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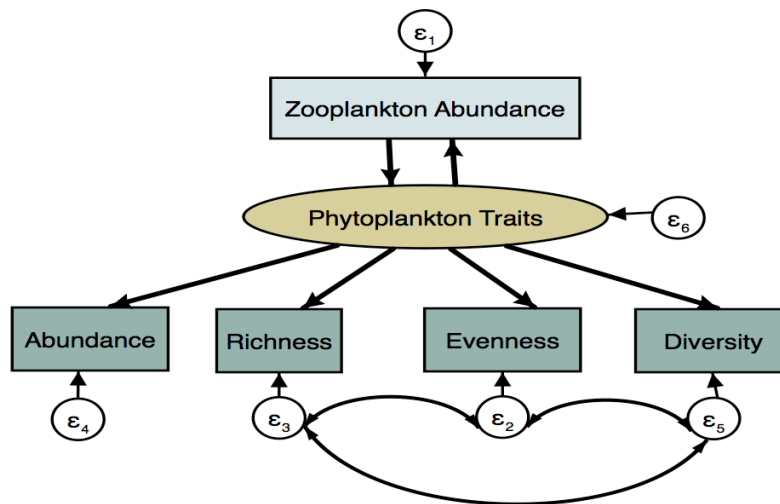
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Relationships between Phytoplankton Richness and Diversity, Zooplankton Abundance, and cyanoHAB Dominance in Utah Lake, 2016

Technical Report

To

Wasatch Front Water Quality Council



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January 19, 2018

SUMMARY

Utah Lake, a remnant of ancient Lake Bonneville, is perhaps one of the most unique shallow freshwater lake ecosystems remaining in the world, despite undergoing a catastrophic ecosystem shift and hysteresis shortly after Euro-American settlement in the mid-1800s. Algal communities in Utah Lake are spatially and temporally variable, uncommonly rich and diverse, and are essential for maintaining most ecological functions in the lake. The ecological importance of their diversity cannot be overestimated. A phytoplankton taxa richness based metric will likely be incorporated into Utah Division of Water Quality's (UDWQ) criteria for assessing aquatic life use designation in Utah Lake. Any loss in Utah Lake's phytoplankton taxa richness would be a sign of impairment and cause for concern. A few phytoplankton taxa, including cyanobacteria (cyanoHABs) can dominate blooms, typically in summer, with cell counts exceeding 100,000 mL⁻¹. Short and long- term effects of blooms on phytoplankton richness and diversity, and ultimately ecosystem function in Utah Lake are unknown. Utah Lake also supports a rich and diverse zooplankton assemblage that varies spatially and temporally. Phytoplankton can have a bottom up control on zooplankton and conversely, zooplankton can have a top down control on phytoplankton that routinely and selectively rely on cyanoHABs as a major part of their diets. Understanding this huge interaction potential between phytoplankton and zooplankton assemblages seems daunting, however critical first steps in collecting and analyzing data have been taken by the Wasatch Front Water Quality Council, including results presented in this report.

Results of these analyses show that phytoplankton assemblages in Utah Lake are spatially and temporally variable with many taxa strong indicators of this variability. Interactions between phytoplankton and zooplankton significantly affected phytoplankton abundance, richness, evenness, diversity, and zooplankton abundances, especially when phytoplankton abundances were high (> 50,000 cell mL⁻¹). CyanoHABs did not appear to affect phytoplankton taxa richness, nor did diatom or green algal blooms. This suggests that Utah Lake's unique and diverse phytoplankton assemblage remains resilient to current levels of blooms, however careful monitoring of phytoplankton assemblages is mandatory, particularly if blooms are expected to increase in intensity or duration. Extensive food web data have been collected in 2017 and will continue to be collected that will add to our knowledge and provide us much needed data to conduct network based food web models. These analyses and models will allow managers to more prudently manage Utah Lake's ecosystem, including water quality, and cyanoHABs based on a solid foundation of sound science.

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Dedication

This report is dedicated to the late Dr. Larry Gray, former aquatic ecology professor at Utah Valley University, Orem, Utah and Utah Lake's leading expert on zooplankton taxonomy and ecology. His absence and expertise will be sorely missed.

Introduction

It is now fully recognized that biodiversity is essential for maintaining most ecological functions and for providing a multitude of ecosystem services (Millennium Ecosystem Assessment 2005, Schabhtt et al. 2013). Phytoplankton diversity within aquatic ecosystems: supports primary productivity, regulates water quality (including cyanHABs¹), minimizes negative effects of environmental changes by enhancing ecosystem resistance and resilience, governs secondary productivity and resource use efficiency, and promotes phytoplankton growth and phosphorus uptake (Schabhtt et al. 2013; McNaughton 1977; Naeem and Li 1997; Chapin et al. 2000). (McCann 2000, Ptacnik et al. 2008; Striebel et al. 2009a; Cardinale 2011). Phytoplankton diversity, abundance, and biomass within an ecosystem are almost always highly spatially and temporally variable (Scheffer 1991; Paerl and Huisman 2008; Winder and Cloern 2010, Schabhtt et al. 2013) with diverse and productive algal assemblages typically having very fast turnover rates that are often sensitive to and reflective of environmental perturbation (Falkowski et al. 1998, Schabhtt et al. 2013).

Utah Lake is a small remnant of one of the most astounding lakes ever known; \cong 32,000-year-old, Lake Bonneville (Eardley et al. 1973). Native Americans thrived in Utah Lake's environs. Early explorers marveled at its beauty and its seemingly limitless bounty and despite irresponsible abuse by those who settled and continue to settle along its shores; Utah Lake's rich biodiversity continues to persist and evolve. Utah Lake underwent a catastrophic ecosystem shift² (Scheffer et al. 1993; Scheffer et al. 2001) and ecological hysteresis³ shortly after Euro-American settlement in the mid-1800s (Carter 2005) and continues at its present alternate stable state (Beisner 2003). Utah Lake is now a eutrophic- to- hypereutrophic, sometimes brackish, turbid, shallow, temperate, highly regulated reservoir with many unquantified cold to warm water springs hidden under its surface. It's very large size (> 96,000 acres), physical, chemical and biological characteristics, including extremely high primary and secondary productivity and biodiversity, combined with its ancient lineage, make Utah Lake perhaps one of the most unique shallow freshwater lake ecosystems remaining in the world (Richards and Miller 2017).

¹ cyanoHAB is the preferred abbreviation for cyanobacteria blooms. Cyanobacteria are not algae. The "H" in cyanoHABs denotes harmful, however most algal blooms that are known to occur in Utah Lake are not considered harmful.

² Catastrophic ecosystem shift is when loss of resilience causes an abrupt switch to a contrasting alternative stable state (Scheffer et al. 2001).

³ Ecological hysteresis is when community recovery is modulated by the biota and not simply the reverse trajectory of the response to an impact (e.g. catastrophic ecosystem shift).

Richards and Miller (2017) showed that phytoplankton assemblages in Utah Lake were spatially and temporally variable and surprisingly, uncommonly rich and diverse (Zimmerman and Cardinale 2014, USEPA National Lakes Assessment: <http://water.epa.gov/type/lakes/NLA>). An estimated > 400 benthic diatom and non-planktonic algal taxa (Dr. Sam Rushforth personal communication), and between 150 to 170 phytoplankton taxa (Richards and Miller 2017) buffer Utah Lake's ecosystem functioning against environmental fluctuations, including cyanoHABs (Chalar 2007).

Phytoplankton taxa richness is widely used in water quality assessment programs to measure ecological response to environmental changes (Lenoir et al. 2008; Ehrlen & Morris 2015; Keith et al. 2015; Urban 2015; USEPA National Lakes Assessment Program) and likely will be incorporated into Utah Division of Water Quality's (UDWQ) criteria for assessing aquatic life use designation in Utah Lake. Any loss in Utah Lake's phytoplankton taxa richness would be a sign of impairment and cause for concern. However, ecologists continue to show that environmental changes can affect ecosystem function well before a change in taxa richness occurs, including relative contributions of individual taxa to ecosystem functions via changes in their abundance or biomass (often measured using evenness and diversity indices) or to changes in assemblage composition (Loreau 1998; Fox 2006; Spaak et al. 2017; Fox & Kerr 2012; Fox 2006; Suding et al. 2008).

Algal blooms have occurred throughout Utah Lake's storied past but may possibly be becoming more common and severe (UDWQ 2017). A few phytoplankton taxa, including cyanobacteria (acronym: cyanoHABs) can dominate these blooms, typically in summer, with cell counts exceeding $100,000 \text{ mL}^{-1}$ (Richards and Miller 2017, Richards 2017). Short and long-term effects of algal blooms and cyanoHABs on phytoplankton richness and diversity and ultimately ecosystem function in Utah Lake are unknown.

Utah Lake also supports a rich and diverse zooplankton assemblage that also varies spatially and temporally (Richards and Miller 2017). There are >> 20 zooplankton taxa occurring in Utah Lake including; cladocera, copepod, and rotifer taxa from several functional groups with different life history and feeding strategies (Richards and Miller 2017).

Phytoplankton assemblages can have a bottom up control on zooplankton assemblages via several mechanisms, including relative abundance, digestibility, nutrient content, etc. Conversely, zooplankton assemblages can have a top down control on phytoplankton assemblages via selective and non-selective grazing and contrary to past assumptions, it is becoming apparent that zooplankton routinely and selectively rely on cyanoHABs in their diets (Woodland et al. 2013; Koski et al. 2002; Vehmaa et al. 2013; Gorokhova and Engstrom-Ost 2009; and Hogfors et al. 2014). Given the rich phytoplankton and zooplankton assemblages in

Utah Lake, there could easily be $\gg 4 \times 10^{24}$ combinations of potential interactions between the two, each of which can influence interactions and food web outcomes, including cyanoHABs. Understanding this huge interaction potential between phytoplankton and zooplankton assemblages seems daunting, however much useful prerequisite insight can be gleaned from analyzing simple metrics including: phytoplankton assemblage richness, diversity, similarity, and abundance, and zooplankton abundance; none of which have been examined until now.

This technical report is a continuation of Utah Lake phytoplankton and zooplankton data analysis collected by members of the Wasatch Front Water Quality Council (WFWQC) in collaboration with several state agencies and universities. Analyses presented in this technical report focus on phytoplankton richness, diversity, similarity, and abundance as related to phytoplankton blooms (including cyanoHABs), and zooplankton abundance. These analyses are a primer of additional analyses that will be conducted after phytoplankton and zooplankton assemblage data are processed from the 2017 and 2018 sampling seasons and are supplemental to past analyses conducted by OreoHelix Consulting and the WFWQC. See Richards and Miller (2017) and Richards (2017) for more details on sample collection dates, locations, and additional ecological analyses of phytoplankton and zooplankton assemblages, as well as benthic assemblages.

Hypothesis tested

Several general hypotheses were tested in these analyses:

1. Spatial and temporal factors affect phytoplankton richness, diversity, similarity, and abundance.
2. Phytoplankton abundance affects phytoplankton richness, diversity, and similarity.
3. Zooplankton abundance affects phytoplankton richness, diversity, similarity, and abundance.
4. Zooplankton abundance is affected by phytoplankton richness, diversity, similarity, abundance, and spatial and temporal factors.
5. cyanoHABs have more of an effect on phytoplankton taxa richness than do diatom (Bacillariophytes) or green algal (Chlorophytes) blooms.

A conceptual path diagram of hypothesized relationships is provided in Figure 1.

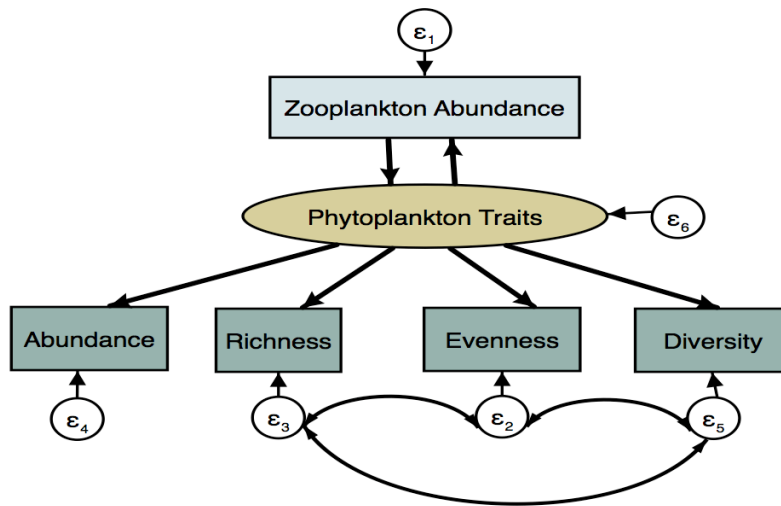


Figure 1. Conceptual path diagram of interactions between phytoplankton and zooplankton in Utah Lake, 2016. Phytoplankton traits (abundance, richness, evenness, and diversity) can be considered a latent variable. Solid black lines with one arrow are causal effects; curved lines suggest correlations; small circles are error estimates.

Methods

Phytoplankton were taxonomically identified and enumerated by Rushforth Phycology, Provo, UT. Zooplankton were taxonomically identified and enumerated by the late Dr. Larry Gray, Utah Valley University, Orem, UT. Data from between 133 and 135 integrated phytoplankton samples were analyzed. A breakdown of number of phytoplankton samples by month and location are in Table 1. See Richards and Miller (2017) for more details of data.

Table 1. List of number of phytoplankton samples by months and sites used in this analysis.

Month	N	Site	N
Feb	2	GB	18
Mar	8	PB	19
Apr	4	ULSP	3
May	5	LM	22
June	12	PL	34
July	14	PM	11
Aug	34	LB	8
Sept	24	SB	11
Oct	18	ULout	4
Nov	10	PA	3
Dec	4		
Total	135	Total	133

Statistical Methods

Five metrics: phytoplankton Richness (number of taxa within a sample), Evenness, Shannon's diversity, phytoplankton cell counts mL^{-1} , and total zooplankton mL^{-1} were computed. Relationships between these were then examined and compared. Phytoplankton taxa richness and abundance, and total zooplankton mL^{-1} were count data truncated at zero and were not normally distributed. Evenness was fractional data, limited in distribution between 0 and 1, and also not normally distributed. Therefore, several regression models where the response (dependent) variables were from non-normal distributions were generated including; linear, truncated Poisson, fractional response, and truncated negative binomial models. Phytoplankton cell counts mL^{-1} were log transformed when used as predictors and models were compared using raw or log transformed data. Model fitness was evaluated, and best-fit models were selected using the lowest log likelihood (ll), Akaikes Information Criteria (AIC) and Bayesian Information Criteria (BIC) values. Incidence rate ratios (IRR) were used instead of regression coefficients for the non-linear models to better help interpret results. IRRs can be interpreted similarly to odds ratios or risk ratios. Regression models were generated with the constant term removed when response variables were expected to be zero at predictor variables equal to zero. Robust standard errors were used in all models. One data entry that had 48 phytoplankton taxa was considered a high leverage point and removed from the analyses. This data was collected from a Provo Bay, June 2016 sample and will be reevaluated to determine if it was an outlier caused by a data entry error or truly had 48 taxa. February and December data had only a few samples each and were removed from most of the analyses. Pairwise comparisons of predicted means vs. grand means from regression models were also generated, where appropriate. All statistical analyses described in this paragraph were performed using Stata/IC 15.1 for Mac (64-bit Intel)(StataCorp 2018).

