Zooplankton Ecology of Lake Tahoe: Composition, Migration, and Influence on Plankton Particle Sizes Final Report

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Executive Summary

The impetus for this work stemmed from many conversations from 2018-2022 by the Tahoe Science Advisory Council and from scientific papers (Chandra et al. 2024) and reports (Cortes et al. 2022) that recommended filling a knowledge gap related to zooplankton dynamics in Lake Tahoe. In lakes, zooplankton can play an important role in transferring carbon (energy) from the lower food web (bacterial and algae) to higher-level consumers like fishes and amphibians, influencing the structure and function of the microbial and phytoplankton part of the food web through the excretion of dissolved organic carbon and nutrients, and grazing particulate matter through feeding. While published studies from Lake Tahoe have not supported the last point, it may be important in moderately productive parts of the lake, like Emerald Bay (Bess et al. 2021; Chandra et al. 2024), the lake's nearshore, or marinas.

An essential component of the Lake Tahoe clarity model, zooplankton-derived estimations inserted into the model are from 1-2 locations within the lake collected through unfunded efforts by UC Davis. In addition, there is no contemporary information about the lake's microzooplankton dynamics (i.e., rotifers and ciliates), and there is no understanding of zooplankton dynamics in vertical and horizontal space (nearshore to offshore). Previous snapshot studies captured some aspects of the variation of zooplankton in space and time. These studies were conducted when the lake was in a different state regarding clarity and algal production. The historical studies show a significant variation of invasive mysid shrimp (*Mysis diluviana*) and native zooplankton, suggesting 'patchiness' in vertical space, perhaps through daily migrations of zooplankton or due to methodological issues at the time of the study or variation within horizontal space (Goldman, 1974; Rybock, 1978, Morgan, 1981; Burgi, et al. 1993). Based on literature from other large lakes, we expect variation in zooplankton dynamics across space and time as zooplankton may migrate in the day and night. Hence, quantifying the contemporary composition and densities within Lake Tahoe could serve as important updates to model inputs (e.g., mass balance, statistical) that try to explain why Lake Tahoe's clarity is changing over time. This project implemented a comprehensive sampling across seasons in time and space to evaluate the dynamics of zooplankton over seasons and quantified the environmental variation in clarity and water quality across the lake. In addition, we investigated the community composition of microzooplankton, vertical migration patterns, and ecological effects of zooplankton on particles across nearshore and pelagic environments.

Clarity and water quality profile measurements can indicate the patch-scale variability of environmental conditions in the lake. Clarity, measured via Secchi disk, varied in time and space, serving as one indicator for how environmental conditions can vary in the lake in horizontal space. For instance, nearshore environments had a 40% lower Secchi disk depth when compared to the pelagic sites in May, except Emerald Bay, which had 55% lower Secchi values than the pelagic sites in May. The lowest Secchi disk values were recorded in May, and they increased up to 52% in July at the same site. In the pelagic habitat, the water quality profiles of temperature, chlorophyll-a, and dissolved oxygen were consistent with seasonal stratification patterns with changes in space and time. In contrast, chlorophyll-a and dissolved oxygen did not exhibit much variation in time and space in the nearshore sites. Both offshore and nearshore sites did not show significant variation by day versus night.

We found that zooplankton composition had distinct differences in community structure between pelagic, nearshore, and embayment sites. Due to its productive mesotrophic status, Emerald Bay showed the highest zooplankton abundance and diversity. Invasive mysid shrimp were observed at pelagic, long-term water quality monitoring sites (MLTP, LTP), and a South shore site with minimal presence in Emerald Bay. Mysids exhibited distinct distributions in space, influenced by sampling location and season. These results highlight the importance of future studies or monitoring programs incorporating collections in time and space, especially if those programs aim to determine more accurate characterizations of mysid dynamics (density, growth rates) and their influence on lake processes. Fortunately, historical snapshot studies have been undertaken from Lake Tahoe to understand the distribution of shrimp, which, if combined with modern tools (i.e., calibrated hydroacoustic instrumentation), can be used to develop a monitoring program for this larger zooplankton within the lake.

Zooplankton results include the first contemporary identification of 16 microzooplankton rotifers with a taxonomic key that can be used for future studies. We found a similar rotifer community between nearshore and offshore environments. We also saw a distinct pattern between Lake Tahoe and Emerald Bay, with the latter's mesotrophic conditions supporting a unique zooplankton community. The common species observed across all sites were the microzooplankton rotifers, *Kellicottia longispina,* and *Polyarthra dolichoptera*. Differences in microzooplankton species abundances align with historical data but highlight shifts potentially attributable to ecological changes in the lake. The density of microzooplankton rotifers and other zooplankton is notably much higher in our collections than in historical collections due to the methods used in this study. The methods employed in this study targeted the depths within the lake where we expected vertical migration in the present-day (e.g., photic zone) and used finer mesh to capture the microzooplankton. In contrast, historical studies used larger mesh-size nets and collected plankton across a more significant part of the water column, potentially diluting the actual concentration of plankton that could influence the area where particles influence lake clarity (e.g., top 40 meters). Thus, before creating a future monitoring program targeting zooplankton, we need to establish clear objectives and have discrete questions and linkages to other efforts (e.g., models) that are trying to understand the drivers of clarity changes in the lake.

The study reveals that while most zooplankton exhibit diel vertical migration, specific taxa (e.g., *Bosmina*, *Epischura,* and *Diaptomus)* display different behaviors depending on the site and season sampled. Also, analyzing the vertical and spatial concentration of macro- and microzooplankton, we found significant day-night differences across nearshore and offshore environments, demonstrating the complexity of their migration patterns with potential combined vertical and horizontal migration patterns. In short, day-to-night samplings need to occur in time and space to develop more accurate mean concentrations for different zooplankton taxa. This more accurate representation can then be used to assess the role of zooplankton on the lake’s water quality and clarity.

Using seminatural experiments with lake water from the nearshore and offshore habitats, we observed minimal impacts of grazing by zooplankton on the finer particle fractions, which are known to control clarity. The higher zooplankton densities may influence the dissolved organic carbon and nutrient concentration within the water, which could affect the functional processes related to microbes and phytoplankton. Exploring the influence of zooplankton and the

contributions of organic carbon and nutrient cycling via similar experiments over time that capture the much higher densities we observed during the monitoring, combined with bioenergetic modeling to understand the role of zooplankton excretion processes on microbe or phytoplankton growth, is warranted before making strong conclusions about the role of zooplankton on the ecosystem dynamics in the lake.

This study reinforces the idea that zooplankton populations are largely heterogenous in Lake Tahoe in horizontal and vertical space and time, adding to a notion that relying on a few stations to characterize zooplankton in the lake may lead to erroneous conclusions about their dynamics (e.g., density, composition) and role in the lake. Specific methods that quantify the density and composition must also consider the mesh size, depth of plankton collections, and preservation methods. In addition, comparing traditional (microscopy) to modern tools (metagenomics for ciliates and rotifers) may allow for a more functional characterization of the role of zooplankton within the lake. Finally, experiments that quantify the influence of zooplankton coupled with monitoring of natural populations in space and time could allow for an understanding of the fate of particles in the presence of different larger and smaller zooplankton taxa or the role of zooplankton in driving pelagic processes like bacterial and phytoplankton growth.

We note that this report has not been peer-reviewed by scientists. Depending on the resources and time available, the authors will try to reformat the report for submission to a peer-reviewed journal.

Background

Understanding the drivers of Lake Tahoe's declining water clarity has interested scientists and managers for many decades, particularly as the lake experiences continued cultural eutrophication and loss of clarity. Monitoring water quality and clarity has primarily been undertaken at two lake sites, providing an important opportunity to understand the intra- and interannual changes in the lake. However, to explain these changes and understand whether internal processes within the lake may influence water quality and clarity, additional variables like zooplankton dynamics need proper characterization within the lake as they can influence several fundamental lake attributes, like the availability of nutrients and organic carbon stimulating phytoplankton and bacterial growth, respectively. In addition, different zooplankton taxa may feed on particles of different sizes (Figure 1, Cortes et al. 2022).

The UC Davis Tahoe Environmental Research Center has monitored zooplankton from a few sites within the lake, providing an important characterization of zooplankton dynamics over time. For example, long-term monitoring has been used to show the decline or resilience of some native zooplankton as invasive mysid shrimp (*Mysis diluviana)* established within the lake (Richards et al. 1975). This largely unfunded effort by our UC Davis colleagues has limitations and utility for understanding how zooplankton influence the lake's water quality since zooplankton composition and density can be highly variable in time and space. In addition, Lake Tahoe's microzooplankton (i.e., ciliates and rotifers) have not been characterized in the present day even though they may play a role in governing the fate of fine particles in the lake, which influences clarity (Figure 1).

This study focused on collecting basic science information that can be used to improve the Lake Tahoe clarity model and support other efforts that are underway to understand how internal lake parameters, like zooplankton, might influence lake conditions. The project focused on quantifying the composition and density of micro- and macrozooplankton across nearshore and offshore lake habitats and the potential vertical migration and distribution during the day and night conditions. These attributes can help determine when and where to monitor zooplankton within the lake. We also determined the densities of invasive, predatory mysid shrimp in time and space; these opossum shrimp can serve as predators of other zooplankton, serve as filter feeders of algae and detritus, play a role in the cycling of carbon and nitrogen, and serve as a food source for the lake's main sport fishes, kokanee salmon (*Oncorhyncus nerka*) and lake trout (*Salvelinus namaycush*). Finally, we evaluate the influence of zooplankton on Lake Tahoe's clarity through a pilot experiment that characterized the changes in particle size distribution using lake water additions with different zooplankton concentrations. We organized the report findings based on the tasks assigned in the work order for this project.

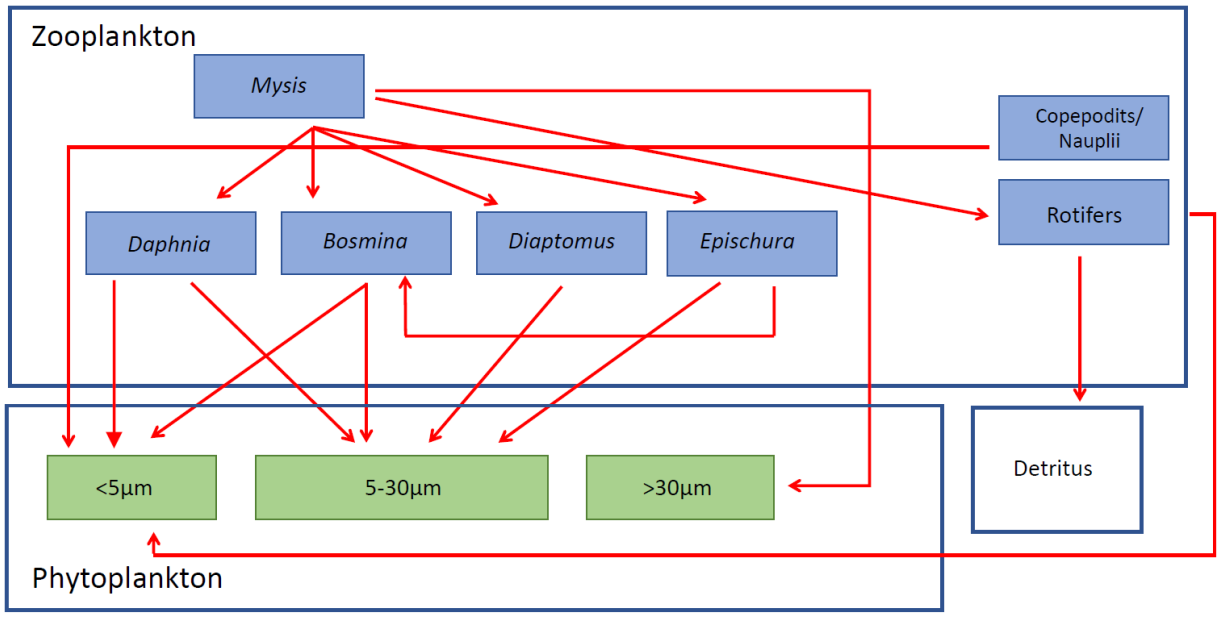


Figure 1. Zooplankton food web connection to particle size classes in Lake Tahoe. The arrows indicate hypothesized but simplified for model purposes, controls on the particle concentrations within Lake Tahoe. Source: Cortes et al. (2022).

Study Tasks

Task 1: Project Coordination.
A committee of scientists and resource management partners from institutions and agencies was created to coordinate and inform them of activities during the project's design and implementation phases. An example of the initial structure of the project and its relationship to the coordination committee is presented in Figure 2. During the project, the following people and their institutions helped guide the project: Steve Sadro, UC Davis; Jason Kuchnicki, Holly Holwager, Dr. Chris Fritsen from the Nevada Division of Environmental Protection; Dr. Melissa Thaw, California's Lahontan Water Quality Control Board; Dan Segan, Tahoe Regional Planning Agency; Laura Patten, League to Save Lake Tahoe; Bob Larsen, Tahoe Science Advisory Council; Phoebe Song, Dane Michels from the US Environmental Protection Agency). Semi-regular meetings were held to provide project updates and preliminary results. We anticipate having a final meeting with our coordination committee in the new year of 2025 to share the results of this project.

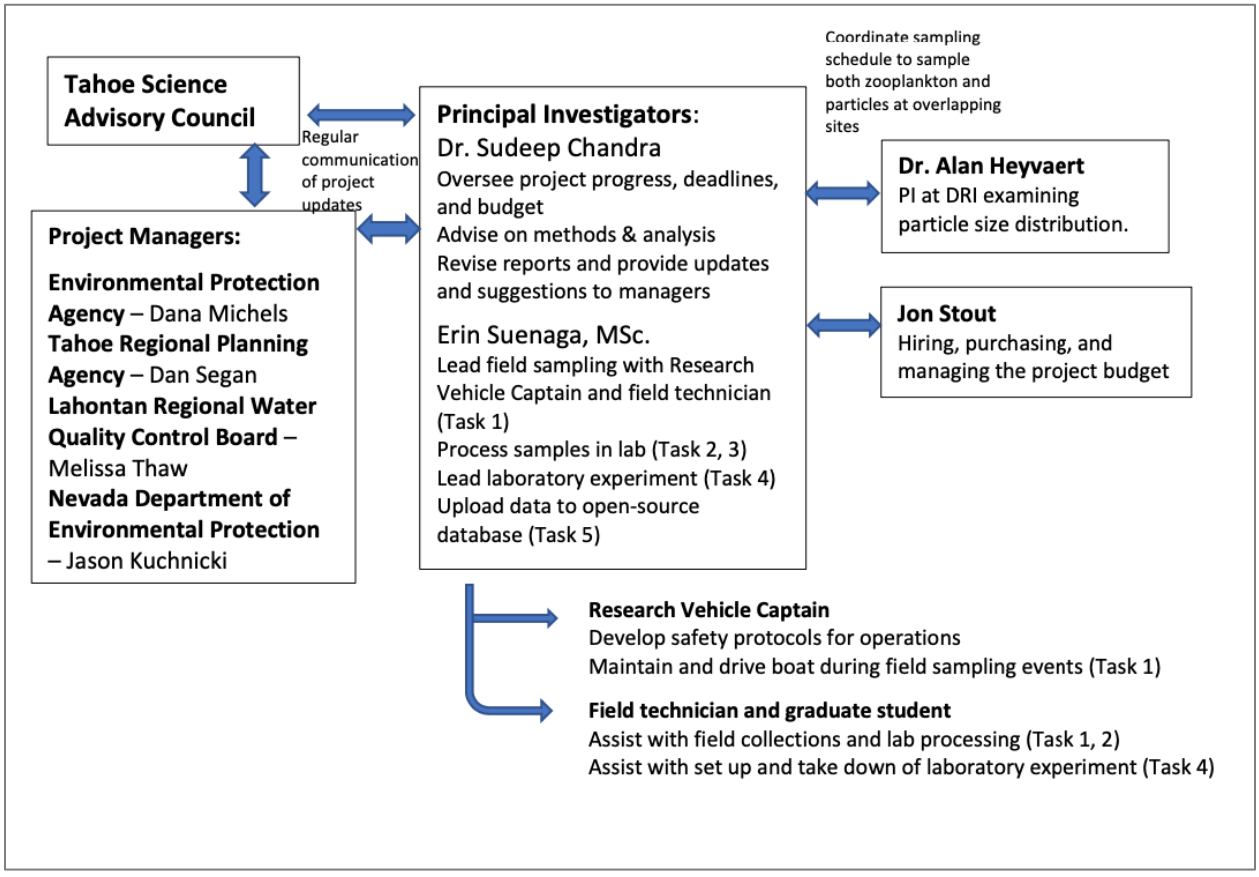


Figure 2. The initial structure of the project lists some of the coordination committee members and management partners who provided feedback during the implementation of the project.

Task 2: Collect macro- and microzooplankton samples from 10 locations around the lake.

Sampling site description

We quantified and identified the zooplankton species composition and density of macro- and microzooplankton at 10 locations around the Lake in May, July, September, and December 2023. The 10 locations included four pelagic sites, two long-term water quality monitoring sites funded by the agencies to UC Davis (MLTP, LTP), and two additional sites in the Southshore and Emerald Bay. Six nearshore sites (Incline Village, Dollar Point, Blackwood, Meek's Bay, Taylor Creek, Glenbrook Bay; Figure 3) were also sampled over time. Locations of sites were selected to encompass the full spatial extent and locations of river inputs into the lake.

Macrozooplankton sampling methodology

To sample macrozooplankton, we used an 80 µm mesh conical, closing net (0.75 m diameter) during the day and night at 10 m intervals from 0 to 110 m for pelagic sites (0-10, 20-30, 40-50, 60-70, 80-90, 100-110 m) or 0-15 m for nearshore sites (0-5, 10-15 m). We preserved the samples in a sucrose Lugol's solution, and the net was rinsed between hauls. To minimize the influence of light on the potential for vertical migration, we sampled the lake around the two weeks surrounding the new moon (May 19, July 17, September 19, and December 12). A winch was used to pull most of the nets to ensure consistency in hauls at a rate of approximately 0.4 m s^{-1}. When needed, the nets were pulled by hand. Daytime samples were taken between 9:30 am and 3:50 pm, and nighttime samples were taken a minimum of 1.5 hours after sunset and 2 hours before sunrise to capture zooplankton migration.

Mysis sampling methodology

Mysids were collected through vertical tows using a 1 m diameter net with 500 µm mesh at the four pelagic sampling sites at night. Samples were preserved in 70% ethanol. In May, samples were taken from 150 m depths at the MLTP, LTP, and south shore sites and down to 60 m in Emerald Bay at the deepest point. In July, September, and December, samples were taken to 200 m depths. Due to weather advisories, we could not collect a mysid sample from the LTP site in December despite repeated attempts to sample the lake. All mysid samples were taken over two hours after dusk when they entered the upper water column to feed and before dawn when they migrated back down to deeper depths. In the laboratory, we enumerated and measured the lengths of all mysids captured in the samples so future studies can determine cohort sizes and growth rates.

Microzooplankton sampling methodology

We sampled for microzooplankton (rotifers and ciliates) using an 8L Van Dorn or Niskin bottle and filtered the water through 10 µm mesh sieves. The pelagic site samples were pooled from water collected at 10, 20, 30, and 40 m for a total of 32 L, and the nearshore site samples were pooled from water collected at 5, 10, and 15 m depths for a total of 24 L. Organisms remaining on the mesh were carefully rinsed into a bottle using deionized (DI) water. Approximately $1/8^{th}$ of an Alka Seltzer tablet was added immediately to the sample bottle. Then, 1-2 hours later, we added 2-3 drops of rose Bengal stain and formalin to make a 3 % (protocol adapted from Thomas et al., 2017; Sweeney et al., 2022).

Water quality measurement profile methodology

At each site, both day and night, profiles for temperature, dissolved oxygen (DO), and chlorophyll-a (chl-a) were taken using a Ruskin RBR *Concerto* or M*aestro.* Profiles were taken to approximately 100 m (the lowest depth recommended by RBR) at the pelagic sites and to approximately 15-20 m at the nearshore sites, trying to avoid hitting the bottom of the lake. We measured clarity at each site during the day using a 30.4 cm diameter Secchi disk. We could not take measurements at some sites because weather conditions prevented accurate readings.

Task 2: Findings and discussion

Four hundred twenty-five samples were collected for zooplankton, including pelagic and nearshore sites. During the sampling period, the Secchi disk varied spatially and temporally; the lowest values were recorded in May (e.g., 8.9 m at Blackwood and 9 m at Glenbrook), while the highest values were measured in July (e.g., 18.9 m at MLTP and LTP). Lower Secchi disk values were observed in May in the pelagic and nearshore environments, while higher measurements were recorded in September (Table 1, Figure 4). Also, nearshore environments had lower (range: 9-16.8 m) Secchi disk depth than the pelagic sites (range: 11-18.9 m) in all the temporal measurements, except for Emerald Bay (range: 6.7- 13.3 m).

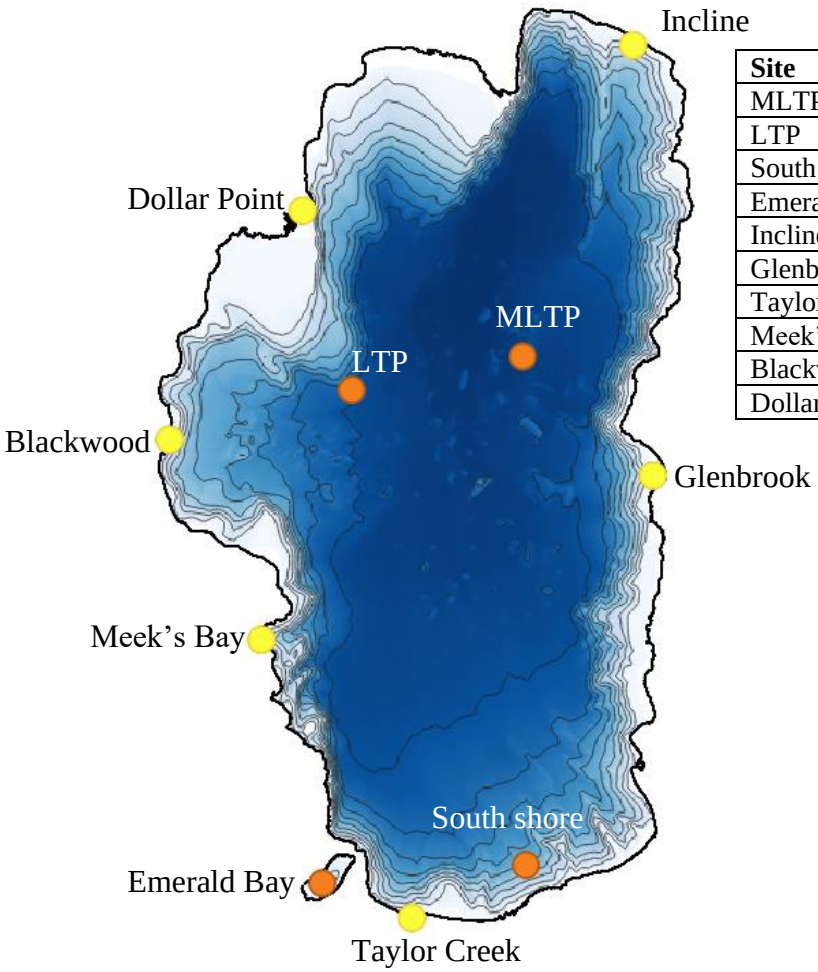
Eighty RBR water quality profile measurements, including temperature, chlorophyll a, and dissolved oxygen, were measured while sampling zooplankton at the 10 stations during the day and night. Measurements recorded by the RBR during May, July, September, and December at the pelagic site LTP for chlorophyll, temperature, and dissolved oxygen were different across months. Day and night measurements had minimal variation (Figures 5 and 6). The temperature profile shows the progression of the thermocline during the summer, with maximum stratification in September. Chlorophyll-a presented the maximum peak of around 27 m between May and Sep. Dissolved oxygen presented the maximum values at around 25 m, with a decreasing trend in depth. The values recorded by the RBR during May, July, September, and December at the nearshore site Glenbrook for chlorophyll-a and dissolved oxygen did not vary temporarily, except for the temperature profile (Figure 6). The temperature profile shows mostly a well-mixed water column, except in May. Chlorophyll-a and dissolved oxygen did not vary through the profile. Day and Night measurements were similar.

Per the deliverable for this task, we have shared a project folder containing data, field notes, and any relevant protocols used during this project so future studies can make comparisons with this study. In brief, the data includes:

- The 425 zooplankton samples collected from the 10 stations, during day and night.
- We anticipate placing the preserved zooplankton samples and copies of the field notes collected during this project at the Natural History Museum at the University of Nevada, Reno, so others can review these samples.
- The 80 RBR measurements, including temperature, chlorophyll a, and dissolved oxygen were measured while sampling zooplankton at the 10 stations during the day and night. Recorded data has been submitted with this report.
- The 40 Secchi measurements at the 10 stations during May, July, September, and December have been submitted with this report.

Table 1. Secchi disk measurements in May, July, September, and December 2023.

	Site	May	July	September	December
Pelagic	**MLTP**	14.8	16.2	18.9	15.2
	LTP	NA	16	18.9	15.2
	Southshore	11	11	17	16.2
	Emerald Bay	6.7	NA	13.3	11.5
Nearshore	**Blackwood**	8.9	NA	16.8	14.5
	Meek's Creek	15.4	NA	16.8	15
	Taylor Creek	NA	13	15.4	15.3
	Dollar Point	14.7	15.8	16.8	NA
	Incline	10.3	15.2	16.7	15.1
	Glenbrook	9	14	13.7	13.7



Site	Coordinates
MLTP	39.131111, -120.00278
LTP	39.121667, -120.07750
South shore	38.958889, -120.00861
Emerald Bay	38.95500, -120.090722
Incline	39.235231, -119.95019
Glenbrook	39.089332, -119.94791
Taylor Creek	38.942264, -120.05881
Meek's Bay	39.038141,-120.120191
Blackwood	39.106781, -120.15740
Dollar Point	39.182901, -120.09638

Figure 3. Pelagic (orange) and nearshore (yellow) sampling sites for macro- and microzooplankton samples in May, July, September, and December 2023, with GPS coordinates for each sampling location. Locations were determined based on historical collections made in the literature and to complement the existing long-term water quality and clarity monitoring funded by the agencies to UC Davis (e.g., sites MLTP and LTP).

