, USA) ranging from 500 to 750× magnification following standard methods (Downing and Rigler, 1984; McCauley, 1984). Net tow samples were filtered through an 80-μm mesh sieve and were diluted to 200–2000 mL depending on the density of each sample. At least three aliquots ranging from 1 to 5 mL were counted for each net tow sample until ~100 individual crustaceans and large rotifers were identified (cladocerans and rotifers to genus, copepods to order) per sample to account for rare taxa. All microscopy was conducted by the same taxonomist (HLW). We used length-weight regressions following Downing and Rigler (1984) to convert length measurements to biomass. We then calculated the standardized zooplankton density for each taxon by dividing the density by the maximum density across all sampling dates.

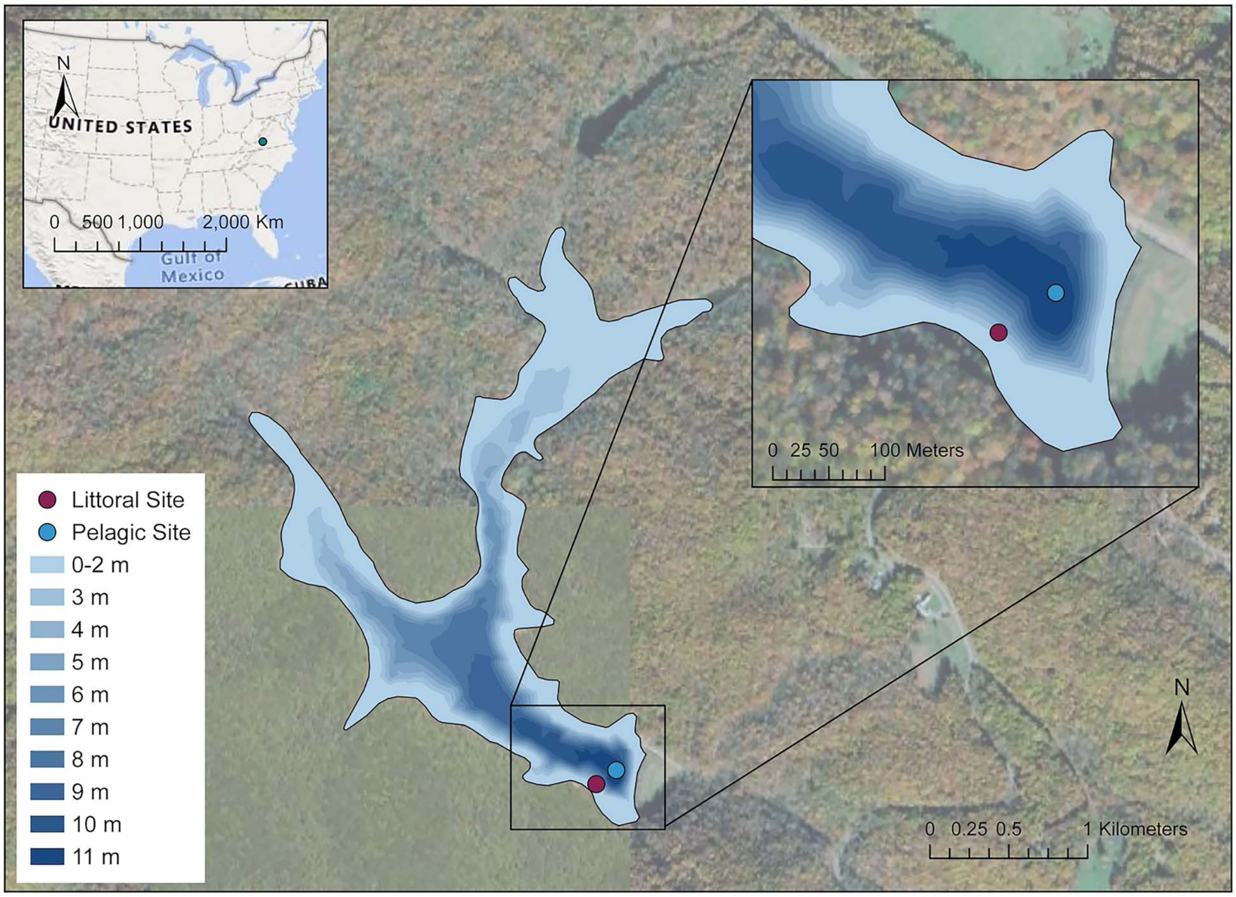


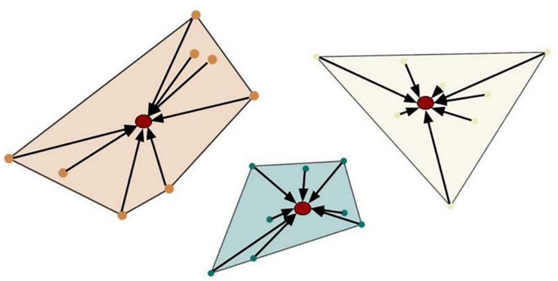
Fig. 1. Map of Beaverdam Reservoir, Vinton, Virginia, USA (37.313° N, 79.816° W). Points depict pelagic (right) and littoral (left) sites, which are located near the reservoir dam.

TN and TP samples were analyzed colorimetrically using a Lachat QuikChem 8 500 Flow Injection Analyzer following persulfate digestion (Carey, Wander, *et al.*, 2023).

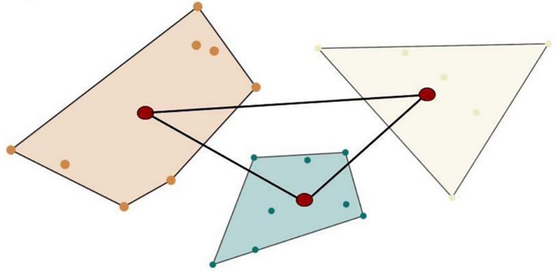
Q1—analysis of spatial and temporal variability

We used a multivariate approach to quantify and statistically compare variability in zooplankton community structure among sites, sampling dates, and hours. Using epilimnetic zooplankton data, we performed Non-metric MultiDimensional Scaling (NMDS) using the *metaMDS()* function in the *vegan* R package (Oksanen *et al.*, 2022). We chose NMDS because it does not assume linear relationships exist in the data and allows for flexibility when choosing a distance metric that summarizes the differences between points in a dataset (McCune and Grace, 2002). We determined the number of dimensions for the NMDS using a scree plot (Fig. S1). Our data consisted of zooplankton densities from 17 dominant (defined as $> 0.1\%$ of total density) taxa averaged across replicates collected for a particular site, sampling date, and hour (Carey *et al.*, 2024). These taxa were as follows: *Bosmina, Ceriodaphnia, Daphnia, Calanoida, Cyclopoida, copepod nauplius, Collotheca, Conochiloides, Conochilus, Gastropus, Kellicottia, Keratella, Lepadella, Monostyla, Polyarthra, Pompholyx* and *Trichocerca*. All density data were Hellinger-transformed to standardize densities among taxa, and absolute values were converted to relative values using the *labdsv* R package (Roberts, 2019). Community data were then converted to a Euclidean distance matrix before performing the NMDS. We looked at groupings between pelagic vs. littoral sites ($n = 2$ sites), among sampling dates ($n = 5$ days), and among hours within each 24-hour period ($n = 11$ hours). We assessed variability among all three scales (sites, sampling dates, and hours of day) using different polygon groupings of the same points in the ordination.