Indicator taxa analysis (ITA) was used to detect and describe the value of different phytoplankton taxa for indicating month and site groupings. Dufrêne and Legendre's (1997) method of calculating taxa indicator values was used. This method combined information on the concentration of taxa abundances by site and by month and the faithfulness of occurrence of a taxon in that particular group. ITA produced maximum indicator values, IVmax, for each taxon in each group. Significance of IVmax was then tested using a Monte Carlo randomization method which randomly assigned sample units to groups 1000 times and calculated an IVmax each time. Probability of Type I error was the proportion of times that the IVmax from the randomized samples were equal to or greater than the original IVmax. The null hypothesis was that IVmax was not greater than would be expected by chance (i.e. that a taxon had no indicator value). Significance was selected at $p \leq 0.05$ (McCune and Grace 2002). Indicator taxa analysis was conducted using PC-ORD Ver. 6.22 (McCune and Mefford 2011).

Results

Phytoplankton Taxa Richness⁴

Summary statistics of phytoplankton abundance, richness, evenness, and diversity by sample are presented in Appendix 4.

Richness vs. Phytoplankton Abundance

Phytoplankton richness was significantly positively affected by phytoplankton abundance (Figure 2 and Table 2). This relationship was expected; the more cells there were, the more taxa were likely to occur. The linear model using phytoplankton richness as the dependent variable and phytoplankton abundance (cells mL⁻¹) as the sole predictor had a decent adjusted $R^2 = 0.43$, although this model had a poorer fit compared with the truncated negative binomial regression model, which had the lowest ll, AIC and BIC of the three models (Appendix 1) (Table 2).

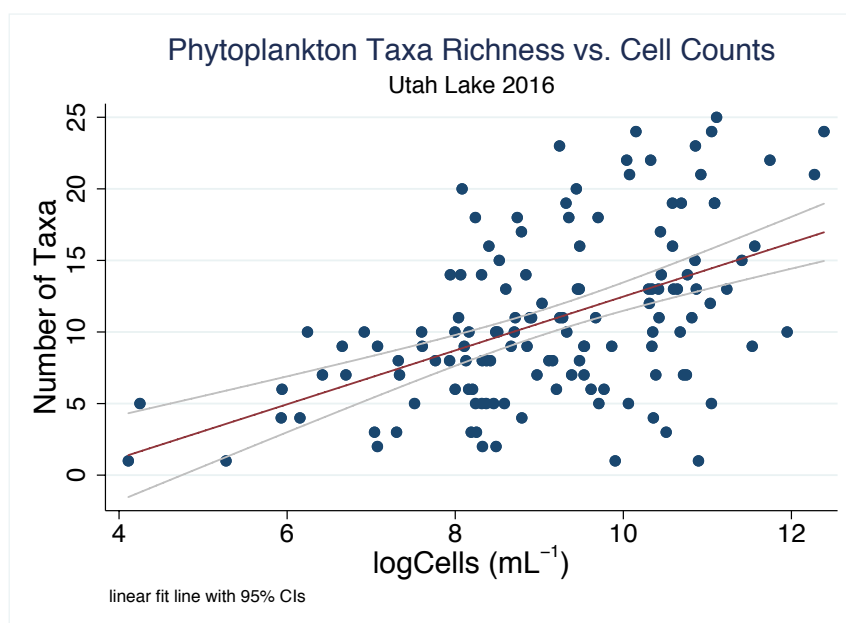


Figure 2. Relationship between the number of phytoplankton taxa and phytoplankton abundance (cells mL⁻¹) (log transformed). Linear regression $R^2 = 0.43$. Truncated negative binomial model had best fit (Appendix 2).

Table 2. Truncated negative binomial regression model results for phytoplankton taxa richness vs. phytoplankton abundance (cells mL⁻¹) (log transformed) (constant removed). $N = 135$; Truncation point: 0; Dispersion = mean; Wald $\chi^2(1) = 3063.71$; Prob > $\chi^2 = 0.0000$; Log likelihood = -405.22442

	Coef.	Std. Err.	z	P > z	[95% Conf. Interval]
logTotalCells	0.253	0.004	55.35	< 0.01	0.244 0.262
/lnalpha	-1.901	0.213			-2.320 -1.482

⁴ Taxa richness as used here is the number of taxa per sample (alpha diversity). It does not include differences of individual taxa between and among samples (i.e. similarity, beta diversity). Some taxa may occur in one sample and not another but the overall number of taxa may not change.

alpha	0.1493	0.031			0.098	0.227
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Phytoplankton Richness by Site and Month

Phytoplankton taxa richness significantly varied among sites and months and their interactions (Figure 3, Table 3, Appendix 5, and Appendix 6). A linear model was considered the best fit with a good $R^2 = 0.70$ (Appendix 2). Phytoplankton richness (number of taxa/sample) was typically greater in late spring/early summer and lowest after July.

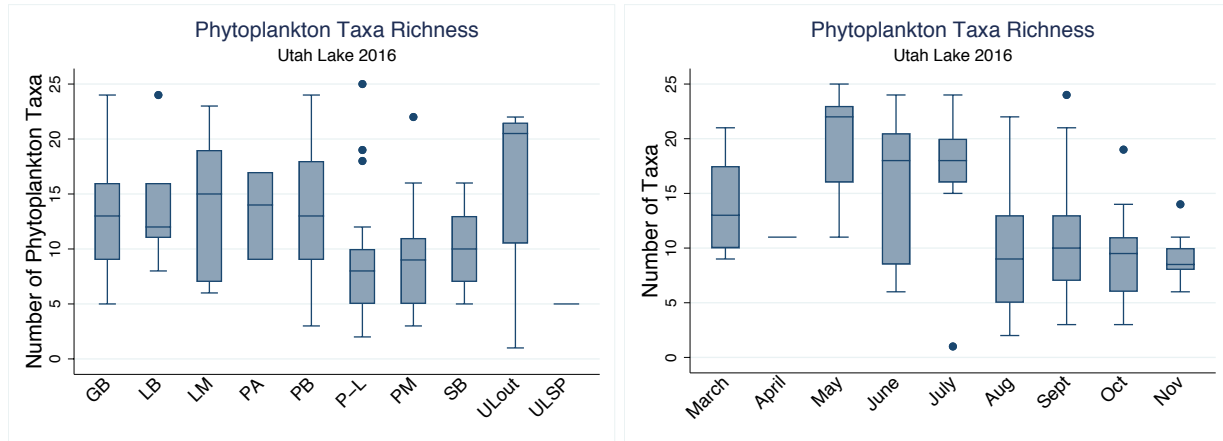


Figure 3. Phytoplankton taxa richness by site and month, Utah Lake 2016.

Table 3. Linear regression results of phytoplankton richness vs sites and months and interactions. $N = 117$; $F(28,65)$; $R^2 = 0.70$, Root MSE = 4.26. May and Pelican-Lindon transect held as baselines.

richness	Robust					
	Coef.	Std. Err.	t	P> t	[95% Conf. Interval]	
monthcode						
March	-8.00	6.64	-1.20	0.23	-21.26	5.26
April	-7.00	6.64	-1.05	0.30	-20.26	6.26
May	0.00	(base)				
June	-7.00	7.67	-0.91	0.37	-22.33	8.33
July	-21.00
Aug	-12.08	6.72	-1.80	0.08	-25.50	1.35
Sept	-10.75	6.75	-1.59	0.12	-24.23	2.73
Oct	-10.83	6.83	-1.59	0.12	-24.47	2.81
Nov	-9.33	6.68	-1.40	0.17	-22.68	4.01
SiteCode						
GB	2.33	0.73	3.20	0.00	0.87	3.79
LB	5.33	0.73	7.30	0.00	3.87	6.79
LM	5.00	6.64	0.75	0.45	-8.26	18.26
P-L	0.00	(base)				
PA	6.08	2.82	2.16	0.03	0.45	11.72
PB	-0.17	0.87	-0.19	0.85	-1.91	1.57
PL	8.00	3.85	2.08	0.04	0.32	15.68
PM	-2.00	6.64	-0.30	0.76	-15.26	11.26
SB	-1.67	0.73	-2.28	0.03	-3.13	-0.21
ULout	4.00	6.64	0.60	0.55	-9.26	17.26

monthcode#SiteCode						
March#GB	2.17	1.60	1.35	0.18	-1.03	5.36
March#LM	4.00	6.64	0.60	0.55	-9.26	17.26
March#PB	1.67	1.67	1.00	0.32	-1.67	5.00
March#PM	1.00	6.64	0.15	0.88	-12.26	14.26
March#ULout	7.00	6.64	1.05	0.30	-6.26	20.26
June#GB	-3.67	4.68	-0.78	0.44	-13.01	5.67
June#LM	5.00	7.67	0.65	0.52	-10.33	20.33
June#PB	10.50	4.39	2.39	0.02	1.73	19.27
June#ULout	5.00	7.67	0.65	0.52	-10.33	20.33
July#GB	22.67	6.95	3.26	0.00	8.80	36.54
July#LB	13.67	6.68	2.05	0.04	0.32	27.01
July#LM	16.00
July#PB	24.17	6.96	3.47	0.00	10.26	38.07
July#SB	20.17	6.70	3.01	0.00	6.79	33.54
Aug#GB	6.74	2.54	2.66	0.01	1.68	11.81
Aug#LB	0.74	1.28	0.58	0.56	-1.81	3.29
Aug#LM	0.08	7.21	0.01	0.99	-14.32	14.47
Aug#PB	4.64	2.80	1.66	0.10	-0.95	10.24
Aug#PM	7.08	9.08	0.78	0.44	-11.05	25.21
Aug#SB	2.74	1.28	2.15	0.04	0.19	5.29
Sept#GB	-1.33	2.02	-0.66	0.51	-5.37	2.70
Sept#LB	2.08	5.45	0.38	0.70	-8.80	12.97
Sept#LM	4.08	7.24	0.56	0.57	-10.38	18.55
Sept#PB	1.92	4.07	0.47	0.64	-6.22	10.05
Sept#PM	-2.25	6.75	-0.33	0.74	-15.73	11.23
Sept#SB	3.75	2.92	1.29	0.20	-2.07	9.57
Oct#GB	5.00	4.62	1.08	0.28	-4.22	14.22
Oct#LB	-1.50	1.75	-0.86	0.40	-5.00	2.00
Oct#LM	-5.17	6.90	-0.75	0.46	-18.94	8.60
Oct#PB	4.00	2.63	1.52	0.13	-1.25	9.25
Oct#PM	2.83	7.40	0.38	0.70	-11.94	17.61
Oct#SB	6.00	2.26	2.66	0.01	1.49	10.51
Nov#LM	-7.67	6.68	-1.15	0.26	-21.01	5.68
Nov#PM	2.33	6.68	0.35	0.73	-11.01	15.68
_cons	18.00	6.64	2.71	0.01	4.74	31.26

Indicator Taxa for Sites and Months

Four sites had significant indicator phytoplankton taxa: Provo Airport site, Provo Bay, Sandy Beach, and Utah Lake outlet (Table 4). The green algae (Chlorophyta) *Desmodesmus* was almost exclusively found in Provo Bay and was also the most dominant bloom taxon in Utah Lake, 2016 (Table 19). This supports Richards and Miller (2017) conclusion that Provo Bay functions much differently than the rest of Utah Lake. Surprisingly, Utah Lake outlet had fifteen phytoplankton indicator taxa. The outlet area was only sampled on four occasions in late spring/early summer but appears to have a unique phytoplankton assemblage which most likely is due to the

cumulative contributions of the entire lake. More emphasis on understanding this portion of the lake is obviously needed.

Table 4. Significant indicator phytoplankton taxa for sites. Only sites that had statistically significant indicator taxa are listed.

Site	Taxon
Provo Airport	<i>Perionella</i> species
	<i>Monoraphidium convolutus</i>
	<i>Crucigenia rectangularis</i>
Provo Bay	<i>Desmodesmus opoliensis</i>
	<i>Desmodesmus communis</i>
	<i>Desmodesmus</i> species
Sandy Beach	<i>Chrysocapsa planktonica</i>
Utah Lake outlet	<i>Oscillatoria</i> species
	<i>Monoraphidium komarakovae</i>
	<i>Kirchneriella lunata</i>
	<i>Chlamydomonas</i> species
	unknown elongate chlorophyte
	<i>Lagerheimia</i> species
	<i>Nitzschia reversa</i>
	Unknown spherical chlorophyte 3
	<i>Ulothrix</i> species
	<i>Monoraphidium arcuatum</i>
	unknown filamentous Cyanophyta species
	<i>Monoraphidium</i> species
	<i>Tetraedron minimum</i>
	<i>Monoraphidium contortum</i>
<i>Pediastrum</i> species	

Seven months had significant indicator taxa: February, March, April, May, June, July, and December (Table 5) suggesting < monthly changes in phytoplankton assemblages until the end of July when cyanoHABs, particularly *Aphanizomenon flos-aquae*, occurred. It was surprising that *Aphanocapsa* sp. (cyanobacteria) were indicators of the phytoplankton assemblage in December and were the most abundant taxon found in that month.

Table 5. Significant indicator phytoplankton taxa for months. Only months that had statistically significant indicator taxa are listed.

Month	Taxon	Month	Taxon
-------	-------	-------	-------

Feb	<i>Cryptomonas</i> species 2	May	<i>Coelastrum microporum</i>
	<i>Monoraphidium irregulare</i>		<i>Chlamydomonas</i> species
	<i>Gymnodinium</i> species		<i>Oocystis</i> species 2
March	<i>Monoraphidium arcuatum</i>		unknown spherical chlorophyta
	Centric diatoms		<i>Oocystis borgei</i>
	unknown filamentous Cyanophyta		Unknown colonial cyanophyte
	<i>Cyillardospermopsis catemca</i>		<i>Gomphosphaeria aponina</i>
	<i>Leptolyngbya</i> species		<i>Crucigenia fenestrata</i>
	<i>Monoraphidium contortum</i>		unknown spherical chlorophyta
	<i>Kirchneriella lunata</i>		June
	<i>Crucigenia rectangularis</i>	<i>Desmodesmus communis</i>	
	pennate diatoms	<i>Nitzschia acicularis</i>	
<i>Monoraphidium convolutus</i>	<i>Actinastrum hantzschii</i>		
April	<i>Kirchneriella lunata</i>	<i>Ankistrodesmus falcatus</i>	
	<i>Monoraphidium griffithii</i>	July	<i>Aphanizomenon flos-aquae</i>
	<i>Scenedesmus</i> species	Dec	<i>Aphanocapsa</i> species
	<i>Micractinium</i> species		

Phytoplankton Richness and Zooplankton Abundance

Phytoplankton taxa richness was not significantly affected by zooplankton abundance (mL^{-1}) using the best-fit truncated negative binomial model with either the untransformed or log transformed zooplankton abundance data (Figure 4). Linear regression results were $R^2 = 0.01$, $p = 0.52$ and the constant term = 10.59 on log transformed zooplankton abundance for interpretive purposes only. The constant term suggests that in the absence of zooplankton, phytoplankton richness was typically around 11 taxa per sample throughout the lake in 2016.

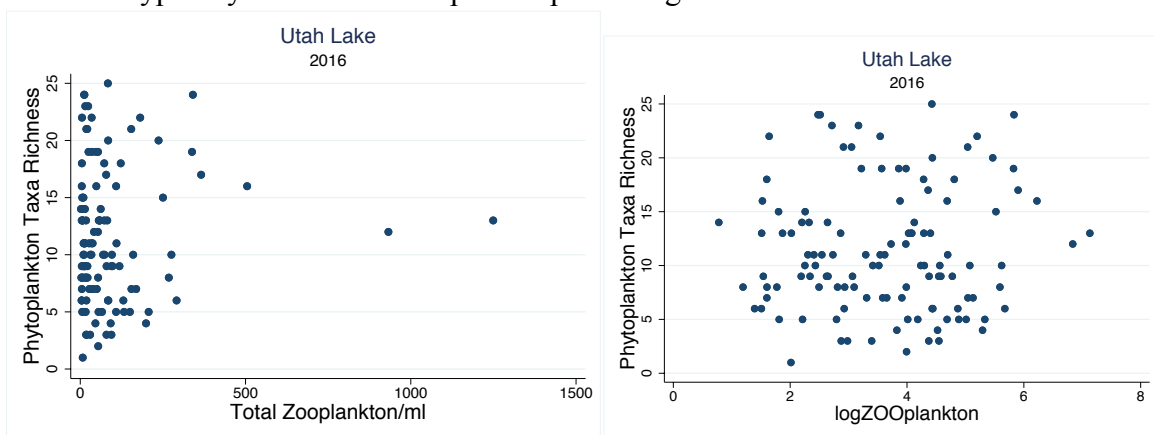


Figure 4. Relationship between phytoplankton richness and zooplankton abundance (total counts mL^{-1}) (untransformed and log transformed zooplankton abundances).