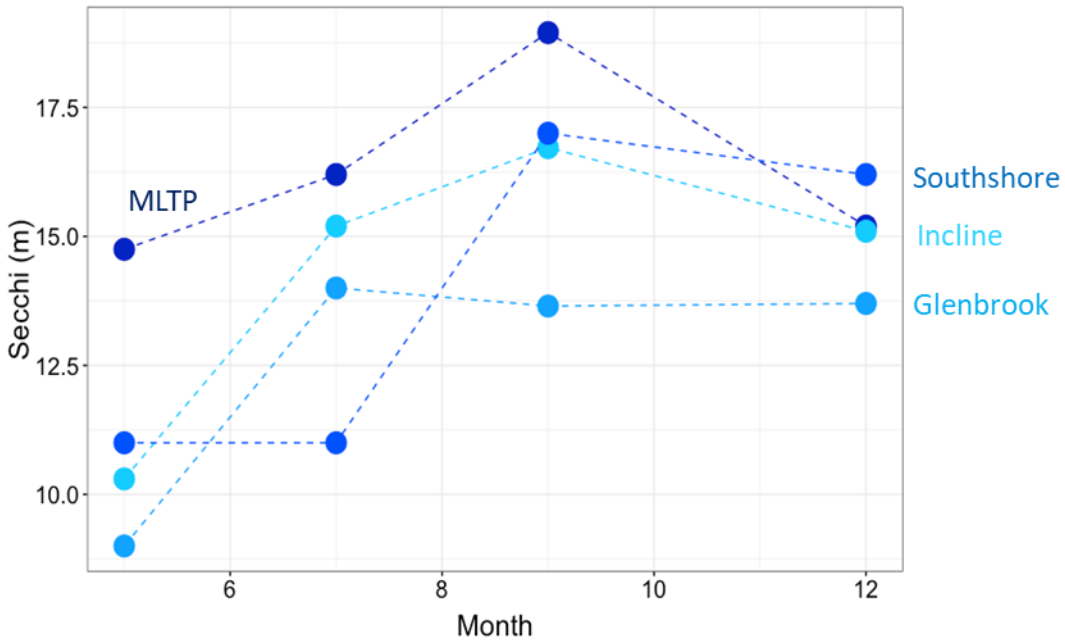


Figure 4. Secchi disk measurement at MLTP, South shore, Incline, and Glenbrook between May – Dec 2023. Note the variability in space and time across and within sites, indicating the environmental conditions across the lake may not be the same as where the long-term monitoring locations are conducted at the MLTP site.

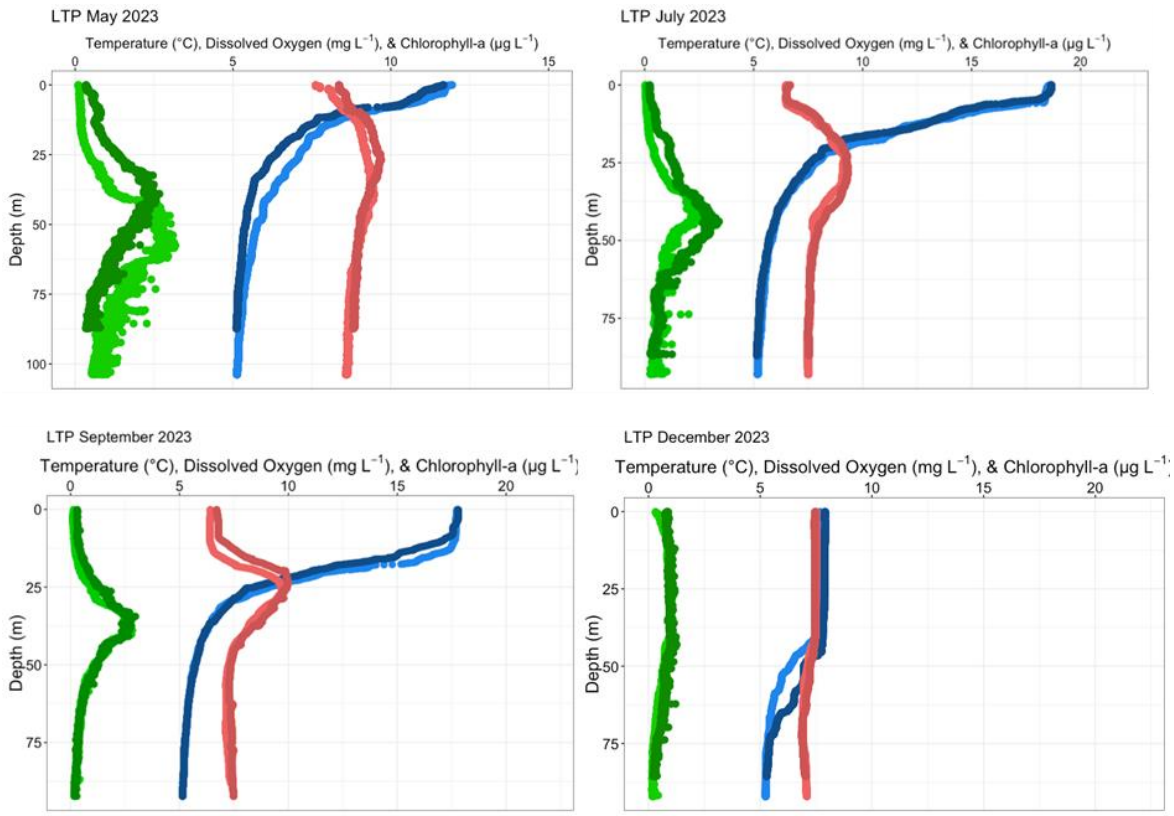


Figure 5. Day and Night RBR measurement of chlorophyll a (Green), dissolved oxygen (Red), and temperature (Blue) between May – Dec 2023 at LPT. Day is the dark shade, and night is the light shade.

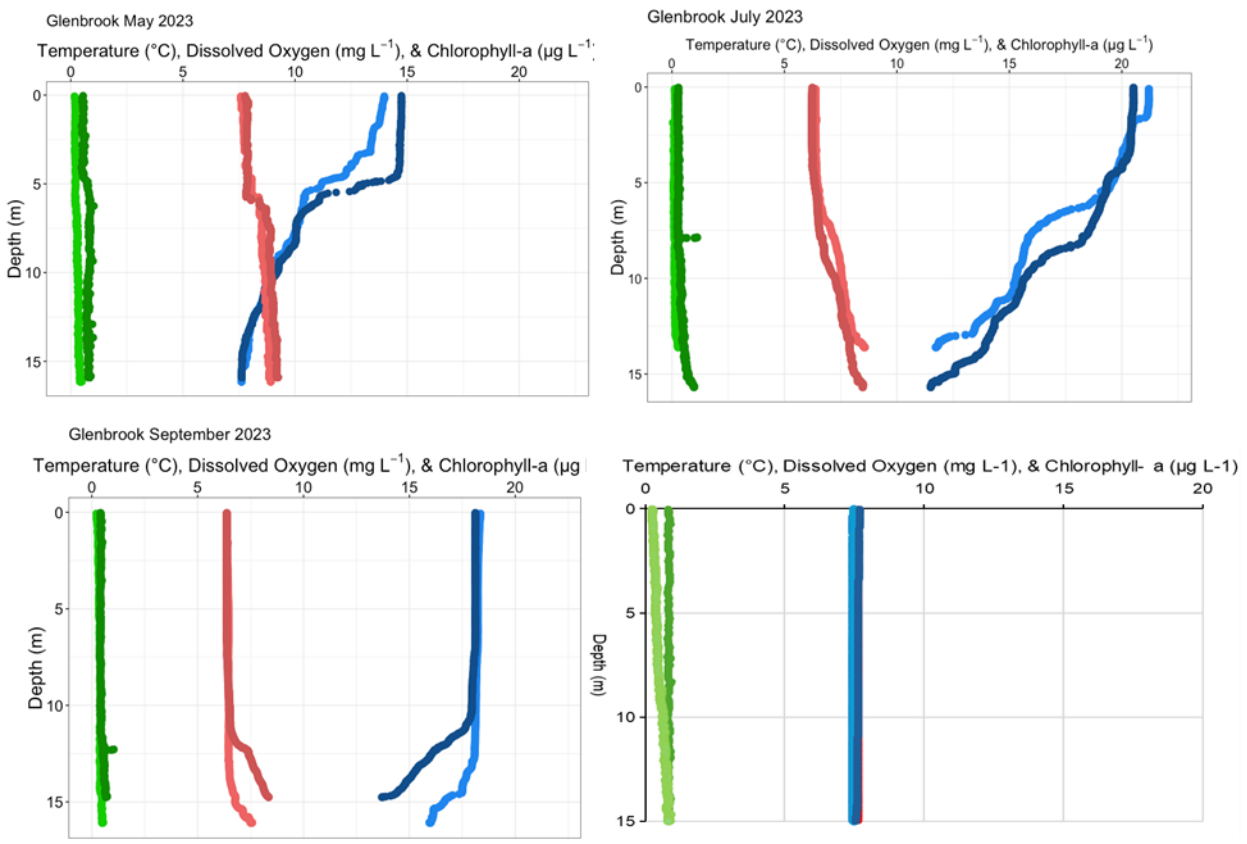


Figure 6. Day and Night RBR measurement of chlorophyll a (Green line), dissolved oxygen (Red line), and Temperature (Blue line) between May – Dec 2023 at Glenbrook. Day is the dark shade, and night is the light shade.

Task 3: Count, identify, and measure macro- and microzooplankton from samples.

All samples collected in Task 2 were transported back to the University of Nevada's Aquatic Ecosystems and Analysis laboratory for enumeration and identification.

Methodology for counting and identification of macrozooplankton and mysids

The zooplankton samples were diluted with DI water to 100 mL (or 200 mL in the case of very high densities), homogenized using a magnetic stir bar and plate, and five 5 mL subsamples were placed into a counting maze for enumeration under a dissection microscope. Zooplankton were identified to the species level, with lengths and egg numbers noted for individual *Daphnia* and *Bosmina*. Copepods were identified by species and age class (adult, juvenile, nauplius), and adults were identified as male or female. Values for each subsample were summed and converted into units of individuals per cubic meter using the net tow volume of either 4.42 m^3 (10 m haul interval for pelagic sites) or 2.21 m^3 (5 m haul interval for nearshore sites). We enumerated and measured the lengths of all mysids captured in the samples under a dissection microscope.

Methodology for counting and identification of microzooplankton

The rotifer samples were enumerated and identified to the species or genus level using a compound microscope at varying magnification levels. We consulted with experts for confirmation on species identification. Individual rotifers were placed onto a microscope slide for speciation, and the trophi (jaw bones) were isolated by dissolving the outer body with concentrated bleach. We examined the structure of the trophi under 100x magnification with oil immersion. The entire sample was analyzed, and concentrations were calculated by dividing the total counts by the volume of water filtered (32 L or 24 L for the pelagic and nearshore sites, respectively). Rotifer samples were enumerated and identified to the species level where possible, and a taxonomic list and identification key were created so others could identify samples in the future. The same samples were used to identify rotifers and ciliates. A set of test samples for ciliate identification were sent to an expert, Dr. David Carron, from the University of Southern California for evaluation.

Task 3: Finding and discussion

Note we could not directly compare densities with historical data because historical samples were collected with larger mesh (80 µm) and long net tows through the water column (0-150 m). We modified methods, using a smaller mesh, sometimes with water collections from discrete depths, so we could ensure the capture of microzooplankton and so we could determine concentrations within the area of the clarity readings at Lake Tahoe. Extending collections using longer net tows as initiated by the historical sampling into the deep waters may reflect the actual density of zooplankton within, affecting the lake's clarity as determined by the lake clarity model or other analysis. Where possible, we compare the species assemblages from historical studies with those from the present day. No notable changes in macrozooplankton composition are identified, but there is some new information related to the composition of rotifers and the dominance of zooplankton during the different times of the year.

Macrozooplankton

In Figures 7-20, we observe the concentrations and distributions of the primary taxa through the water column, across sampling sites and in day and night conditions. We found spatial and temporal differences in the community compositions and densities at Lake Tahoe between nearshore and offshore environments (Figures 7-20; Table 2). In addition, we observed variation in the density of macrozooplankton between day and night at the same site (e.g., Glenbrook and Incline Village location during May sampling). As expected, we observed the highest zooplankton density during July in all the sites, with copepod nauplii being the dominant taxa in all the sites during day and night conditions (Figures 7 and 8), *Epischura* and *Bosmina* were the following most abundant taxa in the nearshore environment and *Cyclopods* and *Epischura* in the offshore sites. Also, Emerald Bay, the lake's more productive embayment, was the only site that presented relatively stable concentrations in time and the highest concentrations of zooplankton, particularly cladocerans. Nevertheless, we found strong spatial variability in density and taxa in May, September and December. In May, we observed higher density offshore than nearshore, also *Cyclopods, Diaptomous, and Epischura* were the most abundant taxa in the nearshore sites (e.g, Incline Village, Dollar Point, and Glenbrook) (Figures 9 and 10), while copepod nauplii and *Cyclopod* dominated offshore sites. During September, density decreased in all the sites, but with an abrupt change in some of the nearshore sites (Incline Village, Blackwood, and Taylor Creek); at the nearshore sites, *Epischura* and *Bosmina* were the dominant taxa, while *Epischura* and *Cyclopods* were most abundant at offshore sites. Finally, during December, all the sites have lower densities, except for Emerald Bay, and *Epischura, Cyclopods, and Diaptomous* were the dominant taxa.

Vertical variability in abundance and composition was also observed (Figures 11-20). In general, *Epischura* and *Leptodiaptomus* calanoid copepods were found in the highest abundance in the top 10 m of the water column in the summer months of July and September. *Diacyclops thomasi*, cyclopoid copepods, were most abundant at the pelagic sites in the 20-70 m depth range. *Daphnia spp* were found in relatively low abundances at most sites during most seasons (<10 individuals m-3), except for Emerald Bay, where concentrations ranged from 0 to 652 individuals m^{-3}. *Bosmina longirostris* concentrations varied greatly across samples, 0 to >6000 individuals m^{-3}. *Bosmina* were observed at the highest concentrations in July, particularly in the nearshore sites of the lake. The concentrations of the different zooplankton taxa were variable between sites and depths, which supports previous studies showing the patchiness of zooplankton communities in Lake Tahoe (Burgi et al. 1993; Folt et al. 1993). The vertical migration of zooplankton is discussed in Task 4.

We compared the zooplankton community structure between the nearshore and pelagic communities in Lake Tahoe during the whole sampling period using a non-metric multidimensional scaling, a distance-based ordination technique (Figure 21). Nearshore, pelagic, and Emerald Bay zooplankton communities were significantly different from each other (ANOSIM, $R=0.35$, $p<0.001$). Emerald Bay communities are characterized by high concentrations of cyclopoid copepods, *Daphnia,* and *Holopedium*. Nearshore sites are comprised of higher concentrations of *Bosmina* and *Epischura*.

Holopedium glacialis was very abundant in July in Emerald Bay. It was not commonly observed in other pelagic or nearshore samples but was consistently found in the more productive embayment of Lake Tahoe.

Table 2. Lake Tahoe macrozooplankton species list identified in samples collected in 2023.

Macrozooplankton species list
Diaptomus sp.
Epischura nevadensis
Cyclopoid sp.
Nauplii sp.
Bosmina longirostis
Daphnia spp.
Chydoridae sp.
Leptodiaptomus tyrelli
Holopedium sp.
Diacyclosps thomasi

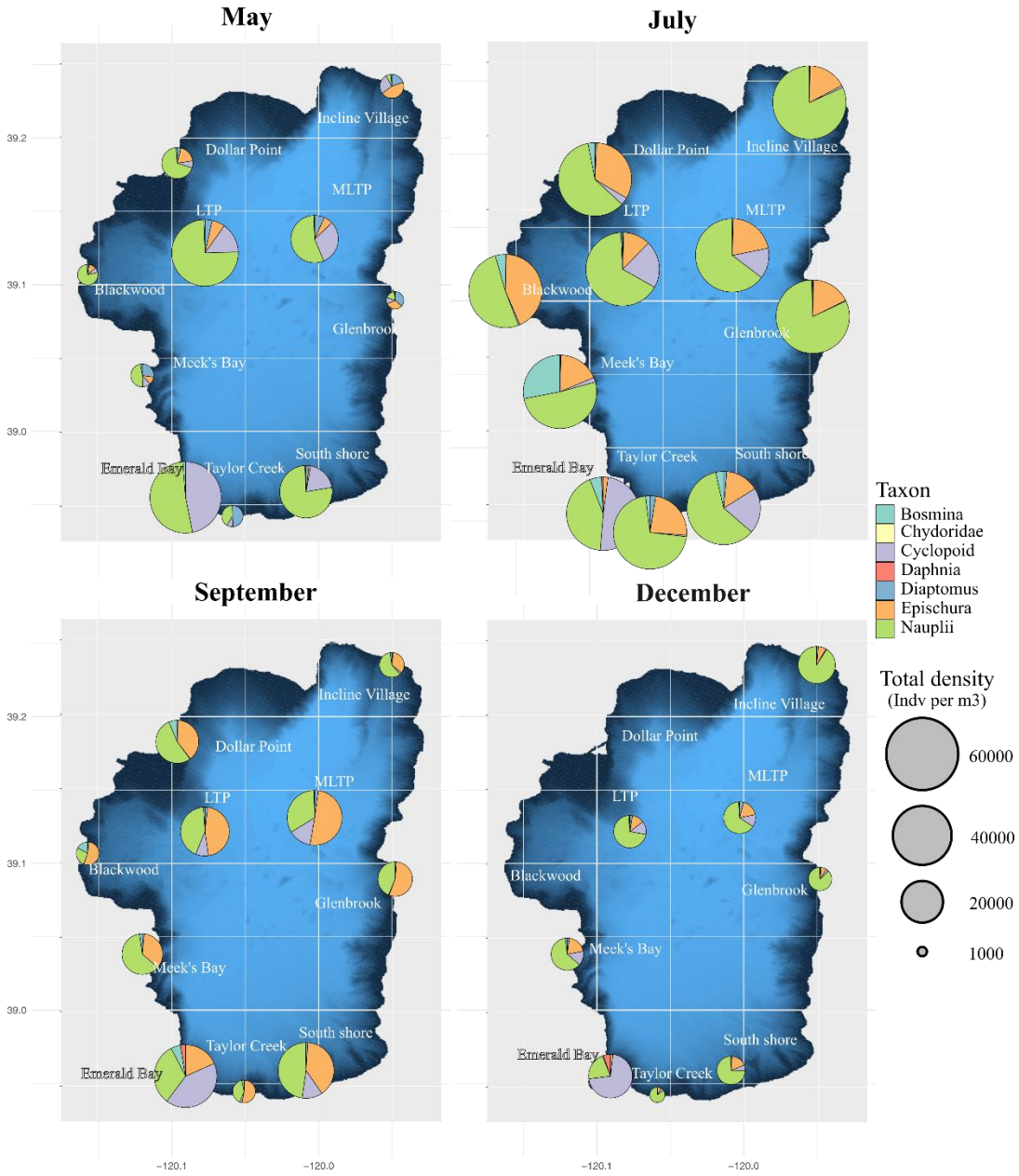


Figure 7. Spatial and temporal variability of the total macrozooplankton concentration and community composition during the day at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meek's Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites.

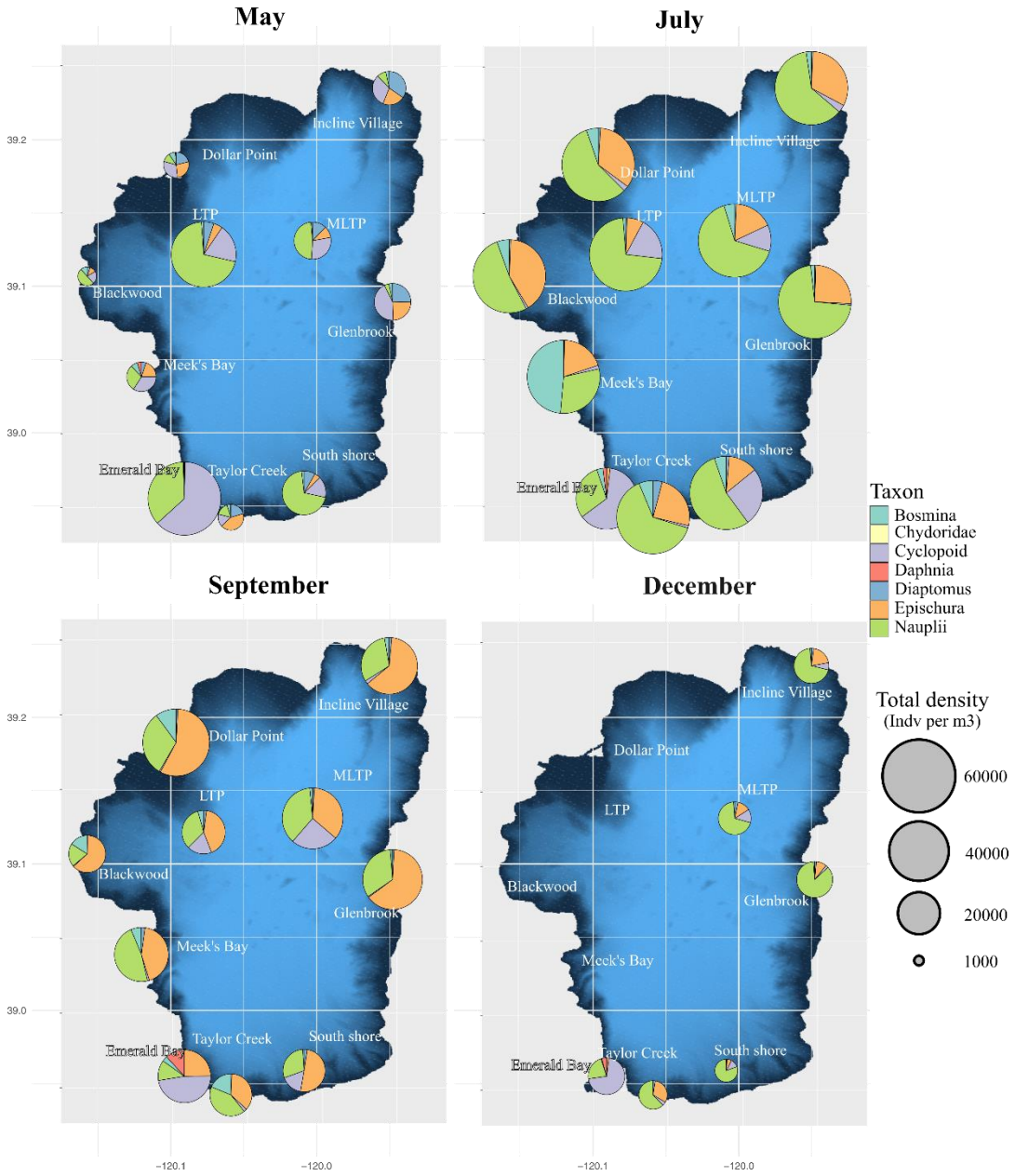


Figure 8. Spatial and temporal variability of the total macrozooplankton concentration and community composition during the night at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meek's Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites.

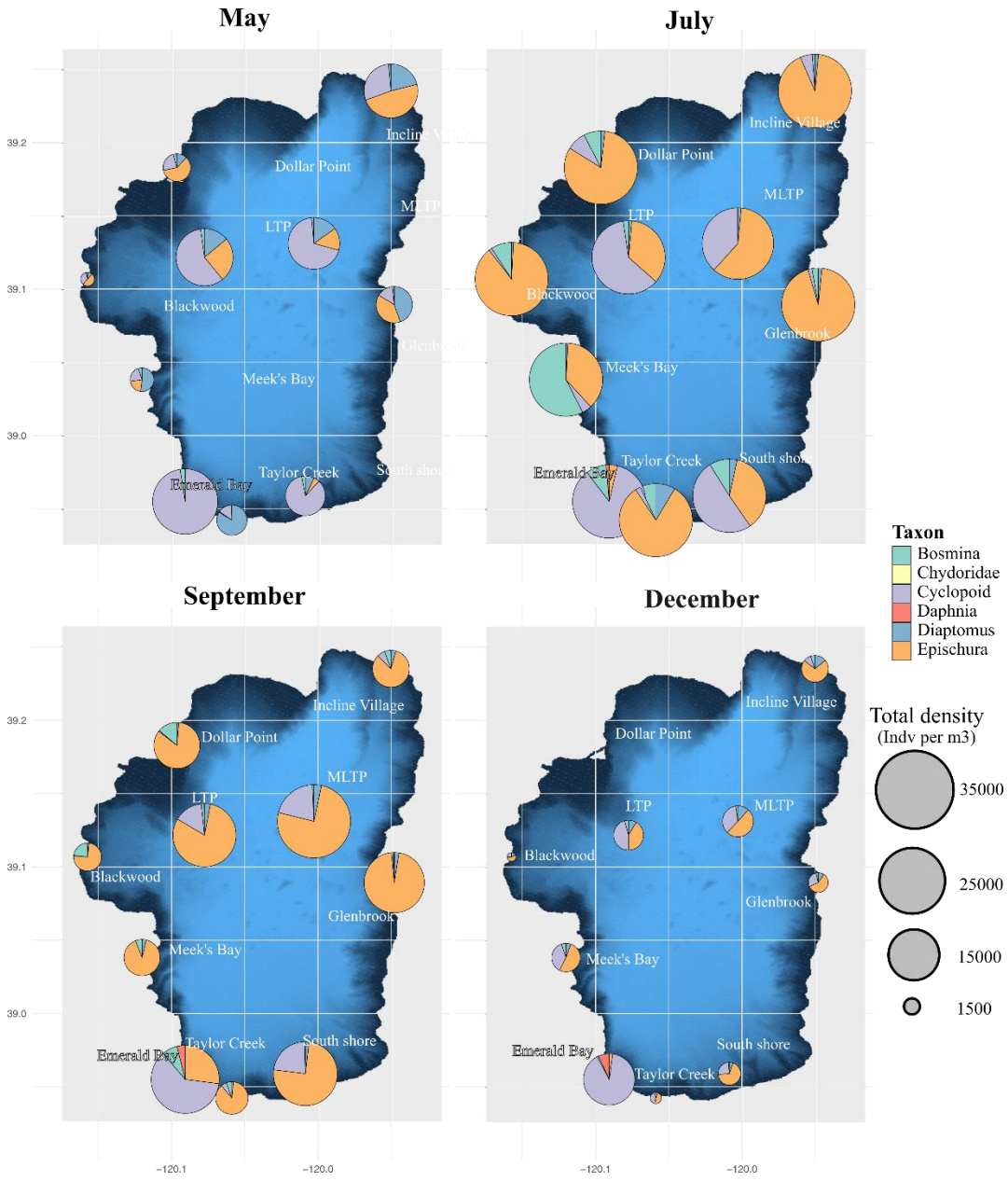


Figure 9. Spatial and temporal variability of the total microzooplankton density and community composition, excluding copepod nauplii during the day at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meek's Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites.

