

Are Zooplankton as Patchy as Phytoplankton?

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Abstract

Phytoplankton and zooplankton form the base of most lake food webs and are the primary sources of energy for higher trophic levels. The distribution of phytoplankton and zooplankton is not constant vertically or horizontally within a lake. Recent studies have shown that the horizontal distribution of phytoplankton is not even across the surface of lakes. However, little is known about the horizontal distribution of zooplankton in the surface waters of lakes or the spatial interactions among zooplankton and phytoplankton. The aim of this study was to quantify the spatial distribution of phytoplankton and zooplankton and determine if their spatial distributions are related. We sampled zooplankton and phytoplankton at night in a 24 point grid in Paul Lake, Michigan in the late spring and early summer of 2016. Phytoplankton and zooplankton were not uniformly distributed horizontally. Instead, there were hotspots of both zooplankton and phytoplankton, and in many instances (11 out of 18) there was positive autocorrelation. Additionally, zooplankton and phytoplankton concentrations were not correlated in space indicating that grazing is likely not a driver of zooplankton or phytoplankton spatial heterogeneity.

Introduction

Phytoplankton are free-floating photoautotrophic organisms common in lake ecosystems. Phytoplankton populations respond to both biotic and abiotic factors. For example, phytoplankton abundances haven been shown to vary in response to grazing pressure by zooplankton (Carpenter et al. 1985). Additionally, nutrient pollution in lakes, termed eutrophication, often results in nuisance algae blooms covering the surface of the water (Heisler et al. 2008). Zooplankton, which are a broad group of small invertebrates that live in the water column (Kalff 2001), play an integral role in food webs as a link between primary producers (phytoplankton) and organisms higher up in the food web. Many zooplankton graze on phytoplankton and therefore can reduce phytoplankton concentrations (Carpenter et al. 1985). In general, phytoplankton and zooplankton make

up the base level of aquatic food webs and play an important role in structuring aquatic ecosystems and ecosystem services.

The distribution of phytoplankton and zooplankton is not uniform throughout lakes. In many lakes, chlorophyll *a*, a pigment in phytoplankton, has a variable vertical distribution with peak concentrations in the metalimnion (Cullen 1982). Recent studies investigating the horizontal spatial distribution of phytoplankton (Crawford et al. 2014) and metabolic rates (Van de Bogert et al. 2012) have shown that these variables are not evenly distributed horizontally across lakes. This observed patchiness in phytoplankton may drive or be driven by patchiness in zooplankton distributions.

In the case of zooplankton, a great deal of work has been performed to understand that vertical heterogeneity in these organisms. It has been shown that zooplankton are not evenly distributed vertically through the water column as they exhibit diel vertical migration (Lampert 1989; Dini And Carpenter 1992; Kalff 2001). In diel vertical migration, zooplankton typically migrate up the water column into the epilimnion during the evening and into the night (Lampert 1989; Dini And Carpenter 1992; Kalff 2001). Although it is clear that zooplankton are not evenly distributed vertically, very little work has focused on understanding the horizontal distribution of zooplankton.

Generally, phytoplankton and zooplankton samples are collected at only one location in a lake (e.g. Carpenter et al. 2011; Pace et al. 2013). Results from collecting samples in one area may not accurately estimate the population if phytoplankton and zooplankton occur in patches. Additionally, researchers have focused on temporal variation in zooplankton and phytoplankton while disregarding the possibility of within-lake spatial variation (Carpenter et al. 2011). Very little work has examined the

horizontal spatial variation in zooplankton and its relationship to the patchy horizontal distribution of algae. Thus, it is imperative to investigate spatial interactions of phytoplankton and zooplankton in lakes in order to better understand and characterize these systems.

Here, we aim to document the relationships between phytoplankton patches and zooplankton patches and gain a better understanding of the magnitude of variability of phytoplankton and zooplankton that exists within a lake. We hypothesize that there will be large spatial variability in both zooplankton and phytoplankton abundances throughout the lake. Thus, sampling in one area may not be an accurate representation of the phytoplankton and zooplankton abundances in the lake. Further, we hypothesize that there will be a direct positive relationship between phytoplankton abundance and zooplankton abundance; meaning that zooplankton will be in dense patches where there are dense patches of phytoplankton. Such a relationship could be driven by zooplankton aggregating in high resource areas.

Methods

Study site- Paul Lake is a northern temperate lake located at the University of Notre Dame's Environmental Research Center in the Upper Peninsula of Michigan. Paul Lake can be best characterized as oligotrophic and has a maximum depth of 12 meters (Kitchell And Kitchell 1980; Dini And Carpenter 1992). Largemouth bass (*Micropterus salmoides*) is the lake's top predator, which feed on smaller planktivorous fish (Kitchell and Kitchell 1980). The low number of planktivorous fish enables large-bodied (and efficient grazers) zooplankton to persist.