Using the Hellinger-transformed Euclidean distance matrix, we determined dispersion and statistical location effects (following Anderson and Walsh, 2013) to identify how zooplankton communities changed across space (pelagic vs. littoral sites) and time (sampling dates and hours of the day). Dispersion describes the spread of data, whereas location describes the distance between multiple groups in multivariate space (Anderson and Walsh, 2013). First, we calculated dispersion for each group, where a single group represented one site, one sampling date, or one hour of the day (Fig. 2a). We calculated dispersion by taking the mean Euclidean distance between every point in a group and its respective group centroid using the *betadisper()* function in the *vegan* R package (Anderson, 2006). To determine whether dispersion vs. statistical location effects were significantly different *among* spatial and temporal scales, we performed a Kruskal-Wallis test for each metric of variability (i.e. dispersion and statistical location effects), followed by Dunn post-hoc tests (using *kruskal.test()* and *dunnTest()* in the *FSA* R package;



a) Dispersion



b) Location

Fig. 2. Conceptual figure depicting dispersion (**a**) and statistical location (**b**), two metrics of community structure variability, in ordination space. Polygons represent distinct groups of zooplankton samples aggregated within one of the focal scales of variability (i.e. site, sampling date, or hour), lines represent the distance in multidimensional space being quantified between groups, and larger points represent the centroid of each group. To calculate dispersion (a), distances from each point to the centroid among all polygons were averaged to summarize differences among groups and quantify variability for each spatial and temporal scale. To calculate statistical location (b), all distances between polygons were averaged to quantify variability for each spatial and temporal scale. Both metrics were calculated using the Euclidean distances of Hellinger-transformed zooplankton density data collected from Beaverdam Reservoir.

Ogle *et al.,* 2020). To determine whether dispersion effects were significantly different *within* spatial and temporal scales, i.e. among the pelagic vs. littoral sites, sampling dates ($n = 5$), or hours of the day ($n = 11$), we calculated the average dispersion for each group (Fig. 2a) and performed three separate Kruskal–Wallis tests followed by Dunn post-hoc tests where appropriate (Table S2).

Second, we calculated the mean distance between each pairwise combination of centroids for pelagic vs. littoral sites, sampling dates, and hours of the day separately to determine the statistical location effect among these different spatial and temporal scales (Fig. 2b). To determine the statistical location effect, we used the *dist()* function in the *stats* package (R Core Team, 2022) and calculated the mean distance between group centroids for sites, sampling dates, and hours of the day. We performed three separate Kruskal–Wallis tests followed by Dunn post-hoc tests to determine whether statistical location effects were significantly different *among* spatial and temporal scales (Fig. 2b). We used this dual approach (dispersion and statistical location effects) to better characterize spatial and temporal variability in zooplankton community structure, as the spread of points within polygons describes how variable community structure is within a single group, while the distance between polygons describes how distinct groups are from each other. We note that dispersion and statistical location values were calculated from a Euclidean distance matrix based on the transformed zooplankton density data, rather than the NMDS output, so that we fully characterized variability in the dataset before dimension reduction. Therefore, these two metrics of variability should be similar to the NMDS output given that the same matrix was used to perform the multivariate analysis.

To account for different numbers of groups within each spatial or temporal scale (e.g. two spatial groups for the littoral and pelagic site samples vs. 11 temporal groups for each hour sampling) as well as different numbers of points within each group, we used a Monte Carlo approach. For sites, sampling dates, and hours of the day, we randomly sampled 10 untransformed zooplankton density data points from two groups within that specific spatial or temporal scale and repeated this process 500 times. Next, we Hellinger-transformed the selected data, converted them into a Euclidean distance matrix, and calculated the mean and standard deviation of the dispersion and statistical location effects for each random sampling. We chose two groups with 10 points each for our Monte Carlo approach because the minimum number of groups within a spatial or temporal scale for our study was two ($n = 2$ sites) and the minimum number of points within a group was 10 (5 days × 2 sites).

Finally, to determine whether zooplankton community structure varied more among sites, sampling dates, or hours of the day, we performed Kruskal–Wallis tests followed by Dunn post-hoc tests. The post-hoc tests were Bonferroni-corrected to account for multiple tests (Ogle *et al.,* 2020) of the mean dispersion and location values from each random sampling of the Monte Carlo approach ($n = 500$).

Q2—environmental driver analysis

To understand which environmental variables were most important for driving differences in zooplankton community structure among sampling dates, we fit environmental variables to our ordination using *envfit()* in the *vegan* R package (Oksanen *et al.,* 2022). These environmental drivers were water temperature, thermocline depth, specific conductance, PAR, Secchi depth, dissolved oxygen, oxycline depth, TN, TP, chlorophyll *a,* wind speed, and air temperature. Of the depth-specific profile data, we focused on conditions at 0.1 m and 10 m to represent epilimnetic and hypolimnetic conditions, respectively. We calculated thermocline and oxycline depth from CTD profiles filtered to 1-m intervals using *thermo.depth()* in the *rLakeAnalyzer* R package (Winslow *et al.,* 2019). We note that we only included epilimnetic, but not hypolimnetic, dissolved oxygen in our analysis because hypolimnetic concentrations were consistently 0 mg/L throughout the summer stratified period. Given limited environmental data across sites and hours of the day, we only performed this driver analysis among sampling dates.