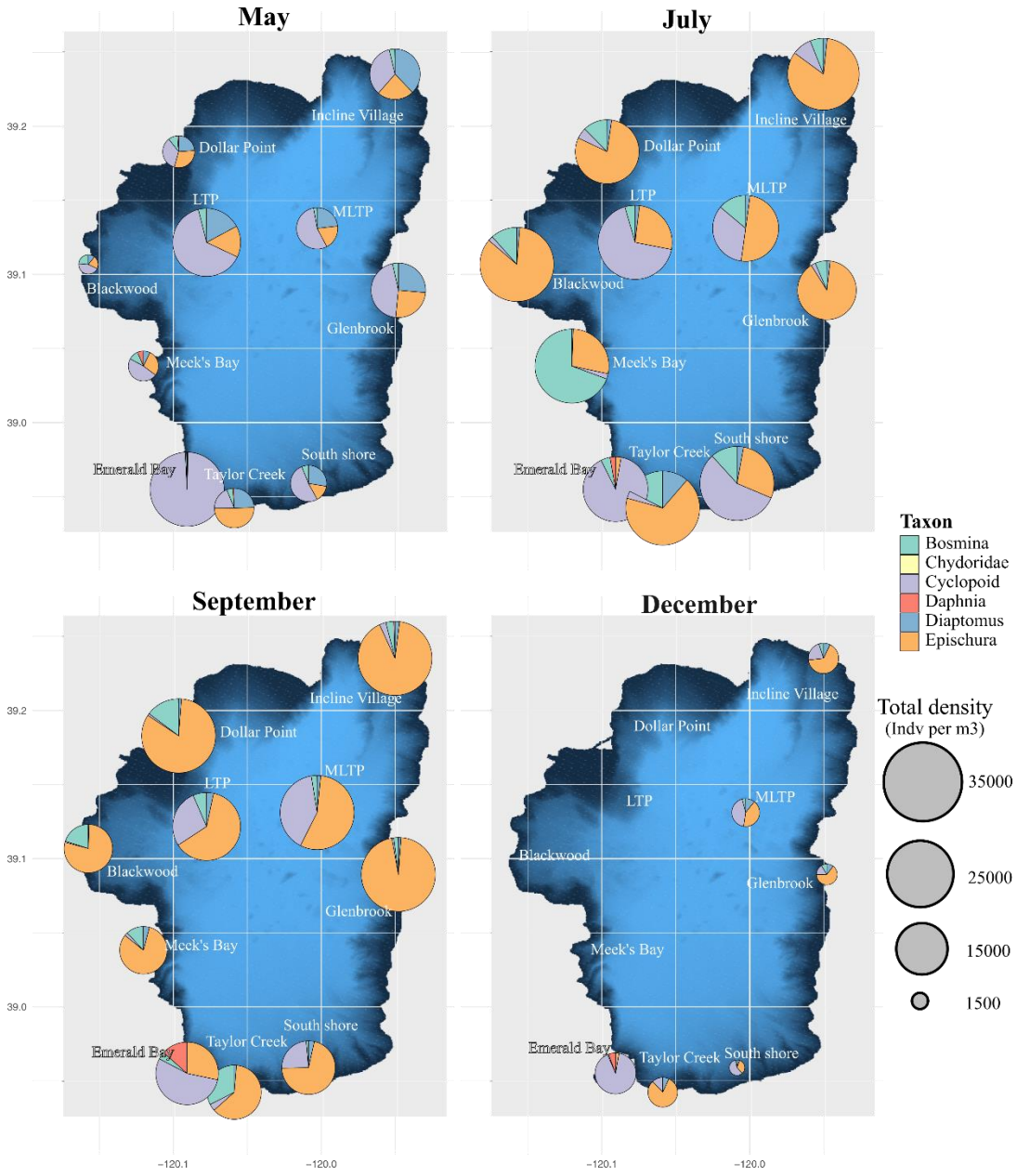


Figure 10. Spatial and temporal variability of the total microzooplankton density and community composition excluding copepod nauplii during the night at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meek's Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites.

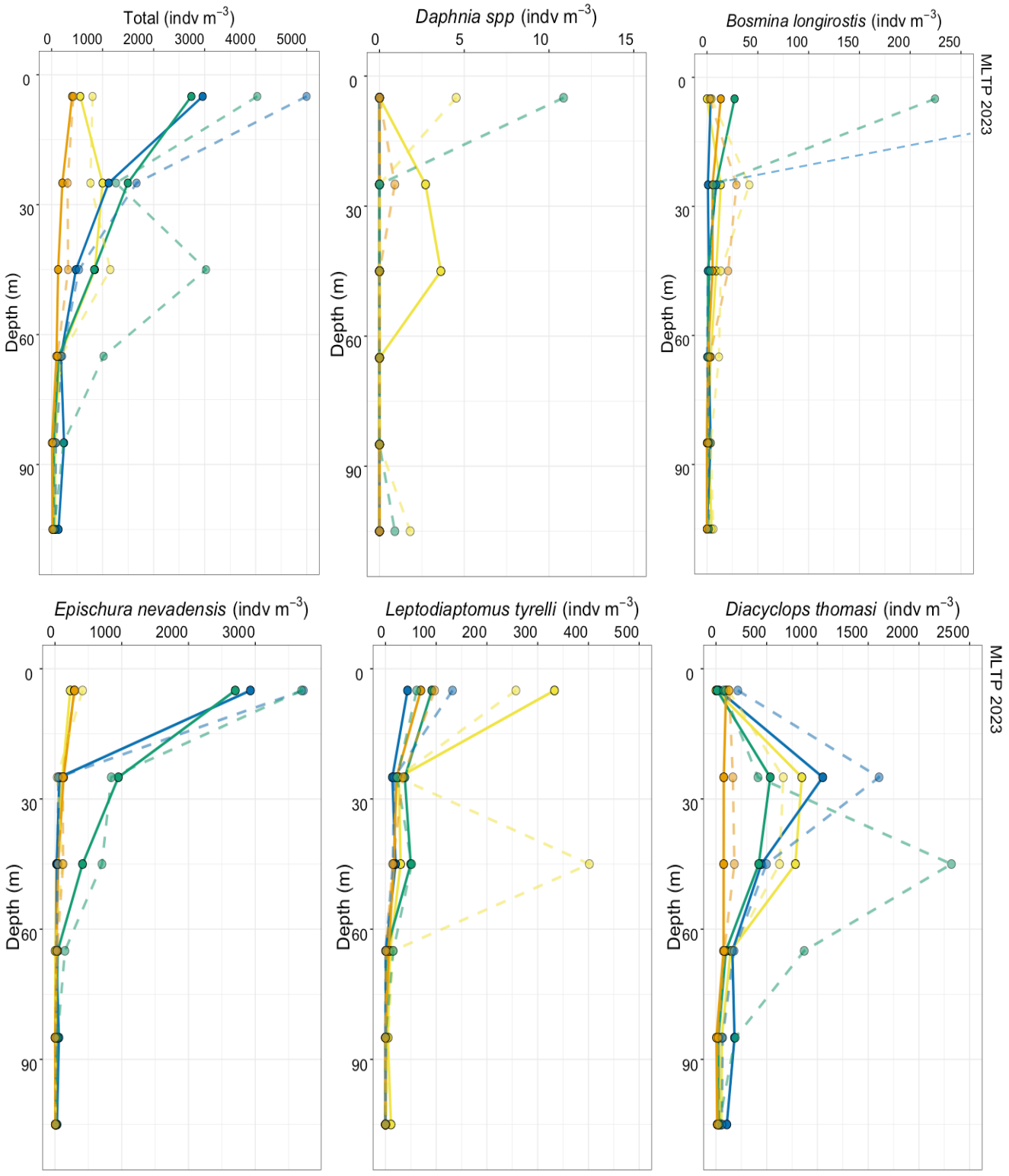


Figure 11. Concentrations of common zooplankton taxa in Lake Tahoe at MLTP site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

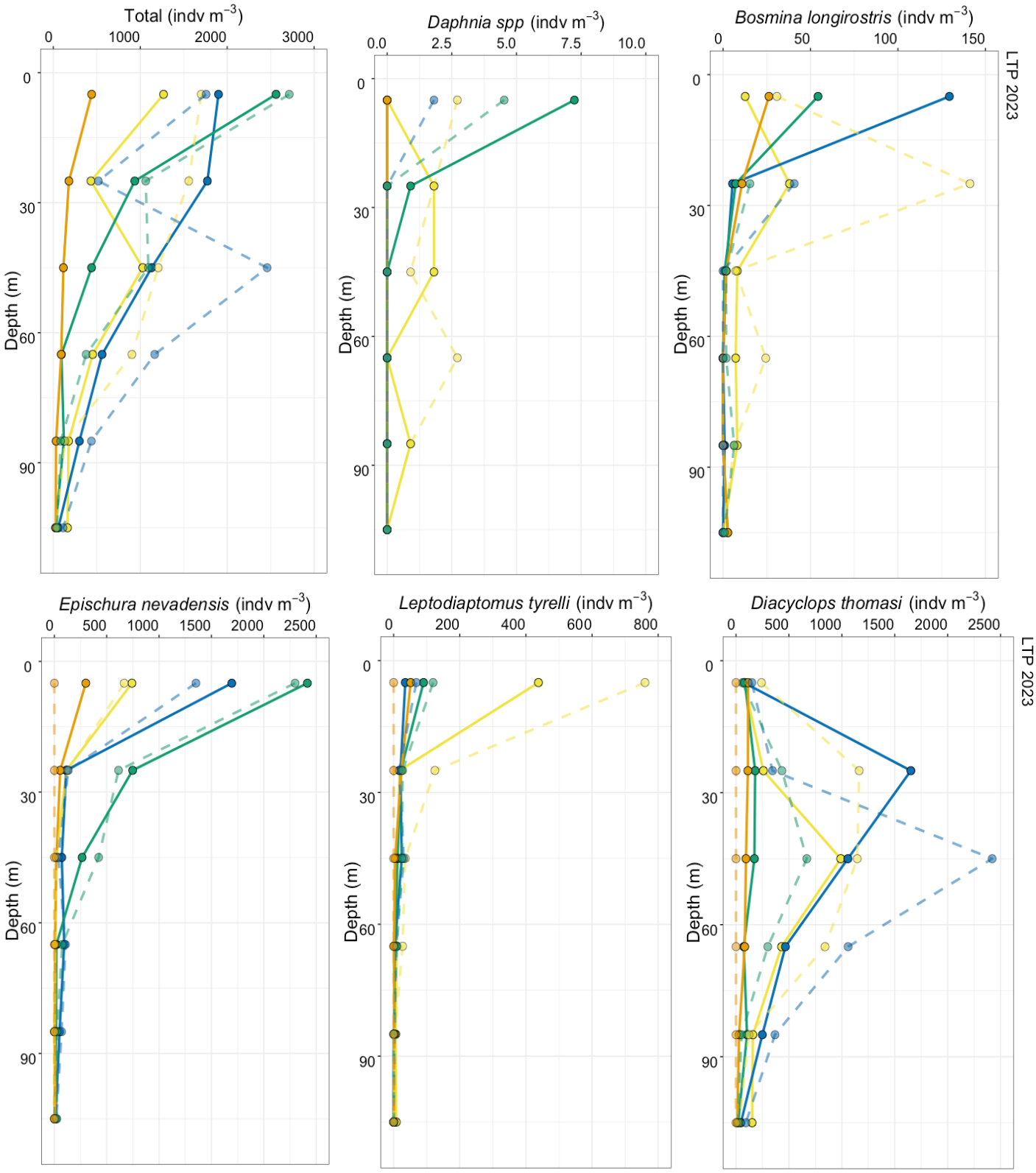


Figure 12. Concentrations of common zooplankton taxa in Lake Tahoe at LTP site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

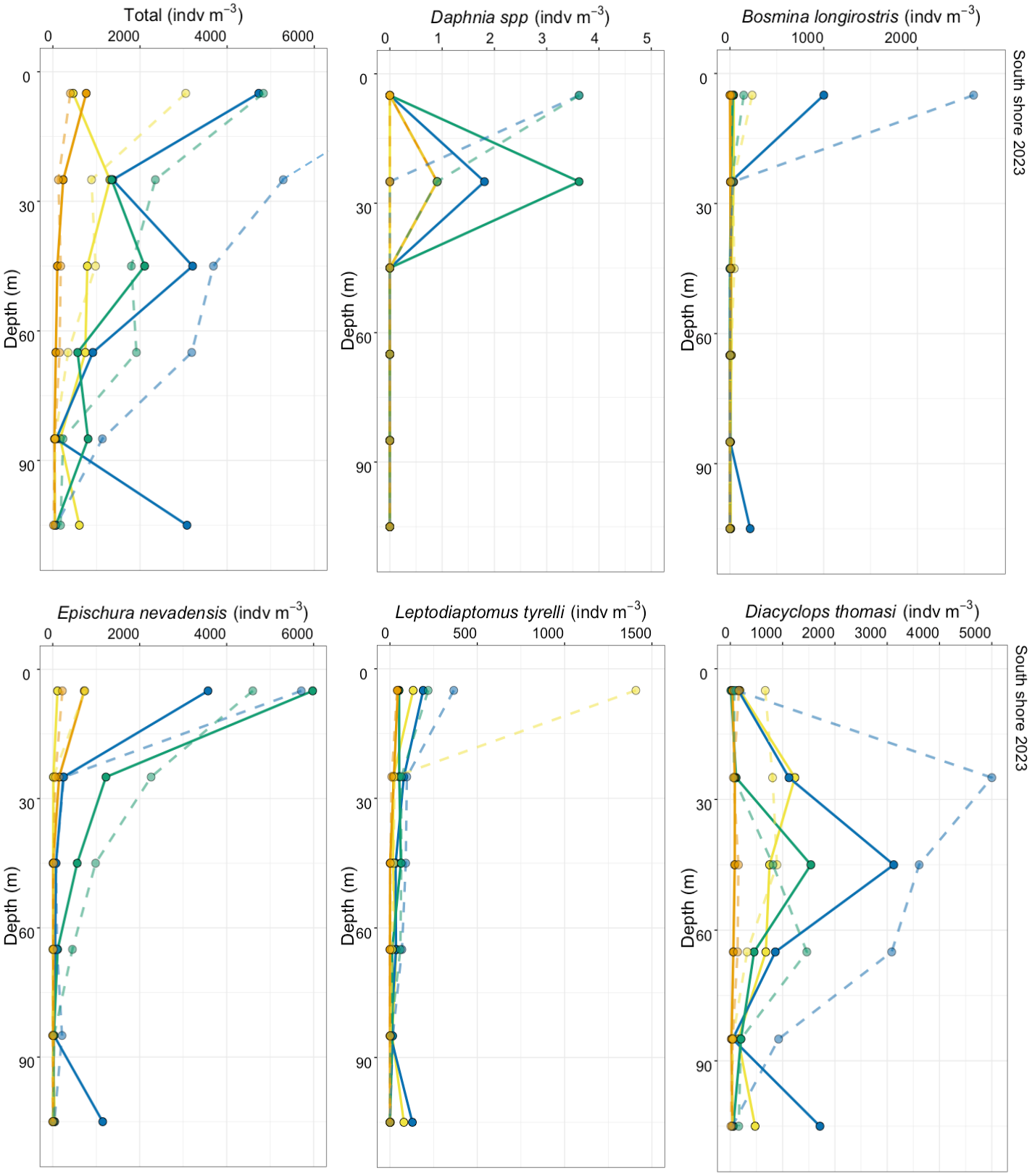


Figure 13. Concentrations of common zooplankton taxa in Lake Tahoe at South shore site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

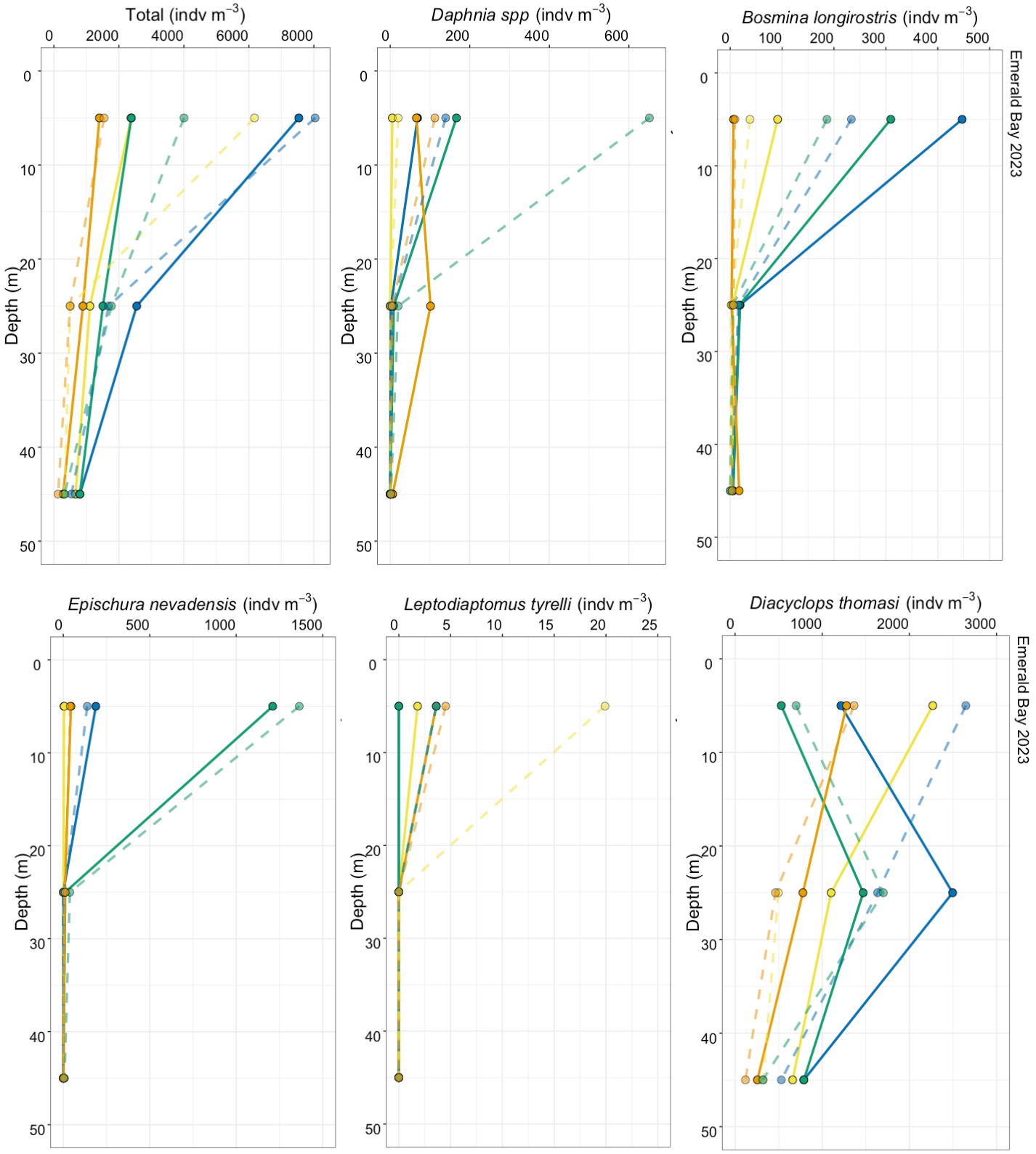


Figure 14. Concentrations of common zooplankton taxa in Lake Tahoe at Emerald Bay site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

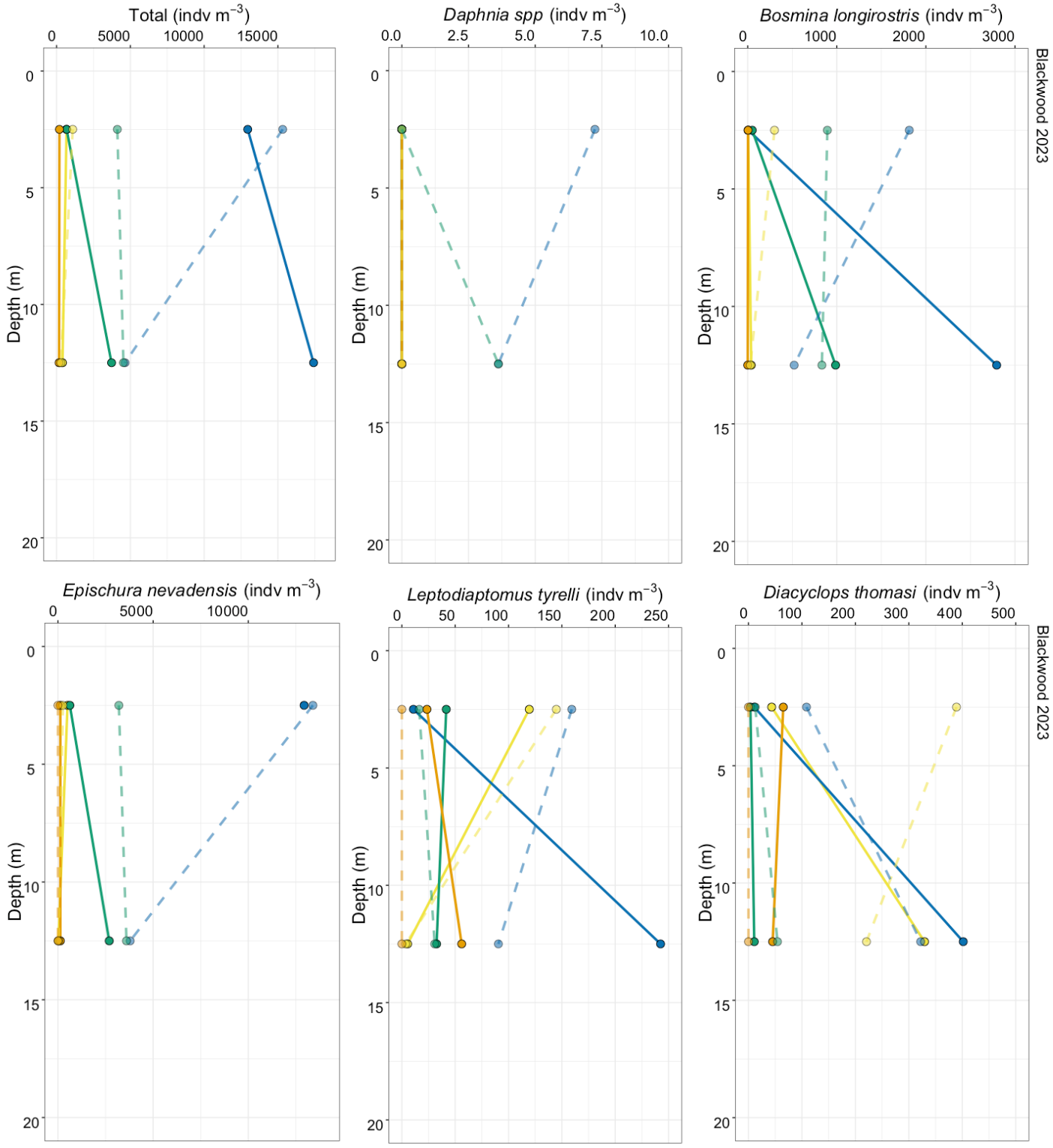


Figure 15. Concentrations of common zooplankton taxa in Lake Tahoe at Blackwood site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

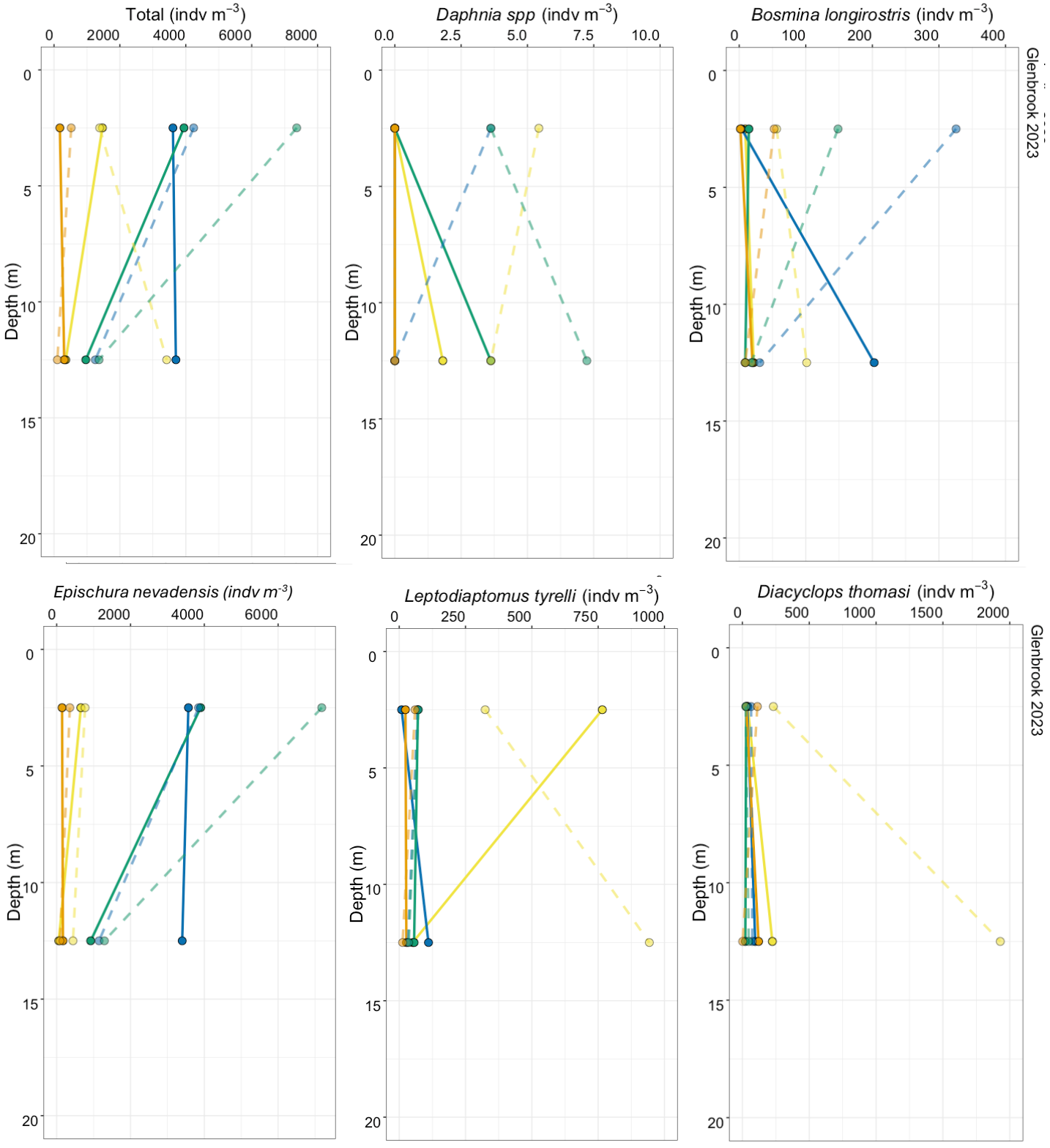


Figure 16. Concentrations of common zooplankton taxa in Lake Tahoe at Glenbrook site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