Study design- We sampled Paul Lake in the summer of 2016 on May 24th, May 30th, and June 13th. Sampling generally occurred between the hours of 22:00 and 00:00. Zooplankton are less likely to be in deeper depths at night and will have migrated up to the epilimnion, which helped mitigate vertical variances in distribution. The pelagic zone of the lake was broken up into a grid of 24 evenly spaced sampling points 15 meters away from one another (Figure 1).

Field sampling- A 3 meter vertical zooplankton tow using a Wisconsin zooplankton net with 153 μm mesh was taken at each of the 24 sampling sites. The samples were then preserved in Lugol's solution. Four subsamples from each site were enumerated for four common taxa: calanoid copepods, cyclopoid copepods, *Holopedium*, and *Daphnia* via microscopy. Zooplankton abundance was then estimated via subsamples as summarized in McCauley 1984. A 2 meter integrated water sample was taken at each sampling site to estimate phytoplankton biomass via chlorophyll a concentration. 200 mL of sample water was filtered using 47 mm GF/F filters (nominal pore size 0.1 μm) to collect phytoplankton cells. The filters were frozen for at least twenty-four hours to lyse the cells and then chlorophyll a was extracted by submerging each filter in 25 mL of methanol for exactly twenty-four hours. Chlorophyll a concentrations were then determined fluorometrically following methods in Marker et al. 1980.

Statistical analysis- Frequency distributions were calculated to look for initial trends and relationships. We then analyzed our data for correlations between zooplankton abundance and phytoplankton biomass across the lake on a given sampling date and also examined how these correlations changed over time. This was done by regressing zooplankton abundance against with phytoplankton abundance. We also examined how

the variance in phytoplankton and zooplankton biomass changes over the season and how the variance in our data changes with respect to abundance using the coefficient of variation. Additionally, patchiness of either phytoplankton or zooplankton may be autocorrelated with itself. Spatial autocorrelation takes into consideration the possibility that sampling sites next to one another may not be independent of each other (Sokal And Oden 1978). Thus, we used Moran's I (Moran 1950) test for spatial autocorrelation to determine if any variable was related to itself through space for a given sampling date. Then, for each sample date, we looked at variability of both a low density taxa (*Daphnia*) and high density taxa (calanoid copepods). This was done visually by creating box and whisker plots of zooplankton abundance at all points standardized to the mean on that sample date ($[\text{abundance at each point} / \text{mean abundance}] * 100$). The resulting "percent of mean" was used to allow for comparisons between taxa and within a given taxa through time.

Results

Chlorophyll *a* concentrations increased from the first sampling date to the second sampling date. Distinct patches of phytoplankton were apparent in all of the weeks (Figure 2). These high concentrations of algae were on the west side during the first and third week. Phytoplankton concentration was found to be positively spatially autocorrelated the first and third night, but not on the second night when there was a wider range and larger amount of variation in the data (Table 1, Moran's I $p < 0.01$).

No relationships between phytoplankton and zooplankton (in terms of total zooplankton and among each taxa) were found (Figures 3-7, linear regression $p > 0.05$).

The frequency distribution of total zooplankton did not change over the three sampling dates. With this being said, there were distinct patches of zooplankton (all taxa considered together) in different areas of the lake each week (Figure 3). Total zooplankton abundance was positively auto correlated the second and third week (Table 1, Moran's $I p < 0.1$ and $p = 0.1$).

The abundance of *Daphnia* declined sharply after the first week of sampling (Figure 4). *Daphnia* were the most abundant on the west side of the lake the second week (Figure 4). When *Daphnia* crashed, they were found to be positively autocorrelated for both the second week and third week (Table 1, Moran's $I p < 0.01$).

Holopedium had one of the highest abundances throughout the study. In contrast to *Daphnia*, *Holopedium* were the most abundant on the east side of the lake. The variability of the distribution of *Holopedium* abundance got smaller as time went on (Figure 5). *Holopedium* were only observed to be positively auto correlated on the first night (Table 1, Moran's $I p < 0.01$).

The frequency distribution of calanoid copepods did not to change over the course of the study. Notably, calanoid copepods were one of the most abundant taxa each week and were found in patches in different locations throughout the lake (Figure 6). Calanoid copepods were also found to be positively autocorrelated during the second and third night (Table 1, Moran's $I p < 0.01$).

Examining the other copepod, we observed a decline in cyclopoid copepods during the last week of the study. Distinct visual patches of cyclopoids occurred each

week (Figure 7). Cyclopoid copepods also exhibited positive autocorrelation during the third week (Table 1, Moran's I $p < 0.01$).

In terms of magnitude, variation was large for both *Daphnia*, which had a small distribution after the first week, and calanoid copepods that had a large distribution. Around 50% of the samples taken each week had abundances that were equal to or greater than 25% away from the median value (Figure 8).

Discussion

The results strongly support the idea that aquatic systems are heterogeneous. Spatial variability and patchiness can be observed for both phytoplankton and zooplankton. This phenomenon cannot be explained by grazing pressure from zooplankton or local phytoplankton suppression by zooplankton as zooplankton abundance was not significantly correlated with phytoplankton abundance for any taxa on any sampling date.