Q3—migration analysis

We calculated DVM and DHM metrics for cladocerans, copepods, and rotifers during each of the five sampling dates. To identify whether DVM was occurring, we calculated the hypolimnetic zooplankton density and biomass (Z_{Hyp}) by subtracting epilimnetic tow data (i.e. zooplankton count and biomass values from 4-m pelagic tows) from the full water column tow data:

$$Z_{\mathrm{Hyp}} = \frac{\left(\frac{1}{\mathrm{propvol}_{\mathrm{full}}} {}^{*} \mathrm{X}_{\mathrm{full}} {}^{*} \frac{1}{\mathrm{NetEff}_{\mathrm{full}}}\right) - \left(\frac{1}{\mathrm{propvol}_{\mathrm{epi}}} {}^{*} \mathrm{X}_{\mathrm{epi}} {}^{*} \frac{1}{\mathrm{NetEff}_{\mathrm{epi}}}\right)}{\mathrm{Vol}_{\mathrm{full}} - \mathrm{Vol}_{\mathrm{epi}}} \tag{1}$$

Where X is the number or biomass (μg) of zooplankton calculated from the full water column tow (X_{full}) or epilimnetic tow (X_{epi}), *propvol* is the proportional volume of the sample (i.e. proportion of the sample counted relative to the total sample volume) for the full water column or epilimnetic tows, *NetEff* is the correction factor calculated by comparing zooplankton tow density to Schindler trap density for each sample (Text S1; Wander *et al.*, 2024), and *Vol* is the unadjusted volume of the tow calculated using the tow depth and the dimensions of the zooplankton net.

Zooplankton epilimnetic and hypolimnetic density and biomass at the pelagic site were used to calculate a proportional DVM metric (DVM_{prop}) as follows:

$$DVM_{prop} = Z_{epi}/\left(Z_{epi} + Z_{hypo}\right)_{Night} - Z_{epi}/\left(Z_{epi} + Z_{hypo}\right)_{Day} \tag{2}$$

Where Z_{epi} is the adjusted density or biomass calculated for each taxon in the epilimnion and Z_{hypo} is the adjusted density or biomass calculated for each taxon in the hypolimnion. Proportional density and biomass during the day were subtracted from the proportional density or biomass calculated for each taxon during the night to get DVM_{prop}, where positive values indicate that zooplankton were performing typical DVM (i.e. migrating to the surface at night and at depth during the day) and negative values indicate that zooplankton were performing reverse DVM. Because our 24-hour sampling campaigns began at noon, we collected $n = 2$ noon samples at the start of the 24-hour period and another $n = 2$ samples at the end. We then calculated DVM_{prop} using the mean of each noon sampling event and then averaged these two DVM_{prop} values together to represent the mean DVM magnitude ± standard error.

Zooplankton density and biomass at the pelagic site vs. littoral site were used to calculate a proportional DHM metric (DHM_{prop}) as follows:

$$DHM_{prop} = Z_{pel}/\left(Z_{pel} + Z_{lit}\right)_{Night} - Z_{pel}/\left(Z_{pel} + Z_{lit}\right)_{Day} \tag{3}$$

Where Z_{pel} is the adjusted density or biomass calculated for each taxon in the pelagic surface waters and Z_{lit} is the adjusted density or biomass calculated for each taxon at the littoral site. Proportional density and biomass during the day were subtracted from the proportional density or biomass calculated for each taxon during the night to get DHM_{prop}, where positive values indicate that zooplankton were performing typical DHM (i.e. migrating to the pelagic site at night and the littoral site during the day) and negative values indicate that zooplankton were performing reverse DHM. Similar to DVM_{prop}, DHM_{prop} was calculated from the two samples collected at both noon sampling events, which were averaged to represent the mean DHM magnitude ± standard error. We note that this metric describes relative change in zooplankton density or biomass between the two sites, though individual zooplankton may not be able to migrate the full distance between the pelagic and littoral site.

All statistical analyses were performed in R v.4.2.2 (R Core Team, 2022). All data and code used to run these analyses are publicly available in the Environmental Data Initiative repository (Carey *et al.*, 2024) and Zenodo repository (Wander *et al.*, 2024), respectively.

RESULTS

Q1: Is zooplankton community structure more variable over space or time?

We observed high variability in zooplankton community structure across spatial and temporal scales (Figs 3 and 4). However, we found that the magnitude of variability in zooplankton community structure was greater among summer sampling dates over three years than between the littoral and pelagic sites or among hours on the same day, as demonstrated by the greatest statistical location effect and smallest dispersion among sampling dates (Fig. 5). Specifically, we observed a greater location effect within sampling dates, but a lower dispersion effect among individual sampling dates, suggesting that community structure is variable among, but not within, sampling dates.

Observed patterns in zooplankton density

Taxon-specific zooplankton density patterns were highly variable among sampling dates and hours in each 24-hour period. Standardized density (i.e. absolute density relative to maximum density) in the epilimnion was greatest for 15–16 June 2021 across all zooplankton taxa and at both sites, with a mean value of 0.44. Conversely, standardized density was smallest for 10–11 July 2019, with a mean value of 0.09 (Fig. 3). Within the zooplankton community, cladocerans and copepods had 62–84% higher mean standardized densities in the epilimnion at night than during the day for all sampling dates and sites (Fig. 3). Conversely, mean standardized rotifer densities in the epilimnion were 15% higher during the day than at night across all sampling dates (Fig. 3). Across all taxa, mean standardized zooplankton density was 0.26 at the pelagic site, which was greater than the mean standardized density observed at the littoral site (0.18; Fig. 3). However, mean standardized density at the pelagic site was 23% greater at night than during the day, whereas mean standardized density at the littoral site was 45% greater at night than during the day (Fig. 3). We note that we did observe a diurnal deficit at the pelagic site in Beaverdam Reservoir, as the mean zooplankton density was 14% greater at night vs. during the day. We also observed an even greater deficit at the littoral site, where mean zooplankton density was 30% greater at night vs. during the day.

Variability in community structure in multidimensional space

Overall, our metrics of variability and NMDS results suggest that while there were differences in epilimnetic community structure among sites and hours of the day, the greatest differences in