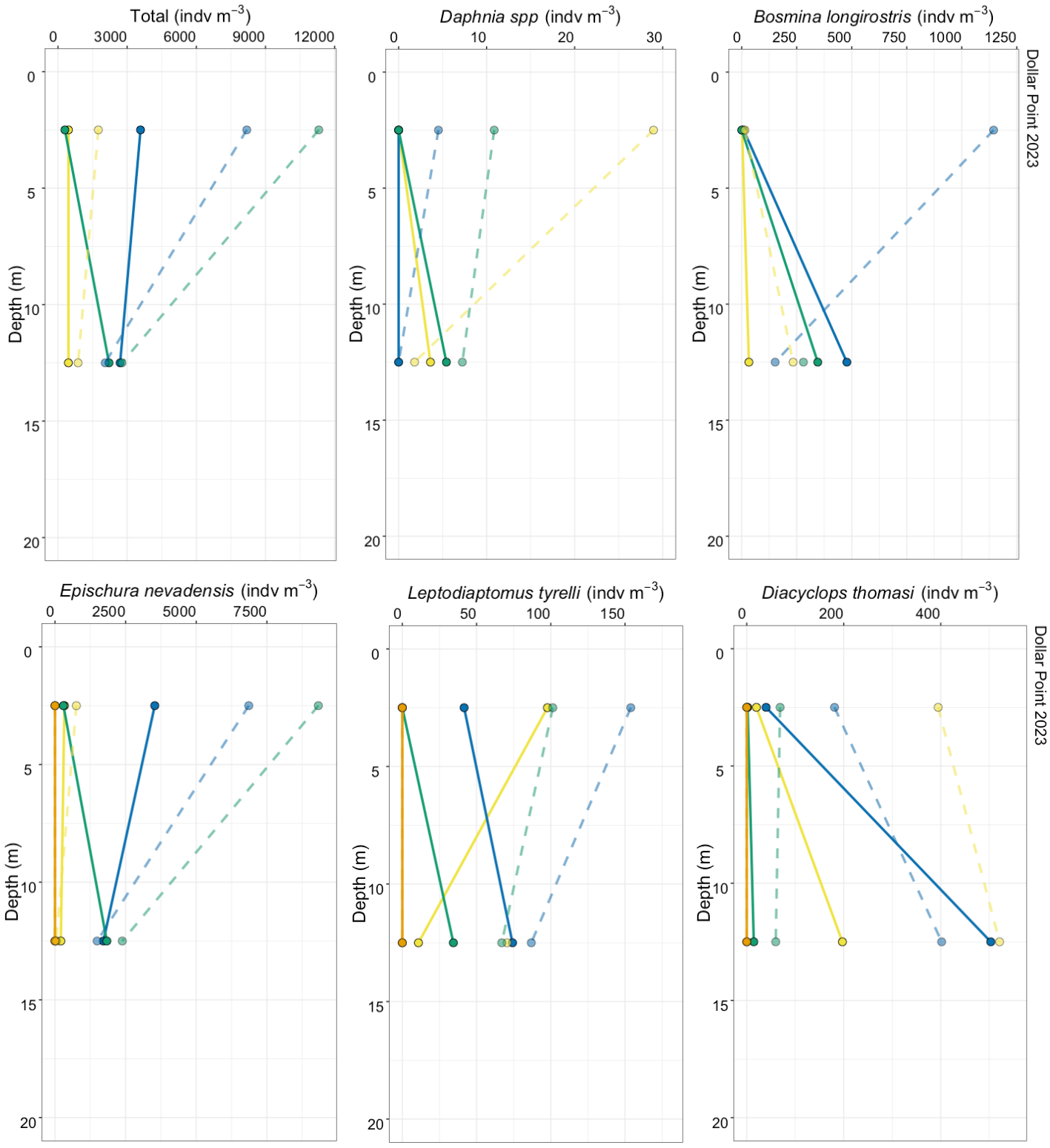


Figure 17. Concentrations of common zooplankton taxa in Lake Tahoe at Dollar Point site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

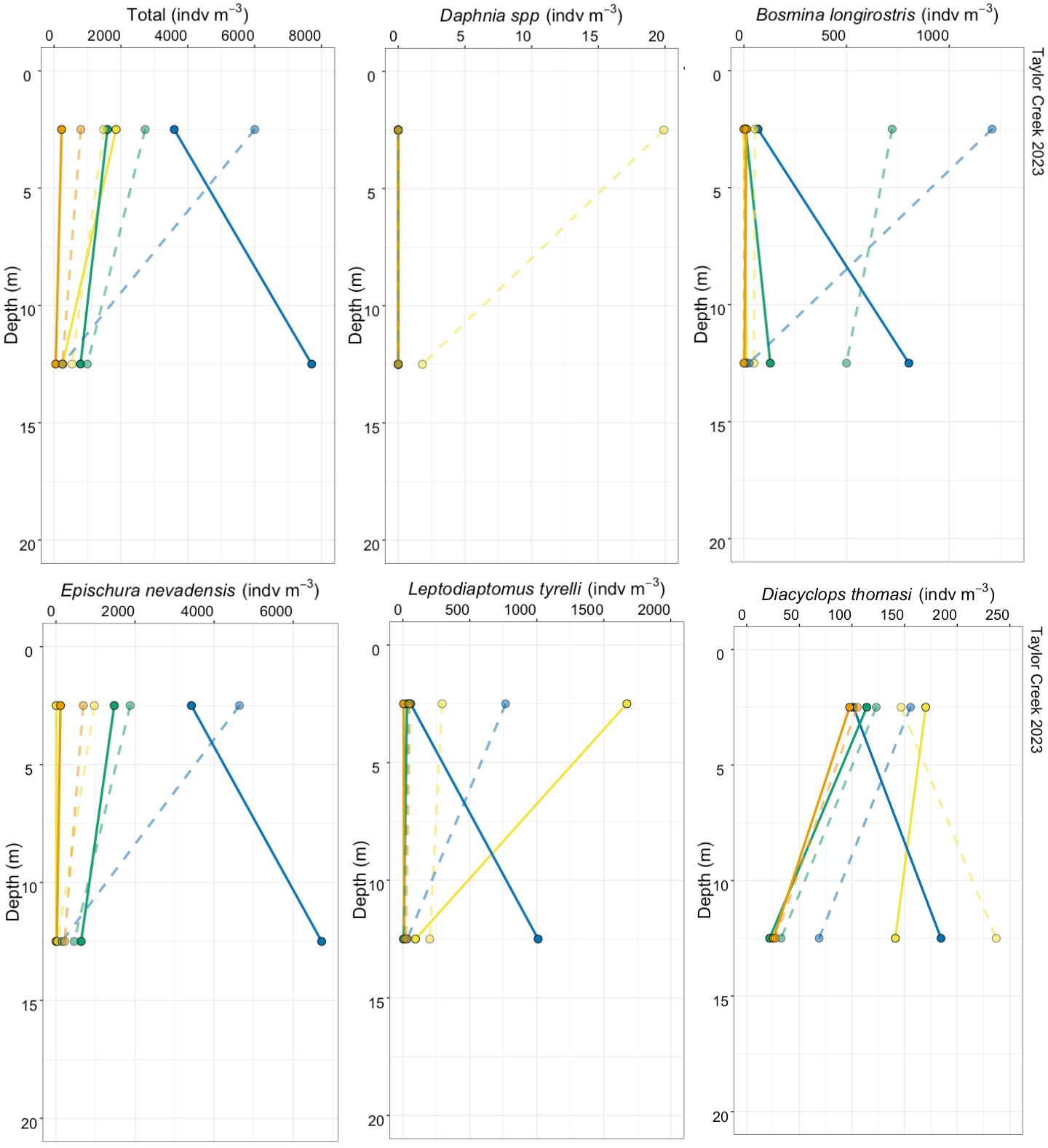


Figure 18. Concentrations of common zooplankton taxa in Lake Tahoe at Taylor Creek site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

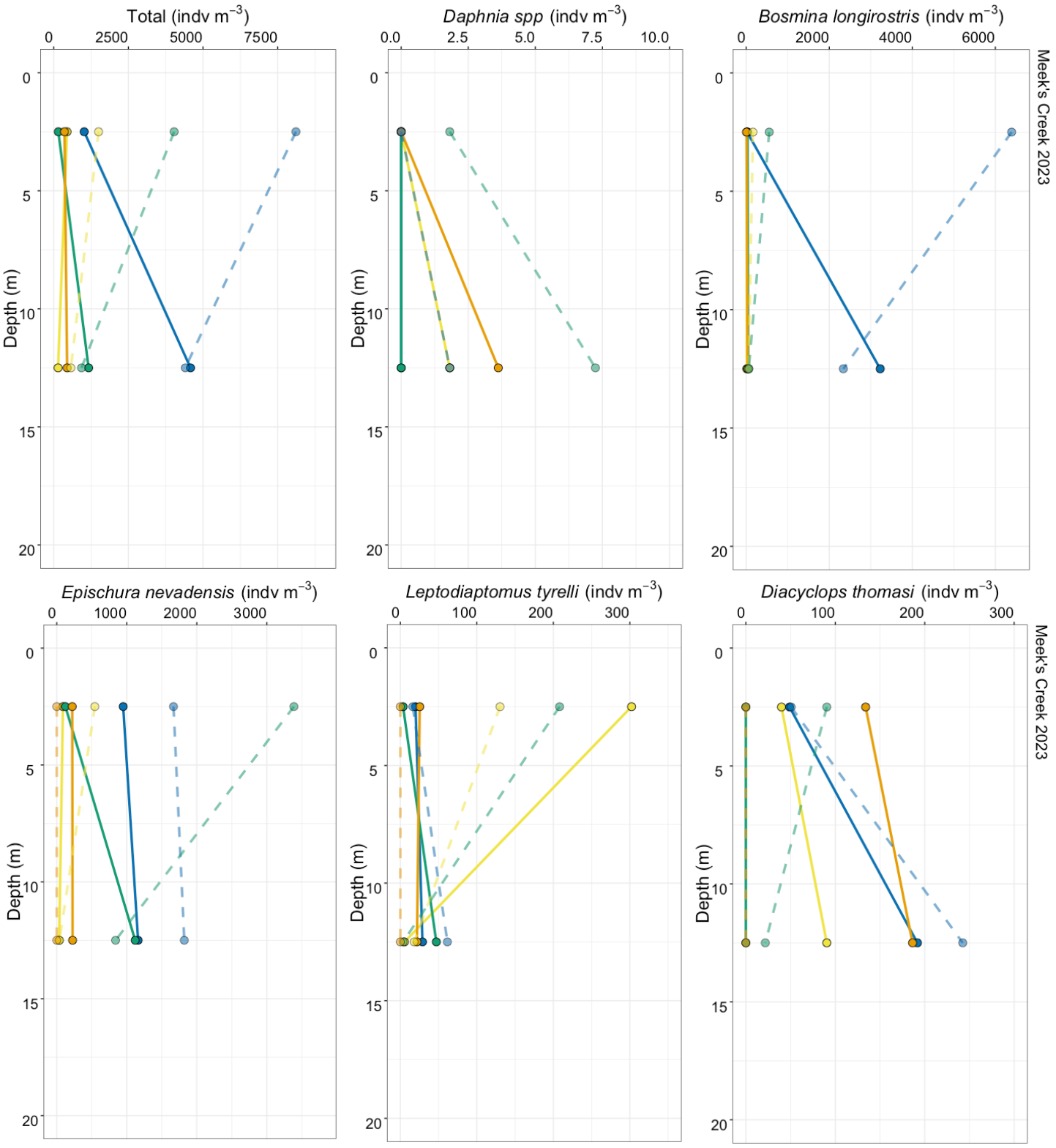


Figure 19. Concentrations of common zooplankton taxa in Lake Tahoe at Meek's Creek site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

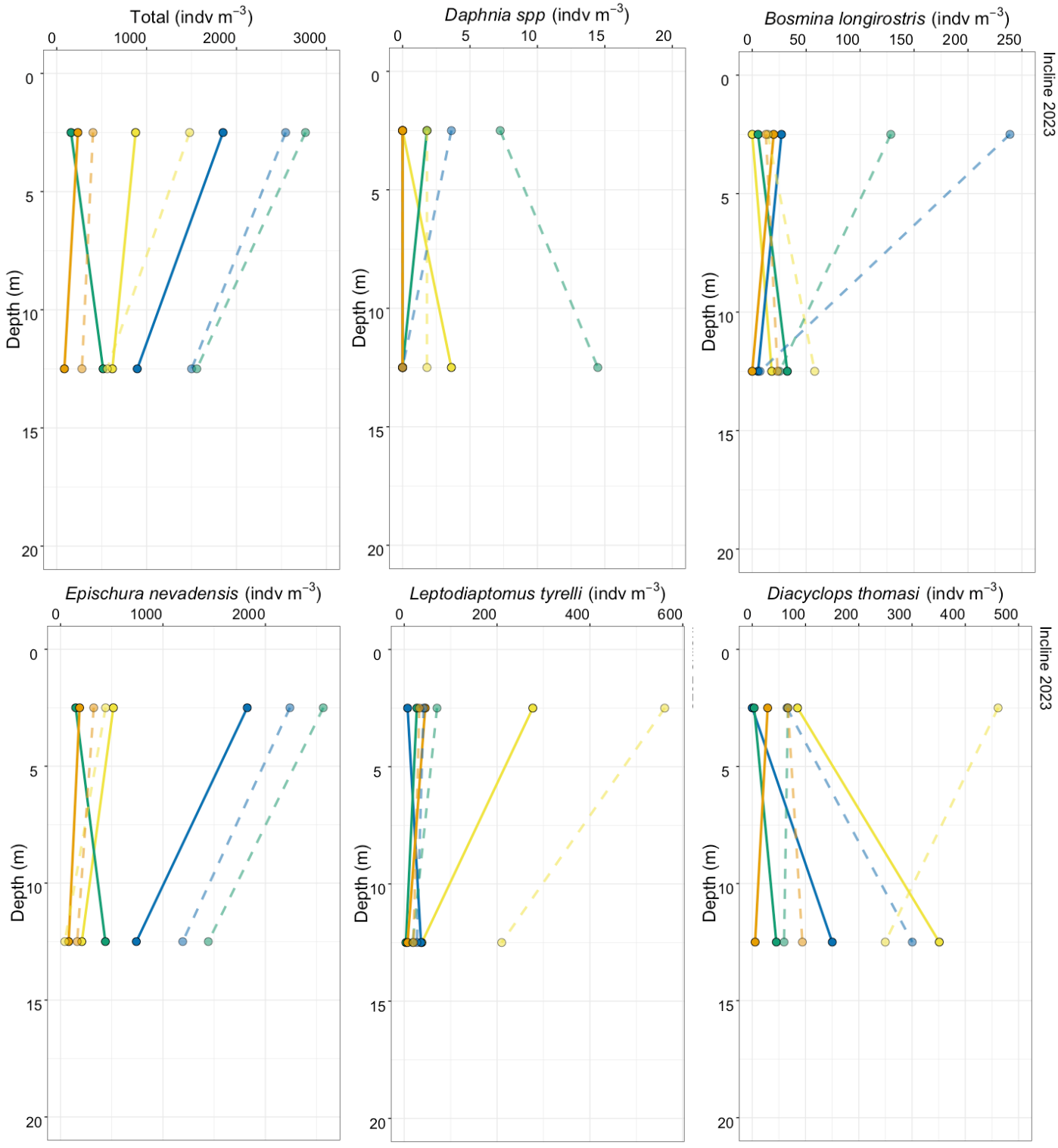


Figure 20. Concentrations of common zooplankton taxa in Lake Tahoe at Incline Village site during the day (solid lines) and night (dashed lines) in May (yellow), July (blue), September (green), and December (orange) 2023.

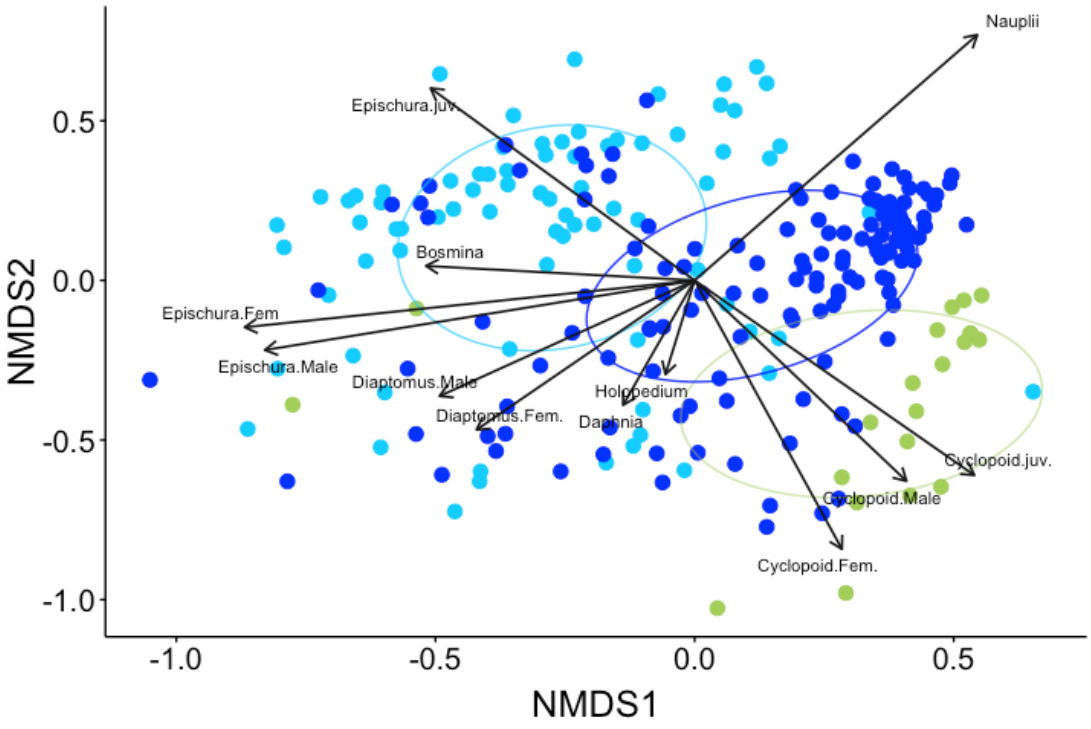


Figure 21. NMDS plot of zooplankton community structure of the nearshore (light blue), pelagic (dark blue), and Emerald Bay (green) habitats in Lake Tahoe during the day and night. ANOSIM, R=0.35, p<0.001.

Mysid shrimp

The cohorts of mysids can be observed in Figure 22. *Mysis diluviana* was identified at MLTP, LTP, and South Shore pelagic locations. Emerald Bay presented only one individual per sample. Thus, these results are not shown in Figure 22. *Mysis diluviana* was found at two maturity stages: Adults (>10 mm) and Juvenile (3-10 mm), and as expected based on the life history of mysids in Lake Tahoe, there is a higher proportion of juveniles in May and adults during September (Table 3). We observed more individuals at LTP and South Shore than at MLTP during September sampling, suggesting substantial spatial variation in the lake, consistent with previous Lake Tahoe studies (Morgan, 1981; Rybock, 1978). The observed seasonal variations in population structure, with juveniles dominating in spring (May) and adults becoming more prevalent in late summer and fall (September), could indicate synchronized reproduction and growth cycles likely driven by environmental factors such as temperature and food availability as discussed in previous research related to mysid shrimp in Lake Tahoe (Morgan, 1981; Rybock 1978).

Table 3. Adults and juvenile counts for *Mysis diluviana* individuals at each station during May, July, September, and December sampling.

Location	**Date**	**Adult**	**Juvenile**
Emerald Bay	May	-	1
Emerald Bay	July	-	1
Emerald Bay	September	-	-
Emerald Bay	December	1	-
LTP	May	11	86
LTP	July	43	20
LTP	September	107	15
MLTP	May	13	47
MLTP	July	38	44
MLTP	September	87	6
MLTP	December	58	6
Southshore	May	36	115
Southshore	July	34	65
Southshore	September	165	18
Southshore	December	73	1

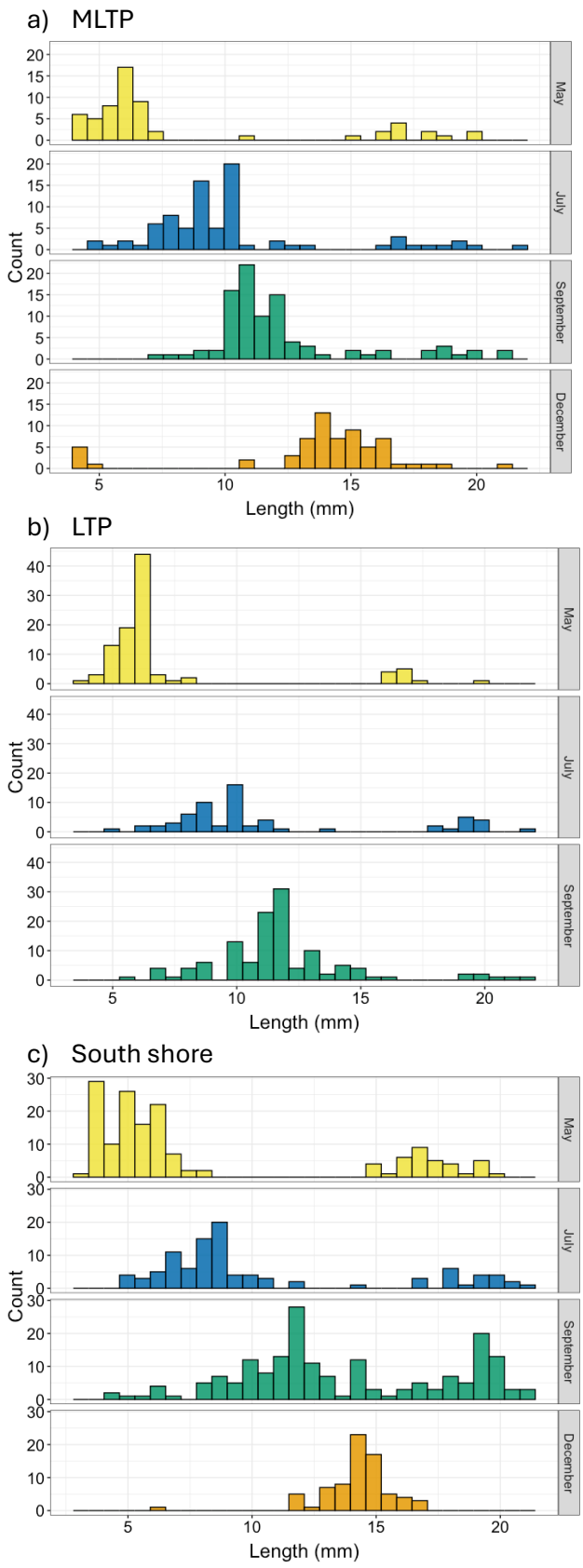


Figure 22. Count data of *Mysis diluviana* taken from Lake Tahoe in May, July, September, and December 2023 at a) MLTP site, b) LTP site, and c) South shore site.

Microzooplankton

Rotifers

We have developed the first list of rotifer taxa and visual identification key or Lake Tahoe that others can use in the future when identifying zooplankton. We identified 16 total species across all nearshore and pelagic sites (Table 4, Figures 23-26). We found spatial and temporal differences in the community compositions and densities at Lake Tahoe that were more site-specific and independent of nearshore and offshore environments. In addition, variation in rotifer density was observed between day and night sampling between and in each site. For instance, rotifer concentration in May was 60 and 20 individuals per L at MLTD and LPT, respectively, and changed to 10 and 60 individuals per L at MLTD and LPT, respectively, during the night. This may be due to horizontal and vertical movements of plankton or transport, although this was not a focus of this study (Figures 23 and 24).

During May, we observed differences in density between and within nearshore and offshore sites. Higher densities were found at MLTP, Dollar Point, and Emerald Bay (close to 60 individuals per L), mid densities in the eastern sites (Incline Village, Glenbrook, and South Shore), and lower densities in the western sites (Blackwood, Meek's Bay, Taylor Creek, and LTP). Dominant taxa were *S. kitina* and *P. dolichoptera,* followed by *K. heimalis* and *K. longispina* in the Northern sites (Incline Village and Dollar Point) and by *K. longispina* and *K. cochlearis* in the Southern sites (Blackwood, LTP, MLTP, South shore, Taylor Creek and Meek's Bay). In July, we found the highest concentration of rotifer at MLTP, Glenbrook, and Taylor Creek and the lowest at Emerald Bay, Dollar Point, and South Shore. *P. dolichoptera* and *K. longispina* were the dominant taxa, but it was site-dependent (Figure 23).

In September, the highest concentrations were observed at Incline Village, MLTP, and Meeks Bay, while the lower concentrations were found at South Shore, Glenbrook, Dollar Point, and LPT. The composition was also variable, with *P. dolichoptera, K. longispina* and *C. unicornis* dominating in Incline Village, Blackwood, Meek's Bay, LTP, and South shore, while *K cochlearis, K. longispina, P. dolichoptera,* and *S. kitina* prevailed at Emerald Bay, MLTD, and Taylor Creek (See Figure 23). Finally, in December, all the sites had similar rotifer densities (~ 40 indv per L), except for Emerald Bay and Taylor Creek, which had lower densities (10-20 indv per L). The rotifer community composition was very similar, consisting of *P. dolichoptera, K. longispina,* and *S. kitina,* except in Emerald Bay, which mainly supported *K. cochlearis*.

Goldman (1974) performed the last comprehensive study on rotifers in Lake Tahoe, where rotifers were sampled alongside zooplankton using an 80µm mesh Clarke-Bumpus sampler net. Goldman noted that the small rotifer known to inhabit unproductive waters, *Chromogaster ovalis,* was a very common species found in the lake during the late fall and winter but became very rare from June through October. We did not detect this species in our samples, which could be attributed to the timing of our sampling, differing sampling methods or identification, or changes in Tahoe's rotifer community. *Syncheata kitina*, a rotifer identified in 2023, had the highest abundances in the May samples while becoming very rare or nonexistent in the summer samples except for two-night samples at Dollar Point and Taylor Creek sites in July and September, respectively. Like Goldman's study, we found *K. longispina* as the most common

and abundant rotifer at all sites sampled. *Keratella* species were also commonly found in almost all sites and were the most abundant rotifer in Emerald Bay. The most common rotifer in our 2023 samples throughout the year was *Polyarthra dolichoptera.* Goldman noted that the 1971 data suggested that *P. dolichoptera* was in decline in Lake Tahoe, but our efforts did not support this conclusion.

We compared the rotifer community structure between the nearshore and pelagic communities Lake Tahoe during the whole sampling period using a non-metric multidimensional scaling (a distance-based ordination technique). Overall, the rotifer communities we observed in the nearshore and pelagic habitats of Lake Tahoe do not differ from each other (Figure 25). However, we did observe a difference in community composition between the main lake and Emerald Bay. Emerald Bay is a more productive, mesotrophic system with lower clarity and higher algal biovolume (Morgan 1981; Morgan et al. 1981; Bess et al. 2021), supporting a different zooplankton community. Finally, connecting current trophic (productivity) and clarity conditions to microzooplankton dynamics could be an excellent way to understand how smaller, perhaps more progressive, changes in the lake are connecting to changes in consumers.

Ciliates

Ciliates could not be identified in the laboratory even after different methodologies were used to concentrate the samples. The initial methodology employed involved directly removing small aliquots from sample bottles for examination using an upright compound microscope. A Sedgwick-Rafter cell was utilized with a total volume of 1 mL; however, ciliates were not detected in any of the samples. It was hypothesized that the abundances of ciliates might have been sufficiently low, leading to their absence in the samples despite the observation of other nano/microplankton taxa, including rotifers, microcrustaceans, various larger and more resilient phytoplankton such as desmids, and a significant quantity of pine pollen.

Subsequently, the samples were allowed to settle for 24 hours. Following this period, a siphoning technique was employed to remove approximately three-quarters of the liquid from the upper portion of the containers, thereby concentrating the remaining material. This method of gentle concentration has been utilized frequently in previous research. After thoroughly mixing the residual volume, a second sampling was conducted using the Sedgwick-Rafter cell to ascertain the presence of ciliates. Once again, ciliates were not identified; however, the presence of the previously noted taxa indicated the success of the concentration method.

In the subsequent phase, the entire remaining volume of the samples was allowed to settle within Utermöhl settling chambers, facilitating the examination of the settled material using inverted microscopy. A significant quantity of debris was present alongside a greater abundance of plankton from the previously observed taxa; however, ciliates remained undetected. Throughout this investigation, not a single clearly identifiable ciliate was observed. Some stray tintinnid loricae were noted, but these were devoid of cellular material. Numerous other planktonic organisms of similar dimensions to ciliates were observed; nonetheless, these organisms were predominantly from more robust taxa, with one sample containing a considerable number of empty *Dinobryon* loricae.