Instead, wind may be an important driver of spatial heterogeneity. There is evidence for phytoplankton that physical forces such as wind create patches of nutrients that spur phytoplankton growth (Caron et al. 2008; Blukacz et al. 2010; Mackay et al. 2011). These nutrient patches could in turn result in patches of phytoplankton, thus creating spatial variability in primary production in lakes. Zooplankton on the other hand may be less vulnerable to wind driven patchiness as they are able to move more quickly throughout the water. Zooplankton also have to balance searching for food with avoiding

predation which could alter their spatial distribution. Research in the future should take into account and quantify what role if any wind has in creating patchiness.

As stated earlier, there were many instances of positive autocorrelation among both phytoplankton and zooplankton. Going hand in hand, there were many observations of low variance to mean ratios, which can be an indicator of autocorrelation. While the dominant driver of patchiness remains unclear, our results show that many plankton are positively autocorrelated, indicative of patchiness, or under-dispersion (cite paper with this statistic).

Interestingly, we observed that the two taxa of cladocerans (*Daphnia* and *Holopedium*) were most abundant on different sides of the lake. *Holopedium* were most abundant on the west side of the lake while *Daphnia* were abundant on the west side. It is possible that this separation could be driven by competitive avoidance since these two taxa occupy similar niches.

Additionally, we observed that all taxa of zooplankton and phytoplankton had high coefficients of variation. Further, we found a wide range and magnitude in percent variability of our samples from each date. This suggests if we were to only sample *Daphnia*, for example, in one area of the pelagic zone of the lake, we could severely overestimate or underestimate the population in the system. This same trend holds for all taxa of zooplankton, total zooplankton and chlorophyll *a*. Sampling in one just one location over time leads to potential mischaracterization of the phytoplankton and zooplankton communities. Thus, if the goal of a study is to understand and characterize

the population of either phytoplankton or zooplankton, we suggest taking multiple samples of the pelagic zone.

In summary, our results show that there is high spatial variability of both phytoplankton and zooplankton. We also show the spatial variability in lake systems are dynamic and the mechanisms driving variability in space over time are still poorly understood. Our hypothesis that planktonic patchiness is driven by zooplankton grazing on phytoplankton was not supported. Another point to consider is that Paul Lake is oligotrophic and therefore primary production is likely nutrient limited. We may observe very different trends in eutrophic lakes, which have higher chlorophyll and potentially more algae blooms. Further emphasis should be put on investigating the physical forces that could affect patchiness such as wind. Thus, we suggest more research be done to comprehend the spatial variability that is observed in lake systems.

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Relevant Figures

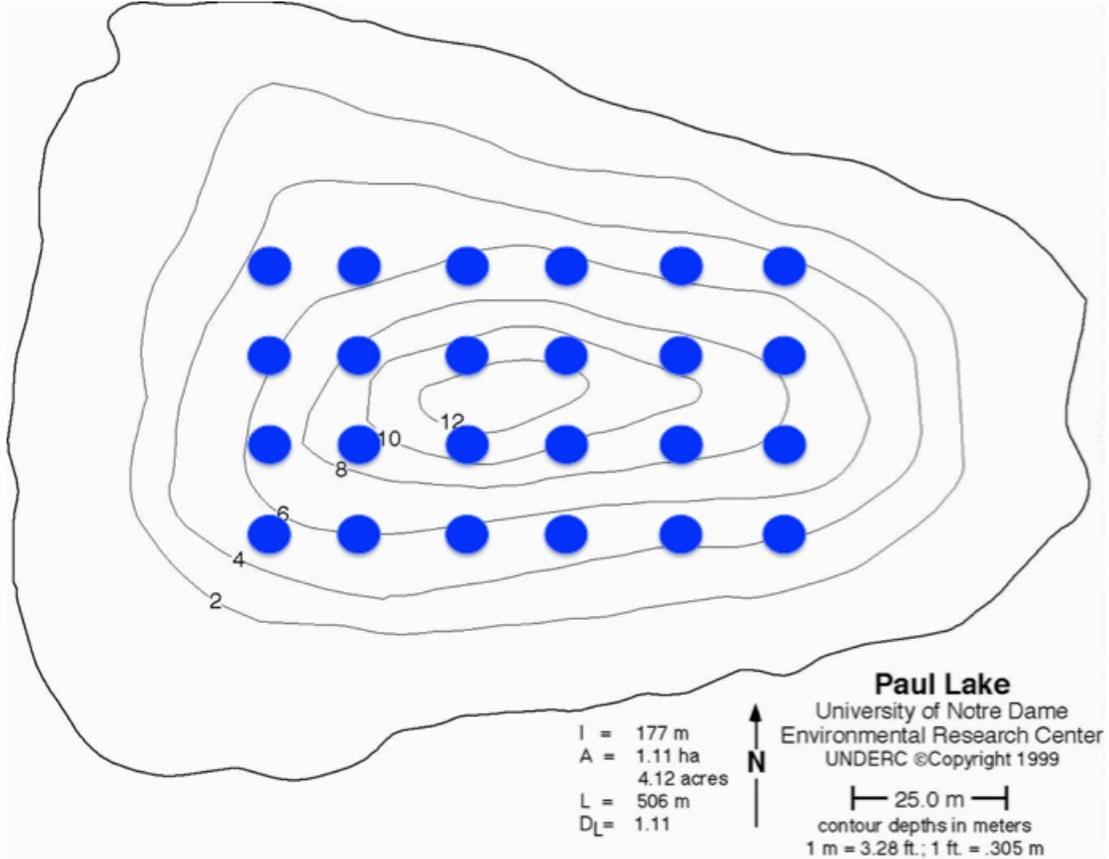
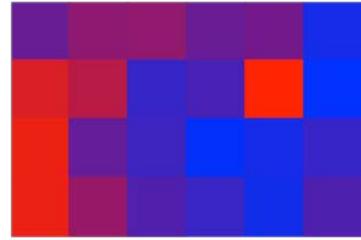
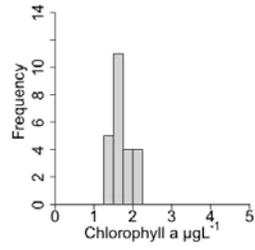
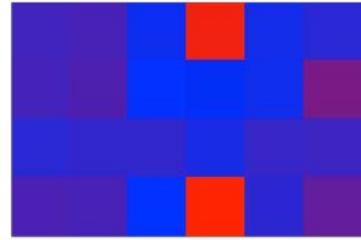
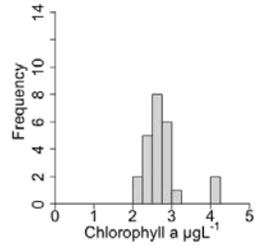