Phytoplankton Abundance

Temporal and Spatial Patterns of Phytoplankton Abundance

The following figures illustrates that total phytoplankton abundances (cells mL⁻¹) were significantly affected by month and were greater in April, May and June than the grand mean and significantly lower in November and likely October than the mean (Figure 5, Table 6, and Appendix 7 **Error! Reference source not found.**) but did not significantly differ between sites (Figure 5 and Table 7). The best-fit linear regression models had a very low $R^2 = 0.08$ for month effects and $R^2 = 0.05$ for site effects showing that phytoplankton abundance was not very well predicted by month or site values when modeled separately.

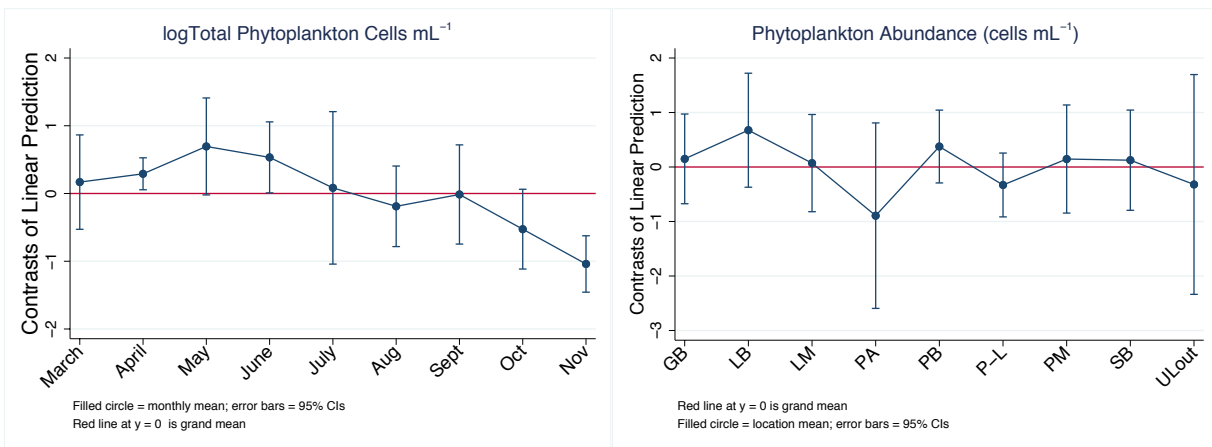


Figure 5. Contrasts of linear predictions of log₁₀ Total phytoplankton cells mL⁻¹ by months and sites with grand mean in Utah Lake 2016

Table 6. Linear regression model results of phytoplankton abundance (cells mL⁻¹) by month. $N = 177$; $R^2 = 0.08$; Root MSE = 1.51.

	Coef.	Robust Std. Err.	t	P>t	[95% Conf. Interval]	
<i>Month</i>						
March	0	(base)				
April	0.123	0.375	0.327	0.744	-0.621 0.866	
May	0.526	0.539	0.977	0.331	-0.541 1.594	
June	0.365	0.461	0.792	0.43	-0.548 1.278	
July	-0.085	0.733	-0.116	0.908	-1.537 1.367	
Aug	-0.357	0.488	-0.732	0.465	-1.324 0.61	
Sept	-0.183	0.546	-0.335	0.739	-1.264 0.899	
Oct	-0.694	0.486	-1.43	0.156	-1.657 0.268	
Nov	-1.208	0.423	-2.855	0.005	-2.047 -0.37	
cons	9.549	0.375	25.466	< 0.001	8.806 10.292	

Table 7. Linear regression model of phytoplankton abundance (cells mL⁻¹)(log transformed) by site. N = 117, R² = 0.05; Root MSE = 1.53.

	Coef.	Robust Std. Err.	t	P>t	[95% Conf. Interval]	
<i>Site</i>						
GB	0	(base)				
LB	0.526	0.685	0.768	0.444	-0.832 1.884	
LM	-0.078	0.609	-0.127	0.899	-1.286 1.131	
PA	-1.042	1.029	-1.013	0.313	-3.082 0.998	
PB	0.227	0.507	0.447	0.656	-0.779 1.232	
P-L	-0.479	0.473	-1.013	0.313	-1.416 0.458	
PM	-0.003	0.658	-0.004	0.997	-1.307 1.302	
SB	-0.024	0.623	-0.039	0.969	-1.259 1.21	
ULout	-0.469	1.201	-0.391	0.697	-2.849 1.911	
cons	9.388	0.408	23.015	< 0.001	8.58 10.197	

There were also no significant differences in phytoplankton abundances between sites using pairwise comparisons of adjusted predictions.

Spatial and temporal relationships between phytoplankton richness-diversity-similarity, phytoplankton cell counts, and zooplankton abundance

Abiotic spatial and temporal factors do not independently affect phytoplankton taxa richness-diversity or phytoplankton or zooplankton abundances. Biotic interactions between phytoplankton and zooplankton assemblages are also important. Therefore, additional regression models than those presented in previous sections were made comparing abiotic⁵ and biotic factors.

Phytoplankton richness

Phytoplankton richness was significantly affected by phytoplankton abundance but not by zooplankton abundance when site and month and their interactions were included in models (Table 8). This relationship between phytoplankton richness and abundance was expected; the more cells there were, the more taxa were likely to be present which was also demonstrated when phytoplankton richness and abundance were modelled separately (see section: Richness vs. Phytoplankton Abundance). Summary statistics are presented in Appendix 4.

The absence of an effect of zooplankton abundance (mL⁻¹) on phytoplankton richness suggests that zooplankton likely did not have a top down control effect throughout 2016. This was also shown in section:

⁵ Site and month were considered abiotic factors in this analysis that include physical and chemical variables not used in these analyses although they implicitly include the biotic factors that were modeled separately.

Phytoplankton Richness and Zooplankton Abundance. Additionally, and as expected, phytoplankton richness was significantly affected by spatial and temporal factors, including interactions between the two (Table 8). The best-fit linear regression model had a very good $R^2 = 0.79$ and a lower ll, AIC, and BIC than other models tested including those with only single predictors presented in previous sections. This shows that phytoplankton richness was affected by both abiotic and biotic factors.

Table 8. Linear regression phytoplankton taxa richness as a function of phytoplankton cells, zooplankton abundance, site, month and site month interactions. Baseline site and month locations = P-L transect and May. $N = 118$; $R^2 = 0.79$; Root MSE = 3.62.

Factor	Coef.	Robust std.err.	t	P > t	95%LCL	95%UCL
Phytoplankton abundance (cells mL ⁻¹)	1.61	0.37	4.36	0.00	0.87	2.35
Zooplankton abundance (mL ⁻¹)	-0.16	0.64	-0.24	0.81	-1.43	1.12
Site						
GB	1.31	0.99	1.33	0.19	-0.66	3.29
LB	4.32	1.39	3.12	0.00	1.55	7.10
LM	3.51	5.12	0.68	0.50	-6.72	13.73
PA	10.14	1.37	7.40	0.00	7.40	12.88
PB	-0.54	0.97	-0.56	0.58	-2.47	1.39
PM	-1.16	5.09	-0.23	0.82	-11.32	9.00
SB	-0.37	1.15	-0.32	0.75	-2.67	1.93
ULout	3.88	5.09	0.76	0.45	-6.28	14.05
ULSP	-1.34	1.29	-1.04	0.30	-3.93	1.24
Month						
March	-8.79	5.17	-1.70	0.09	-19.12	1.54
April	-6.51	5.09	-1.28	0.21	-16.67	3.65
June	-3.71	6.20	-0.60	0.55	-16.09	8.67
July	-13.54	1.78	-7.62	0.00	-17.09	-9.99
Aug	-9.21	5.34	-1.73	0.09	-19.88	1.45
Sept	-12.22	5.13	-2.38	0.02	-22.46	-1.97
Oct	-8.37	5.36	-1.56	0.12	-19.08	2.34
Nov	-6.41	5.26	-1.22	0.23	-16.93	4.10
Site by Month						
GB#March	6.48	2.49	2.60	0.01	1.50	11.45
GB#June	-6.42	4.61	-1.39	0.17	-15.64	2.79
GB#July	17.93	5.56	3.23	0.00	6.83	29.03
GB#Aug	4.15	2.89	1.43	0.16	-1.63	9.92
GB#Sept	3.31	1.91	1.73	0.09	-0.51	7.13

GB#Oct	4.14	2.70	1.53	0.13	-1.26	9.54
GB#Nov	0.00	(omitted)				
LB#July	5.06	5.61	0.90	0.37	-6.15	16.26
LB#Aug	-2.32	1.84	-1.26	0.21	-6.01	1.36
LB#Sept	5.19	4.08	1.27	0.21	-2.95	13.34
LB#Oct	-2.02	2.37	-0.85	0.40	-6.75	2.71
LB#Nov	0.00	(omitted)				
LM#March	4.55	5.28	0.86	0.39	-6.00	15.10
LM#June	3.26	6.16	0.53	0.60	-9.04	15.57
LM#July	12.14	1.71	7.10	0.00	8.72	15.55
LM#Aug	0.45	5.97	0.08	0.94	-11.49	12.39
LM#Sept	6.78	5.28	1.28	0.20	-3.76	17.32
LM#Oct	-2.79	5.63	-0.50	0.62	-14.03	8.46
LM#Nov	-6.34	5.24	-1.21	0.23	-16.80	4.12
PA#Sept	0.00	(omitted)				
PB#March	4.02	1.38	2.91	0.01	1.26	6.77
PB#June	6.17	4.25	1.45	0.15	-2.32	14.66
PB#July	17.05	6.17	2.76	0.01	4.72	29.37
PB#Aug	1.43	2.91	0.49	0.63	-4.40	7.25
PB#Sept	4.59	2.80	1.64	0.11	-1.00	10.18
PB#Oct	4.07	2.88	1.41	0.16	-1.68	9.82
PB#Nov	0.00	(omitted)				
PM#March	2.44	5.12	0.48	0.64	-7.79	12.66
PM#Aug	4.50	6.63	0.68	0.50	-8.75	17.75
PM#Sept	1.16	5.17	0.22	0.82	-9.16	11.48
PM#Oct	-0.49	5.84	-0.08	0.93	-12.16	11.18
PM#Nov	-0.93	5.24	-0.18	0.86	-11.39	9.53
SB#July	9.95	5.83	1.71	0.09	-1.71	21.60
SB#Aug	-0.70	2.27	-0.31	0.76	-5.25	3.84
SB#Sept	5.86	1.72	3.40	0.00	2.41	9.31
SB#Oct	3.03	2.19	1.39	0.17	-1.34	7.39
SB#Nov	0.00	(omitted)				
ULout#March	6.29	5.12	1.23	0.22	-3.93	16.51
ULout#June	2.82	6.14	0.46	0.65	-9.46	15.09
ULout#July	0.00	(omitted)				
ULSP#Aug	0.00	(omitted)				

Phytoplankton Abundance

Phytoplankton abundances (cells mL⁻¹) were significantly positively associated with phytoplankton richness and zooplankton abundances (mL⁻¹) (Table 9) and were also significantly affected by many of the sites and months and their interactions (Table 9). This significant positive relationship shows that higher phytoplankton abundances were not only due to increases in cyanobacteria but to increases in other phytoplankton taxa as well. The significant differences in abundance by sites and months are somewhat in contrast to results when abundance vs sites and months were modelled separately. This was because in these more complete models, other factors were taken into consideration. These more complete models also had lower log likelihood, AIC, and BIC values showing that they were better fits and consequently explained more of the variability than the simplified models even though there were more predictors in the models.

Table 9. Negative binomial regression of phytoplankton abundance as a function of phytoplankton richness, zooplankton abundance, site, month and site month interactions. N = 117; Log pseudolikelihood = -1246.46; Pseudo R² = 0.05.

Factor	IRR	Robust Std.Err.	z	P > z	95% Conf. Intervals	
Phytoplankton richness	1.177	0.033	5.757	0.000	1.113	1.244
Zooplankton abundance	1.001	0.001	2.342	0.019	1	1.002
Site						
GB	11.266	3.446	7.918	0.000	6.186	20.518
LB	30.857	19.244	5.499	0.000	9.088	104.763
LM	1.471	0.068	8.365	0.000	1.344	1.61
PA	9.078	8.87	2.258	0.024	1.337	61.618
PB	4.715	2.567	2.848	0.004	1.622	13.704
P-L	2.944	1.236	2.572	0.01	1.293	6.705
PM	147.931	72.023	10.263	0.000	56.969	384.136
SB	22.361	9.69	7.17	0.000	9.563	52.284
ULout	1	(base)				
ULSP	10.686	4.11	6.159	0.000	5.028	22.711
Month						
March	4.036	0.173	32.596	0.000	3.711	4.389
April	1.961	0.571	2.312	0.021	1.108	3.471
May	1.396	0.086	5.399	0.000	1.237	1.576
June	1	(base)				
July	0.375	0.202	-1.817	0.069	0.13	1.08
Aug	0.432	0.341	-1.064	0.287	0.092	2.029
Sept	0.202	0.168	-1.924	0.054	0.04	1.031
Oct	0.117	0.09	-2.794	0.005	0.026	0.527
Nov	0.049	0.038	-3.829	0.000	0.01	0.228

Site by Month						
GB#March	0.023	0.006	-13.245	< 0.001	0.013	0.04
GB#June	1	(base)				
GB#July	0.117	0.123	-2.045	0.041	0.015	0.915
GB#Aug	1.499	1.386	0.438	0.661	0.245	9.173
GB#Sept	4.255	4.055	1.52	0.129	0.657	27.54
GB#Oct	3.031	3.351	1.003	0.316	0.347	26.455
GB#Nov	4.16	3.468	1.71	0.087	0.812	21.311
LB#July	0.833	0.277	-0.549	0.583	0.435	1.598
LB#Aug	0.489	0.218	-1.602	0.109	0.204	1.174
LB#Sept	0.692	0.49	-0.519	0.603	0.173	2.773
LB#Oct	1.113	0.572	0.209	0.834	0.407	3.048
LM#March	1.064	0.093	0.711	0.477	0.897	1.263
LM#May	1.326	0.055	6.789	< 0.001	1.222	1.438
LM#June	1	(base)				
LM#July	1.261	0.571	0.512	0.609	0.519	3.062
LM#Aug	9.039	5.101	3.902	< 0.001	2.991	27.317
LM#Sept	22.181	22.025	3.121	0.002	3.168	155.305
LM#Oct	24.357	21.384	3.637	< 0.001	4.358	136.127
LM#Nov	43.116	16.482	9.846	< 0.001	20.382	91.207
PB#March	0.164	0.108	-2.753	0.006	0.045	0.594
PB#June	1	(base)				
PB#July	1.367	1.166	0.367	0.714	0.257	7.273
PB#Aug	8.846	7.192	2.681	0.007	1.798	43.531
PB#Sept	6.466	5.34	2.26	0.024	1.281	32.633
PB#Oct	4.053	3.213	1.765	0.078	0.857	19.165
PB#Nov	10.294	7.014	3.422	0.001	2.708	39.135
P-L#March	1.163	0.323	0.543	0.587	0.675	2.003
P-L#May	0.611	0.205	-1.467	0.143	0.316	1.18
P-L#June	1	(base)				
P-L#Aug	6.742	6.081	2.116	0.034	1.151	39.491
P-L#Sept	64.301	56.742	4.718	< 0.001	11.405	362.536
P-L#Oct	12.422	11.503	2.721	0.007	2.023	76.284
P-L#Nov	12.874	11.005	2.989	0.003	2.41	68.759
PM#March	0.006	0.005	-6.232	< 0.001	0.001	0.031
PM#May	0.01	0.007	-7.063	< 0.001	0.003	0.036
PM#Aug	0.138	0.075	-3.658	< 0.001	0.048	0.399
PM#Sept	0.165	0.1	-2.959	0.003	0.05	0.544
PM#Oct	0.73	0.306	-0.75	0.453	0.321	1.661

ULout#March	1	(base)				
ULout#May	1	(base)				
ULout#June	1	(base)				
ULout#July	1	(base)				
_cons	437.672	248.692	10.703	< 0.001	143.709	1332.95
/lnalpha	-0.436	0.15			-0.731	-0.141
alpha	0.646	0.097			0.481	0.868

Zooplankton abundance

Zooplankton abundance (mL^{-1}) was not affected by phytoplankton richness but was affected by phytoplankton abundance (cells mL^{-1}) and by site and month factors and their interactions (Figure 6, Figure 7, Figure 8, and Table 10). There was a very large positive effect of phytoplankton abundance on zooplankton abundance as illustrated by the IRR = 475 (Table 10). This further supports our understanding of Utah Lake ecosystem and that zooplankton and phytoplankton abundances are intimately linked and when phytoplankton abundances were low, zooplankton abundances were low, and vice versa. This is in contrast with the effects of zooplankton abundance on phytoplankton abundance in which we found no effect of zooplankton abundance on phytoplankton abundance (see previous section, Phytoplankton Abundance) and suggests that there is likely a bottom up effect of phytoplankton abundance on zooplankton abundance throughout the year. Pairwise comparisons of model predicted zooplankton abundances by months and sites are in Appendix 8 and Appendix 9.