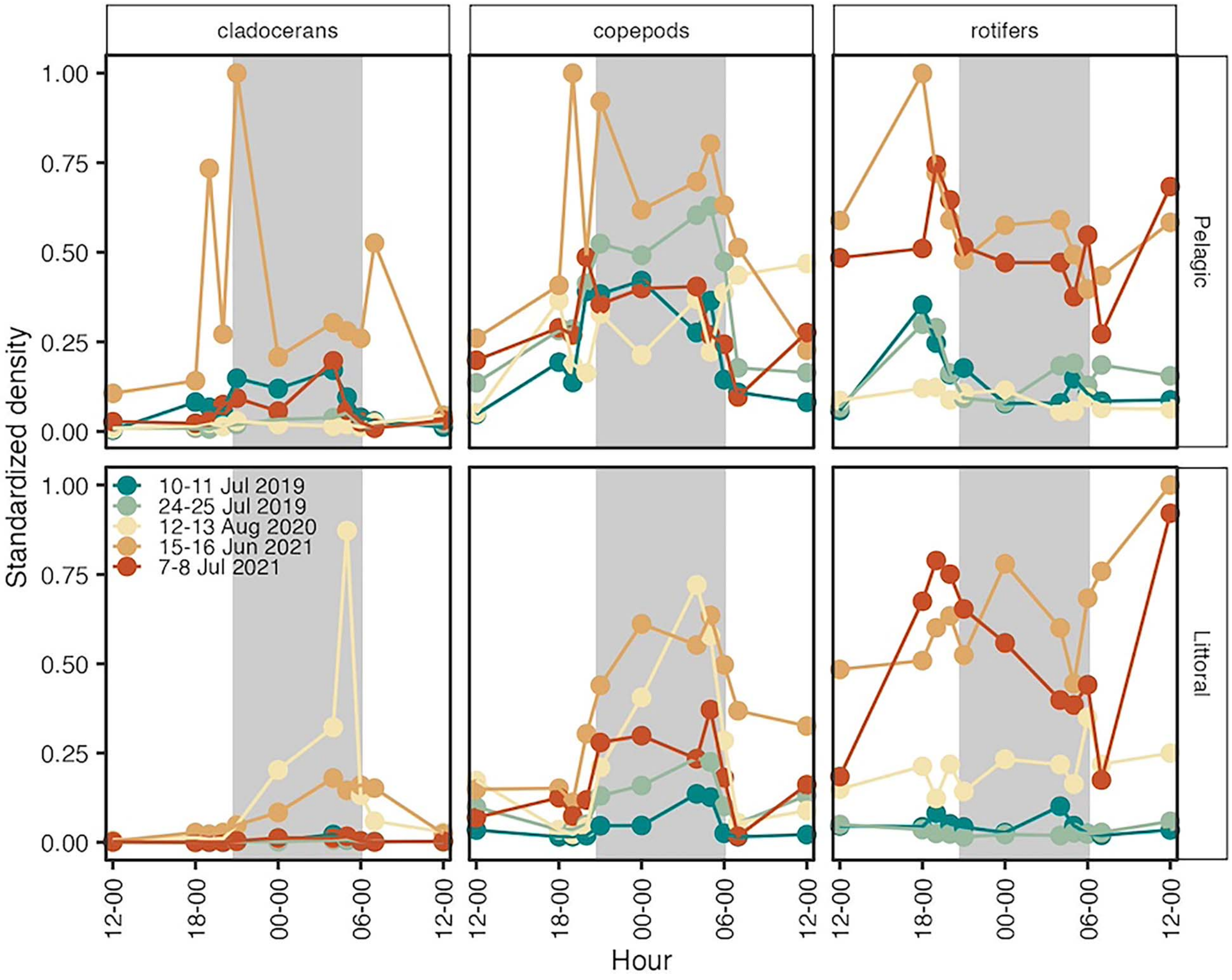


Fig. 3. Standardized epilimnetic zooplankton density for three taxa, calculated as the observed density divided by the maximum density across all sampling dates, for each 24-hour sampling date during the summers of 2019–2021. Top panels depict standardized epilimnetic zooplankton density over time at the pelagic site, bottom panels depict standardized epilimnetic zooplankton density over time at the littoral site. Columns represent different zooplankton taxa (Cladocera, Copepoda, Rotifera). Colored lines correspond to each of the five 24-hour sampling dates. Error bars represent standard error. Shading represents sunset to sunrise during each 24-hour period. Zooplankton density values before standardization are shown in Fig. S6.

zooplankton community structure occurred over longer-term temporal scales (i.e. among sampling dates; Figs 4 and 5). We chose four dimensions in our NMDS application, as we observed rapid reduction of stress until the fourth dimension ($k = 4$, stress = 0.046; Fig. S1). The dispersion effect was smallest among sampling dates (0.23 ± 0.04) and greatest among hours of the day (0.27 ± 0.04, $P < 0.001$; Fig. 5, Table S2), indicating that zooplankton community structure within a single sampling date was more tightly clustered, and therefore less variable, than within an hour of the day. Conversely, the statistical location effect among group centroids resulted in the greatest variability among sampling dates (0.36 ± 0.08) and the smallest variability among hours of the day (0.20 ± 0.09, $P < 0.001$; Fig. 5, Table S2), indicating that zooplankton communities observed on different sampling dates were more distinct than zooplankton communities observed at different hours of the day.

We found different patterns of variability within each spatial and temporal scale. However, variability was only significantly different between sites, in which dispersion was 34% greater at the littoral site than the pelagic site ($P < 0.001$; Fig. 6, Table S3). Variability in average dispersion on 12–13 August 2020 was only significantly greater than the 15–16 June 2021 sampling date ($P < 0.001$; Fig. 6, Table S3). However, there were no significant differences in average dispersion among hours of the day ($P = 0.91$, Table S3), despite greater variability in sunrise and sunset hours than daytime or nighttime hours (Fig. S2).

Q2: Which environmental drivers best explain variability in zooplankton community structure?

We found that the differences in zooplankton community structure among sampling dates were associated with changes in environmental conditions (Fig. 7). We observed distinct clustering of zooplankton community structure among the two 2019 sampling dates, which differed from 2020 and 2021 sampling dates. In 2019, zooplankton community structure was associated with