The conclusion drawn from this analysis is that the screening process utilized to concentrate ciliates during sample collection was overly harsh, resulting in an inability to obtain quantitative estimates from the samples. Retaining live ciliates on filtering screens would not be optimal for determining abundance. It is customary to preserve a larger volume of unfiltered water before gentle concentration by settling the preserved sample, mirroring the methodology attempted in this study. Additionally, it is worth noting that the lack of successful ciliate identification is unlikely attributable to inadequate preservation of the samples, as the organisms observed appeared to be well-preserved. The hypothesis remains that the primary issue stemmed from the initial screening process.

Per the deliverable for this task, field notes and any relevant protocols used during this project so future studies can make comparisons with this study have been submitted along with this report. In brief, the data includes:

- Identification and count of 425 samples of macrozooplankton collected from the 10 stations and during day and night.
- Identification and count of 125 samples of rotifers.
- Pictures and descriptions of rotifers identified in Lake Tahoe 2023 samples.
- Measurements and counts of the Mysis individuals collected in the pelagic sites during May, July, September, and December sampling.

Table 4. Lake Tahoe rotifer species identified in previous studies compared to those identified in samples collected 2023.

Historical ID (Goldman, 1974; UC Davis monitoring data)	**2023 (this study)**
Kellicottia longispina	*Kellicottia longispina*
Keratella cochlearis	*Keratella cochlearis*
Keratella quadrata	*Keratella hiemalis*
Notholca (striata type)	*Notholca caudata (?)*
Notholca (squamula type)	*Notholca labis (?)*
Ascomorpha spp.	*Gastropus stylifer*
Lecane spp.	*Lecane ludwigii*
Monostyla spp.	*Lecane bulla*
Chromogaster ovalis	*Polyarthra dolichoptera*
Polyarthra vulgaris	*Syncheata kitina*
Syncheata spp.	*Conochilus unicornis*
Conochilus unicornis	*Trichocera spp.*
Trichocera spp.	*Trichotria tetractys*
Ploesoma truncatum	*Lapedella spp.*
Epiphanes (?)	*Collotheca spp.(?)*
	Bdelloidea spp.

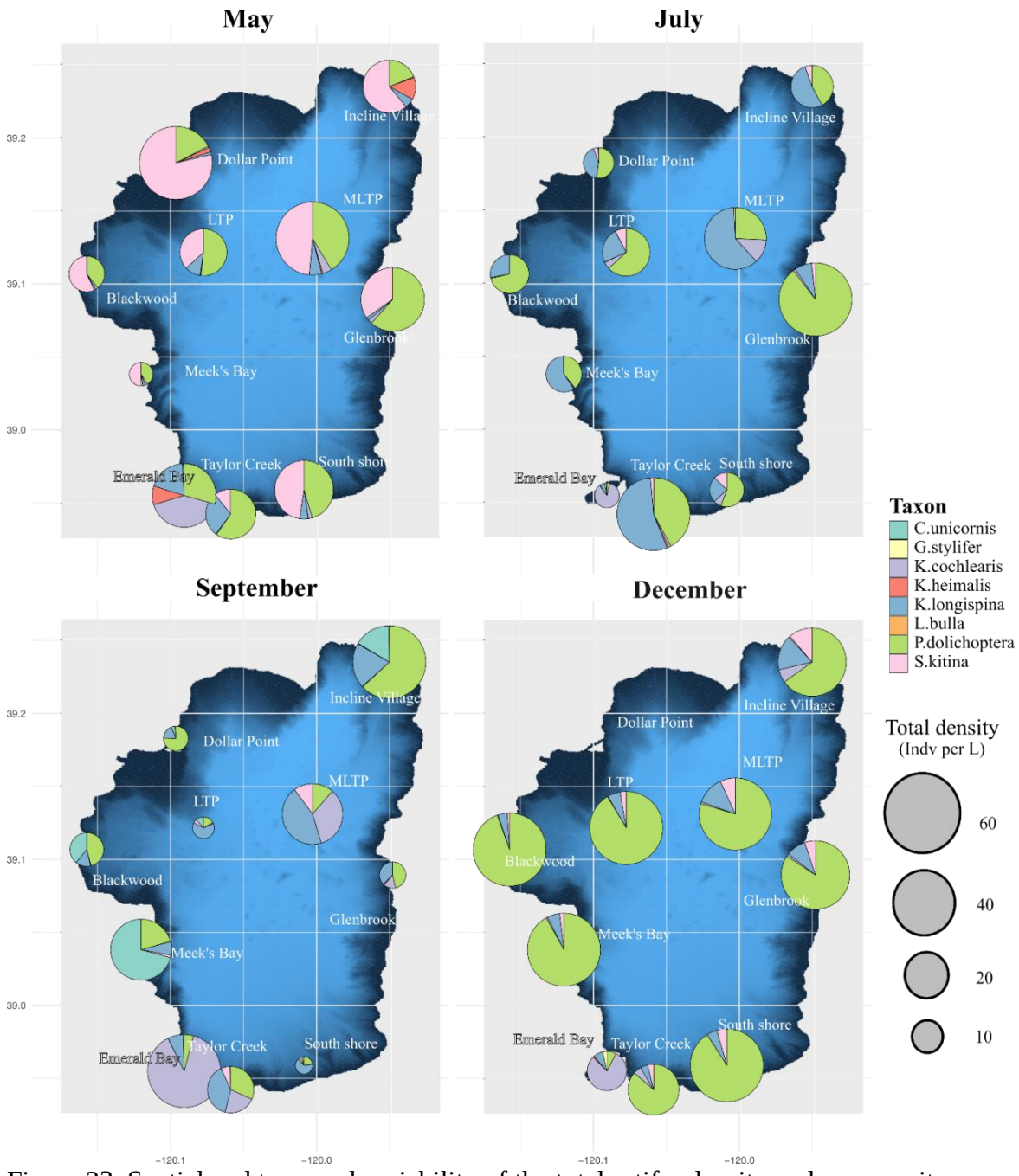


Figure 23. Spatial and temporal variability of the total rotifer density and community composition during the day at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meek's Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites. We include only those species whose density proportion was higher than 0.04 in all the samples.

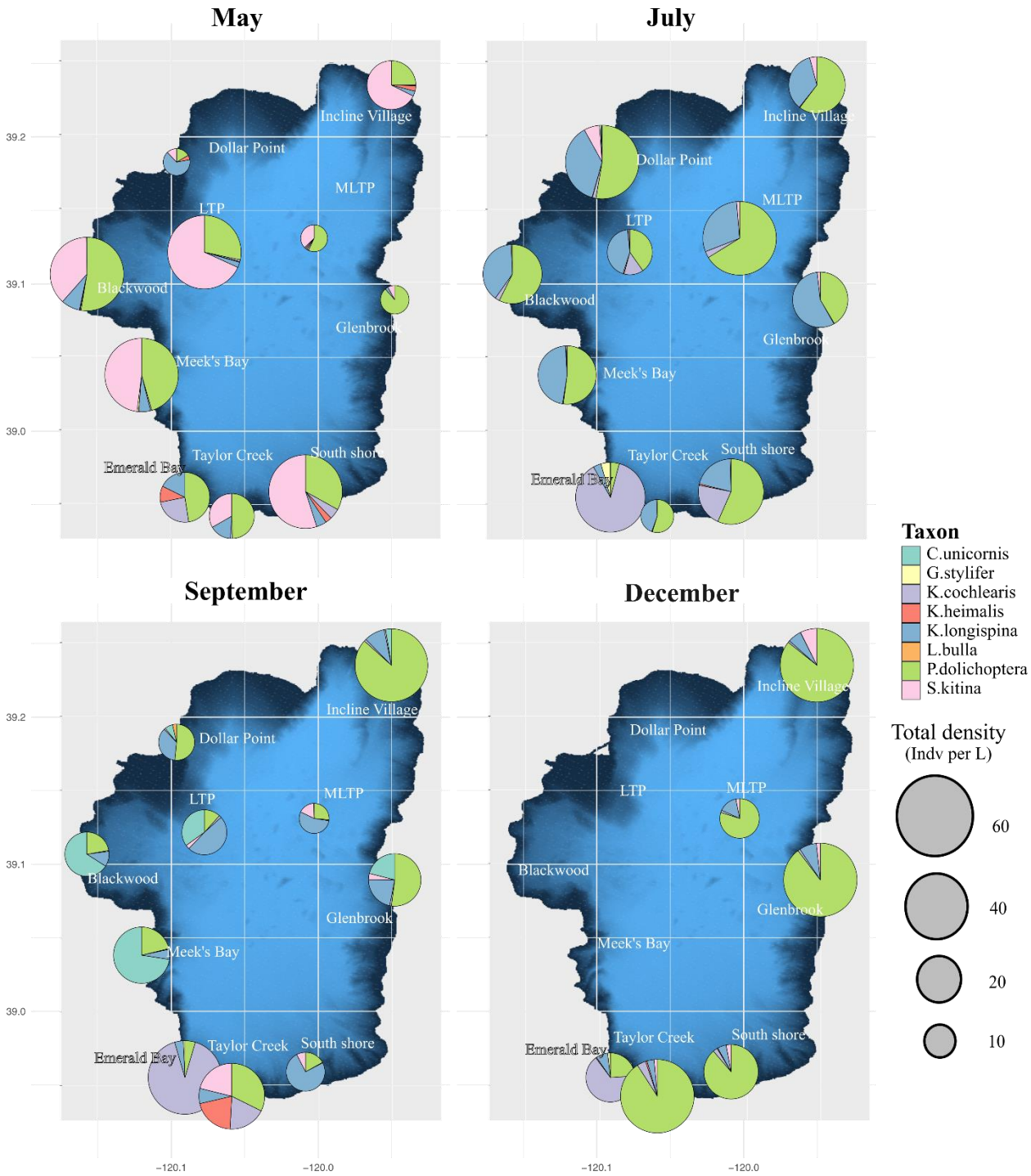


Figure 24. Spatial and temporal variability of the total rotifer density and community composition during the night at Lake Tahoe. Total densities correspond to an integrated sample of 0-15 m for nearshore (Blackwood, Dollar Point, Glenbrook, Incline, Meeks Creek, Taylor Creek), 0-50 m for Emerald Bay, and 0-110 m for pelagic (LTP, MLTP, Southshore) sites. We include only those species whose density proportion was higher than 0.04 in all the samples.

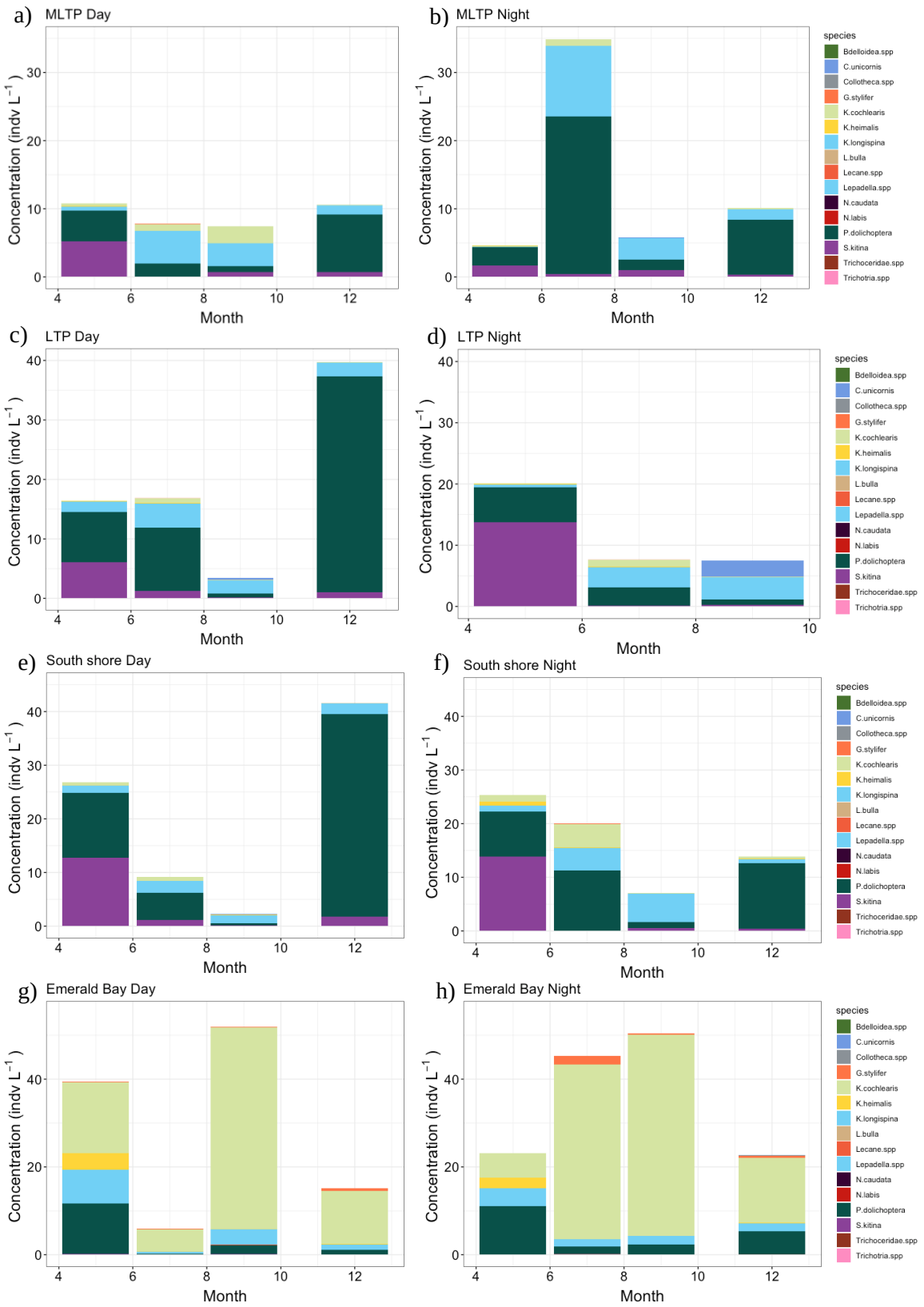
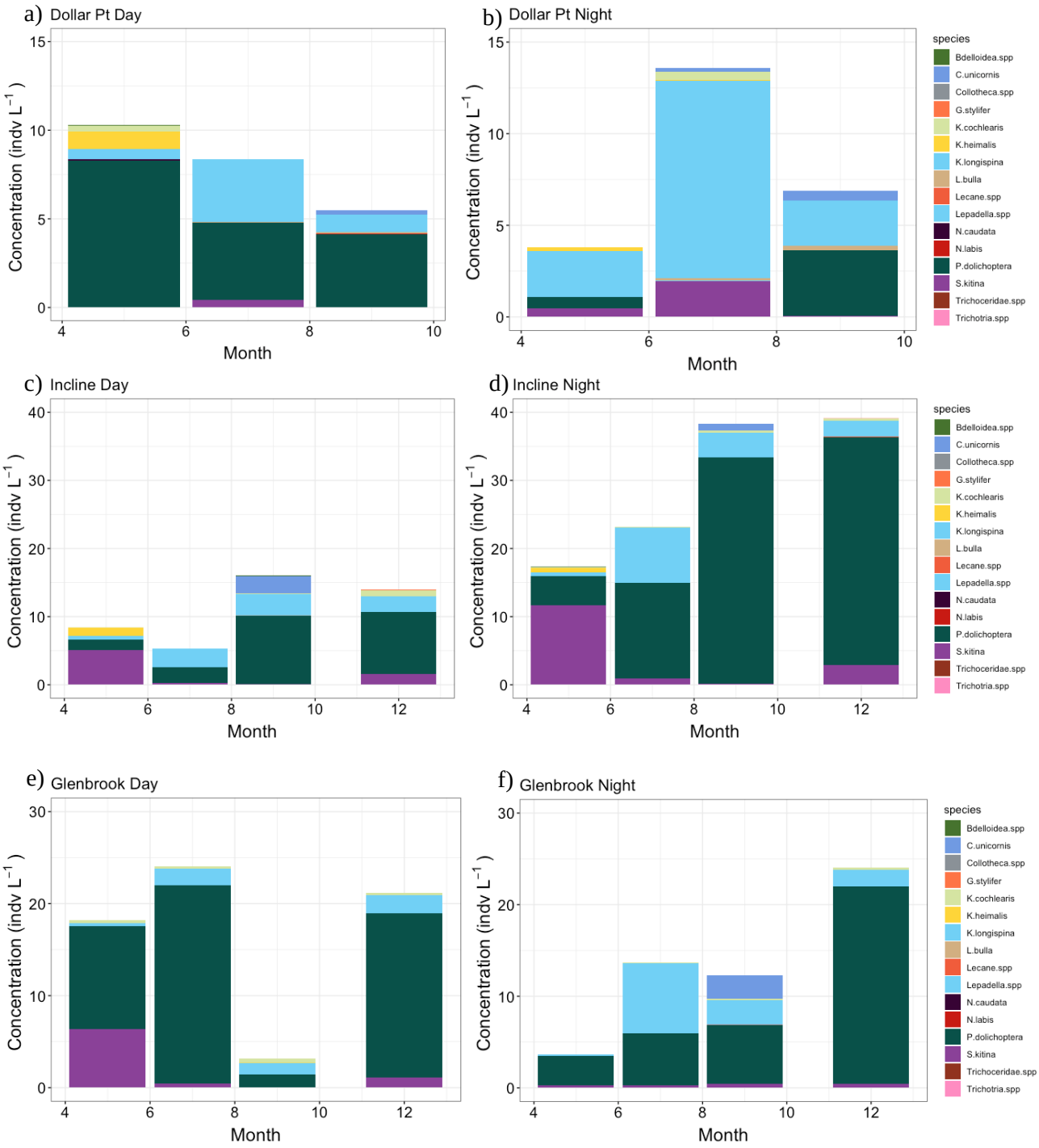


Figure 25. Community composition of rotifers in Lake Tahoe in pelagic sampling sites MLTP (a, b), LTP (c, d), South shore (e, f), and Emerald Bay (g,h) during the day and night).


a) Dollar Pt Day
b) Dollar Pt Night
c) Incline Day
d) Incline Night
e) Glenbrook Day
f) Glenbrook Night
Concentration (indv L^{-1})
Month
species
Bdelloidea.spp
C.unicornis
Collotheca.spp
G.stylifer
K.cochlearis
K.heimalis
K.longispina
L.bulla
Lecane.spp
Lepadella.spp
N.caudata
N.labis
P.dolichoptera
S.kitina
Trichoceridae.spp
Trichotria.spp

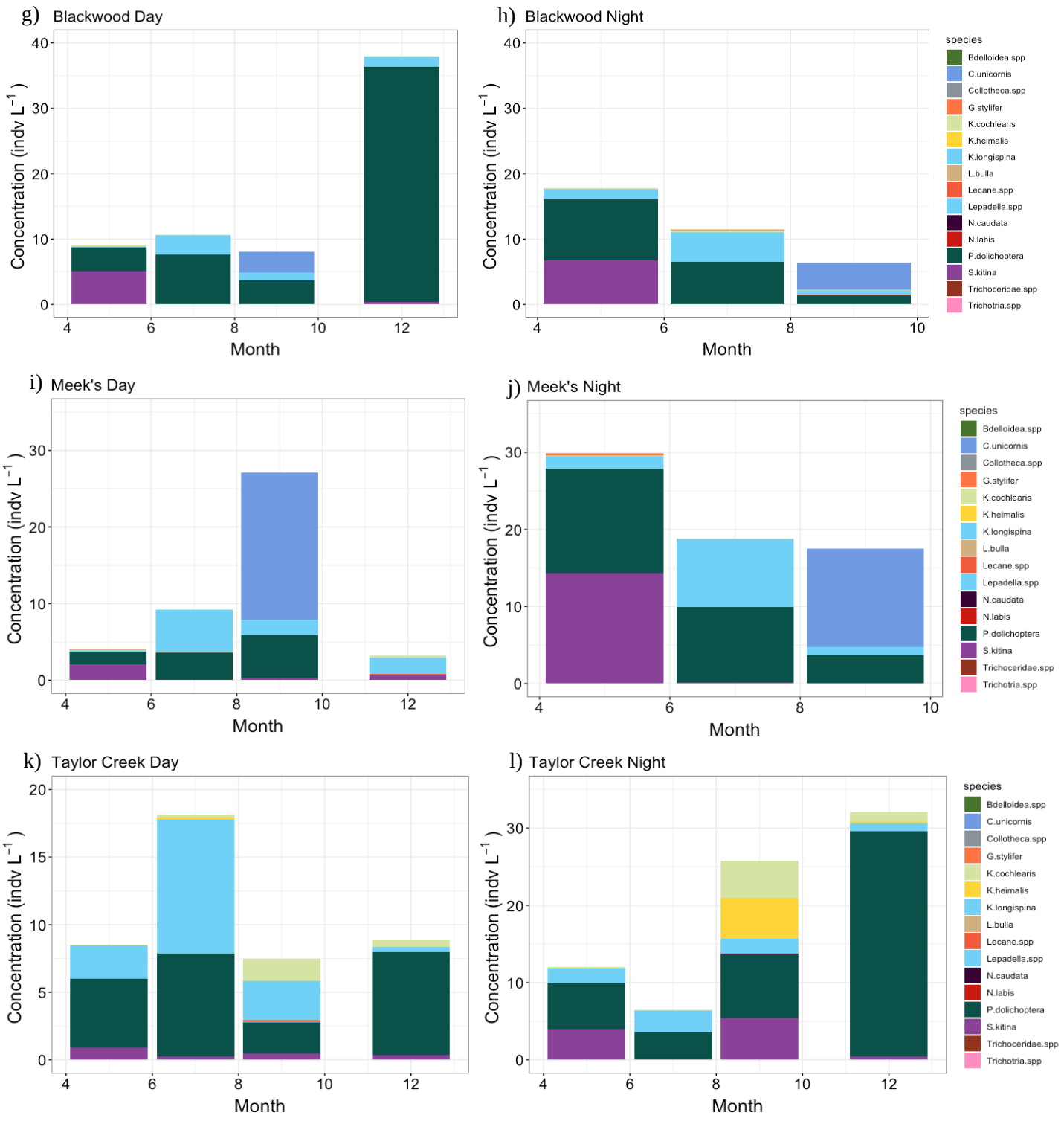


Figure 26. Community composition of rotifers in Lake Tahoe in nearshore sampling sites Dollar Point (a, b), Incline (c, d), Glenbrook (e, f), and Blackwood (g,h), Meek's Bay (i, j), and Taylor Creek (k, l) during the day and night).

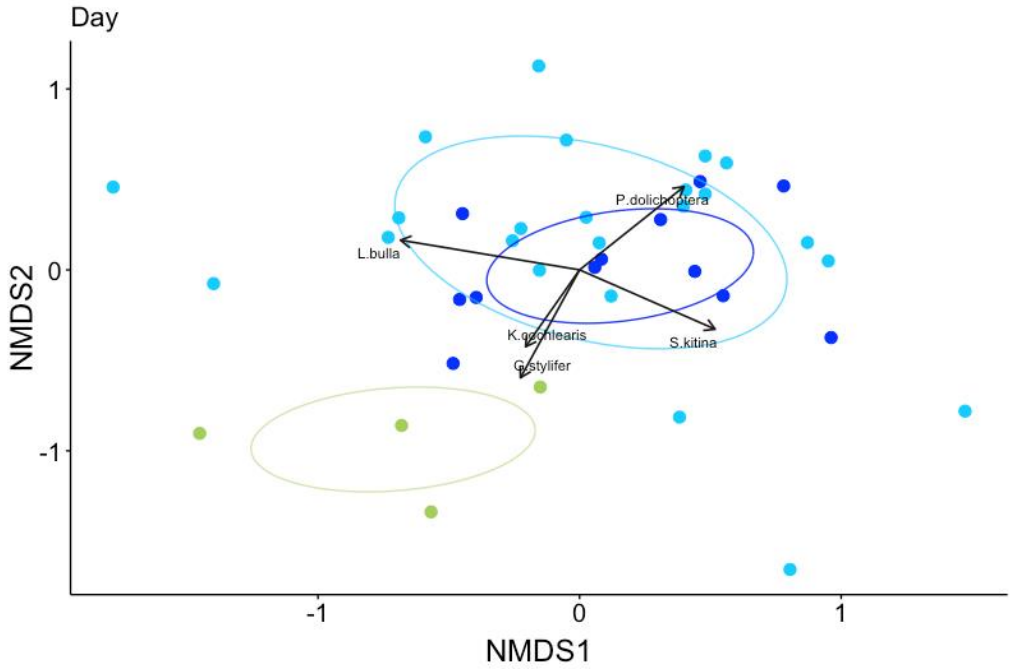


Figure 27. NMDS plot of rotifer communities in the nearshore (light blue), pelagic (dark blue), and Emerald Bay (green) of Lake Tahoe from samples taken in May, July, September, and December 2023.

Task 4: Quantify diel vertical migration of macro- and microzooplankton using collected diurnal samples.

To quantify diel vertical migration of macro- and microzooplankton, we collected zooplankton (Figures 28-30) and microzooplankton (Figure 31) samples during the day and night at least 1.5 hours after sunset and 2 hours before sunrise. We subtracted the pooled profile daytime values from the pooled nighttime values to get concentrations of zooplankton that migrate through the water column.

Task 4: Findings and discussion

We also examined differences in migration patterns in the different zooplankton taxa in the pelagic and nearshore sites. Many taxa exhibit diel vertical migration, where nighttime values were higher than daytime values. Emerald Bay presented distinct patterns of migration of *Bosmina* in all sampled months, where daytime values were higher than nighttime, which was not expected given the literature on cladoceran migration that suggests higher densities during nighttime.

We observed a distinct pattern of *Epischura* in nearshore sites during the July sampling period, with daytime values higher than nighttime values at Glenbrook, Taylor Creek, and Blackwood. The same occurred with *Diaptomus* during May and July at Taylor Creek. Also, in Figures 11-20, we observe that for some taxa, the concentration of zooplankton at the surface during the night was much higher than the sum of surface and depth concentration during the day. Therefore, we suspect that zooplankton could migrate vertically and horizontally (e.g., from the nearshore to the offshore). Also, spatial plots shown in Figures 7-10 and 23-24 suggest important differences in the concentration of macro- and microzooplankton during day and night in nearshore and offshore environments, suggesting that migration patterns of macro- and microzooplankton are very complex. Thus, having an actual representative zooplankton concentration would require additional space and time monitoring.