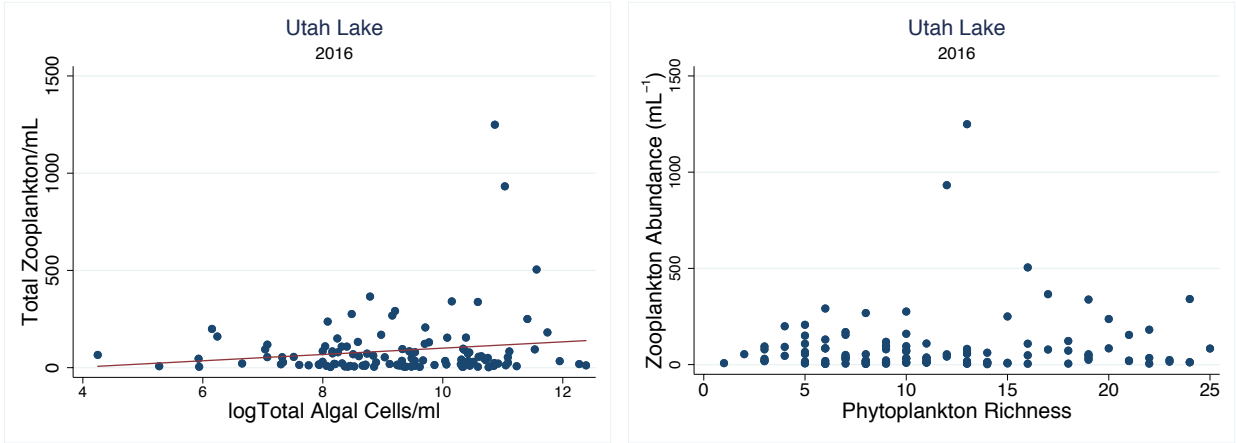


Figure 6. Relationship between zooplankton (mL^{-1}) abundance phytoplankton abundance (\log total cells mL^{-1}). and phytoplankton richness.

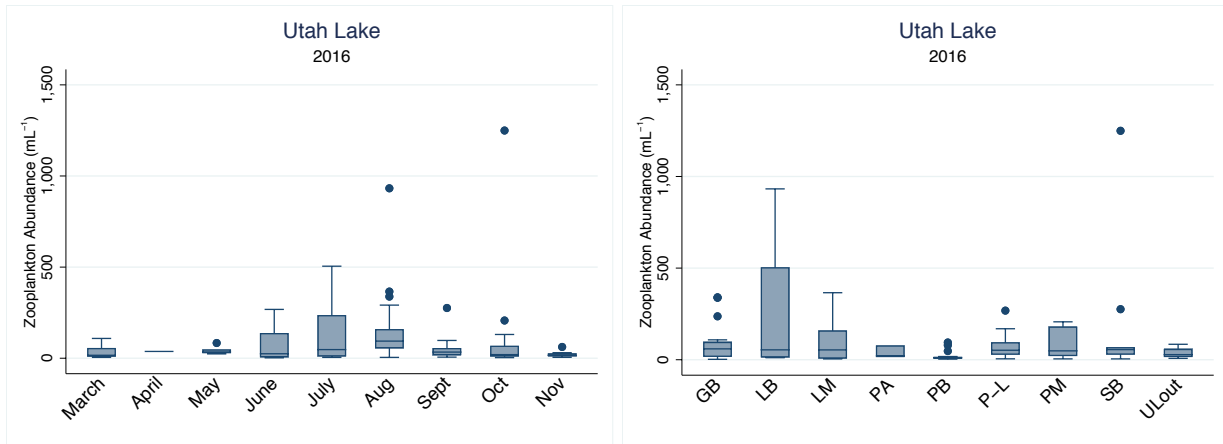


Figure 7. Relationship between zooplankton (mL⁻¹) abundances and months and sites in Utah Lake, 2016.

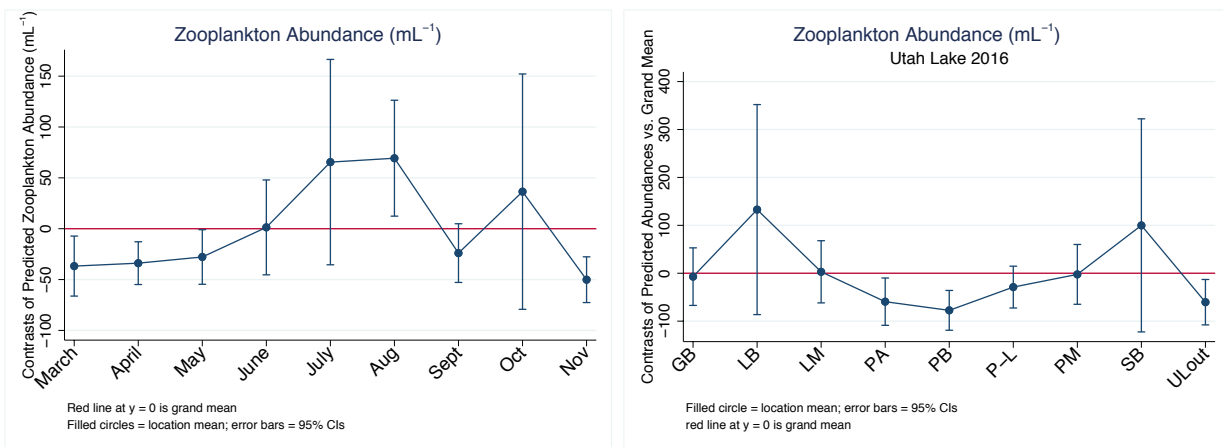


Figure 8. Contrasts of truncated negative binomial model predictions of zooplankton abundances (mL⁻¹) with grand mean by months and sites in Utah Lake, 2016.

Table 10. Effects of phytoplankton richness and abundance, site, and month on zooplankton abundance (mL⁻¹). Truncated negative binomial regression results.

	IRR	Robust Std. Err.	z	P > z	95% LCL	95% UCL
Phytoplankton richness	0.987	0.037	-0.338	0.735	0.918	1.063
Phytoplankton abundance (cells mL ⁻¹)	475	0.14	4.096	0.000	1.225	1.777
Site						
GB	0.156	0.134	-2.156	0.031	0.029	0.845
LB	0.185	0.103	-3.044	0.002	0.062	0.548
LM	3.999	2.451	2.261	0.024	1.203	13.293
PA	0.036	0.027	-4.503	< 0.001	0.009	0.153
PB	0.138	0.09	-3.018	0.003	0.038	0.499
P-L	4.699	3.347	2.172	0.03	1.163	18.977
PM	0.019	0.01	-7.707	< 0.001	0.007	0.052
SB	0.134	0.056	-4.818	< 0.001	0.059	0.304

ULout	1	(base)				
ULSP	0.698	0.258	-0.973	0.331	0.338	1.441
Month						
March	0.394	0.261	-1.406	0.16	0.108	1.443
April	0.212	0.06	-5.466	< 0.001	0.122	0.37
May	0.918	0.565	-0.138	0.89	0.275	3.068
June	1	(base)				
July	0.976	0.461	-0.052	0.959	0.387	2.463
Aug	7.179	4.715	3.001	0.003	1.982	26.009
Sept	39.092	27.423	5.226	< 0.001	9.885	154.595
Oct	90.777	74.3	5.508	< 0.001	18.25	451.518
Nov	12.818	6.093	5.366	< 0.001	5.049	32.543
Site by Month						
GB#March	61.242	60.366	4.175	< 0.001	8.872	422.741
GB#June	1	(base)				
GB#July	72.495	79.361	3.913	< 0.001	8.482	619.627
GB#Aug	2.857	3.216	0.933	0.351	0.315	25.939
GB#Sept	0.622	0.796	-0.371	0.71	0.051	7.635
GB#Oct	0.136	0.166	-1.633	0.102	0.012	1.491
GB#Nov	0.298	0.239	-1.512	0.13	0.062	1.431
LB#July	38.171	10.868	12.792	< 0.001	21.846	66.693
LB#Aug	11.187	0.836	32.297	< 0.001	9.662	12.953
LB#Sept	0.205	0.156	-2.083	0.037	0.046	0.911
LB#Oct	0.021	0.012	-6.67	< 0.001	0.007	0.064
LM#March	0.582	0.358	-0.879	0.379	0.174	1.947
LM#May	0.127	0.072	-3.645	< 0.001	0.042	0.385
LM#June	1	(base)				
LM#July	0.78	0.407	-0.476	0.634	0.281	2.167
LM#Aug	0.301	0.201	-1.801	0.072	0.081	1.112
LM#Sept	0.006	0.005	-5.86	< 0.001	0.001	0.034
LM#Oct	0.001	0.001	-8.117	< 0.001	0	0.004
LM#Nov	0.016	0.005	-13.375	< 0.001	0.009	0.03
PB#March	5.087	4.277	1.934	0.053	0.979	26.438
PB#June	1	(base)				
PB#July	5.613	3.027	3.199	0.001	1.951	16.152
PB#Aug	0.973	0.664	-0.04	0.968	0.255	3.705
PB#Sept	0.059	0.036	-4.613	< 0.001	0.018	0.196
PB#Oct	0.027	0.023	-4.345	< 0.001	0.005	0.139
PB#Nov	0.349	0.156	-2.36	0.018	0.146	0.837

P-L#March	0.125	0.082	-3.16	0.002	0.034	0.453
P-L#May	0.291	0.197	-1.827	0.068	0.077	1.094
P-L#June	1	(base)				
P-L#Aug	0.125	0.098	-2.661	0.008	0.027	0.578
P-L#Sept	0.003	0.002	-8.529	< 0.001	0.001	0.011
P-L#Oct	0.003	0.003	-6.209	< 0.001	0.001	0.02
P-L#Nov	0.013	0.01	-5.613	< 0.001	0.003	0.06
PM#March	22.143	15.902	4.313	< 0.001	5.419	90.474
PM#May	84.451	49.887	7.51	< 0.001	26.533	268.799
PM#Aug	59.016	38.769	6.207	< 0.001	16.285	213.87
PM#Sept	1.132	0.6	0.233	0.815	0.4	3.2
PM#Oct	1.647	1.33	0.618	0.536	0.338	8.017

Evenness

Phytoplankton taxa evenness did not significantly differ among sites but did among months (Figure 9, Table 11, Appendix 10, and Appendix 11). These differences in evenness help confirm that Utah Lake's phytoplankton assemblages are both spatially and temporally dynamic.

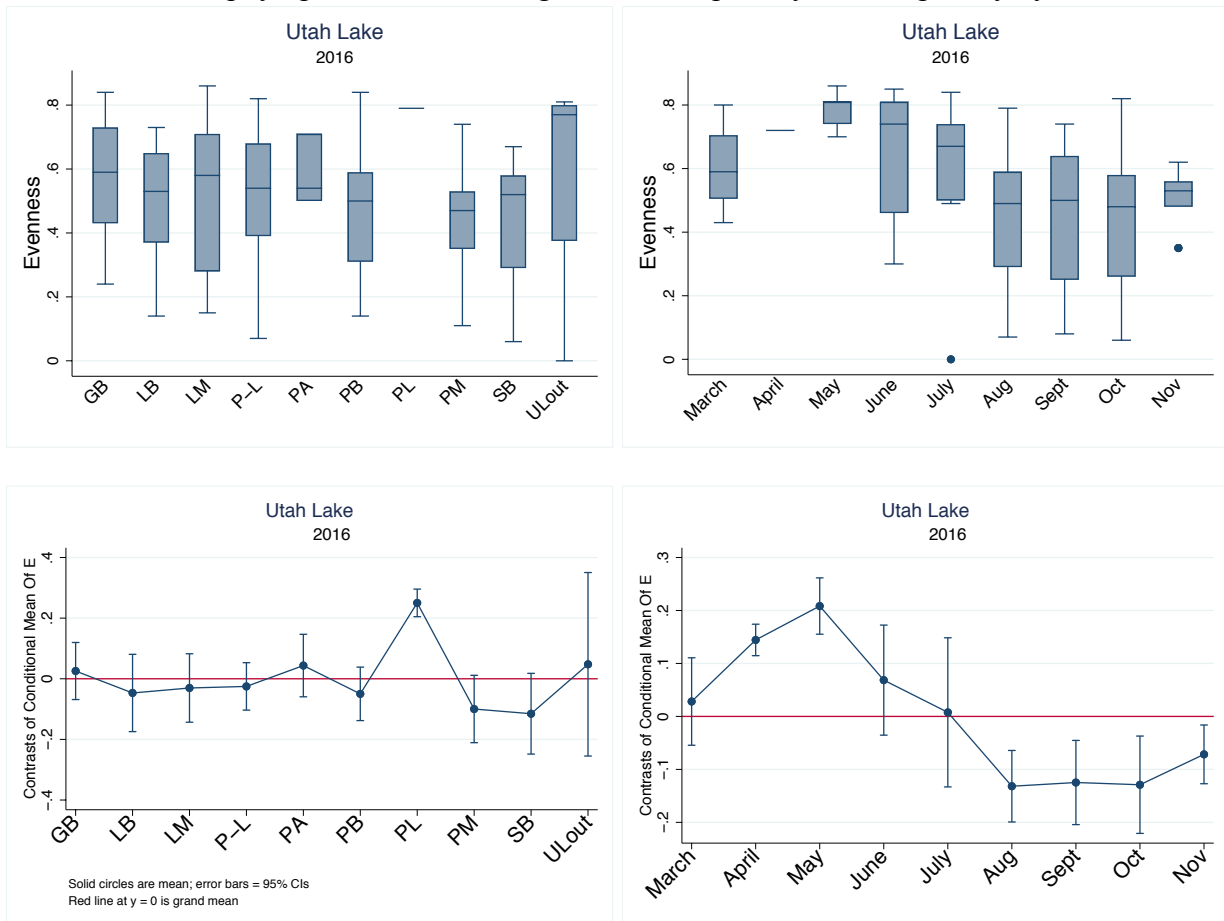


Figure 9. Relationships between phytoplankton taxa evenness and sites and months in Utah Lake, 2016, including contrasts of fractional probit regression model predictions with grand means.