Figure 1 Bathymetric map of Paul Lake obtained from University of Notre Dame (UNDERC). Blue dots represent sampling grid with 24 evenly spaced sampling points throughout the pelagic zone (>4m).

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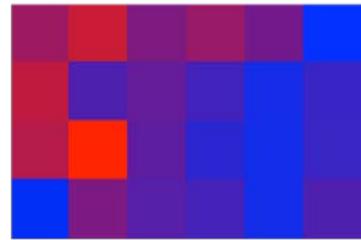
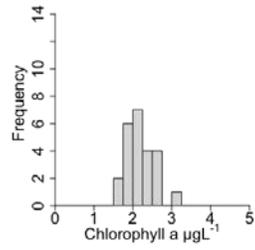


Figure 2 Heat maps and frequency distributions of chlorophyll a concentrations. Heat maps are in a blue (low concentration) to red (high concentration) gradient.

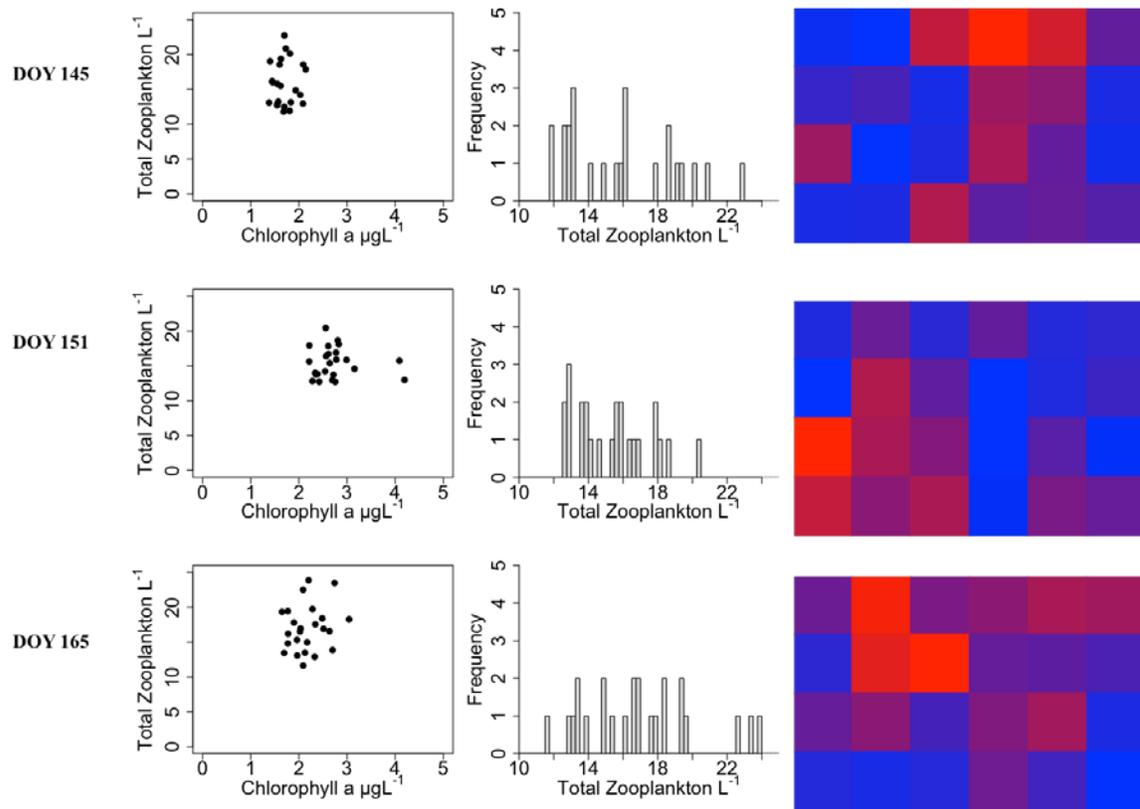