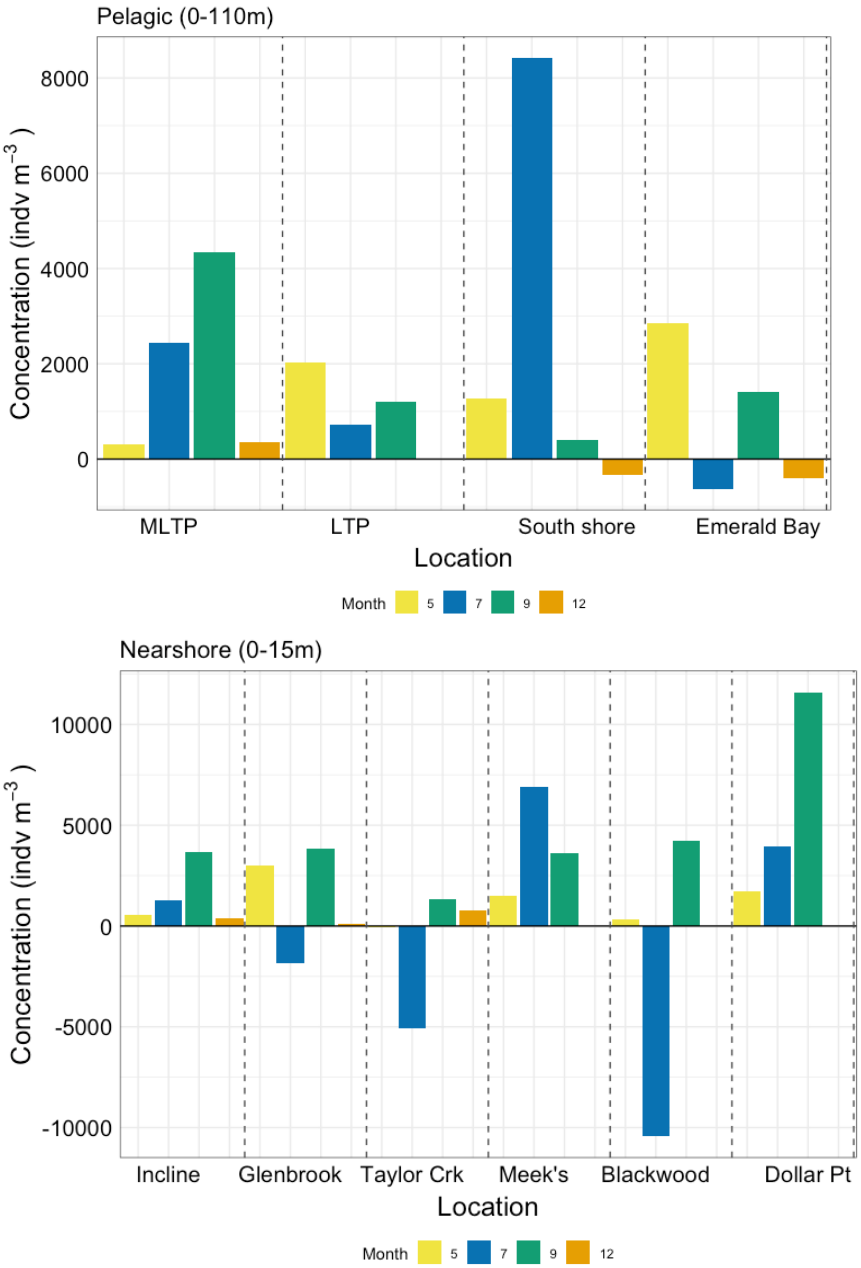


Figure 28. Total concentrations difference of migrating zooplankton (Night – Day) from the a) pelagic and b) nearshore sites in Lake Tahoe in May (yellow), July (blue), September (green), and December (orange) 2023. A number more than zero indicates taxa are migrating to shallow waters, as expected in the literature.

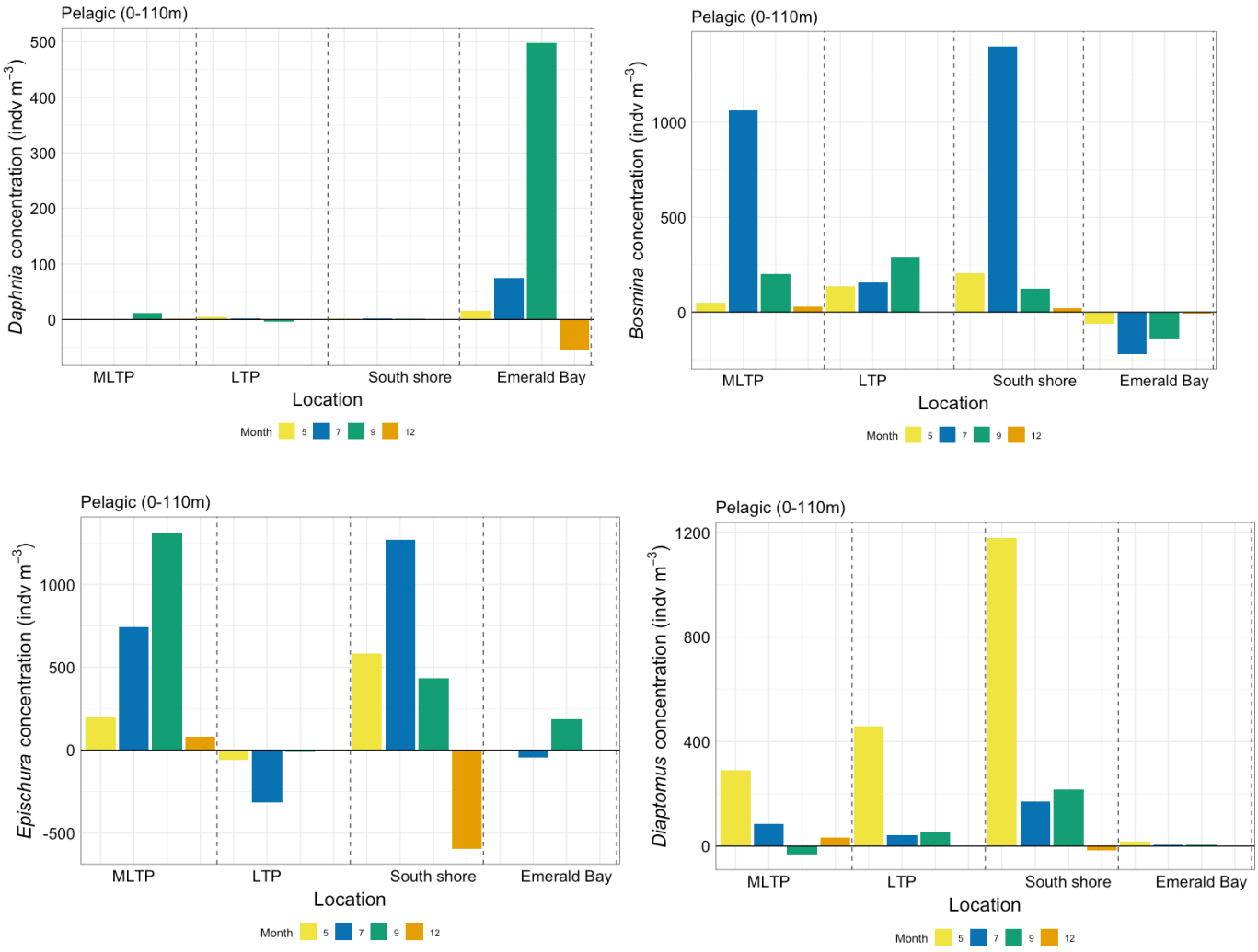


Figure 29. Concentrations difference (Night – Day) of migrating zooplankton taxa in pelagic sites of Lake Tahoe. A number more than zero indicates taxa are migrating to shallow waters, as expected in the literature.

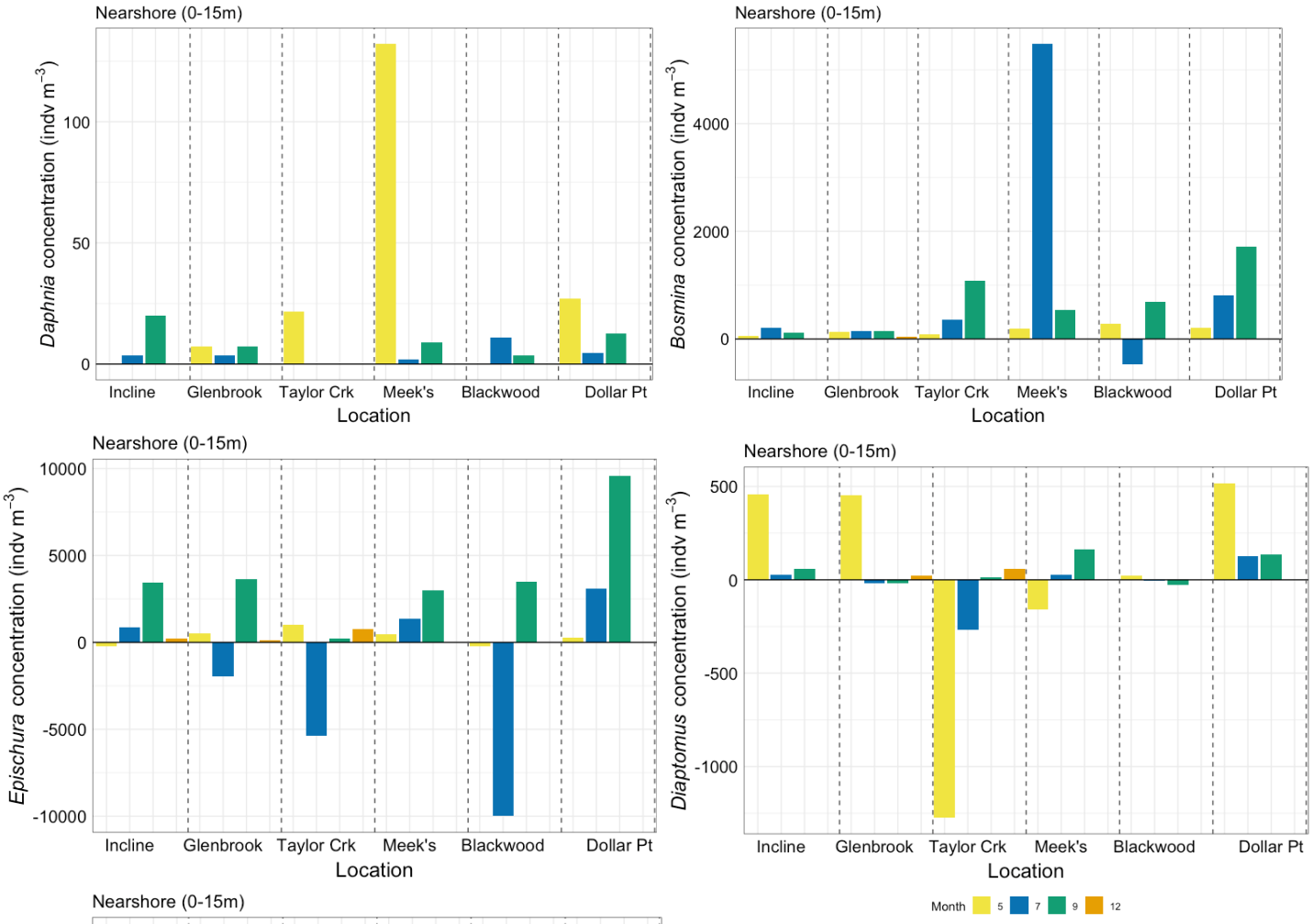


Figure 30. Concentrations difference (Night – Day) of migrating zooplankton taxa in nearshore sites of Lake Tahoe. A number more than zero indicates taxa are migrating to shallow waters, as expected in the literature.

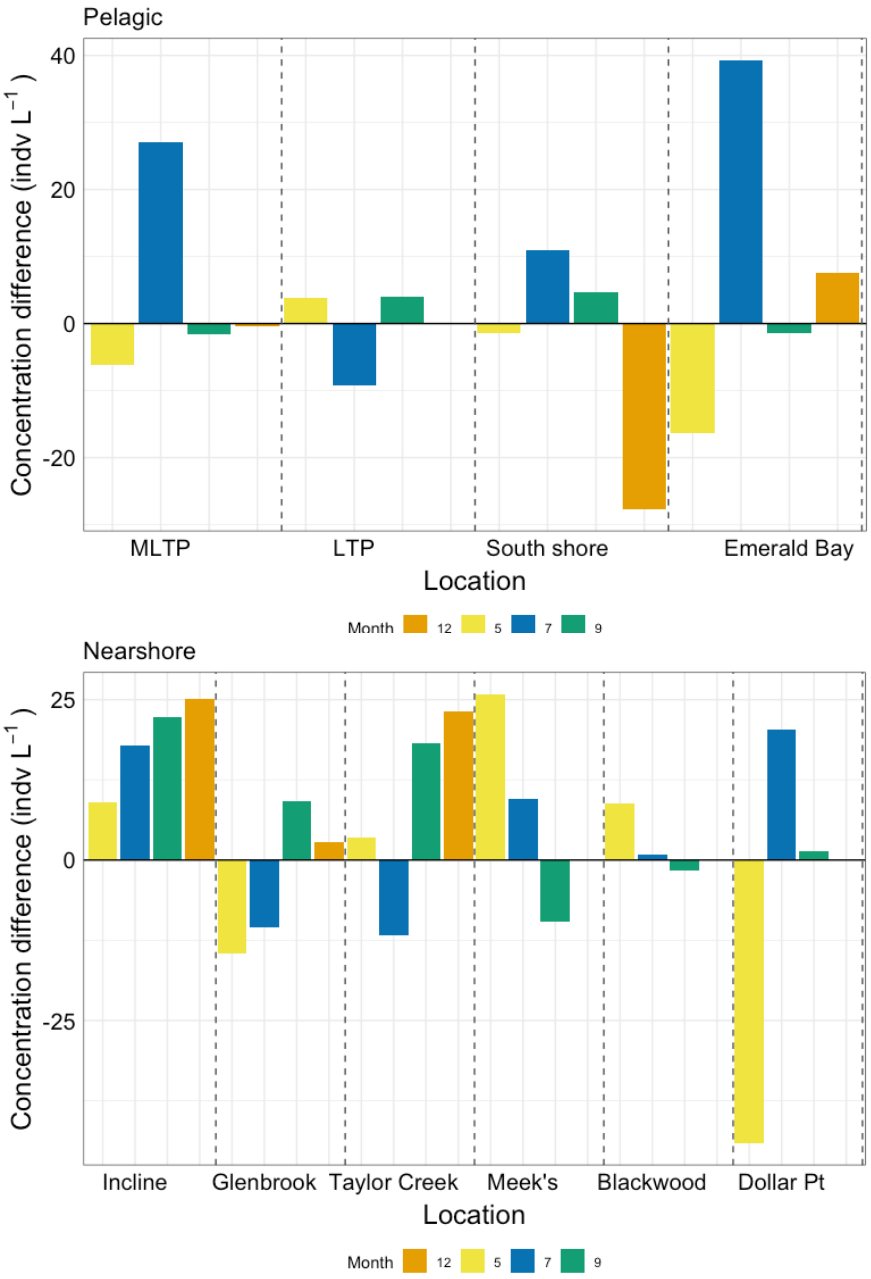


Figure 31. Concentration difference (Night – Day) of migrating rotifers in a) pelagic and b) nearshore sites in Lake Tahoe in May (yellow), July (blue), September (green), and December (orange) 2023. A number more than zero indicates taxa are migrating to shallow waters, as expected in the literature.

Task 5: Quantifying the effects of zooplankton communities on particle size distributions affecting clarity.

We used seminatural experiments with lake water and zooplankton to simulate nearshore and offshore conditions along a gradient of zooplankton densities. Glenbrook was chosen as the nearshore sampling location, with water collected at 5, 10, 12, and 15 m on December 3, 2024. MLTP served as the offshore sampling location. An integrated lake water sample for the experiment was collected using a Van Dorn sampler (4.2 L) from 10, 20, 30, and 50 m depths on December 4, 2024. The water was carefully filtered through a 50 µm mesh sieve to remove any macro-zooplankton present before placement in pre-cleaned sampling containers (16.8 L total volume for each treatment). During the water filtration for each individual mesocosm, measures were taken to create target zooplankton densities used within the experiments:

1. Reference- no zooplankton added,
2. Half, the concentration at half the density found within the lake,
3. Ambient, the density found within the lake, and
4. Double- the zooplankton concentration twice that found within the lake.

For buckets receiving half of the ambient zooplankton density, 2.1 L of water for each depth was passed through two separate 50 µm sieves. The contents from one sieve screen were washed into a 500 mL bottle with filtered lake water to keep zooplankton alive during transport, while the contents remaining on the other sieve were discarded. All filtered water was retained in the pre-cleaned mesocosm container for the half-density treatment. For mesocosms with ambient zooplankton densities, 4.2 L of water for each depth was filtered through one 50 µm mesh sieve. All zooplankton captured on the filter were washed into a 500 mL bottle with filtered lake water. All filtered water was retained in the pre-cleaned mesocosm container for the ambient density treatment. For mesocosms containing double the ambient zooplankton density, a total of 8.4 L or two Van Dorn's per depth, were filtered through one 50 µm mesh sieve. Half of the lake water filtered for each depth was retained and placed into the mesocosm container for the experiment, while the remainder was discarded. All zooplankton captured on the filter were washed into a 500 mL bottle with filtered lake water to keep zooplankton alive during transport. To create the reference treatment, 4.2 L of water for each depth was filtered into a clean mesocosm container through a 50 µm mesh sieve. All zooplankton captured on the filter reference water were preserved with sucrose Lugol's solution for identification and enumeration. Six replicates were created for each zooplankton treatment and the control for nearshore (n = 24) and offshore conditions (n = 24).

At the laboratory, zooplankton were added into the mesocosm containers with zooplankton added into the same water (i.e., container) they were removed from while creating target population densities in the field. After the zooplankton additions, water in the mesocosm containers was stirred for 1 minute to suspend all particles before a LISST 200-X particle size analyzer was placed in the container to gather pre-treatment data. An RBR Maestro was placed in the mesocosm immediately after for chlorophyll-a measurements. The LISST and RBR were rinsed in deionized water between samples to remove particles and minimize contamination between mesocosm treatments. After collecting pre-treatment data, the mesocosms were placed

in an 18°C temperature chamber with an 18/6 hour dark/light cycle and incubated undisturbed for 36 hours.

After incubation, another set of LISST and RBR measurements were collected using the previously described methods for post-treatment conditions. In addition, 180 mL of water from each replicate was filtered through pre-combusted Whatman GF/F filters with a pore size of 0.6-0.8 µm for total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and soluble reactive phosphorus. The filter disk was immediately frozen for chlorophyll-a analysis. Filtered samples were analyzed for DOC and TDN using a Shimadzu TOC-V. The phosphorus sample has been frozen for future analysis. Methanol extractions of chlorophyll-a were analyzed fluorometrically using a Turner 10-AU fluorometer.

Once instrument profiles and chemistry samples had been taken, the mesocosm water was filtered through a 50 µm mesh sieve to remove the macrozooplankton in the buckets. The zooplankton were preserved with sucrose Lugol's solution for enumeration and identification. To process LISST measurements and analyze the particle concentration, we used the LISST-200X software and considered clean water background measurements performed before the experiment, selecting the irregular shape model to examine the particle concentration. LISST measurement provides particle concentration of 36 log-spaced classes ranging from 1.00 to 500 µm. In this study, we focused on particle size analysis in particles below 50 µm to avoid the influence of macrozooplankton.

We analyzed the zooplankton effect on particles for each treatment (1. Reference- no zooplankton, 2. Half, 3. Ambient, and 4. Double) independently using linear models using generalized least squares (GLS) with treatments modeled as a fixed effect. We evaluated the models that meet the assumption of normality (using Shapiro's Test $p > 0.05$) and homoscedasticity (using Levene's Test $p > 0.05$). Tests for the significance of the fixed effects in the models were performed via the Wald Chi Square statistic (Zuur et al., 2009) using the gls functions in the nlme R package. Multiple treatment comparisons were performed with Tukey's HSD post hoc test (emmeans R package; Lenth, 2021).

Task 5: Findings and discussion

Nearshore

We found a decrease in particle concentration across all treatments at the end of the experiment compared with the initial conditions between 20-50 µm (Figure 32). Figure 32 summarizes the mean values of grain size particle distribution for each experiment; further information about grain size distribution in each treatment can be found in the Supplementary material-B Figures A-D. The particle concentration between 7.11 and 20 µm increased at the end of the experiment in all the treatments compared with the beginning of the experiment. This size range includes the most abundant phytoplankton in Lake Tahoe, *Cyclotella ocellata* (12 µm). Finally, we also observed a decrease in particle concentration at the end of the experiment compared with the initial conditions between 2.63-7.11 µm.

Comparing statistical significance between treatments of selected particle fractions, we found that particles of <2.63 µm and between 3.11-4.33 µm were much higher at the end of the

experiment compared with the initial conditions at Half (half the zooplankton density found within the lake), Ambient (density of zooplankton found within the lake), and Double (twice the density of zooplankton found within the lake) treatments than the Reference (No zooplankton) (Figure 33). But, overall, there were no significative differences between the treatments according to Tukey's HSD post hoc test, except between Half, Ambient, and Reference treatments in fraction <2.63 µm (see Table 5 for more information), indicating a minimal role of zooplankton on these fractions when aggregated.

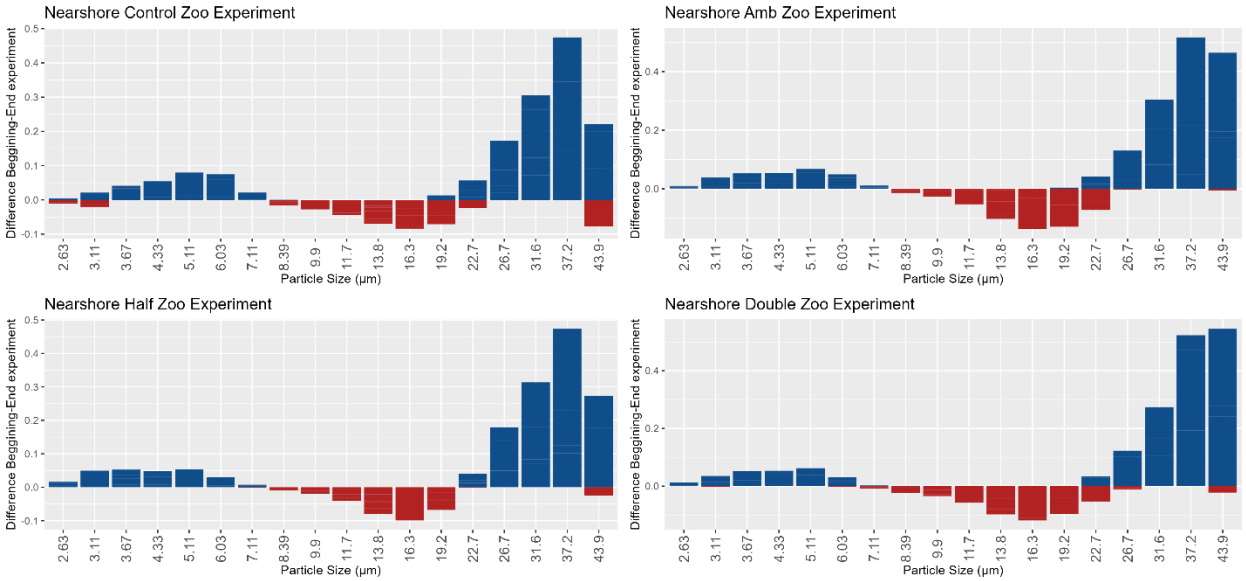


Figure 32. Mean difference between the beginning and end of each treatment's nearshore experiment for particle sizes 0-44 um. Negative values indicate a higher concentration of particles at the end of the experiment, while positive values indicate lower concentration of particles at the end of the experiment.

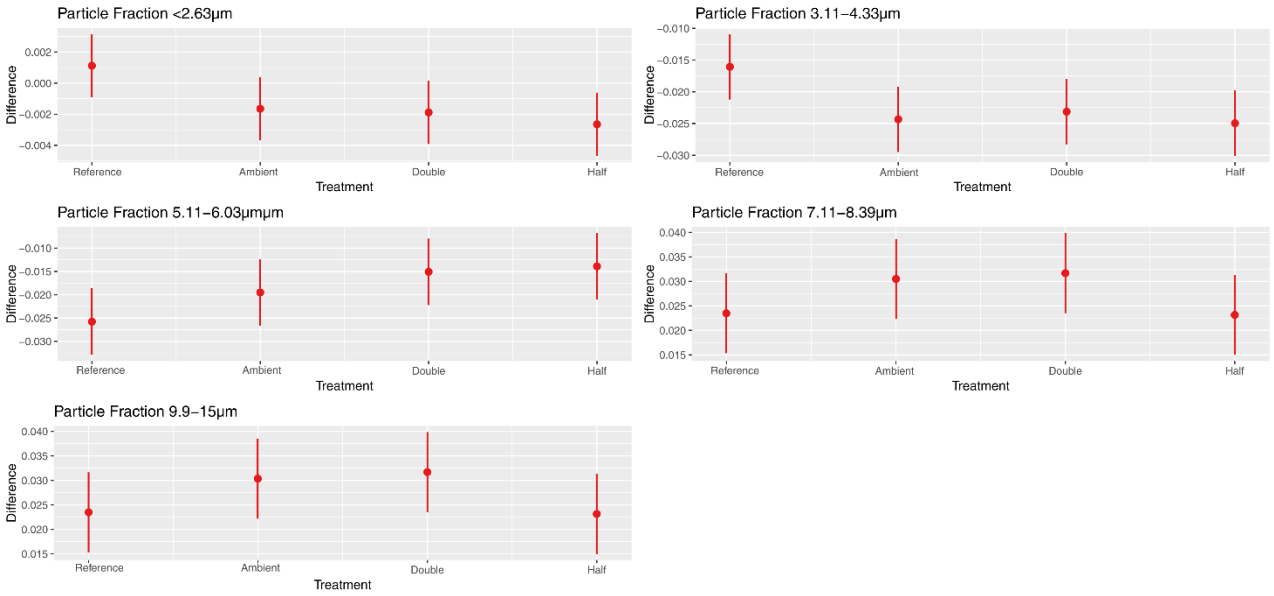


Figure 33. Mean and standard error differences between the beginning and end of the nearshore experiment for each treatment for the analyzed particle fraction. Higher negative values indicate a higher concentration of particles at the end of the experiment.

Table 5. Tukey's HSD post hoc test pairwise comparison between the treatments.

Experiment	**Particle Fraction**	**contrast**	**p value**
Offshore	<2.63 µm	Ambient-Reference	0.97
		Ambient-Double	1.00
		Ambient-Half	0.84
		Reference-Double	0.97
		Reference-Half	0.98
		Double-Half	0.84
	3.11-4.33 µm	Ambient-Reference	0.51
		Ambient-Double	1.00
		Ambient-Half	0.95
		Reference-Double	0.41
		Reference-Half	0.20
		Double-Half	0.96
	5.11-6.03 µm	Ambient-Reference	0.58
		Ambient-Double	0.94
		Ambient-Half	1.00
		Reference-Double	0.23
		Reference-Half	0.50
		Double-Half	0.95
	7.11-8.39 µm	Ambient-Reference	0.88
		Ambient-Double	1.00
		Ambient-Half	0.96
		Reference-Double	0.92

Experiment	Particle Fraction	contrast	p value
		Reference-Half	0.57
		Double-Half	0.91
		Ambient-Reference	0.88
		Ambient-Double	1.00
		Ambient-Half	0.96
		Reference-Double	0.92
		Reference-Half	0.57
	9.9-15 µm	Double-Half	0.91
Nearshore		Ambient - Reference	0.22
		Ambient - Double	1.00
		Ambient - Half	0.89
		Reference- Double	0.16
		Reference - Half	0.06
	<2.63 µm	Double - Half	0.94
		Ambient - Reference	0.24
		Ambient - Double	0.72
		Ambient - Half	1.00
		Reference- Double	0.78
		Reference - Half	0.19
	3.11-4.33 µm	Double - Half	0.63
		Ambient - Reference	0.58
		Ambient - Double	0.80
		Ambient - Half	0.66
		Reference - Double	0.15
		Reference - Half	0.10
	5.11-6.03 µm	Double - Half	0.99
		Ambient - Reference	0.94
		Ambient - Double	0.28
		Ambient - Half	1.00
		Reference - Double	0.10
		Reference - Half	0.92
	7.11-8.39 µm	Double - Half	0.31
		Ambient - Reference	0.94
		Ambient - Double	0.28
		Ambient - Half	1.00
		Reference - Double	0.10
		Reference - Half	0.92
	9.9-15 µm	Double - Half	0.31

Dissolved organic carbon (DOC) values at the end of the nearshore experiment ranged between 0.62-1.83 mg L^{-1} with lowest values observed in the Double treatment (2 times the ambient concentration of zooplankton) and highest at the Ambient treatment (Figure 34). No significant

differences between the treatments were observed except between Ambient and Double treatments (p= 0.001). Total dissolved nitrogen (TDN) was mostly below the detection limit of the employed analytical methodology; only some values were above the detection limit (50 µg L^{-1}) with a maximum concentration of 75.62 µg L^{-1} (see Table 6 for more information).