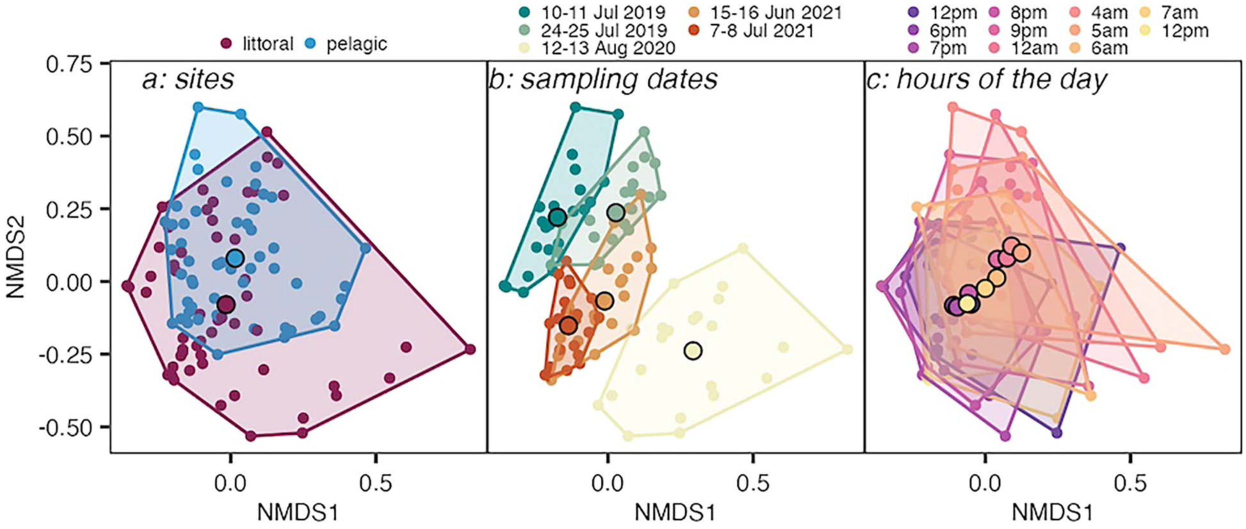


Fig. 4. Non-metric MultiDimensional Scaling (NMDS) plots for axes 1 and 2 (k = 4, stress = 0.046) showing variability in community structure across three different scales: (**a**) sites (*n* = 2), (**b**) sampling dates (*n* = 5), and (**c**) hours of the day (*n* = 11). Panel a: colored polygons represent pelagic and littoral sites; points within each polygon are for all samples collected at each site for all sampling dates and hours of the day (*n* = 55 per polygon). Panel b: colored polygons represent sampling dates; points within each polygon are for all samples collected at both sites and all hours of the day for each sampling date (*n* = 22 per polygon). Panel c: colored polygons represent hours of the day; points within each polygon are for all samples collected at both sites and across all sampling dates (*n* = 10 per polygon). The larger point near the middle of each polygon is the group centroid. Note that points across all three ordinations are the same and that panels only differ in the grouping of points. Axes 3 and 4 are shown in Figs S7–S8. Dispersion and statistical location effects were calculated using the Hellinger-transformed Euclidean distance matrix of zooplankton density data.

low total nutrient concentrations and colder hypolimnetic temperatures. The 10–11 July 2019 sampling date was additionally associated with deeper thermocline, oxycline, and Secchi depths, while the 24–25 July 2019 sampling date was associated with higher hypolimnetic specific conductance and epilimnetic chlorophyll *a* concentration (Figs 7and S3). In 2020, zooplankton community structure was associated with higher hypolimnetic chlorophyll *a*, water temperature, epilimnetic PAR, TN and TP (Figs 7 and S3). The two 2021 sampling dates were associated with higher epilimnetic dissolved oxygen; June 2021 was additionally associated with low epilimnetic chlorophyll *a*, temperature, and epilimnetic and hypolimnetic specific conductance, whereas July 2021 was additionally associated with shallow Secchi depths and high epilimnetic specific conductance (Figs 7 and S3). We note that there were k = 4 dimensions in our application of NMDS and that the same 11 environmental variables associated with axes 1 and 2 were also associated with axes 3 and 4 (Figs S4 and 5). We report p-values and correlation coefficients for each driver as they relate to the NMDS output in Table S4 and correlation coefficients between each pair of drivers used in this analysis in Table S5.

Q3: How does zooplankton migration vary among taxa and over time?

We observed variable migration behavior among sampling dates and taxa; however, cladocerans, copepods, and rotifers showed a slightly greater magnitude of DHM vs. DVM on most sampling dates (Fig. 8). During 2019 sampling dates, zooplankton exhibited either typical DVM and typical DHM or no migration behavior, and magnitudes of migration behavior varied among both sampling dates and taxa (Fig. 8). In 2020, rotifers exhibited DVM and DHM at relatively small magnitudes (Fig. 8c), while cladocerans and copepods exhibited larger magnitudes of both reverse DVM and reverse DHM (Fig. 8a and b). Copepods generally exhibited similar migration behavior as cladocerans across all sampling dates (Fig. 8a and b). Rotifers exhibited migration behavior at a smaller magnitude overall (Fig. 8c) compared to cladocerans and copepods. However, we did observe some evidence of rotifers exhibiting typical DVM and typical DHM on 2019 and 2020 sampling dates, and reverse DVM and reverse DHM in 2021 (Fig. 8c). In 2021 (*n* = 2 sampling dates), there was minimal evidence of typical DVM, but we did observe reverse DHM (Fig. 8). Overall, the magnitude of typical and reverse DVM and DHM were often similar to each other during each sampling date, despite some taxon-specific differences (Fig. 8).

DISCUSSION

Overview

Our study characterized spatial and temporal variability in zooplankton community structure and identified drivers of community variability. We found that zooplankton community structure varied among sites, sampling dates, and hours of the day for the three focal taxa (cladocerans, copepods and rotifers). However, across all three scales, zooplankton variability was greatest among sampling dates over three consecutive years, rather than among sites or hours of the day. Consequently, despite increased recent attention on the importance of identifying night vs. day differences in zooplankton dynamics (e.g. Doubek *et al.*,

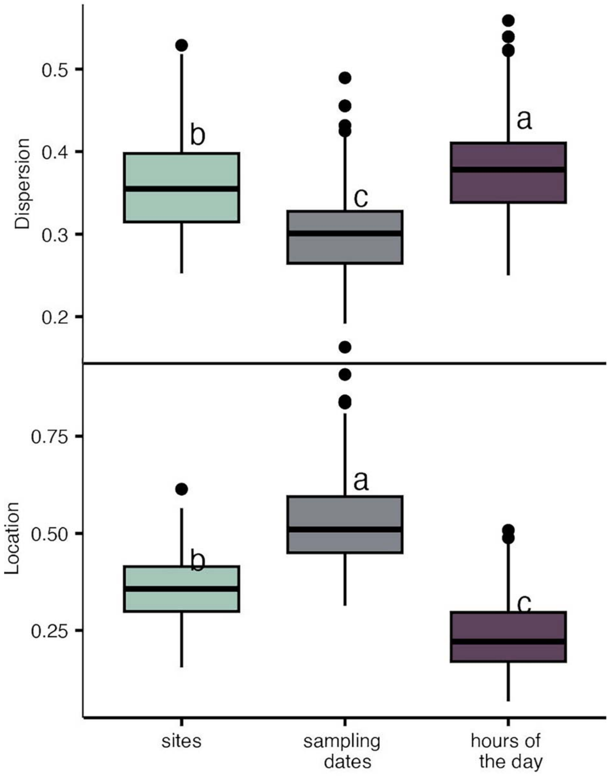


Fig. 5. Boxplots of dispersion (top) and location (bottom) effects among sites, sampling dates, and hours of the day. Boxes indicate median ± one quartile; upper and lower whiskers depict maximum and minimum values, respectively, while points indicate outliers. Letters depict significant differences following a post-hoc Dunn test, where a is the greatest variability and c is the smallest variability. Each boxplot includes $n = 500$ variability calculations from Monte Carlo sampling. Note that the scale with both the greatest location effect and the lowest dispersion effect corresponds to the scale with the highest variation.