Figure 3 Heat maps, scatter plots, and frequency distributions of total zooplankton abundances. Heat maps are in a blue (low concentration) to red (high concentration) gradient. No significant relationship was detected between total zooplankton and chlorophyll *a* (regression $p > 0.05$).

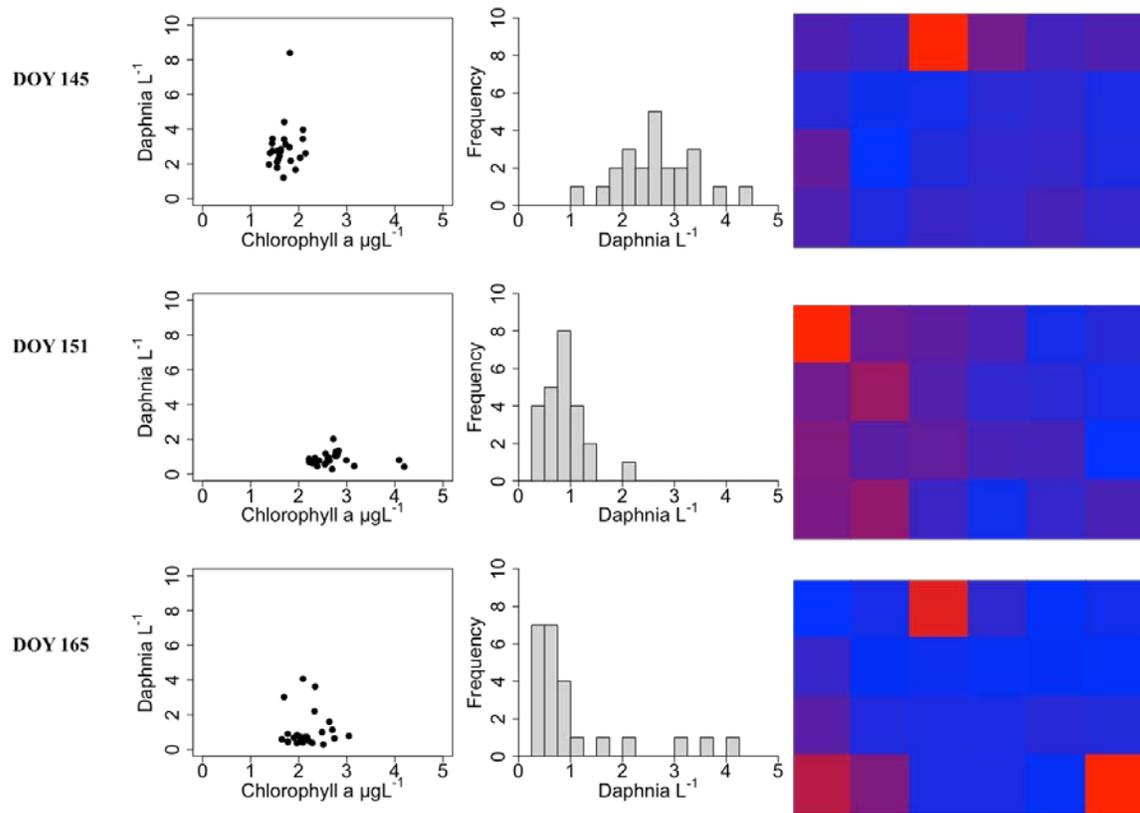


Figure 4 Heat maps, scatter plots, and frequency distributions of *Daphnia* abundances. Heat maps are in a blue (low concentration) to red (high concentration) gradient. No significant relationship was detected between *Daphnia* and chlorophyll *a* (regression $p > 0.05$).