Table 11. Fractional probit regression results of the effects of several factors; phytoplankton richness, abundance, zooplankton abundance, sites and months on phytoplankton taxa evenness.

Fractional probit regression	Number of obs	=	117
	Wald chi2(49)	=	1.56e+10
	Prob > chi2	=	0.0000
Log pseudolikelihood = -73.754935	Pseudo R2	=	0.0903

E	Coef.	Robust Std. Err.	z	P> z	[95% Conf. Interval]	
richness	0.07	0.01	6.76	0.00	0.05	0.10
logtotalcells	-0.27	0.03	-7.95	0.00	-0.34	-0.20
zooplanktontotal	-0.00	0.00	-1.96	0.05	-0.00	0.00
SiteCode						
GB	0.00	(base)				
LB	-0.24	0.03	-7.31	0.00	-0.30	-0.17
LM	0.02	0.28	0.06	0.95	-0.54	0.57
P-L	0.16	0.29	0.57	0.57	-0.41	0.73
PA	-0.16	0.36	-0.46	0.65	-0.86	0.53
PB	-0.05	0.28	-0.18	0.86	-0.60	0.50
PL	-0.13	0.31	-0.43	0.67	-0.73	0.47
PM	-0.27	0.28	-0.96	0.34	-0.82	0.28
SB	-0.19	0.05	-4.09	0.00	-0.28	-0.10
ULout	0.38	0.29	1.34	0.18	-0.18	0.94
monthcode						
March	0.00	(base)				
April	0.42	0.03	13.44	0.00	0.36	0.48
May	-0.23	0.04	-6.32	0.00	-0.31	-0.16
June	0.24	0.40	0.60	0.55	-0.54	1.03
July	-0.39	0.53	-0.73	0.46	-1.42	0.65
Aug	0.28	0.33	0.84	0.40	-0.37	0.93
Sept	-0.16	0.36	-0.44	0.66	-0.87	0.55
Oct	-0.19	0.40	-0.48	0.63	-0.98	0.60
Nov	-0.10	0.28	-0.35	0.73	-0.64	0.45
monthcode#SiteCode						
March#GB	0.00	(base)				
March#LM	0.00	(base)				
March#P-L	0.00	(base)				
March#PB	0.00	(base)				
March#PM	0.00	(base)				
March#ULout	0.00	(base)				
May#LM	0.71	0.03	20.33	0.00	0.64	0.78
May#P-L	0.33	0.28	1.20	0.23	-0.21	0.88
May#PM	0.73	0.06	12.15	0.00	0.61	0.84
June#GB	0.00	(base)				
June#LM	0.21	0.42	0.50	0.62	-0.61	1.03
June#P-L	-0.06	0.43	-0.14	0.89	-0.90	0.78
June#PB	-0.38	0.51	-0.74	0.46	-1.37	0.62
June#ULout	-0.66	0.41	-1.60	0.11	-1.47	0.15
July#GB	0.00	(base)				
July#LB	1.12	0.47	2.38	0.02	0.20	2.05
July#LM	0.38	0.53	0.73	0.47	-0.65	1.42
July#PB	0.37	0.57	0.65	0.52	-0.74	1.47
July#SB	0.70	0.51	1.37	0.17	-0.30	1.71
July#ULout	-5.36	0.62	-8.68	0.00	-6.57	-4.15
Aug#GB	0.00	(base)				
Aug#LB	0.47	0.30	1.59	0.11	-0.11	1.05
Aug#LM	-0.78	0.36	-2.15	0.03	-1.48	-0.07
Aug#P-L	-0.54	0.36	-1.48	0.14	-1.25	0.18
Aug#PB	-0.26	0.36	-0.74	0.46	-0.97	0.44
Aug#PM	-0.20	0.33	-0.60	0.55	-0.86	0.45
Aug#SB	0.42	0.20	2.17	0.03	0.04	0.81
Sept#GB	0.00	(base)				
Sept#LB	0.10	0.34	0.30	0.76	-0.57	0.77
Sept#LM	-0.17	0.43	-0.40	0.69	-1.02	0.67
Sept#P-L	0.32	0.42	0.77	0.44	-0.50	1.14
Sept#PB	-0.16	0.43	-0.37	0.71	-1.01	0.69
Sept#PM	0.84	0.36	2.37	0.02	0.15	1.54
Sept#SB	-0.17	0.43	-0.39	0.70	-1.00	0.67
Oct#GB	0.00	(base)				
Oct#LB	0.28	0.30	0.94	0.35	-0.31	0.87
Oct#LM	-0.12	0.45	-0.26	0.79	-0.99	0.76
Oct#P-L	0.06	0.44	0.15	0.88	-0.79	0.92
Oct#PB	-0.41	0.43	-0.96	0.34	-1.25	0.43
Oct#PM	0.30	0.64	0.47	0.64	-0.95	1.55
Oct#SB	0.08	0.34	0.25	0.81	-0.59	0.76
Nov#GB	0.00	(base)				
Nov#LM	-0.34	0.29	-1.16	0.25	-0.92	0.24
Nov#P-L	-0.20	0.29	-0.68	0.50	-0.77	0.37
Nov#PB	-0.00	0.28	-0.00	1.00	-0.56	0.55
Nov#PM	0.07	0.28	0.27	0.79	-0.47	0.61
_cons	1.81	0.37	4.89	0.00	1.08	2.53

Diversity

Shannon's diversity significantly differed among sites and among months (Figure 10, Table 12, Appendix 12, and Appendix 13). These differences in diversity helps confirm that Utah Lake's phytoplankton assemblages are both spatially and temporally dynamic.

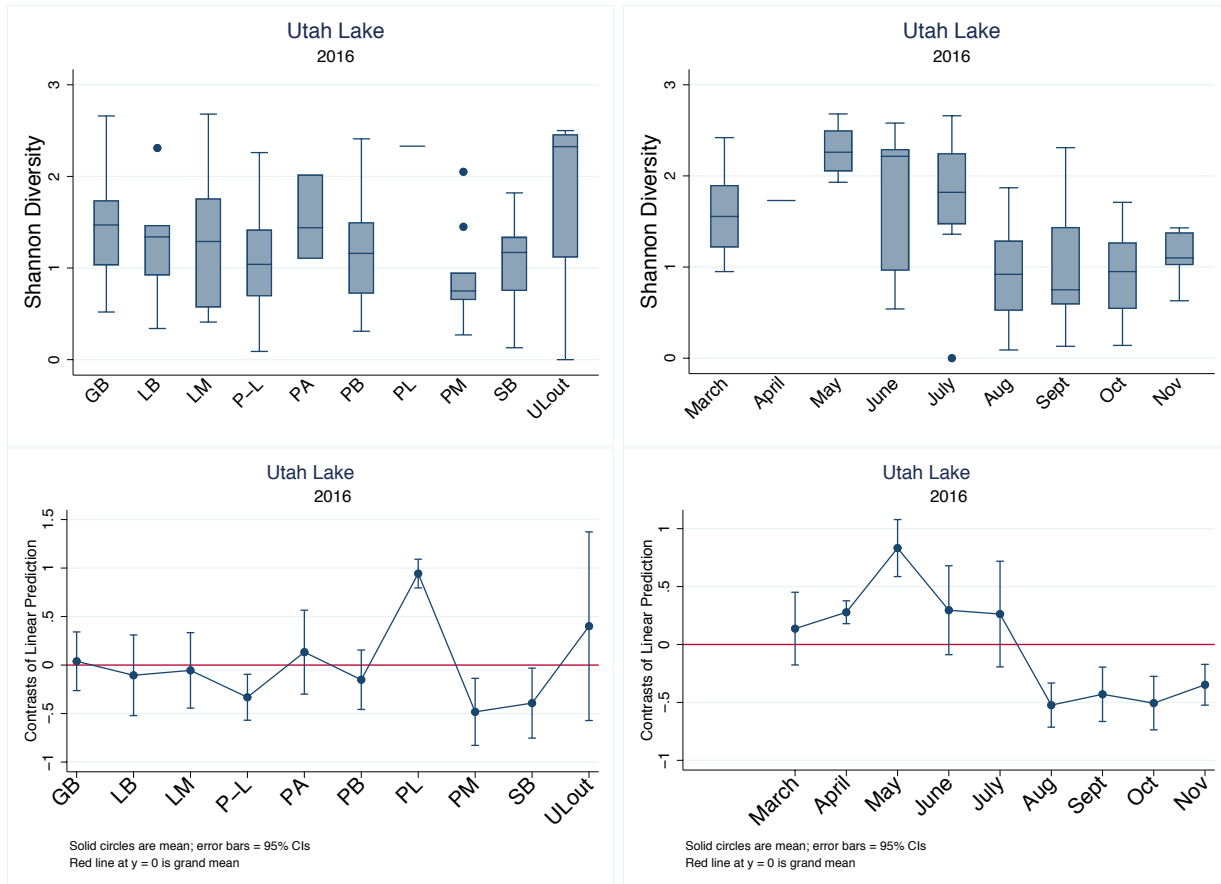


Figure 10. Relationships between phytoplankton taxa diversity and sites and months in Utah Lake, 2016, including contrasts of linear regression model predictions with grand means.

Table 12. Linear regression results of the effects of several factors; phytoplankton richness, abundance, zooplankton abundance, sites and months on phytoplankton taxa diversity.

Linear regression	Number of obs	=	117
	F(31, 62)	=	.
	Prob > F	=	.
	R-squared	=	0.8041
	Root MSE	=	.39898

H	Robust				[95% Conf. Interval]	
	Coef.	Std. Err.	t	P> t		
richness	0.10	0.01	8.11	0.00	0.08	0.13
logtotalcells	-0.19	0.04	-5.05	0.00	-0.27	-0.12
zooplanktontotal	-0.00	0.00	-2.11	0.04	-0.00	-0.00
SiteCode						
LB	-0.21	0.04	-5.65	0.00	-0.29	-0.14
LM	-0.13	0.33	-0.39	0.70	-0.78	0.52
P-L	-0.03	0.33	-0.08	0.94	-0.69	0.63
PA	0.00	0.41	0.01	0.99	-0.81	0.82
PB	-0.14	0.32	-0.44	0.66	-0.79	0.50
PL	0.00	0.41	0.00	1.00	-0.82	0.82
PM	-0.35	0.32	-1.07	0.29	-0.99	0.30
SB	-0.20	0.06	-3.40	0.00	-0.32	-0.08
ULout	0.28	0.33	0.86	0.39	-0.38	0.94
monthcode						
April	0.43	0.03	12.62	0.00	0.36	0.50
May	-0.19	0.04	-4.59	0.00	-0.27	-0.11
June	0.10	0.50	0.20	0.84	-0.90	1.10
July	-0.36	0.67	-0.53	0.60	-1.70	0.99
Aug	0.13	0.39	0.32	0.75	-0.66	0.91
Sept	-0.31	0.41	-0.75	0.46	-1.14	0.52
Oct	-0.36	0.58	-0.63	0.53	-1.52	0.80
Nov	-0.14	0.32	-0.46	0.65	-0.78	0.49
monthcode#SiteCode						
May#LM	0.64	0.04	15.23	0.00	0.55	0.72
May#P-L	0.33	0.33	0.97	0.33	-0.34	0.99
May#PM	0.70	0.08	9.27	0.00	0.55	0.86
June#LM	0.39	0.52	0.74	0.46	-0.65	1.42
June#P-L	0.12	0.53	0.22	0.83	-0.95	1.18
June#PB	-0.30	0.74	-0.41	0.69	-1.78	1.18
June#ULout	-0.43	0.51	-0.85	0.40	-1.46	0.59
July#LB	0.83	0.62	1.35	0.18	-0.40	2.06
July#LM	0.52	0.68	0.77	0.45	-0.83	1.88
July#PB	0.38	0.71	0.53	0.60	-1.05	1.80
July#SB	0.54	0.68	0.79	0.43	-0.82	1.90
July#ULout	-1.08	0.75	-1.44	0.16	-2.57	0.42
Aug#LB	0.36	0.31	1.19	0.24	-0.25	0.97
Aug#LM	-0.52	0.44	-1.17	0.25	-1.41	0.37
Aug#P-L	-0.32	0.42	-0.77	0.44	-1.16	0.51
Aug#PB	-0.23	0.43	-0.55	0.58	-1.08	0.62
Aug#PM	-0.17	0.41	-0.41	0.68	-0.99	0.65
Aug#SB	0.31	0.25	1.24	0.22	-0.19	0.80
Sept#LB	0.12	0.42	0.28	0.78	-0.73	0.97
Sept#LM	0.01	0.50	0.02	0.98	-0.98	1.00
Sept#P-L	0.37	0.45	0.82	0.42	-0.53	1.26
Sept#PB	-0.09	0.50	-0.18	0.86	-1.10	0.92
Sept#PM	0.52	0.40	1.28	0.21	-0.29	1.32
Sept#SB	-0.00	0.44	-0.01	0.99	-0.88	0.87
Oct#LB	0.32	0.49	0.64	0.52	-0.67	1.30
Oct#LM	0.09	0.62	0.15	0.89	-1.15	1.33
Oct#P-L	0.26	0.61	0.42	0.67	-0.97	1.48
Oct#PB	-0.13	0.60	-0.22	0.83	-1.34	1.07
Oct#PM	0.33	0.78	0.42	0.67	-1.23	1.89
Oct#SB	0.23	0.53	0.44	0.66	-0.82	1.29
Nov#LM	-0.20	0.34	-0.58	0.57	-0.88	0.49
Nov#P-L	-0.04	0.33	-0.11	0.92	-0.70	0.63
Nov#PB	0.05	0.32	0.16	0.87	-0.60	0.70
Nov#PM	0.09	0.32	0.28	0.78	-0.54	0.72
_cons	2.07	0.44	4.74	0.00	1.20	2.94

Relationships During High Phytoplankton Abundances

Stronger interaction effects between phytoplankton and zooplankton were expected than presented in the previous sections. This lack of findings may have been due to when either or both phytoplankton and zooplankton assemblages were below carrying capacity or their production was low (e.g. non-summer months) and interactions were not strong enough to have an effect. Upon closer inspection of the data, it appeared that zooplankton abundance was most variable when phytoplankton abundance was approximately $\geq 50,000$ cells mL^{-1} (Figure 11).