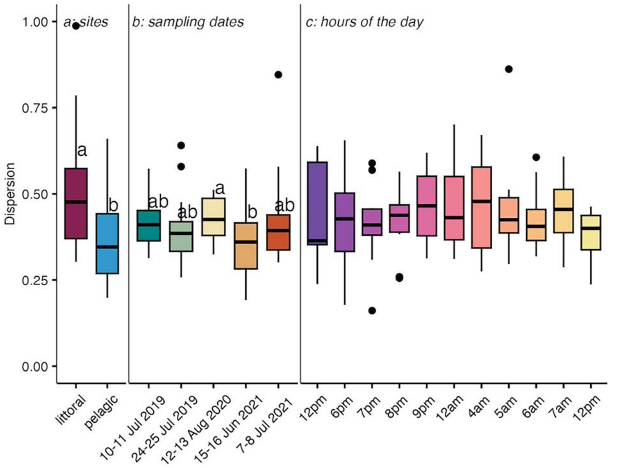


Fig. 6. Boxplots of dispersion values within sites (**a**), sampling dates (**b**), and hours of the day (**c**). Boxes indicate median ± one quartile; upper and lower whiskers depict maximum and minimum values, respectively, while points indicate outliers. Significant differences in dispersion within sampling dates are represented by letters, where a has a greater dispersion than b. Dispersion values among sampling dates or hours of the day were not significantly different from each other. Note that the number of dispersion values within each panel differs among sites ($n = 55$), sampling dates ($n = 22$), and hours of the day ($n = 10$). Greater dispersion corresponds to greater variation among groups.

2020) and other studies that assess changes in community structure from a single mid-summer sampling event (Dodson *et al.*, 2009; Vedenin *et al.*, 2019), our work reaffirms the importance of sampling multiple days over a summer and among multiple summers to best characterize zooplankton community dynamics (Sommer *et al.*, 1986, 2012). Finally, environmental variables explained some of the variability in zooplankton community structure among sampling dates and likely also contributed to dynamic migration behaviors. Below, we discuss our findings and consider how environmental drivers and migration behavior result in spatial and temporal variability in zooplankton community structure.

Q1: Is zooplankton community structure more variable over space or time?

Our results indicate that temporal variability over multi-year timescales is greater than hourly or spatial variability. Specifically, we found that most of the variability in zooplankton community structure was due to differences among sampling dates, as the greatest statistical location effect and the smallest dispersion between samples in multidimensional space were observed at this scale. This result is similar to the few other studies that compared spatial and temporal variability in zooplankton dynamics. For example, O'Connor *et al.* (2023) found that seasonal differences in community dynamics among zooplankton species were greater than spatial differences across five sites. Similarly, Shiel *et al.* (2006) found that seasonal variability was greater than spatial variability, based on sampling that occurred during six distinct sampling events within three different river systems. Our work builds on these previous studies by additionally quantifying zooplankton variability at temporal scales shorter than 1 day. Because variability in zooplankton community structure was not significantly different across hours of the day, our study suggests that the exact time at which sampling occurs within a 24-hour period is likely less important for characterizing variability in community structure than the date of sampling. Ultimately, our analysis supports the idea that sampling across multiple days over multiple years is the best way to characterize zooplankton community structure.

Variability in zooplankton community structure was greater among sampling dates than between sites and among hours, despite that we only considered variability during the summer stratified period (June–August), albeit across 3 years. Zooplankton often exhibit predictable patterns of succession, as documented in the PEG model (Sommer *et al.*, 1986), though these patterns can vary stochastically and in response to a variety of abiotic factors (e.g. turbidity, water temperature, Secchi depth; Dejen *et al.*, 2004; Rettig *et al.*, 2006; Hu *et al.*, 2014). Therefore, had our study extended across different seasons (i.e. sampling in fall, winter, and/or spring, in addition to summer) similar to O'Connor *et al.* (2023) and Shiel *et al.* (2006), we would likely

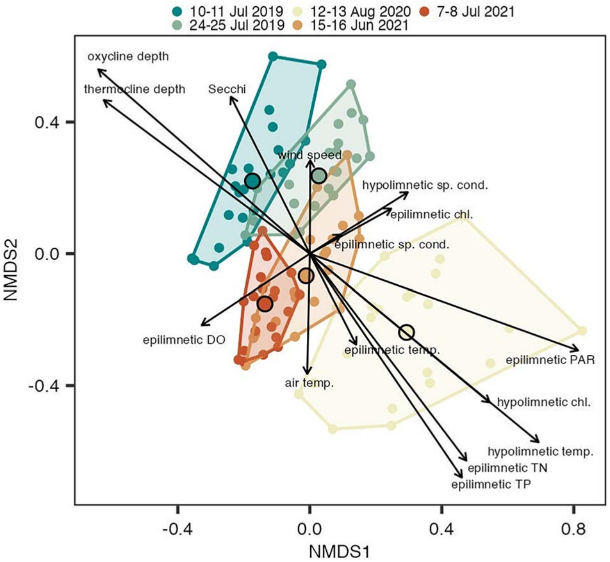


Fig. 7. Non-metric MultiDimensional Scaling (NMDS) plot for axes 1 and 2 (k = 4, stress = 0.046) for zooplankton community structure among sampling dates in Beaverdam Reservoir. Colors correspond to different sampling dates. Arrows represent environmental variables fit onto ordination, where longer arrows are stronger predictors of community structure and shorter arrows are weaker predictors. Secchi = Secchi depth, epilimnetic sp. cond. = epilimnetic specific conductance, hypolimnetic sp. cond. = hypolimnetic specific conductance, epilimnetic chl. = epilimnetic chlorophyll *a* concentration, hypolimnetic chl. = hypolimnetic chlorophyll *a* concentration, epilimnetic DO = epilimnetic dissolved oxygen, epilimnetic temp. = epilimnetic temperature, hypolimnetic temp. = hypolimnetic temperature, epilimnetic PAR = epilimnetic photosynthetically active radiation, epilimnetic TN = epilimnetic total nitrogen, epilimnetic TP = epilimnetic total phosphorus, air temp. = average 24-hour air temperature, wind speed = average 24-hour wind speed. Axes 3 and 4 are shown in Figs S4-S5.