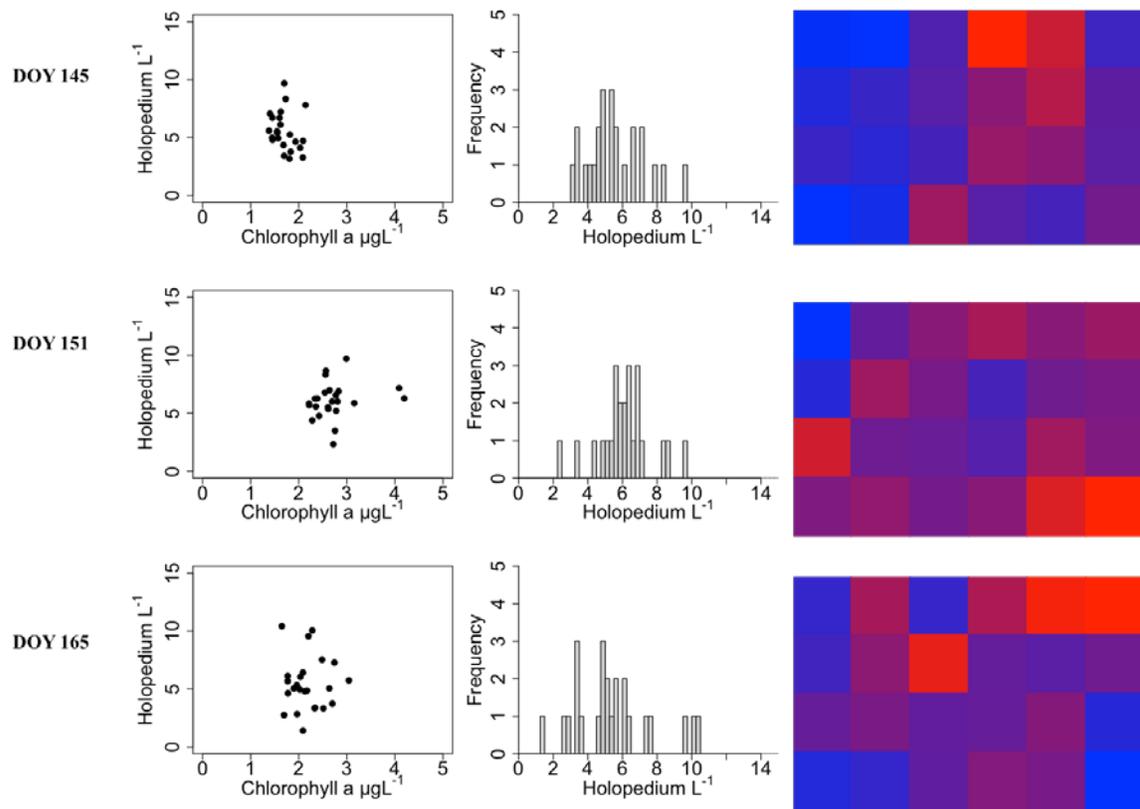


Figure 5 Heat maps, scatter plots, and frequency distributions of *Holopedium* abundances. Heat maps are in a blue (low concentration) to red (high concentration) gradient. No significant relationship was detected between *Holopedium* and chlorophyll *a* (regression $p > 0.05$).