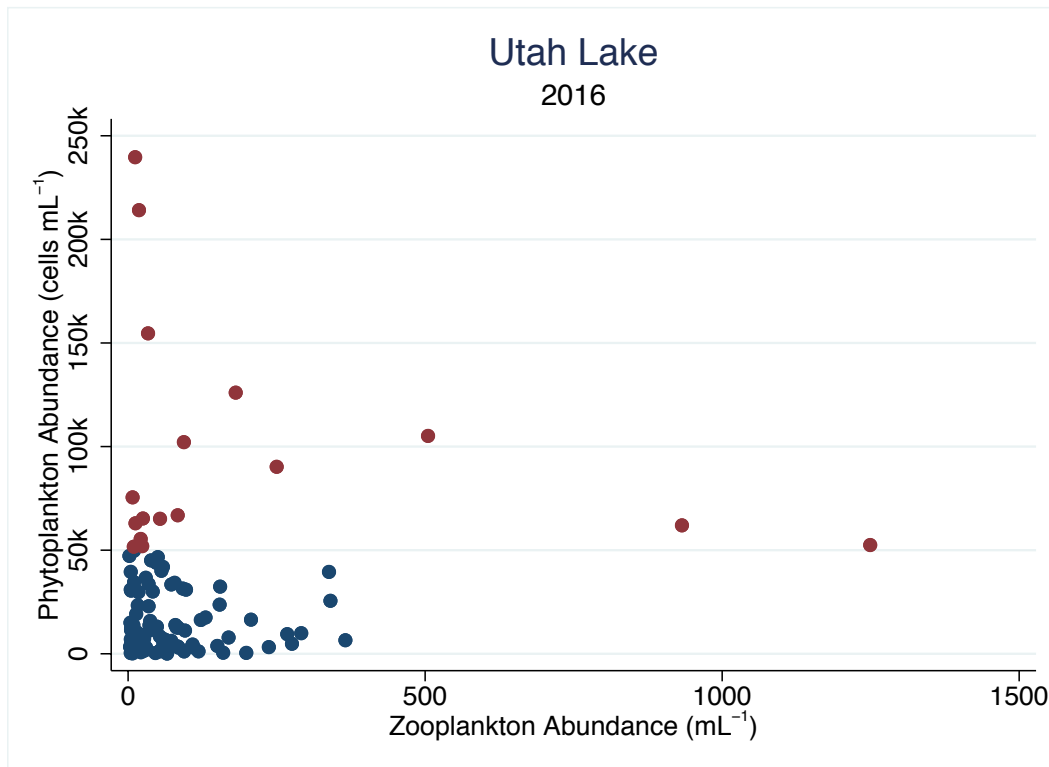


Figure 11. Relationship between phytoplankton abundance and zooplankton abundance. Red dots are zooplankton abundances when phytoplankton abundances were $> 50,000$ cells mL^{-1} .

Subsequently, only those data where phytoplankton abundances were $> 50,000$ cells mL^{-1} were used in the following analyses ($N = 17$ samples). These adjusted results show that zooplankton abundances (mL^{-1}) did not significantly affect phytoplankton taxa richness (Figure 12 and Table 13) but phytoplankton richness negatively affected zooplankton abundance (Table 14).

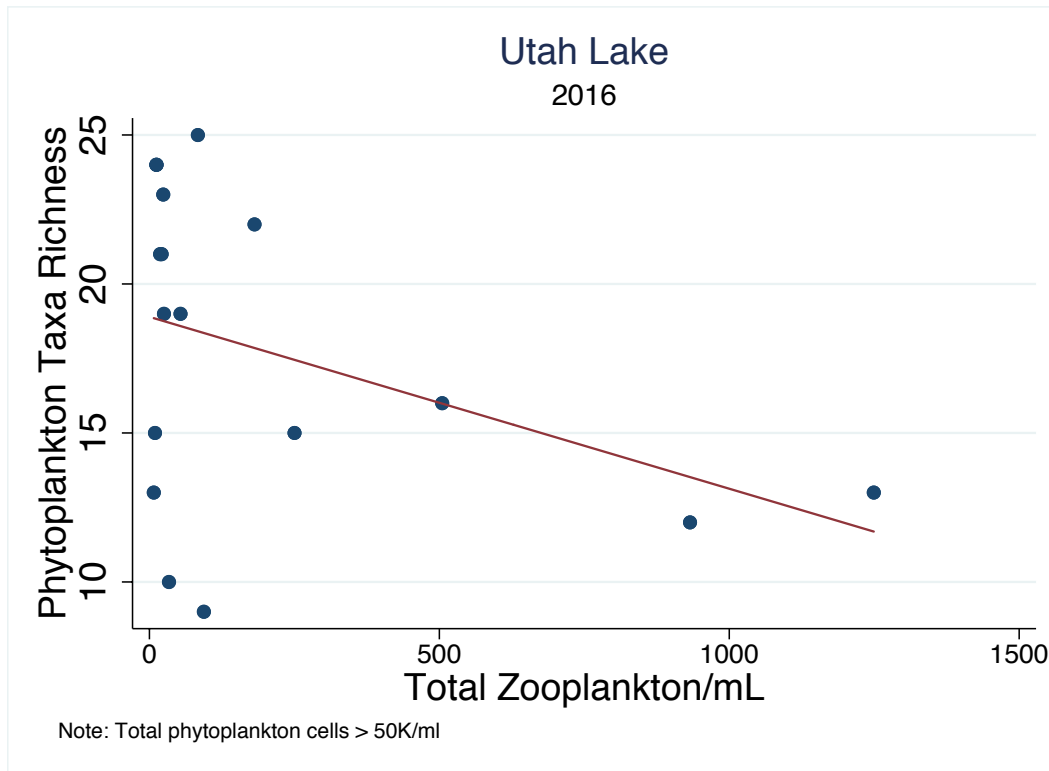


Figure 12. Relationship between phytoplankton abundance and zooplankton abundance using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used.

Table 13. Linear regression results of the effect of zooplankton abundance on phytoplankton richness using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used.

. regress richness zooplanktontotal

Source	SS	df	MS	Number of obs	=	17
Model	69.0841197	1	69.0841197	F(1, 15)	=	2.84
Residual	364.445292	15	24.2963528	Prob > F	=	0.1124
				R-squared	=	0.1594
				Adj R-squared	=	0.1033
Total	433.529412	16	27.0955882	Root MSE	=	4.9291

richness	Coef.	Std. Err.	t	P> t	[95% Conf. Interval]
zooplanktontotal	-.0057675	.0034203	-1.69	0.112	-.0130577 .0015228
_cons	18.89762	1.388771	13.61	0.000	15.93753 21.85772

Table 14. Truncated negative binomial regression results of the effect of phytoplankton richness on zooplankton abundance using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used.

Negative binomial regression		Number of obs	=	17
		Wald chi2(1)	=	9.67
Dispersion	= mean	Prob > chi2	=	0.0019
Log pseudolikelihood	= -100.48165	Pseudo R2	=	0.0341

zooplanktontotal	IRR	Robust Std. Err.	z	P> z	[95% Conf. Interval]	
richness	.8260638	.0507521	-3.11	0.002	.7323473	.931773
_cons	4228.258	4981.501	7.09	0.000	420.0708	42559.88
/lnalpha	.400184	.185026			.0375396	.7628284
alpha	1.492099	.2760772			1.038253	2.144333

There was also a negative relationship between zooplankton abundance and phytoplankton abundance (Figure 13), which appeared to be both bottom-up (phytoplankton abundance negatively affected zooplankton) (Table 15) and top-down (zooplankton abundance negatively affected phytoplankton abundance (Table 16).

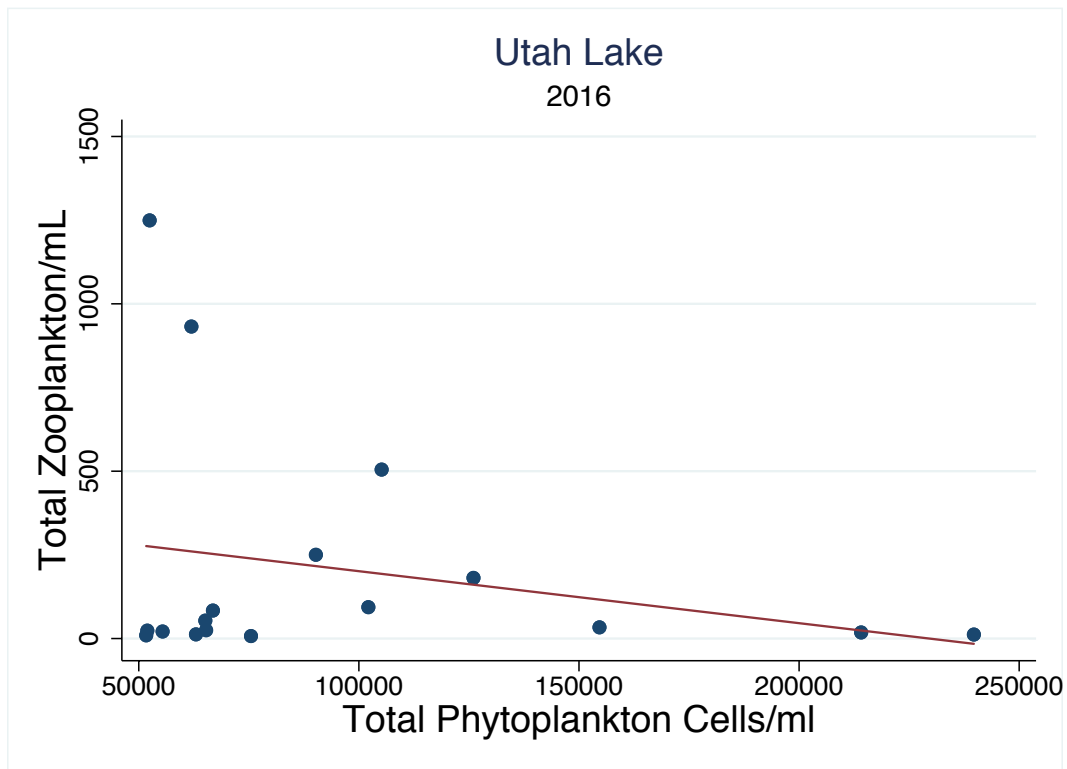


Figure 13. Relationships between zooplankton abundance and phytoplankton abundance using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used.

Table 15. Truncated negative binomial regression results of the effect of zooplankton abundance on phytoplankton richness using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used.

Negative binomial regression		Number of obs	=	17
		Wald chi2(1)	=	12.59
Dispersion	= mean	Prob > chi2	=	0.0004
Log pseudolikelihood	= -102.01551	Pseudo R2	=	0.0194

	IRR	Robust Std. Err.	z	P> z	[95% Conf. Interval]	
zooplanktontotal						
totalcellsmL	.9999838	4.56e-06	-3.55	0.000	.9999749	.9999928
_cons	791.0039	542.6294	9.73	0.000	206.1833	3034.615
/lnalpha	.5309306	.1805784			.1770034	.8848578
alpha	1.700514	.3070762			1.193635	2.42264

Table 16. Truncated negative binomial regression results of the effect of zooplankton abundance on phytoplankton abundance using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used

Negative binomial regression		Number of obs	=	17
		Wald chi2(1)	=	5.54
Dispersion	= mean	Prob > chi2	=	0.0186
Log pseudolikelihood	= -204.8375	Pseudo R2	=	0.0046

	IRR	Robust Std. Err.	z	P> z	[95% Conf. Interval]	
totalcellsmL						
zooplanktontotal	.9994995	.0002127	-2.35	0.019	.9990827	.9999164
_cons	105684.5	17912.3	68.25	0.000	75812.82	147326.3
/lnalpha	-1.513952	.2573085			-2.018267	-1.009636
alpha	.2200388	.0566178			.1328856	.3643515

The following regression models suggest that zooplankton abundances were not affected by phytoplankton richness (Table 17), that is, zooplankton did well no matter how many phytoplankton taxa there were. However, and as anticipated, zooplankton abundances were

positively affected by phytoplankton abundances (Table 17). Zooplankton abundances were also significantly affected by month and site and their interactions (Table 17).

Table 17. Truncated negative binomial regression results of the effect of phytoplankton richness and abundance and sites and months on zooplankton abundance using a subset of the total data where only those values of phytoplankton abundances > 50,000 cells mL⁻¹ were used