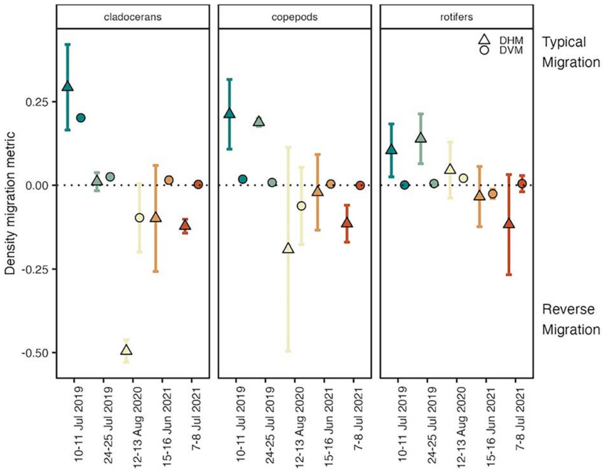


Fig. 8. Zooplankton diel vertical migration (DVM) or diel horizontal migration (DHM) metrics calculated using density data during each sampling date from 2019–2021 for cladocerans (**a**), copepods (**b**), and rotifers (**c**). Colors represent distinct sampling dates. Metrics were averaged using data from both noon samples that were collected 24-hours apart; error bars represent standard error from the two averaged values. Points above the dotted line at 0 represent days during which typical DVM (circles) or typical DHM (triangles) were observed for each taxon. Points on or near the dotted line represent days during which minimal to no migration was observed. Points below the dotted line represent days when zooplankton were observed to exhibit reverse DVM (circles) or reverse DHM (triangles). Migration metrics generated with biomass data yielded similar patterns (Fig. S9).

have seen even greater temporal variability. We also note that zooplankton community structure among days vs. years is likely different, in which annual variability in zooplankton communities may be greater than variability among days, particularly when the days are within a week of each other and environmental conditions are relatively similar. Finally, our results suggest that differences in sample timing within a summer across years had a minimal effect on zooplankton community structure, as the clustering of distinct years, but not months, in our NMDS ordination (Fig. 4) suggests that differences are likely driven by environmental factors, rather than timing of summer sampling.

Although the spatial variability among zooplankton communities was never greater than the temporal variability among sampling dates and hours of the day, we did observe greater variability in community structure at the littoral site than the pelagic site, as well as both DVM and DHM for all sampling dates within the reservoir. Consequently, spatial variability may still be important for overall zooplankton community dynamics. Within a lake, spatial variability in zooplankton may be due to both active migration within a lake to avoid predators (e.g. Lauridsen *et al.*, 1999; Masson *et al.*, 2001), and passive transport from wind-induced currents (Lacroix and Lescher-Moutoué, 1995). Zooplankton taxa have variable swimming speeds, potentially resulting in differences in DHM behavior among taxa. For example, cyclopoid swimming speeds range from 1 to 5.5 mm/s (Williamson 1986); therefore, it is possible for cyclopoids to migrate between 43 and 238 m in 12 hours. Conversely, *Keratella* have swimming speeds ranging from 0.15 to 0.75 mm/s (Obertegger *et al.*, 2018) and therefore may only be able to swim 7–32 m in 12 hours. Given that the distance between the pelagic and littoral site is ~ 40 m, *Keratella* that were observed to exhibit DHM may only be partially migrating, as they cannot swim this full distance twice a day (Fig. S13). Regardless, we note that because we sampled the pelagic and littoral sites at the same time, we were not capturing the migration distance of individual zooplankton, but instead capturing the general movement of zooplankton on these different sampling dates.

Our sampling design likely resulted in an underestimation of spatial variability in zooplankton communities because our two sites were relatively close to each other at ~ 40 m apart, which may not be fully representative of a reservoir with a surface area of 0.28 km^2. For example, in larger lakes, more distinct spatial gradients of environmental conditions, including water temperature, nutrients, and chlorophyll *a*, have been associated with high spatial variability of zooplankton (e.g. Patalas and Salki, 1992; Pinel-Alloul *et al.*, 1999). Microhabitats with different environmental conditions (e.g. temperature, food availability, anoxia) may also result in migration as organisms optimize their fitness (Lampert *et al.*, 2003), in addition to avoiding predators. Therefore, future studies aiming to identify spatial variability in zooplankton community structure variability should focus on sampling at multiple sites that span a larger range of environmental conditions. Regardless, our work highlights that differences in zooplankton community structure can still emerge even over small spatial scales (∼40 m) and may vary over time due to migration behavior.

Q2: Which environmental drivers best explain variability in zooplankton community structure?

Variability in zooplankton community structure was associated with multiple environmental drivers. Specifically, the sampling date with the greatest variability in zooplankton community structure (12–13 August 2020) was associated with high hypolimnetic chlorophyll *a*, water temperature, epilimnetic PAR, and total nutrients (Figs 7 and S3), suggesting that more eutrophic conditions could promote greater variability in zooplankton communities. Across all sampling dates over the three-year study period, the August 2020 sampling date was the latest day sampled in the summer stratified season and had a greater extent of hypolimnetic anoxia than was observed on any of the June or July dates sampled in 2019 and 2021 (Fig. S10). The prevalence of hypolimnetic anoxia may have interacted with taxon-specific functional traits, as we observed that rotifers and copepods, which exhibit higher tolerance to low oxygen conditions, were more abundant than large cladocerans, which are often sensitive to anoxia (Vanderploeg *et al.*, 2009). Moreover, cladoceran average size was smallest in August 2020 compared to other sampling dates (Fig. S11). Additionally, a greater extent of anoxia in the hypolimnion may have led to habitat overlap of predators and prey in the epilimnion, which can increase predation as fish and zooplankton are compressed into a smaller volume of the water column (Dillon *et al.*, 2021). Increased overlap between fish predators and zooplankton likely further favored the dominance of smaller, less conspicuous taxa (e.g. rotifers, as we observed in Beaverdam Reservoir) and those that are better at evading predators (Lazzaro, 1987). The interaction between anoxia, which is often associated with high nutrient and chlorophyll *a* concentrations, and zooplankton functional traits likely explain why zooplankton community structure was more variable in August 2020.

Differences in community structure between 2019, 2020, and 2021 were related to differences in environmental drivers, as 2019 sampling dates had low epilimnetic nutrient concentrations and low hypolimnetic temperatures (Figs 7 and S3). We also saw larger cladocerans and copepods at the pelagic site during the two sampling dates in July 2019 (Fig. S11), suggesting that predation pressure was either reduced or zooplankton were able to more effectively avoid predators via migration. Given high chlorophyll *a* concentrations in the epilimnion and the presence of colder hypolimnetic conditions and deeper thermocline and Secchi depths, variability in zooplankton community structure in 2019 was likely related to migration behavior. Although migrating often incurs costs for zooplankton that remain in habitats with poor food availability and colder temperatures during the day, the threat of predation from remaining in the surface waters during the day could motivate this trade-off (Loose and Dawidowicz, 1994). However, there are several drivers that we did not measure in this study (e.g. phytoplankton community structure, fish population densities and predatory zooplankton abundance) that may be associated with zooplankton community variability and motivate future work.

Q3: How does zooplankton migration vary among taxa and over time?