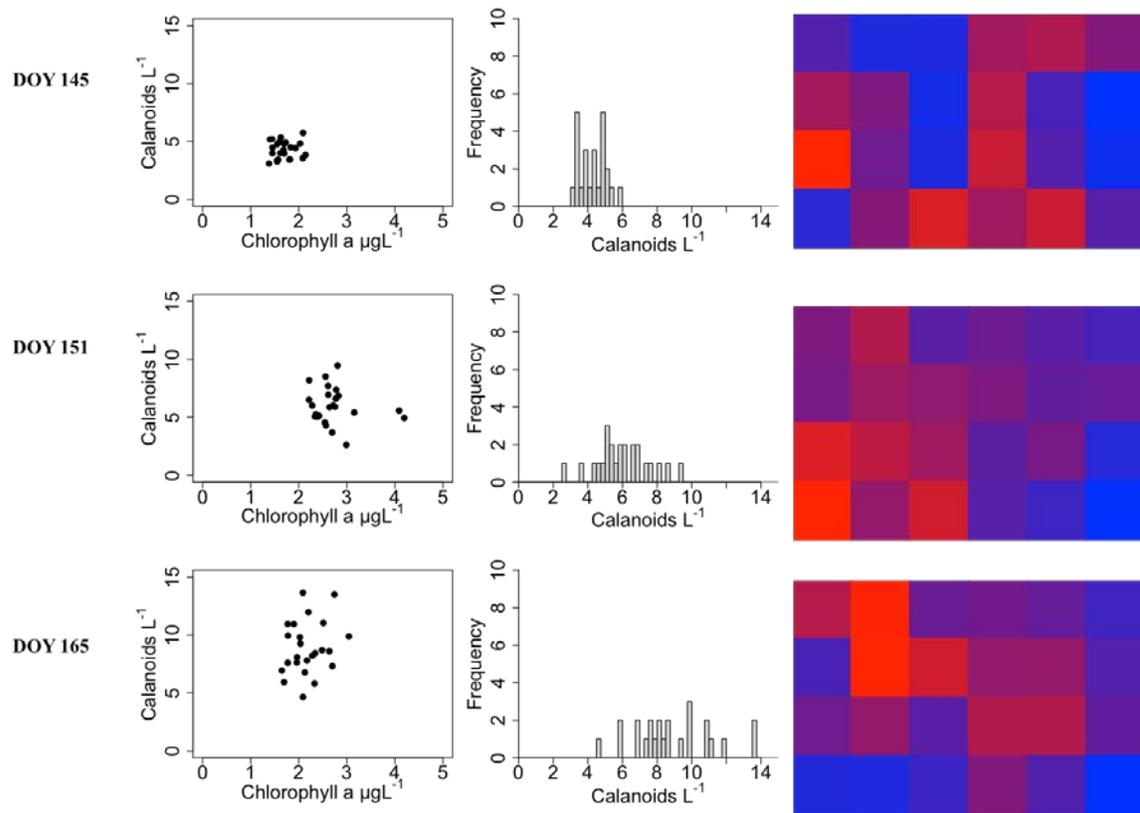


Figure 6 Heat maps, scatter plots, and frequency distributions of calanoid copepods abundances. Heat maps are in a blue (low concentration) to red (high concentration) gradient. No significant relationship was detected between calanoid copepods and chlorophyll *a* (regression $p > 0.05$).

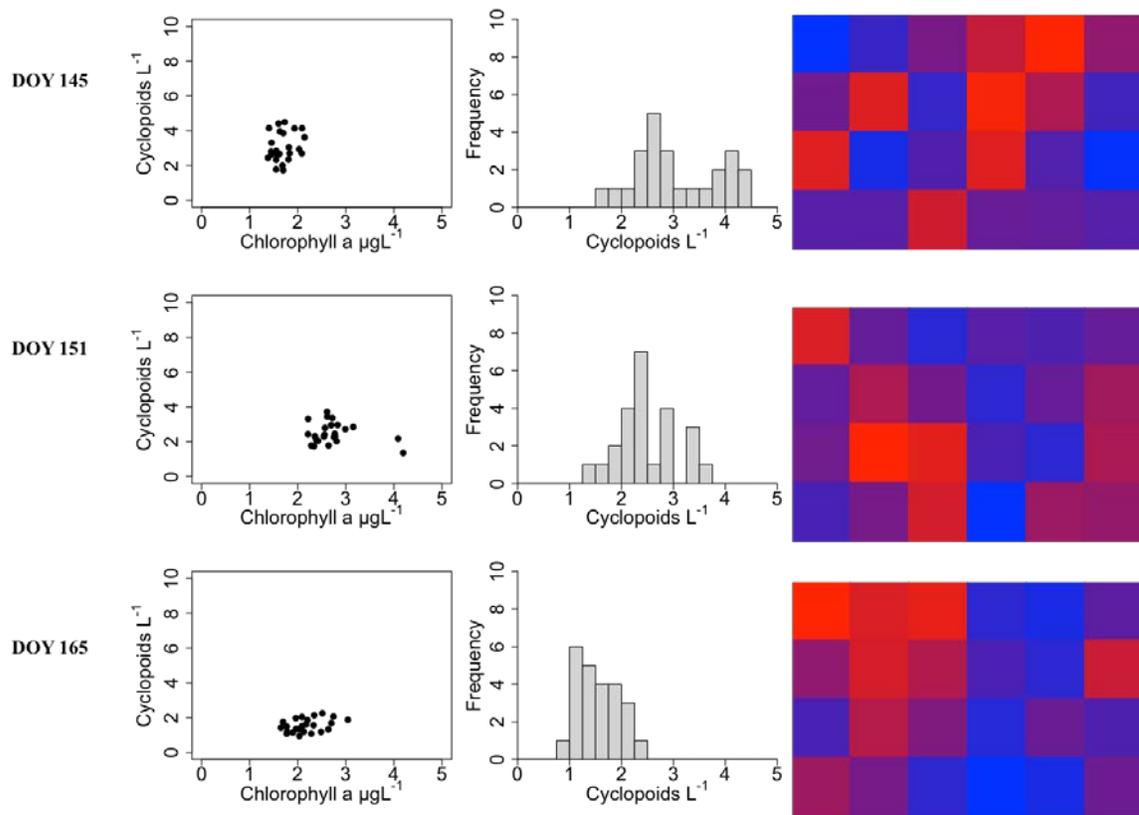


Figure 7 Heat maps, scatter plots, and frequency distributions of cyclopid copepods abundances. Heat maps are in a blue (low concentration) to red (high concentration) gradient. No significant relationship was detected between cyclopid copepods and chlorophyll *a* (regression $p > 0.05$).