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Negative binomial regression          Number of obs   =      17
                                     Wald chi2(7)     =      .
Dispersion = mean                    Prob > chi2      =      .
Log pseudolikelihood = -64.273744    Pseudo R2       =      0.3822

```

zooplanktontotal	Robust					[95% Conf. Interval]	
	IRR	Std. Err.	z	P> z			
richness	0.932	0.042	-1.569	0.117	0.853	1.018	
logtotalcells	18.190	18.642	2.830	0.005	2.440	135.576	
sitecode	(base)						
GB	1.000						
LB	445.619	318.366	8.537	0.000	109.859	1807.561	
LM	47.871	46.646	3.970	0.000	7.090	323.219	
PB	6.956	9.274	1.455	0.146	0.510	94.892	
P-L	84.620	97.847	3.838	0.000	8.774	816.073	
PM	22.188	22.909	3.002	0.003	2.932	167.882	
SB	61.671	7.092	35.842	0.000	49.226	77.262	
ULout	34.673	25.203	4.878	0.000	8.342	144.119	
monthcode	(base)						
March	1.000						
May	1.220	0.505	0.480	0.631	0.542	2.748	
June	0.050	0.042	-3.530	0.000	0.009	0.263	
July	0.204	0.179	-1.810	0.070	0.036	1.141	
Aug	1.326	0.671	0.559	0.576	0.492	3.574	
Sept	0.016	0.018	-3.758	0.000	0.002	0.139	
Oct	22.150	21.637	3.171	0.002	3.265	150.263	
_cons	0.000	0.000	-3.191	0.001	0.000	0.000	
/lnalpha	-21.658	.			.	.	
alpha	0.000	.			.	.	

Phytoplankton richness was slightly (coef. = -0.002) but significantly (p < 0.01) negatively affected by zooplankton abundance but positively affected by phytoplankton abundance (Table 18). This suggests that zooplankton may have had slight preferences or avoidance of some phytoplankton taxa. Phytoplankton richness was also affected by site and month (Table 18).

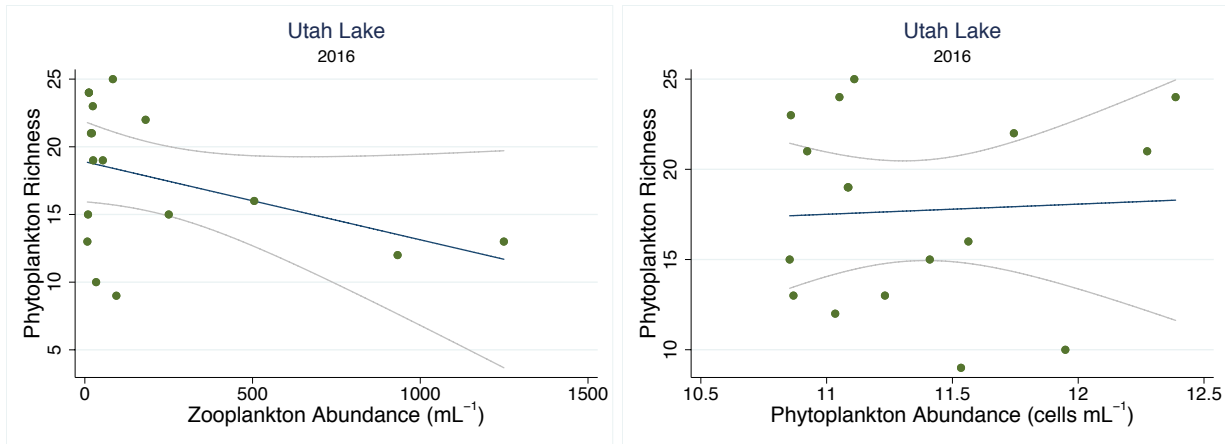


Figure 14. Relationships between phytoplankton richness and zooplankton and phytoplankton abundance when phytoplankton abundances were $> 50,000$ cells mL^{-1} . $N = 17$.

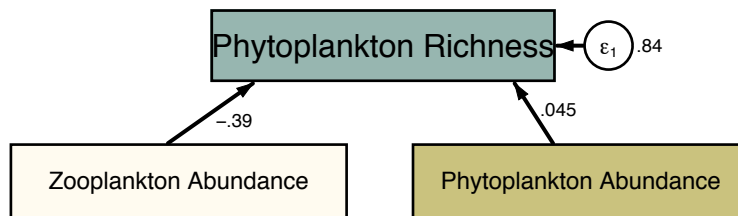


Figure 15. Conceptual path diagram showing relationship between phytoplankton richness and zooplankton and phytoplankton abundance when phytoplankton abundances $> 50,000$ cells mL^{-1} .

Table 18. Truncated Poisson regression results of the effect of and phytoplankton and zooplankton abundances and sites and months on phytoplankton richness using a subset of the total data where only those values of phytoplankton abundances $> 50,000$ cells mL^{-1} were used.

<i>Leptolyngbya</i> species	Cyanobacteria	152558	0.08
<i>Fragilaria virescens</i>	Bacillariophyta	114400	0.06
<i>Phormidium</i> species	Cyanobacteria	107151	0.05
<i>Sphaerocystis schroeteri</i>	Chlorophyta	100738	0.05
<i>Cyanodictyon planktonicum</i>	Cyanobacteria	99820	0.05
<i>Dolichospermum flosaquae</i>	Cyanobacteria	86604	0.04
<i>Aphanizomenon flos-aquae</i>	Cyanobacteria	80524	0.04
<i>Aphanocapsa</i> species	Cyanobacteria	73346	0.04
centric diatoms	Bacillariophyta	61015	0.03
<i>Microcystis aeruginosa</i>	Cyanobacteria	41440	0.02
pennate diatoms	Bacillariophyta	39932	0.02
<i>Coelastrum</i> species	Chlorophyta	30600	0.02
<i>Crucigeniella rectangularis</i>	Chlorophyta	27136	0.01
<i>Monoraphidium dybowskii</i>	Chlorophyta	26222	0.01
<i>Pediastrum duplex</i> var. <i>clathratum</i>	Chlorophyta	24000	0.01
<i>Nitzschia acicularis</i>	Bacillariophyta	19321	0.01

Cyanobacteria accounted for almost 50% of the cell counts when phytoplankton cell counts were high, whereas diatoms and green algae contributed about equally (Figure 16).

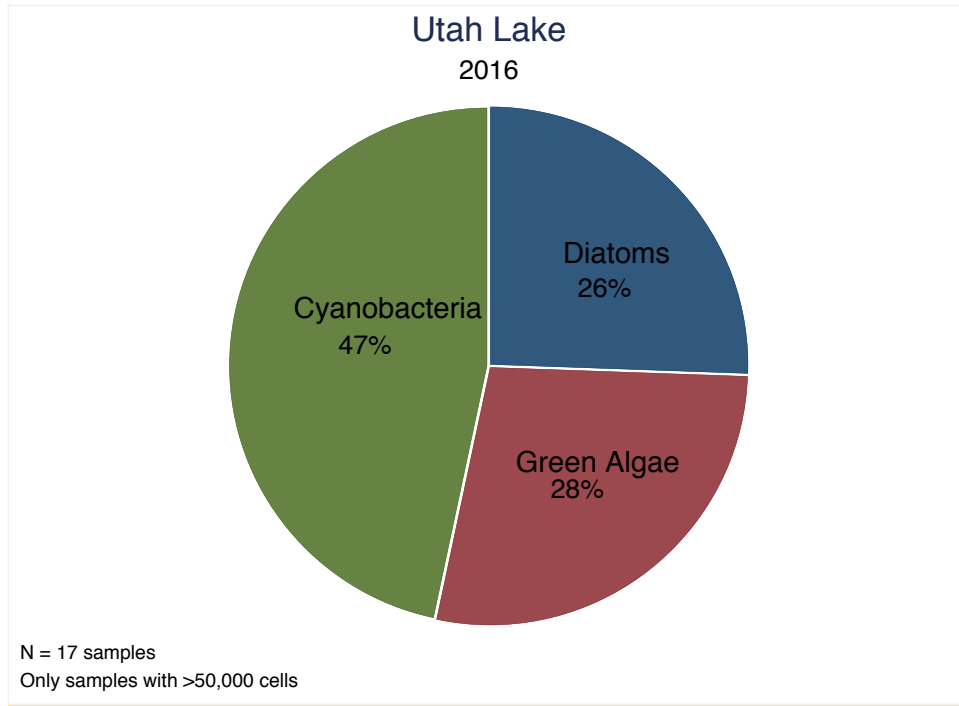


Figure 16. Percentages of cyanobacteria, diatoms (Bacillariophyta), and green algae (Chlorophyta) taxa when phytoplankton cell counts were > 50,000 mL⁻¹.

CyanoHABs did not have a significantly greater effect on phytoplankton taxa richness than did diatoms or green algae, even though cyanoHABS made up almost twice as much of the cell counts during high phytoplankton abundance (Figure 16, Figure 17, and Table 20).

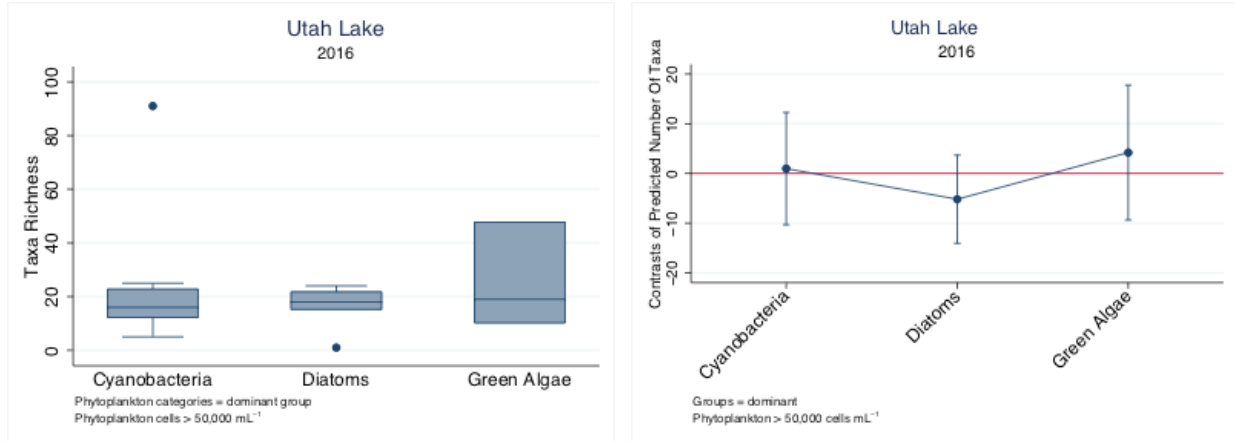


Figure 17. Relationship between phytoplankton taxa richness and major groups of phytoplankton (cyanobacteria, diatoms, and green algae) when phytoplankton abundance > 50,000 cells mL⁻¹. First graph is box plot of raw taxa richness; second graph is contrasts with grand mean taxa richness based on regression model results in Table 22.

Table 20. Truncated negative binomial regression results of phytoplankton taxa richness vs whether cyanobacteria, diatoms, or green algae were the dominant group when phytoplankton abundances were > 50,000 cells mL⁻¹.

Truncated negative binomial regression	Number of obs	=	20
Truncation point: 0	Wald chi2(2)	=	1.50
Dispersion = mean	Prob > chi2	=	0.4723
Log pseudolikelihood = -78.647905	Pseudo R2	=	0.0063

taxarichness	Robust		z	P> z	[95% Conf. Interval]	
	IRR	Std. Err.				
D						
Diatoms	0.72	0.27	-0.86	0.39	0.35	1.51
Green Algae	1.14	0.56	0.28	0.78	0.44	2.99
_cons	22.32	6.85	10.12	0.00	12.24	40.72
/lnalpha	-0.74	0.49			-1.70	0.22
alpha	0.48	0.23			0.18	1.25

Evenness

Richness positively affected evenness, whereas phytoplankton and zooplankton abundance negatively affected evenness .

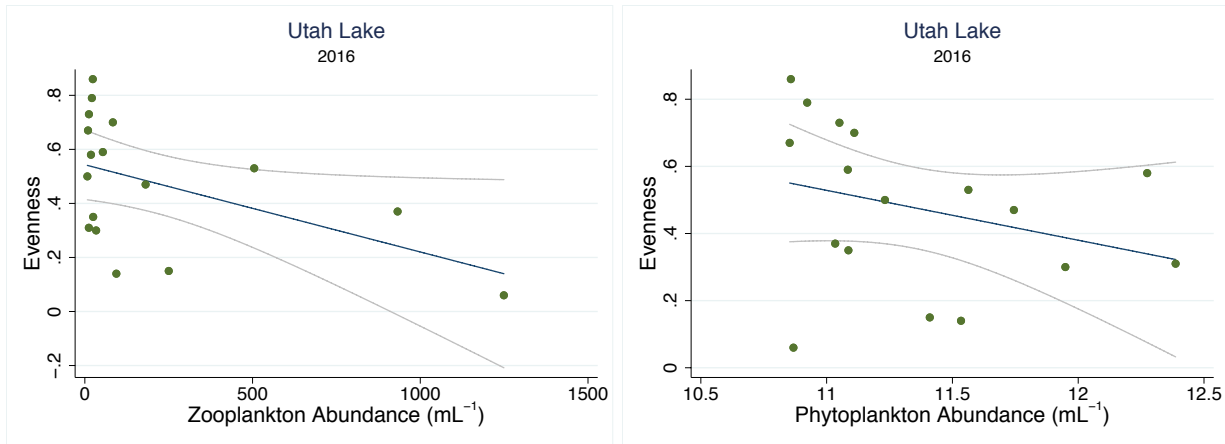


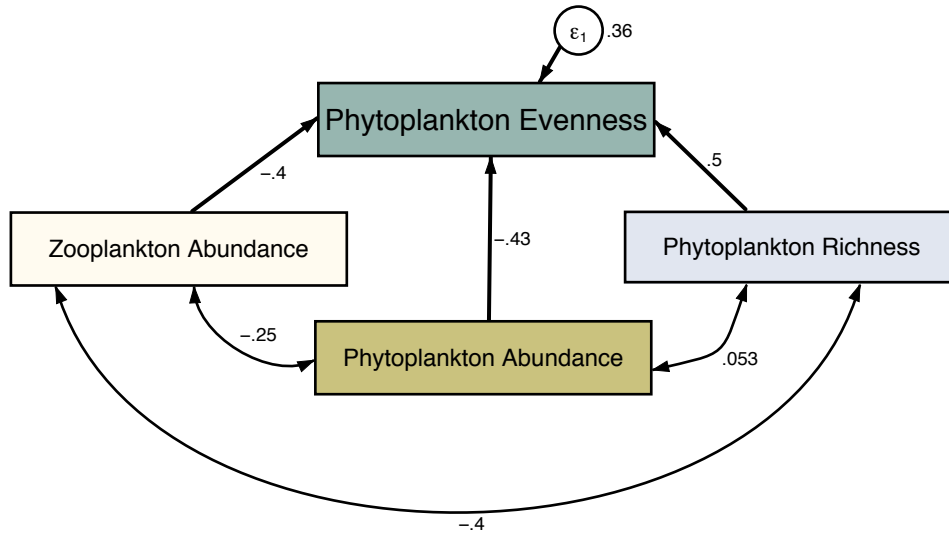
Figure 18. Relationship between phytoplankton taxa evenness and zooplankton and phytoplankton abundances when phytoplankton abundances were > 50,000 cells mL⁻¹.

Table 21. Fractional probit regression results of the effects of several predictor variables on phytoplankton evenness when phytoplankton cells were > 50,000 mL⁻¹.

Fractional probit regression	Number of obs	=	17
	Wald chi2(1)	=	6.63e+14
	Prob > chi2	=	0.0000
Log pseudolikelihood = -9.7712192	Pseudo R2	=	0.1694

E	Robust		z	P> z	[95% Conf. Interval]	
	Coef.	Std. Err.				
richness	0.14	0.00	5.1e+12	0.00	0.14	0.14
logtotalcells	-3.35	0.00	-4.0e+12	0.00	-3.35	-3.35
zooplanktontotal	0.01	0.00	3.8e+12	0.00	0.01	0.01
monthcode						
March	0.00	(base)				
May	-0.30	0.00	-1.2e+12	0.00	-0.30	-0.30
June	1.04	0.00	2.7e+12	0.00	1.04	1.04
July	3.34	0.00	2.3e+12	0.00	3.34	3.34
Aug	-0.74	0.00	-4.4e+12	0.00	-0.74	-0.74
Sept	3.88	0.00	4.6e+12	0.00	3.88	3.88
Oct	-5.49	0.00	-1.7e+07	0.00	-5.49	-5.49
SiteCode						
GB	0.00	(base)				
LB	-9.13	0.00	-2.9e+07	0.00	-9.13	-9.13
LM	-5.05	0.00	-1.6e+07	0.00	-5.05	-5.05
P-L	-5.40	0.00	-1.7e+07	0.00	-5.40	-5.40
PB	-2.93	0.00	-9.3e+06	0.00	-2.93	-2.93
PM	-3.57	0.00	-1.1e+07	0.00	-3.57	-3.57
SB	-8.13	0.00	-2.6e+07	0.00	-8.13	-8.13
ULout	-5.11	0.00	-1.6e+07	0.00	-5.11	-5.11
monthcode#SiteCode						
March#LM	0.00	(base)				
March#ULout	0.00	(base)				
Oct#GB	0.00	(base)				
_cons	39.37	0.00	1.2e+08	0.00	39.37	39.37

A simplified structural equation model (SEM) was generated to further illustrate these interactions (Figure 19). This SEM had very good fits and explained about 64% of the variability between these interactions (Table 22).



Equation level goodness of fit; $R^2 = 0.64$
 Overall goodness of fit: $\chi^2 = 17.53$; $p = 0.001$
 N = 17

Figure 19. Structural equation mode (SEM) of the interactions between phytoplankton richness, evenness, abundance, and zooplankton abundance (mL-1). See Table X for SEM results.

Table 22. Structural equation model (SEM) results of the interactions between phytoplankton richness, evenness, abundance, and zooplankton abundance (mL-1).

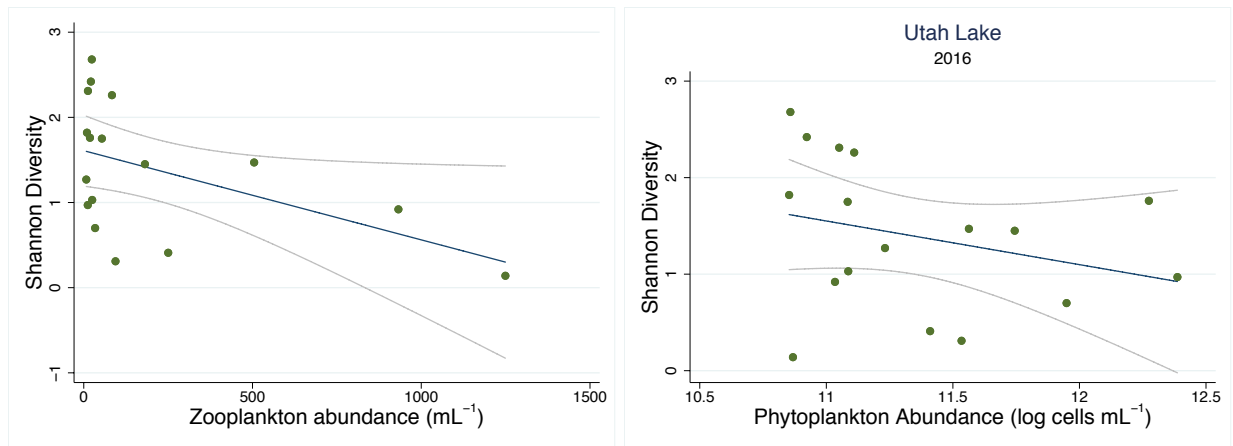


Figure 20. Relationship between phytoplankton diversity and zooplankton and phytoplankton abundance when phytoplankton abundances were > 50,000 cells mL⁻¹.

Table 23. Linear regression model results showing the relationship between phytoplankton diversity (Shannon H) and zooplankton and phytoplankton abundance when phytoplankton abundances were > 50,000 cells mL⁻¹.

Linear regression	Number of obs	=	17
	F(2, 14)	=	10.12
	Prob > F	=	0.0019
	R-squared	=	0.4195
	Root MSE	=	.6275

H	Coef.	Robust Std. Err.	t	P> t	[95% Conf. Interval]	
zooplanktontotal	-.0012825	.0002868	-4.47	0.001	-.0018976	-.0006673
logtotalcells	-.6893739	.2966541	-2.32	0.036	-1.325634	-.053114
_cons	9.482248	3.383816	2.80	0.014	2.224686	16.73981

Discussion

Results presented in this report and Richards and Miller (2017) confirm that Utah Lake's unique phytoplankton assemblages are both spatially and temporally dynamic and resilient to blooms. Any management strategies and in particular, prudent management of cyanoHABs, need to strongly consider these dynamics (Chalar 2009).

Results presented in this report also showed that when cyanoHABs were most abundant; phytoplankton taxa richness appeared to decline, which could be cause for concern. However dominance by cyanoHABs did not affect phytoplankton taxa richness any more than did diatom or green-algal blooms, nor did they appear to cause extinction of phytoplankton taxa. The most plausible explanations for an apparent decline in phytoplankton taxa richness when cyanoHABs and diatom and green algal blooms occurred were a result of: field sampling error, laboratory subsampling error, and the nature of the taxa richness metric. Preliminary analyses conducted in

2017 show that phytoplankton taxa composition and abundances can vary significantly within < 100 m in Utah Lake (Richards unpublished data). Thus, samples collected as singletons at any location can bias findings. In addition, samples examined in the laboratory are intensely subsampled. It is well known that when subsampling is performed on samples that are dominated by a relatively few taxa, uncommon and rare taxa are often overlooked and taxa richness estimates become biased towards reporting fewer taxa (Richards 2016). In addition, Richards and Miller (2017) conducted two separate, well-established multimetric statistical methods on Utah Lake 2016 phytoplankton assemblages. Both methods showed that phytoplankton assemblages were dissimilar among sites and among months, further supporting the conclusion that measures other than taxa richness by itself are necessary to understand diversity of phytoplankton assemblages in Utah Lake and that more importantly, the apparent seasonal change and decrease in taxa richness in the summer months did not reflect a true loss of diversity. Contrarily, Richards and Miller (2017) reported that taxa diversity in Utah Lake was apparently greatest in June and August (Figure 21).

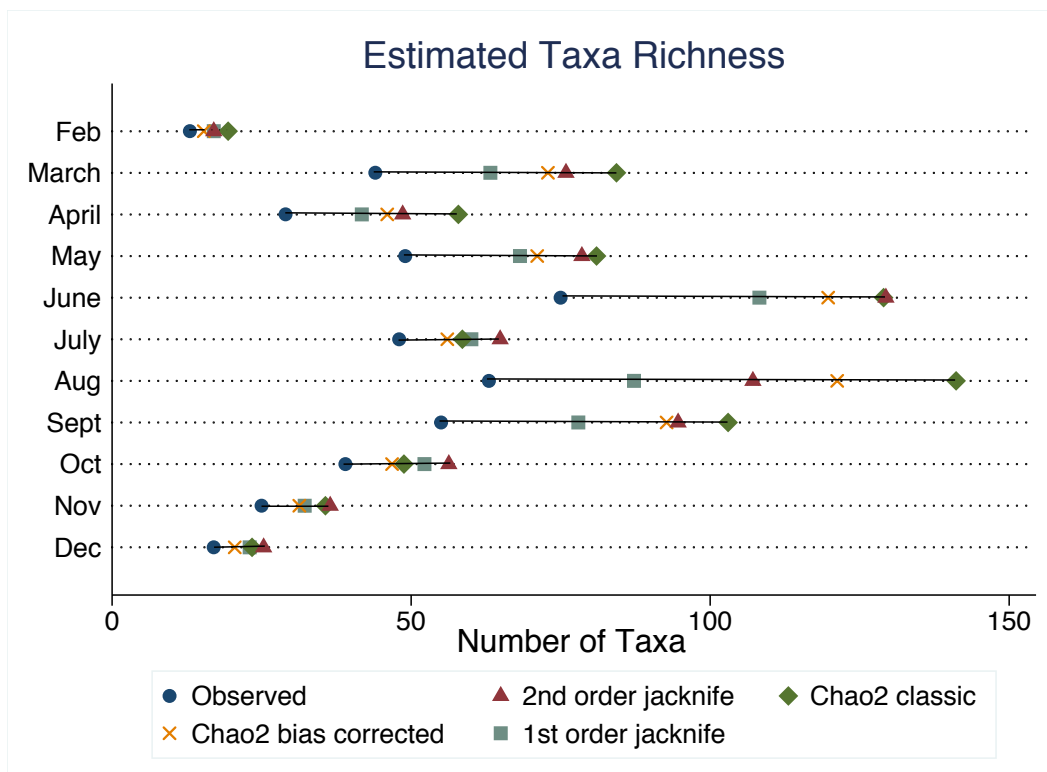


Figure 21. Estimated phytoplankton taxa richness by month in Utah Lake 2016. Estimates include observed and four species area curve based estimates: 1st order jackknife; 2nd order jackknife; Chao2 classic; and Chao2 bias corrected (McCune and Mefford 2011)(from Richards and Miller 2017).

In addition, the taxa richness metric is only a measure of how many taxa were encountered in a sample (i.e. alpha diversity). Taxa richness does not measure beta diversity, the number of different taxa in a location. Figure 21 clearly shows that there was not a loss of taxa during blooms but in fact diversity likely increased during the blooms, albeit with many taxa occurring