Chlorophyll-a values at the end of the experiment ranged from 0.46 to 0.82 µg L^{-1}, with the highest values observed in the Ambient, Half, and Double treatments (with half, and double referencing to the half and double density of ambient zooplankton found within the lake) and lowest in the reference treatment (without zooplankton) (Figure 35). Nevertheless, there were no significant differences between each pair of treatments. We observed a decrease in chlorophyll-a at the end of the experiment compared to initial chlorophyll-a values obtained with the RBR for all the treatments (Figure 36).

Ambient zooplankton community composition at the nearshore experiment has a total concentration of 13.4 indvs per L and it was dominated by the rotifers *Keratella and Kellicottia*, and the copepod *Nauplii sp.* (Figure 37). *Keratella* and *Kellicottia* are considered polyphagous rotifers, which feed from fine detritus/organic aggregates, pico- and nanoplankton, and 20–50 µm microplankton (Gilbert, 2022). Also, both *Kellicottia* and *Keratella* species prefer particles and cells in the 2–10 µm range, with larger individuals or species tend to prefer larger particles within this range (Rublee, 1998). On the other hand, copepod nauplii feed primarily <5 µm plankton (Cortes et al. 2022).

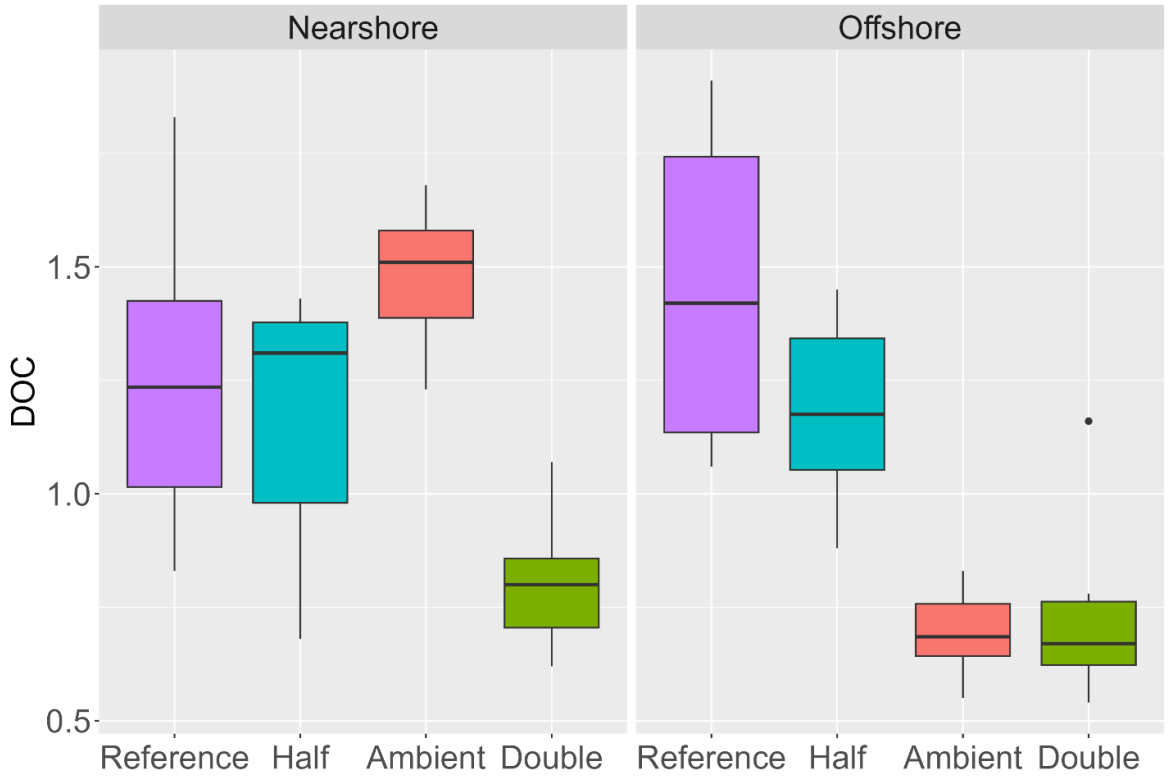


Figure 34. DOC concentration (mg L^{-1}) for each treatment at the Nearshore and offshore experiments. These concentrations were measured in the laboratory and corresponded to samples recovered at the end.

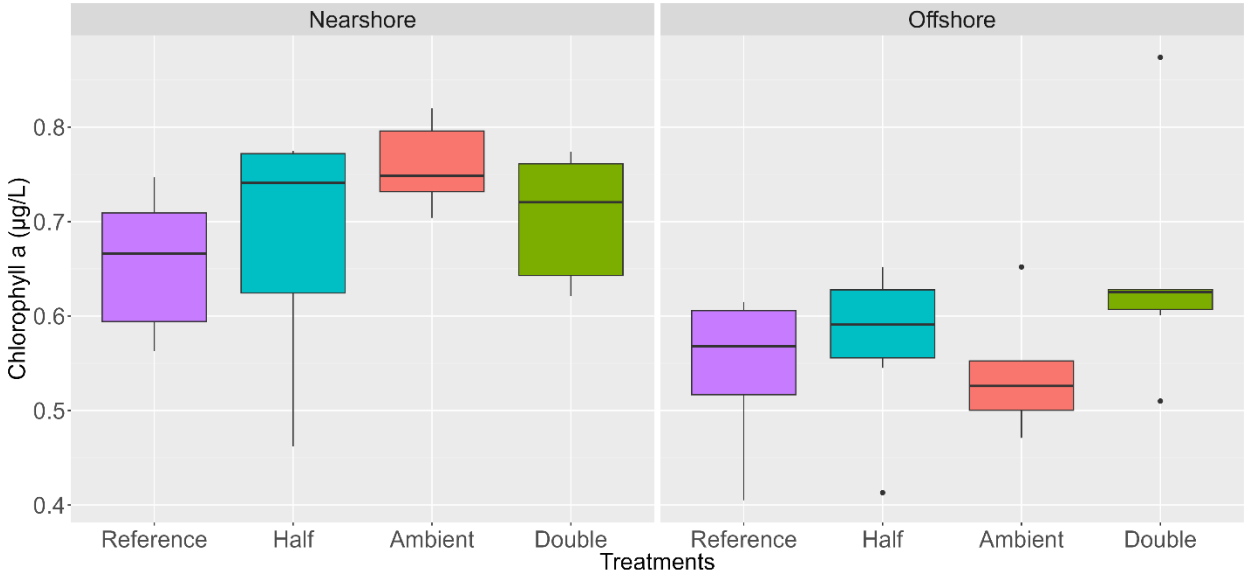


Figure 35. Chlorophyll-a concentration for each treatment at the Nearshore and offshore experiments. These concentrations were measured in the laboratory and corresponded to samples recovered at the end.

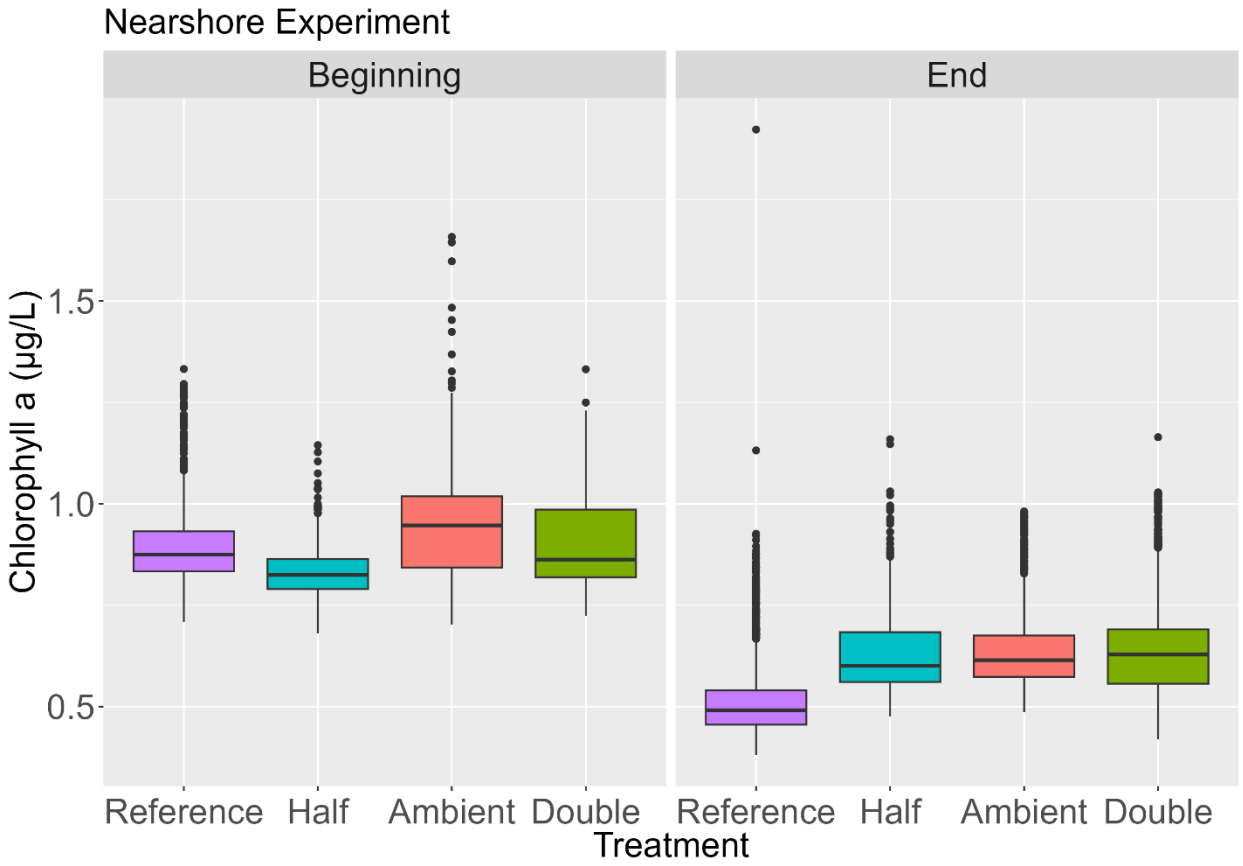


Figure 36. Chlorophyll-a concentration measured at the beginning and end of the nearshore experiment using RBR.

Table 6. DOC, TDN, and chlorophyll-a concentration by the end of the nearshore and offshore experiment. BDL: Below Detection Limit (50 ppb for TDN)

Site	**Treatment**	**Replicates**	**DOC (mg L^{-1})**	**TDN (µg L^{-1})**	**Chl a (µg L^{-1})**
Nearshore	Reference	1	0.83	BDL	0.56
		2	0.98	BDL	0.58
		3	1.35	60.17	0.63
		4	1.45	BDL	0.70
		5	1.12	BDL	0.71
		6	1.83	58.29	0.75
	Half	7	0.89	BDL	0.59
		8	1.25	BDL	0.46
		9	0.68	BDL	0.76
		10	1.38	BDL	0.78
		11	1.43	75.62	0.72
		12	1.37	BDL	0.78

Site	Treatment	Replicates	DOC (mg L^{-1})	TDN (µg L^{-1})	Chl a (µg L^{-1})
	Ambient	13	1.55	55.53	0.82
		14	1.36	56.21	0.73
		15	1.47	BDL	0.75
		16	1.23	BDL	0.70
		17	1.68	71.71	0.81
		18	1.59	BDL	0.74
	Double	19	0.85	BDL	0.76
		20	0.62	BDL	0.77
		21	0.69	BDL	0.63
		22	0.75	BDL	0.76
		23	1.07	BDL	0.69
		24	0.86	BDL	0.62
Offshore	Reference	25	1.08	69.86	0.59
		26	1.06	BDL	0.55
		27	1.91	63.03	0.61
		28	1.3	BDL	0.62
		29	1.54	BDL	0.51
		30	1.81	BDL	0.40
	Half	31	1.2	BDL	0.41
		32	1.39	BDL	0.65
		33	1.02	BDL	0.54
		34	1.15	BDL	0.59
		35	1.45	57.78	0.59
		36	0.88	BDL	0.64
	Ambient	37	0.68	50.17	0.50
		38	0.55	BDL	0.50
		39	0.78	52.33	0.55
		40	0.83	BDL	0.47
		41	0.63	BDL	0.55
		42	0.69	BDL	0.65
	Double	43	0.63	BDL	0.63
		44	1.16	BDL	0.62
		45	0.62	BDL	0.63
		46	0.78	BDL	0.87
		47	0.71	BDL	0.51
		48	0.54	BDL	0.60

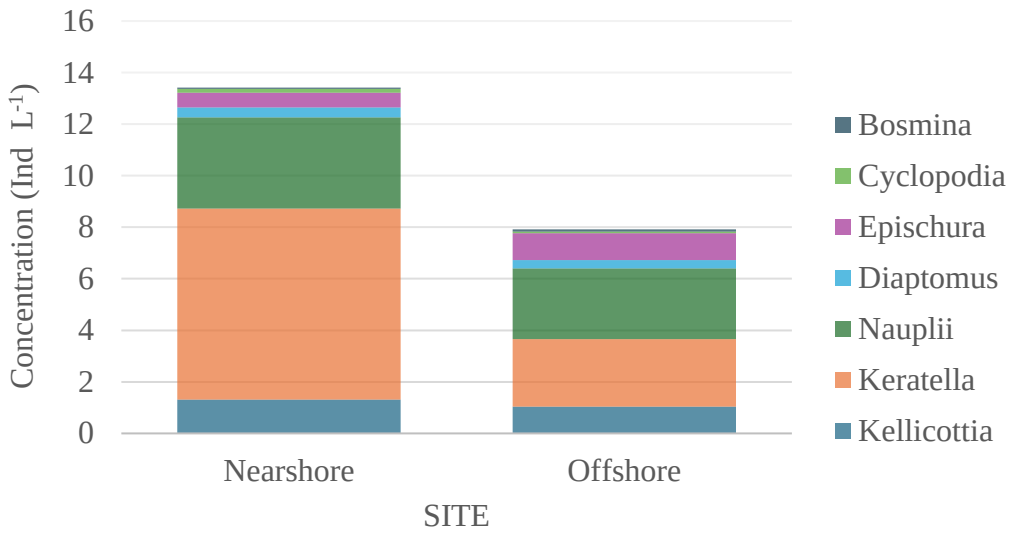


Figure 37. Ambient community composition at nearshore (Glenbrook) and offshore (MLTP) of the experimental mesocosms.

Offshore

We focused on particle size analysis in particles below 50 µm to minimize the influence of zooplankton. Also, we did not include replicate 17 (of the Ambient treatment) in the analysis because their particle distribution in the smaller fraction differed significantly from the other Ambient replicates (See supplementary material- Part B, Figure F). Figure 38 summarizes the mean values of the grain size particle distribution for each experiment; the Supplementary material- Part B Figures E-H provide further information about the grain size distribution in each treatment.

Comparing statistical significance between treatments of selected particle fractions, we found that the particle fractions between 3.11-4.33 µm and 5.11-6.03 µm were higher at the end of the experiment compared with the initial conditions in all the treatments (this is Half, Ambient and Double density of zooplankton found in offshore lake water). Still, the reference experiment (No zooplankton added to lake water) had a higher concentration than the other ones at the end of the experiment (Figure 38). In the larger particle fractions (7.11- 8.39 µm and 9.9-15 µm), all the treatments had higher concentrations of particles at the end of the experiment than the initial conditions in the reference experiment. In particle fraction of <2.63 µm, there was an increase of particles in this range at the end of the experiment, having all the treatment positive differences between initial and final conditions (Figure 39). Nevertheless, the statistical differences between the treatments were insignificant between any pair of treatments and at any particle fraction ranges (Table 5).

At the end of the offshore experiment, DOC ranged between 0.54-1.81 mg L^{-1}, with the lowest values observed in the Ambient and Double treatments (Ambient and double density of zooplankton found in offshore lake water) and highest at Reference and Half treatments (No zooplankton and Half density of zooplankton found in offshore lake water)(Figure 34). The differences between the Ambient and Double treatment with the Reference treatment were

significant (p- 0.0002 and 0.0005, respectively) (Table 5). No significant differences were found between the Reference and Half treatments (p= 0.6041). TDN concentrations mainly were below the detection limit of the employed methodology. Only some values were slightly above the detection limit (50 µg L-1) with a maximum concentration of 69.86 µg L-1 (see Table 6 for more information).

Chlorophyll-a values measured in the laboratory at the end of the experiment ranged from 0.40 to 0.87 µg L^{-1}, and there were very similar between the treatments, with the highest values observed in the Double treatment and the lowest in the Ambient treatment (Figure 34). Nevertheless, there were no significant differences between each pair of treatments, indicating no major changes in phytoplankton biomass. However, chlorophyll in oligotrophic lakes may not be a sensitive measure of changes over short periods of time. Like the nearshore experiment, we observed a decrease in chlorophyll-a at the end of the experiment compared to initial chlorophyll-a values obtained with the RBR for all the treatments. Still, the Double treatment did not decrease as much as in the other treatments, which aligns with the higher chlorophyll concentration measured in the lab compared to the other treatments (Figure 40).

Ambient zooplankton community composition at the offshore experiment has a total concentration of 7.9 indvs per L and it was dominated by the rotifers *Keratella and Kellicottia*, and the copepod *Nauplii sp.* (Figure 37).

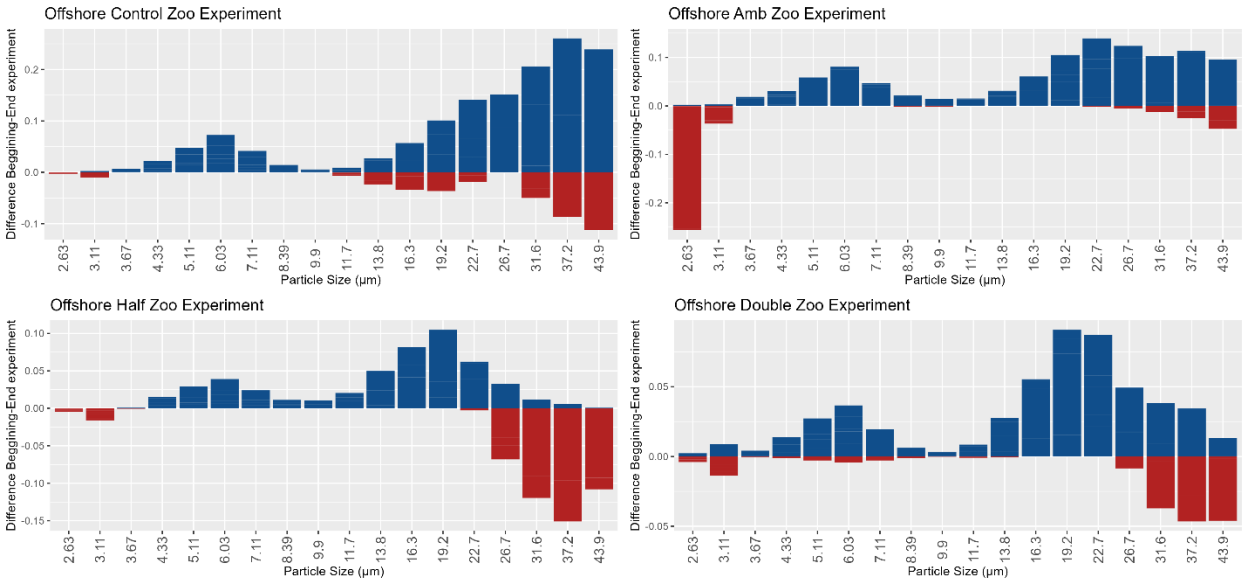


Figure 38. Average difference between the beginning and end of each treatment's nearshore experiment for particle sizes below 50 µm; negative values indicate a higher concentration of particles at the end of the experiment, while positive values indicate lower concentration of particles at the end of the experiment. These results do not include replicate 17.

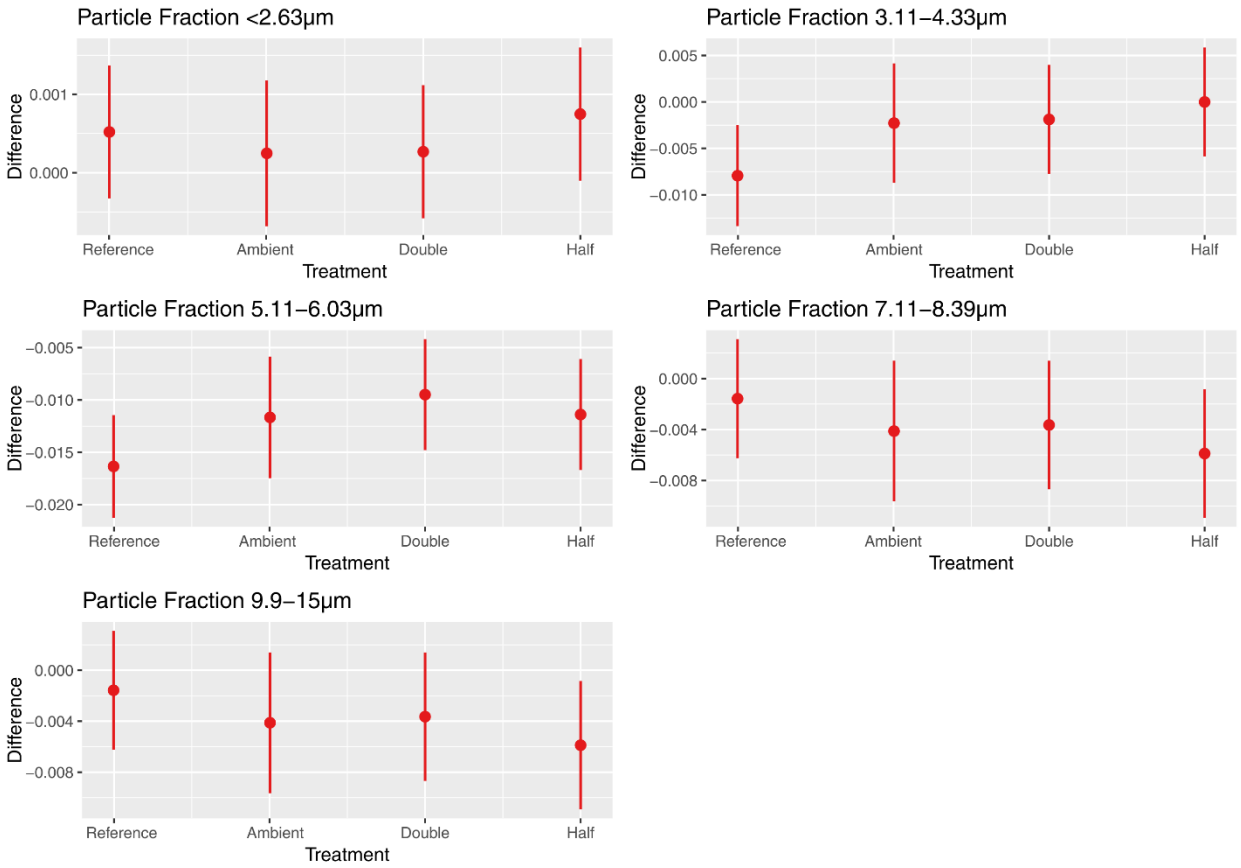


Figure 39. Mean and Standard error differences between the beginning and end of each treatment's offshore experiment for the analyzed particle fraction; higher negative values indicate a higher concentration of particles at the end of the experiment. These results do not include treatment 17.

Figure 40. Chlorophyll-a concentration representing algal biomass at the beginning and end of the offshore experiment using RBR.

In summary, the zooplankton community does not appear to control particles through direct feeding, particularly in the finer particle ranges (0-5 um) that influence lake clarity. Zooplankton could have some influence on altering nutrients or dissolved organic carbon (Bess et al. 2022), where dissolved organic carbon increases in offshore experiments using mid-lake water. This snapshot experiment was conducted once when the zooplankton densities were presumably very low compared to midsummer. It may be helpful to repeat these experiments in space and time, coupling them with lake wide monitoring of zooplankton. In addition, modeling the excretion rates of plankton and calculating potential nutrient and carbon contributions for stimulating bacterial and algal growth may aid in understanding the direct and indirect influences of zooplankton communities on pelagic ecosystem processes. Future experimental methods should consider mixing lake water to reduce the settling of particles out of the water column.

Task 6: Coordination with Desert Research Institute, Dr. Alan Heyvaert's particle evaluation project.

We coordinated, collected, and distributed samples from the sampling sites for the particle evaluation project to Dr. Alan Heyvaert. Per his contract, we also contributed staff and students to analyze particle size for those samples.

Task 7: Reporting, data distribution, and findings communication.
We have provided project updates through short reports and communication with the steering committee. We will present our final findings to the committee after the report has been submitted in January 2025. Data links for the project are embedded in the project for download. Data curation, field campaigns that had to be adjusted due to weather, and zooplankton laboratory analysis took additional time that was not anticipated. As a result, we could not complete the short communications piece for this project. We created a key that other scientists and the public can use to identify rotifers, which has been a major need for Lake Tahoe (see supplemental).

Conclusions and Recommendations.

The last studies evaluating the variation of native zooplankton in time and space occurred in the early 1970s, with other studies evaluating the ecology of mysid shrimp, including their distribution in time and space, in the late 1970s to early1980s. Most of the historical studies have focused mainly on larger macrozooplankton rather than quantifying microzooplankton (ciliates and rotifers), which can play a role in eating smaller particles in the lake; the fine particles (<5 um) in Lake Tahoe govern water clarity dynamics over time. Surprisingly, water quality monitoring programs funded by the agencies have not financed a program that quantifies zooplankton in space or time from Lake Tahoe, despite the scientific literature from lakes of similar type suggesting high spatial variability in zooplankton populations and important roles in governing carbon and nutrient dynamics over time. Without this information, inputs into the models (i.e., statistical, mass-balance, process) evaluating clarity may be using poorly constrained information, resulting in gaps in our understanding of the role of zooplankton in governing the water quality, including Lake Tahoe's clarity.

This study found significant heterogeneity in space and time in clarity and water quality conditions, having us reflect a little more about the actual within-lake variability in these parameters measured over time but not characterized by the long-term monitoring program funded by the agencies. Lake Tahoe's nearshore habitats and Emerald Bay exhibited less clarity than the offshore ones, where long-term monitoring locations have been used to measure lake health over time. As expected, the temperature varies in space (nearshore versus offshore), with more variation in the day versus night and more so via season, suggesting that monitoring programs that measure water quality do not have to consider the time of day as sampling protocols are developed in the future except when measuring clarity via Secchi disk.