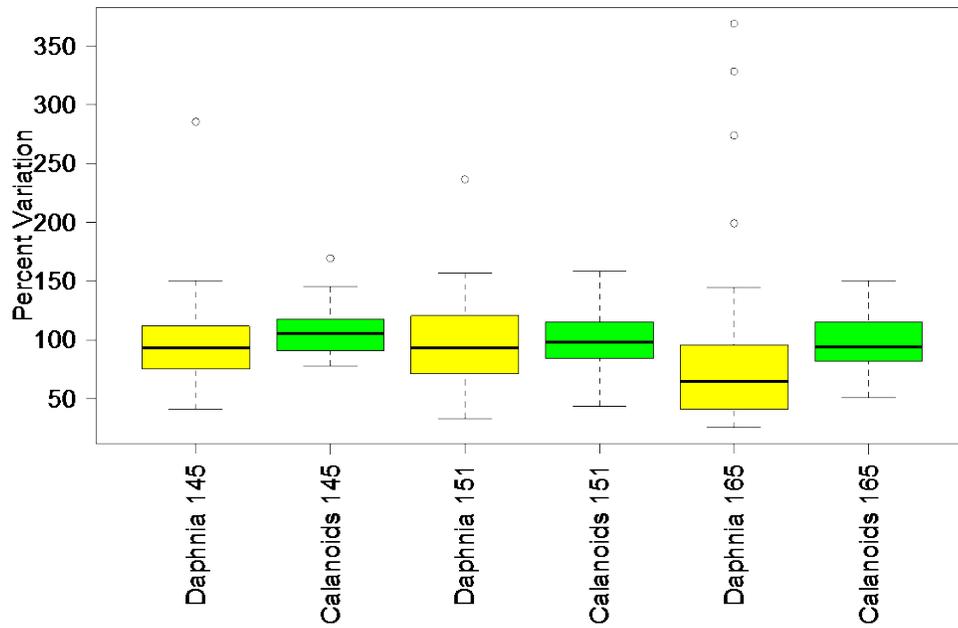


Figure 8 Box and whisker plots of percent variation for and Daphnia and calanoid copepods. Percent variation was calculated by takes the sample value divided by the mean times one hundred (1 sample measurement /mean*100).

Table 1 Summary table for regression analysis and Moran's I test results ("O" = "Observed" values and 'E'="Expected" values for phytoplankton and zooplankton.

DOY	Variable	Related To Chlorophyll <i>a</i> ?	Regression Statistics	Auto Correlated?	Moran's I Statistics
145	Chlorophyll <i>a</i>	N/A	N/A	YES	O=0.08 E=-0.04 P<0.01
145	Total Zooplankton	NO	T ₂₂ =0.15 r ² =0.00 p=0.88	NO	O=0.02 E=-0.04 P=0.06
145	Daphnia	NO	T ₂₂ =0.85 r ² =0.03 p=0.40	NO	O=-0.03 E=-0.04 P=0.48
145	Holopedium	NO	T ₂₂ =-1.07 r ² =0.04 p=0.29	YES	O=0.11 E=-0.04 P=0.01
145	Calanoids	NO	T ₂₂ =0.33 r ² =0.00 p=0.74	YES	O=-0.03 E=-0.04 P=0.75
145	Cyclopoids	NO	T ₂₂ =0.96 r ² =0.04 p=0.34	NO	O=-0.03 E=-0.04 P=0.63
151	Chlorophyll <i>a</i>	N/A	N/A	NO	O=-0.09 E=-0.04 P=0.12
151	Total Zooplankton	NO	T ₂₂ =-0.32 r ² =0.00 p=0.75	YES	O=0.06 E=-0.04 P<0.01
151	Daphnia	NO	T ₂₂ =-0.40 r ² =0.01 p=0.69	YES	O=0.16 E=-0.04 P<0.01
151	Holopedium	NO	T ₂₂ =0.90 r ² =0.04 p=0.38	NO	O=0.01 E=-0.04 P=0.07
151	Calanoids	NO	T ₂₂ =-0.82 r ² =0.03 p=0.42	YES	O=0.16 E=-0.04 P<0.01
151	Cyclopoids	NO	T ₂₂ =-1.10 r ² =0.05 p=0.28	NO	O=-0.02 E=-0.04 P=0.53
165	Chlorophyll <i>a</i>	N/A	N/A	YES	O=0.10 E=-0.04 P<0.01
165	Total Zooplankton	NO	T ₂₂ =0.89 r ² =0.03 p=0.39	YES	O=0.3 E=-0.04 P=0.01
165	Daphnia	NO	T ₂₂ =0.08 r ² =0.01 p=0.94	YES	O=0.15 E=-0.04 P<0.01
165	Holopedium	NO	T ₂₂ =-0.08 r ² =0.00 p=0.94	NO	O=0.01 E=-0.04 P=0.11
165	Calanoids	NO	T ₂₂ =1.02 r ² =0.05 p=0.34	YES	O=0.03 E=-0.04 P=0.11
165	Cyclopoids	NO	T ₂₂ =1.93 r ² =0.14 p=0.06	YES	O=0.09 E=-0.04 P<0.01