We found that zooplankton exhibited both DVM and DHM simultaneously throughout the study period, emphasizing the value of considering both migration behaviors within the same ecosystem. We observed a slightly greater magnitude of DHM over DVM for all taxa, suggesting that the metabolic cost of remaining in anoxic conditions in the hypolimnion for extended periods of time may outweigh the risk of predation within littoral habitats (Doubek *et al.*, 2018). Because DVM and DHM are rarely studied together, we can only compare our results to a handful of studies that have observed both behaviors within the same waterbody (e.g. Carrillo *et al.*, 1989; DeStasio, 1993; Masson *et al.*, 2001; Meerhoff *et al.*, 2007; Antón-Pardo *et al.*, 2021). These studies attribute the presence of both migration strategies to light and predation pressure. Although Meerhoff *et al.* (2007) reported the presence of both DVM and DHM, they found that DVM was generally more prevalent, likely because fish predators use littoral macrophytes as a refuge. In BVR, a variety of environmental conditions may allow for DVM and DHM to occur simultaneously, including both vertebrate and invertebrate predation (Lampert, 1993; Lauridsen and Buenk, 1996).

We observed substantial plasticity in zooplankton migration behavior across all taxa during our study period (Fig. 8). These changes in migration behavior were likely due to taxon-specific functional traits and changing environmental conditions among years. We found that higher wind speed resulted in lower magnitudes of migration for cladocerans and copepods; however, there was no evident relationship between rotifer migration and other environmental drivers (Fig. S12). Additionally, zooplankton that exhibit typical DHM over typical DVM (as observed for cladocerans and copepods in 2019) suggests that they may not be able to tolerate hypolimnetic anoxia and, therefore, use the littoral habitat as a refuge from visual predators during the day instead (Vanderploeg *et al.*, 2009). Alternatively, typical DVM may have been more prevalent than typical DHM if predators (i.e. fish) were abundant at the littoral habitat during the day (Burks *et al.*, 2002). We observed the greatest magnitude of reverse DVM and reverse DHM in 2020, which was likely to avoid predators (i.e. fish) that were exhibiting typical migration behaviors and using the hypolimnion or littoral habitat during the day (Ohman *et al.*, 1983; Burks *et al.*, 2002; Lévesque *et al.*, 2010). Additionally, hypolimnetic temperatures and food resources (as indicated by chlorophyll *a*) were greater in 2020 than all other sampling dates, potentially providing a metabolic advantage for taxa that remained at depth during the night (Fig. S3; Haney, 1988).

While less is known about rotifer migration relative to the migration of larger, more motile zooplankton, we observed both DVM and DHM among rotifers. We observed that rotifers exhibited typical DVM and typical DHM in 2019 and 2020 sampling dates ($n = 3$), and reverse DVM and reverse

DHM during the 2021 sampling dates (n = 2), but these migrations occurred at smaller magnitudes compared to those of crustaceans. The smaller migration extent may be because rotifers experienced less planktivory given their small size and therefore did not experience as strong of a pressure to migrate as a predator-avoidance behavior (Brooks and Dodson, 1965). Given the prevalence of both invertebrates and crustacean zooplankton in BVR, rotifers likely altered their migration depending on the behavior of their predators (Gilbert and Hampton, 2001; Bezerra-Neto *et al.*, 2009). For example, rotifers exhibiting reverse DVM may have done so to avoid cladocerans that were exhibiting typical DVM (Dumont, 1972).

Overall, rotifers likely play important roles within the zooplankton community, but have often been overlooked, particularly in migration studies (Likens and Gilbert, 1970; Nowicki *et al.*, 2017; Karpowicz *et al.*, 2019). In the past, researchers have often focused more on crustacean migration than rotifer migration because rotifers are generally smaller, less motile, slower swimmers, and less susceptible to predation (de Paggi, 1995; Armengol and Miracle, 2000; Karabin and Ejsmont-Karabin, 2005), which may have led to an underestimation of rotifers' contribution to zooplankton migration and overall ecosystem functioning. However, this study and others (e.g. Carrillo *et al.*, 1989; Gilbert and Hampton, 2001) have documented substantial DVM and DHM behavior in rotifers, which can contribute up to 70–90% of total zooplankton biomass, thereby dominating zooplankton communities relative to crustaceans (Orcutt and Pace, 1984; Baranyi *et al.*, 2002). In Beaverdam Reservoir, rotifers comprised up to 50% of the total zooplankton biomass, motivating the need for future work on the magnitude and drivers of their migration behavior.

Overall, variability in migration behavior may partially explain variability in zooplankton community structure. During the 2020 sampling date, we observed the most variability in zooplankton community structure, which coincided with the greatest magnitude of reverse migration for crustacean zooplankton. Because reverse migration is often documented as a response to invertebrate predators (e.g. predatory zooplankton or *Chaoborus* that exhibit DVM), it is possible that invertebrate densities were higher in 2020 than all other sampling dates, though we do not have the data to test this hypothesis. Conversely, we found that low variability in zooplankton community structure in 2019 coincided with a greater magnitude of typical migration (Fig. S14). Consequently, these observations suggest that variability in zooplankton community structure is positively related to reverse migration and inversely related to typical migration. However, given the low range in variability across sampling dates, more data are needed to confirm this pattern. Studies focused on understanding how environmental variability affects migration behavior will help clarify the connection between zooplankton community structure variability and migration behavior.

CONCLUSIONS

This study quantified the relative importance of zooplankton dynamics between a pelagic vs. littoral site, among sampling dates, and among hours of the day to improve our understanding of variability in zooplankton community dynamics within a waterbody. We found that the greatest variability was observed among sampling dates over three consecutive summers rather than sites or hours of the day, which may be associated with both environmental drivers and migration behavior. Despite recent attention on the importance of diel variability in structuring zooplankton communities, our work suggests that monitoring programs should prioritize sampling across multiple days over multiple years to avoid underestimating variability in zooplankton community structure. Moreover, we demonstrate that zooplankton taxa may exhibit multiple migration patterns (typical and reverse DVM and DHM) within a single waterbody over sampling dates that span multiple years. Altogether, our study highlights the remarkable variability in both zooplankton community structure and migration behavior, underscoring the need to continually integrate spatial and temporal monitoring to better understand patterns of zooplankton community structure and behavior in freshwater ecosystems.

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SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

AUTHOR CONTRIBUTIONS

HLW and CCC conceptualized this study. HLW coordinated and led all sampling efforts, counted all zooplankton samples, and led the writing of this manuscript with CCC. HLW, ASL, MEL, DWH, WMW, and CCC helped with field sampling. ASL collated and processed CTD data. HLW, WMW, and DWH analyzed and processed chemistry data. HLW conducted all data analyses with substantial help from BLB and MEL. CCC secured funding for sampling and lab analyses. All authors contributed to drafting the manuscript and approved the final submitted version.

DATA AVAILABILITY

All data are available in the Environmental Data Initiative repository (https://portal.edirepository.org/nis/mapbrowse?scope=edi&identifier=197&revision=3; https://portal.edirepository.org/nis/mapbrowse?packageid=edi.197.2; https://portal.edirepository.org/nis/mapbrowse?scope=edi&identifie

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