Macrozooplankton includes native and non-native animals that are more visible to the trained eye and feed on particles in various size ranges depending on the taxa's life history or feeding modes. While zooplankton diversity and density are different in Emerald Bay versus the main

water body of Lake Tahoe, there is significant heterogeneity across space (horizontal and vertical) and time within Lake Tahoe. While the variation of zooplankton community composition was different in space, there were major differences in the density of macrozooplankton between day and night at the same site. The seasonal variability was evident, with higher densities observed in summer (July) and major declines in winter (December), except in Emerald Bay. Lake Tahoe's nearshore and offshore community composition varied by season, with the most common species found in the nearshore including *Bosmina* and *Epischura*, while offshore sites were dominated by *Epischura, Cyclopods* and early life stage of copepods called nauplii. Invasive shrimp dominate the pelagic sites, except Emerald Bay, contrary to historical published studies from Lake Tahoe from the 1970s and 80s which found shrimp across the pelagic zone of Tahoe and Emerald Bay.

In terms of microzooplankton, smaller animals that have not been well characterized in Lake Tahoe since the 1970s that can feed on finer particles in the lake, there were similar communities of rotifers in the nearshore and pelagic habitats but different abundances at specific sites. Seasonal differences were observed, with high rotifer densities in spring (May) and variable densities throughout summer and fall which is different than the historical studies from the 1970s. Some species, like *Synchaeta kitina*, were abundant in early spring but declined in summer, while others, like *P. dolichoptera*, remained common year-round. Rotifer densities were highest in nearshore environments during May and July, while pelagic habitats often had lower densities. There were seasonal shifts in dominant species, with *Keratella cochlearis* and *P. dolichoptera* dominating at different times and locations. As expected, Emerald Bay supported unique rotifer communities due to its higher productivity and algal biomass.

Zooplankton can migrate in lakes vertically and horizontally across the water column, but this can depend on the species or life stages of specific taxa. UC Davis's current unfunded collection of zooplankton has focused on understanding zooplankton populations during the day and is limited to two sites in the lake. Building from their work, sampling day and night across the lake, we show that zooplankton migration varies among species and across locations. Generally, zooplankton (micro- and macro-) migrate to deeper waters during the day and rise to shallower waters at night. Still, some dominant species, like *Bosmina* and *Epischura*, displayed different migration behaviors depending on the site and season. At some sites, vertical concentrations during the night were much higher than expected in shallow waters, suggesting vertical and horizontal migrations or movements, particularly across nearshore and offshore environments.

Combining the findings related to understanding the macro- and microzooplankton dynamics in Lake Tahoe in space and time, and with the focus on describing migration, we believe that a monitoring approach that only incorporates 1-2 stations approach will not be sufficient if we are trying to evaluate zooplankton's role on water quality and clarity over time. In addition, the historical studies from the 1970s to the present day used long, vertical net hauls from two locations using larger mesh nets (80 um). Future monitoring programs must consider sampling across time and horizontal space (offshore and nearshore) to accurately understand the densities and composition that would serve as input variables in various modeling efforts. Furthermore, samplings in vertical space should occur within the target depths, which contributes to the clarity, or other parts of the lake that may be of interest (e.g., deep productivity maxima). Finer mesh screens within nets need to occur to capture a more accurate picture of rotifer dynamics,

and methods need to be developed to capture microzooplankton ciliate dynamics. A monitoring program built around time (within and across seasons and years with different climatic conditions) and space (across lake habitats) will lead to an actual understanding of the ecology of zooplankton within the lake.

When evaluating the fate of particles due to zooplankton feeding and potential excretion, which can stimulate the bacterial and algal parts of the lake's water quality condition, we observed no statistical differences across treatments in the nearshore or offshore environments when it comes to particle reduction, but there were nuances in the relative increase or decrease of particle fractions across the experiments that may be worth exploring further. Previous research also suggests relatively minor roles of direct zooplankton grazing on lake particles or algal dynamics. However, zooplankton can excrete carbon and nutrients that may stimulate different players in the water column, like bacteria or phytoplankton (Bess et al., 2021). While we didn't see any significant impacts from zooplankton on nutrient and carbon excretion potential in the nearshore, we did see that populations similar to the ambient, or double the ,lake concentrations contributed to the dissolved organic pool in the offshore.

We caution against the over-interpretation of these experiments; they were conducted as pilot experiments at one time in the lake under a particular set of conditions. Coupling these semi-natural grazing experiments along the nearshore and offshore with monitoring and modeling could inform when and how zooplankton influence ecological processes in the pelagic zone. It may be useful to undertake experiments that evaluate the role of zooplankton feeding on particles under different loading conditions of particles from the watershed along the shoreline as well.

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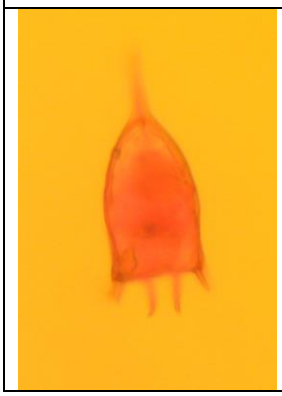
Supplementary materials-A

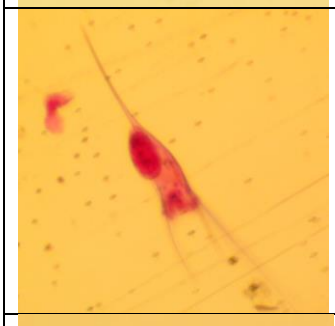
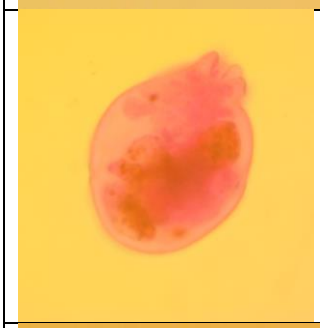
Lake Tahoe rotifer community key – 2023 – with notes on their feeding and ecology.

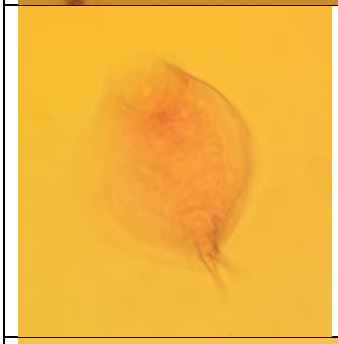
Resources used to produce the key along with identification and processing by Erin Suenaga with identification confirmation and contributions from Dr. Stephanie Hampton (Carnegie Institution for Science) and Dr. Ian Duggan (University of Waikato).

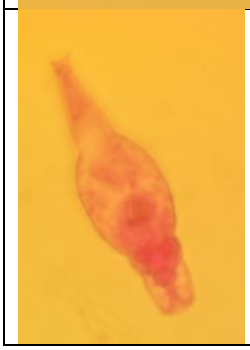
Gilbert, John J. 2022. Food niches of planktonic rotifers: Diversification and implications. *Limnology and Oceanography*. 67: 2218:2252

Bogdan, K.G, and J.J. Gilbert. Seasonal patterns of feeding by natural populations of Keratella, Polyarthra, and Bosmina: Clearance rates, selectivities, and contributions to community grazing. *Limnology and Oceanography*. 27(5): 918-934.

	***Polyarthra dolichopteria*** Tolerant to environmental and seasonal changes (Liang et al. 2019, 2022) Raptorial feeding mode (Pourriot 1977; Gilbert 2022), macrophagous algivores – generally eat nanoalgae (20-50µm) and small microalgae (probably rarely eat fine detritus/organic aggregates or picoplankton Reproduce by cyclic parthenogenesis, resting eggs (dormant stages) will be produced to escape unsuitable conditions Distribution of species driven by geography and environmental parameters whose importance is different in low- and high-altitude lakes (Obertegger et al. 2014) Prefer unflagellated algal cells (Bogdan & Gilbert, 1981)
	***Keratella cochlearis*** Can be found in most freshwater lakes and ponds globally (Green 1987) Polyphagous – eating detritus/organic aggregates, picoplankton, nanoplankton and some larger algae and ciliates. Direct relationships between clearance rates and temperature were found for Keratella feeindg on *chlamydamonas* (large algal cells) and *Rhodotorula (6 x 2.5 µm)* (Bogdan & Gilbert, 1982) Gilbert & MacIsaac (1989, 1991) did experiments looking at interference and exploitative competition of cladocerans on *Keratella.* K.c can coexist with small but not large cladocerans, but populations would be suppressed.

	***Keratella hiemalis*** Polyphagous – eating detritus/organic aggregates, picoplankton, nanoplankton and some larger algae and ciliates. In Lake Erken (Sweden), *K.h* spring maximums coincided with appearance of chrysomonads Generally observed in higher elevations than other species of *Keratella* (Tausz et al. 2019)
	***Kellicottia longispina*** Polyphagous with a diet consisting of fine detritus/organic aggregates, picoplankton, and nanoplankton (Gilbert 2022 lists studies). Co-occurring competitor of *Keretella cochlearis* (Hoffman 1983)
	***Syncheata kitina*** Predominantly macrophagous algivores, unlikely to ingest bacteria and detritus Eurythermal, but highest densities seen above 7C in Loch Leven, Scotland (May et al. 1993)
	***Gastropus stylifer*** *Gastropus* are raptorial, macrophagous algivores, with some species eating much smaller cells. *G. stylifer* has been observed feeding on contents of flagellated algae (Wesenberg-Lund 1930; Pourriot 1965)
	***Conochilus unicornis*** Colonial species Consumes fine detritus/organic aggregates picoplankton and small nanoplankton (<=10µm) Lots of clearance rate studies on this species summarized in Gilbert 2022 – most efficient on food smaller than <5µm

	***Lecane bulla*** One of the most diverse genera of Monogononta rotifers *genus *Monostyla* and *Lecane* were combined (Koste 1978, Sharma 1978) Generally found in tropical systems, but are widespread cosmopolitans and inhabit wide range of environmental conditions (Arroyo-Castro 2021) – thermal generalists (Saucedo-Rios et al. 2017) Fed green algae *Nonnochloropsis oculate* when propagated for laboratory experiments
	***Lepadella spp.*** Littoral, benthic rotifer species (Koste 1978)
	***Trichotria tetractis*** Bacteriovores
	***Trichocera* spp.** Raptorial feeders (Pourriot 1970) Some species have been seen feeding on the eggs of other rotifers, chrysophytes, diatoms, and cryptophyte flagellates

	***Lecane ludwigii ercodes***
	***Notholca*** Macrophagous algivores – mostly feed on pennate or centric diatoms No evidence of feeding on detritus or picoplankton
	***Notholca*** Macrophagous algivores – mostly feed on pennate or centric diatoms No evidence of feeding on detritus or picoplankton
	***Bdelloidea spp.*** *different order from all other rotifers IDed that are order Monogononta Completely asexual reproduction Resistant to extreme environmental changes Possibly eat unicellular algae (Melone and Fontaneto 2005)

Supplementary material-B

Zooplankton grazing on particles experiment, additional figures.

Figure A. Particle size distribution for each reference treatment at the nearshore experiment.

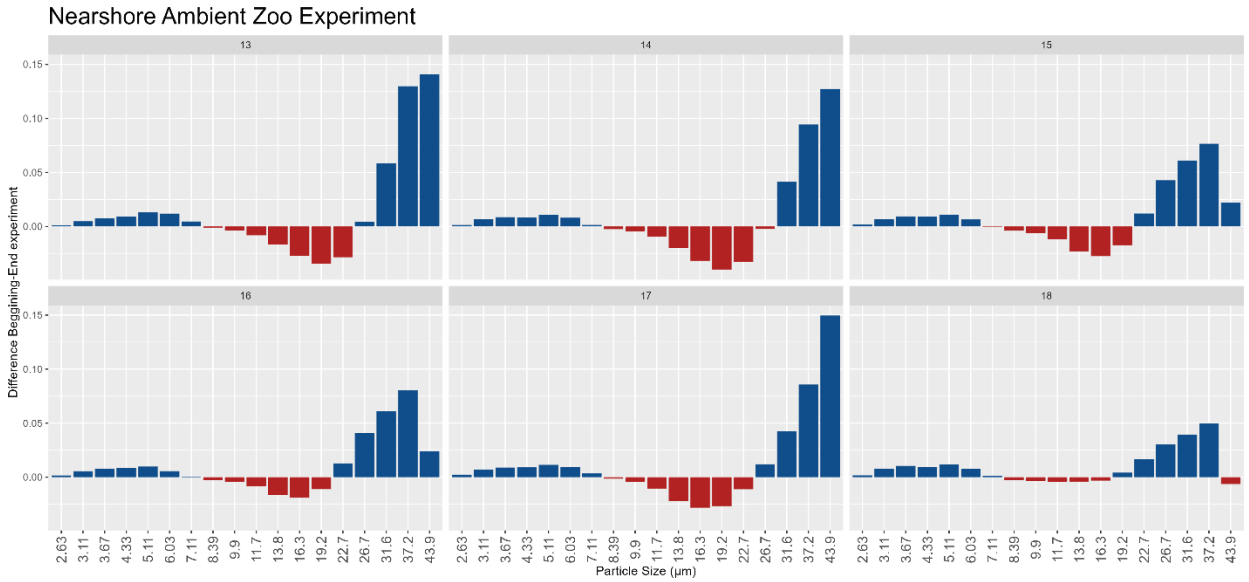


Figure B. Particle size distribution for each Ambient treatment at the nearshore experiment.

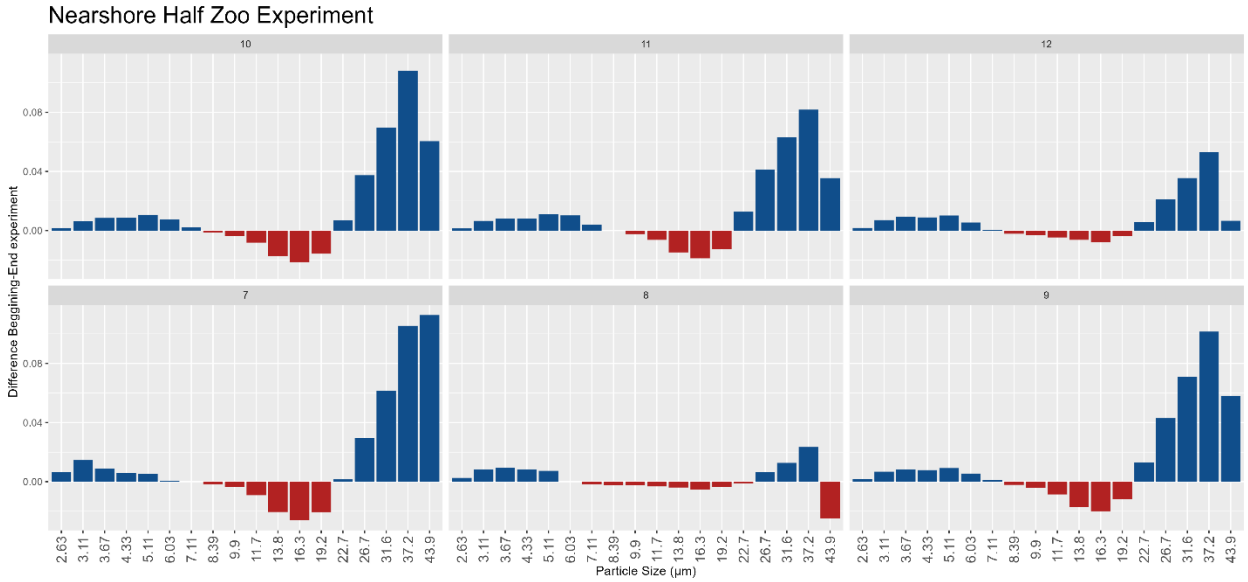


Figure C. Particle size distribution for each Half ambient treatment at the nearshore experiment.

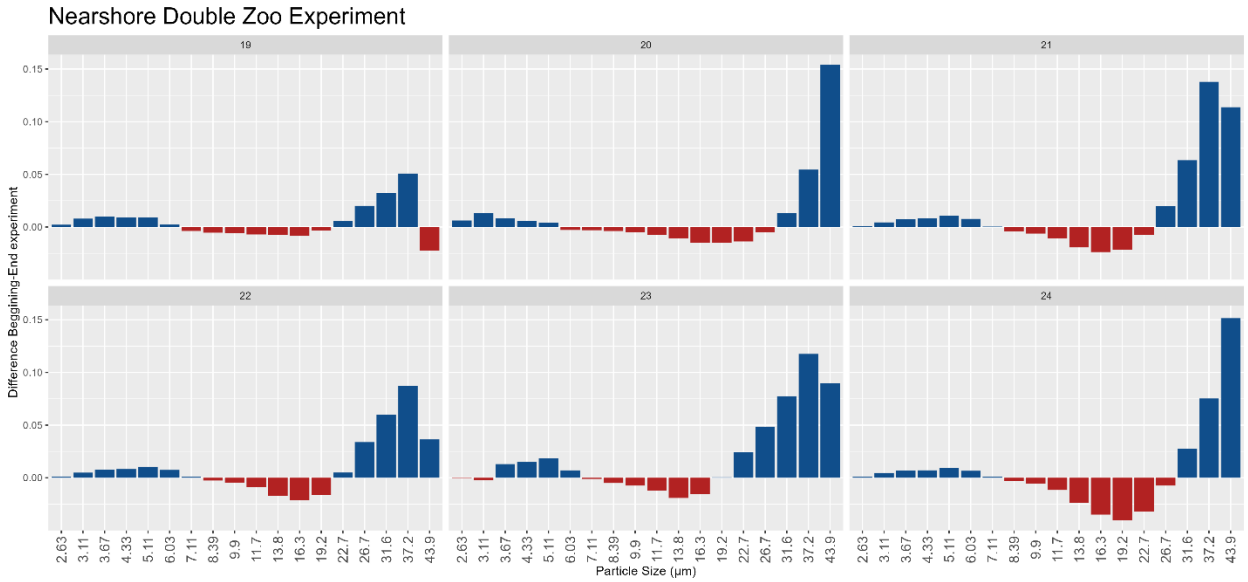


Figure D. Particle size distribution for each Double treatment at the nearshore experiment.

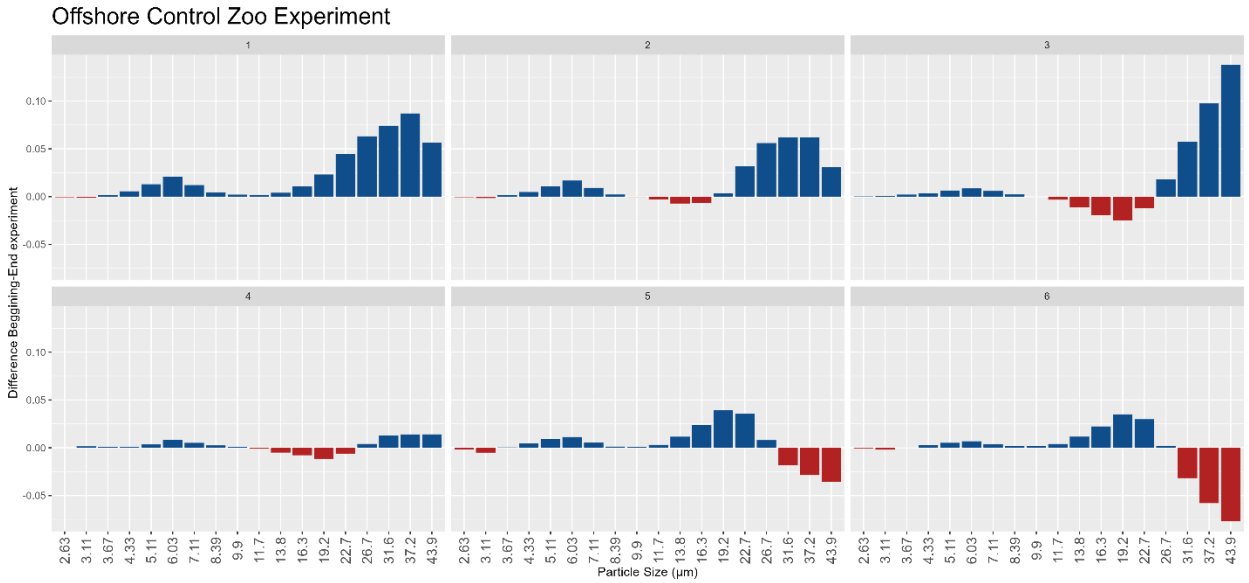


Figure E. Particle size distribution for each reference treatment at the offshore experiment.

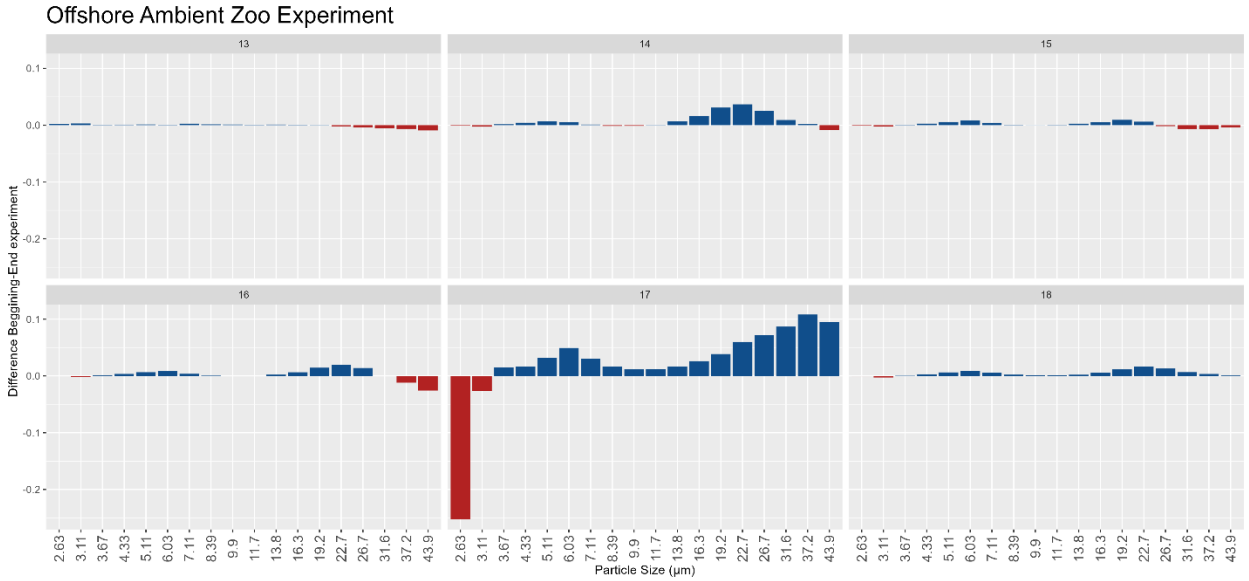


Figure F. Particle size distribution for each Ambient treatment at the offshore experiment.

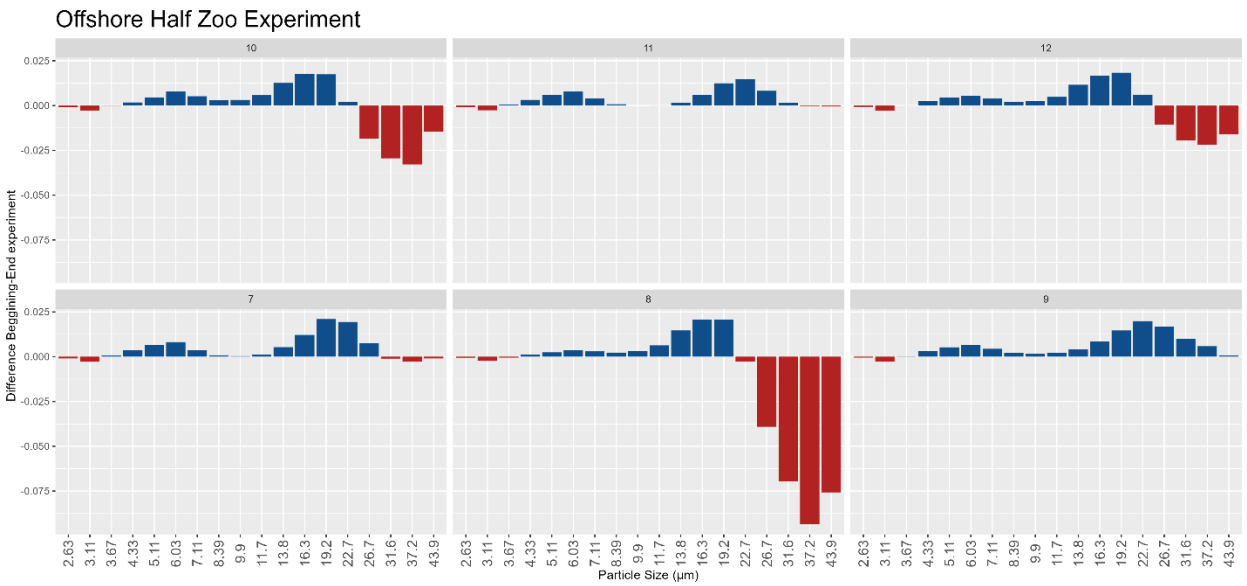


Figure G. Particle size distribution for each half treatment at the offshore experiment.

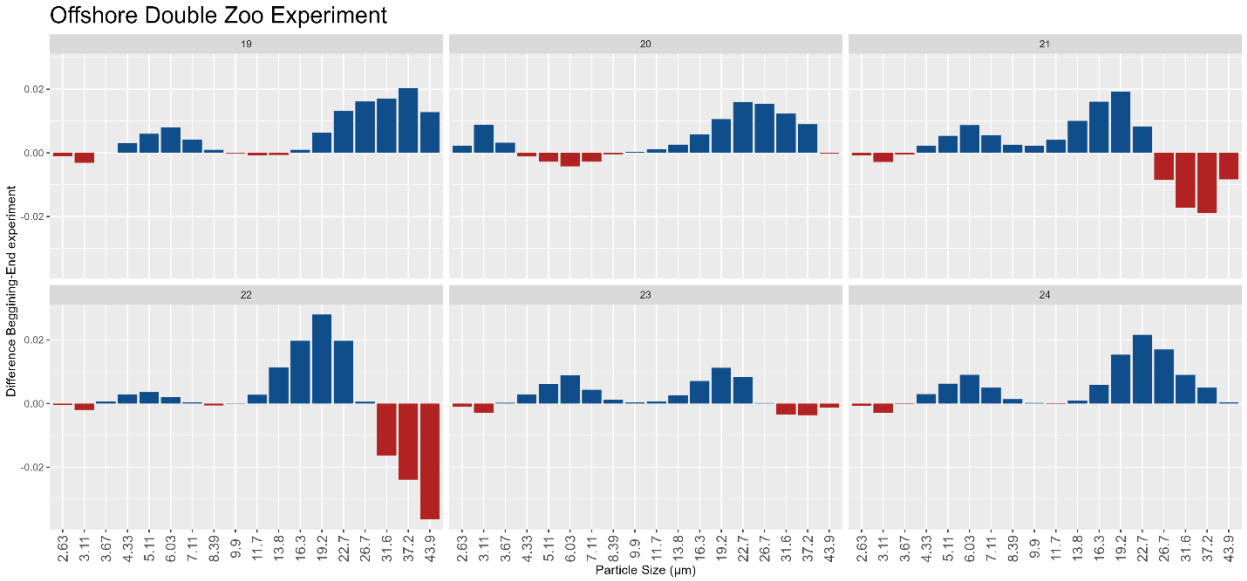


Figure H. Particle size distribution for each Double treatment at the offshore experiment.