at low abundances. Richards and Miller (2017) reported that 33 taxa occurred as singletons and 18 occurred as doubletons out of the 124 taxa or about 41% of the taxa found in 2016 were considered rare and uncommon. This phenomenon of rare and uncommon taxa being more numerous than common taxa is strongly grounded in community ecological theory. There also appeared to be a noticeable shift in the phytoplankton taxa assemblage this past year (2017) with at least 15-20 new taxa observed in 2017 compared with the past, including more cryptomonads (Sam Rushforth, personal communication, preliminary assessment). Although there appears to be a highly diverse and robust phytoplankton assemblage in Utah Lake and that blooms do not negatively affect the assemblage; any further shift in assemblage composition and relative abundances should warrant monitoring, especially if blooms become more intense and prolonged. However, traditional biomonitoring techniques often do not explain these ecological responses because they lack the key ingredient: species interactions within the food web (citation). Thus food web level analysis is mandatory if we are to understand Utah Lake's ecology and manage cyanoHABs.

Results in this report also show that phytoplankton richness was affected by zooplankton abundance and vice versa. This relationship may also be the result of field sampling and lab subsampling error however, if those biases were taken into account there would probably be more noticeable interactions between phytoplankton taxa and zooplankton abundance than reported here. This analysis did not examine direct and indirect interactions between phytoplankton taxa and zooplankton taxa because there were not enough data to adequately address this question and the variability associated with these interactions was great. Thus, any results would have been considered circumstantial. Many Utah Lake phytoplankton and zooplankton samples collected in 2017 are being analyzed using DNA barcoding to determine diet preferences of zooplankton. DNA barcoding and analysis is critical. The additional 2017 combined with 2016 data that will incorporate DNA analysis will provide a robust enough dataset to further investigate relationships between phytoplankton, zooplankton, and chemical and water quality parameters, particularly with one of the most important drivers of phytoplankton assemblages changes, water temperature (Schabhttle et al. 2013).

There has also been an ongoing carp removal program in Utah Lake. Carp are well known to severely affect zooplankton assemblages, which results in cascading effects throughout the entire food web, including cyanoHABs. An obvious effect of carp on zooplankton assemblages is that larger sized zooplankton taxa are removed from the system. Larger sized zooplankton have different feeding strategies than smaller sized zooplankton. This size effect appears to be occurring in Utah Lake where zooplankton have much smaller body sizes in Utah Lake than in Farmington Bay of the Great Salt Lake (Richards unpublished data and personal observation). One major difference in these ecosystems is the near absence of carp in Farmington Bay. It will be important to monitor what food web changes occur in the near future after carp are kept at low biomass levels in Utah Lake. It may be that simply removing carp could reduce cyanoHABs to a

large extent. In addition to the negative effects of carp on zooplankton assemblages, carp and catfish contribute to the turbidity of Utah Lake (obviously, wind is the main contributor to Utah Lake's turbidity). It has recently been established that turbid shallow lakes are unique ecosystems compared to the widely accepted shallow lake models and both phytoplankton and zooplankton assemblages and interactions are strongly affected by turbidity (Somogyi et al. 2017).

Although it has been shown that functional richness and traits can often outperform taxonomic richness in predicting ecosystem functioning (Abonyi et al. 2017), analyses presented in this report relied on phytoplankton taxa richness relationships. Functional richness and traits of Utah Lake's phytoplankton assemblages are presently being compiled for important future analyses.

Additional Next Steps

Network analyses are a promising approach to understanding Utah Lake's foodweb. For example, Gray et al. 2014 suggest that, "links between taxa are almost as important as the taxa themselves and these links can influence biodiversity and ecosystem functioning (Kremen 2005; Thompson et al. 2012) and a system's sensitivity to environmental change (Tylianakis, Tscharntke & Lewis 2007; Gray et al. 2014. Keystone species, for instance, can be identified through a network approach (e.g. Jordan 2009), helping to focus monitoring efforts towards those that are ecologically most significant, since highly connected species often determine network stability and vulnerability to cascading secondary extinctions (e.g. Dunne, Williams & Martinez 2002). A network approach can also help improve efficiency by identifying and tracking those species or interactions that are most sensitive to change; thus, keystone and indicator nodes could help provide novel early warning systems for detecting impending regime shifts or catastrophic ecosystem collapse (Aizen, Sabatino & Tylianakis 2012). Some systems show clear signs in their network structure of impending regime shifts which have consequences for ecosystem functioning (e.g. Rawcliffe et al. 2010), whereas other networks experience significant network rearrangements without affecting some network metrics (Raffaelli & Friedlander 2012)". Network based food web models for Utah Lake have been initiated by OreoHelix Consulting and the WFWQC that will continue to be developed as more data is acquired.

Conclusion

Findings presented in this report provide critical baseline data and information on the diversity, richness, and somewhat tenable resilience of Utah Lake's unique phytoplankton assemblages and their interactions with other portions of the food web. These results build on past analyses by Richards and Miller (2017) and combined with 2017 data and analyses will lead to a solid understanding of these relationships, which is crucial to understanding Utah Lake's ecosystem,

including cyanoHABs, and mandatory for any hope of managing the lake both scientifically and prudently.

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Appendices

Appendix 1. Goodness of fit results for three regression models of number of phytoplankton taxa (dependent) vs. phytoplankton cells mL⁻¹ (log transformed)(independent). The lower the ll, AIC, and BIC values the better the fit.

Regression Model	N	ll (model)	df	AIC	BIC
Linear	118	-492.83	1	987.66	990.56
Truncated Poisson	118	-443.52	1	889.03	891.94
Truncated Negative Binomial	118	-405.22	2	814.45	820.26

Appendix 2. Goodness of fit results for three regression models of number of phytoplankton taxa (dependent) vs. site (independent). The lower the ll, AIC, and BIC values the better the fit.

Regression Model	N	ll	df	AIC	BIC
Linear	118	- 395.48	8	806.96	829.12
Truncated Poisson	118	-724.84	8	1465.69	1487.85
Truncated Negative Binomial	118	-450.44	8	918.88	943.82

Appendix 3. Goodness of fit results for three regression models of number of phytoplankton taxa (dependent) vs. month (independent). The lower the ll, AIC, and BIC values the better the fit.

Regression Model	N	ll (model)	df	AIC	BIC
Linear	117	-381.38	7	776.76	796.10
Truncated Poisson	135	-562.18	7	1138.36	1157.70
Truncated Negative Binomial	135	-440.28	8	896.57	918.66

Appendix 4. Phytoplankton summary stats by sample including richness, evenness, diversity

Percent of cells empty = 90.917

Matrix total = 0.34811E+07

Matrix mean = 0.21108E+03

Variance of totals of Sites = 0.16447E+10

CV of totals of Sites = 154.95%

 S = Richness = number of non-zero elements in row

E = Evenness = $H / \ln(\text{Richness})$

H = Diversity = $-\sum (P_i \cdot \ln(P_i))$ = Shannon's diversity index

D = Simpson's diversity index for infinite population = $1 / \sum (P_i^2)$

where P_i = importance probability in element i (element i
 relativized by row total)

Site Abbreviation	Site Code	Month	Mean	Stand.Dev.	Sum	Min	Max	S	E	H	D'
PB615	5	June	1933.048	17035.184	239698.0000	0.000	189000.000	24	0.305	0.968	0.3707
LM216	3	Feb	59.613	528.529	7392.0000	0.000	5852.000	11	0.376	0.902	0.3631
PM216	7	Feb	6.548	53.807	812.0000	0.000	588.000	7	0.507	0.986	0.4518
LM316	3	March	525.274	3276.603	65134.0000	0.000	35294.000	19	0.593	1.747	0.6807
PM316	7	March	56.476	469.731	7003.0000	0.000	5141.00	9	0.431	0.946	0.4385
ULout316	9	March	446.935	1629.329	55420.0000	0.000	9800.000	21	0.793	2.415	0.8856
MdLk316	6	March	252.048	1877.870	31254.0000	0.000	18744.000	10	0.468	1.077	0.5479
PBc316	5	March	48.565	332.899	6022.0000	0.000	3539.000	10	0.586	1.35	0.6161
PBm316	5	March	105.169	709.649	13041.0000	0.000	7059.000	13	0.536	1.375	0.6277
GBn316	1	March	43.887	191.397	5442.0000	0.000	1500.000	13	0.797	2.045	0.8398
GBs316	1	March	35.863	206.608	4447.0000	0.000	1740.000	16	0.622	1.725	0.7264
LM416	3	April	32.895	242.911	4079.0000	0.000	2660.000	14	0.524	1.383	0.5557

ULSP416	3	April	30.556	157.679	3789.0000	0.000	1582.000	18	0.702	2.029	0.7789
PM416	7	April	34.887	278.118	4326.0000	0.000	2828.00	8	0.418	0.869	0.4836
PLb516	6	April	127.903	687.446	15860.0000	0.000	5600.000	11	0.719	1.725	0.7608
PLa516	6	May	58.387	272.839	7240.0000	0.000	2240.000	11	0.806	1.932	0.8173
PLc516	6	May	539.073	2249.038	66845.0000	0.000	16800.000	25	0.700	2.255	0.8527
LM516	3	May	418.919	1307.279	51946.0000	0.000	8400.000	23	0.855	2.682	0.914
ULout516	9	May	184.895	632.256	22927.0000	0.000	3584.000	22	0.808	2.496	0.8984
PM516	7	May	105.726	502.129	13110.0000	0.000	4550.000	16	0.741	2.053	0.8115
GBn616	1	June	381.081	1545.255	47254.0000	0.000	10808.000	14	0.834	2.202	0.8604
GBs616	1	June	120.919	1143.783	14994.0000	0.000	12600.00	6	0.299	0.535	0.2762
PLb616	6	June	76.532	503.862	9490.0000	0.000	4800.00	8	0.627	1.304	0.6452
PLa616	3	June	131.516	542.687	16308.0000	0.000	4704.000	18	0.780	2.256	0.8557
PLc616	6	June	63.581	518.516	7884.0000	0.000	5600.00	7	0.485	0.945	0.4599
LM616	3	June	191.274	649.802	23718.0000	0.000	4824.000	21	0.848	2.581	0.8996
PM616	7	June	89.823	371.087	11138.0000	0.000	3280.000	19	0.792	2.333	0.8554
ULout616	9	June	101.548	425.708	12592.0000	0.000	3360.000	20	0.745	2.233	0.8514
GBn616b	1	June	154.806	1277.458	19196.0000	0.000	13876.00	9	0.427	0.939	0.4472
PBe616	5	June	245.871	999.655	30488.0000	0.000	6600.000	22	0.730	2.256	0.8597
PBm616	5	June	92.815	331.997	11509.0000	0.000	2200.000	18	0.835	2.413	0.8896
PBw616	5	June	1806.347	6411.909	223987.0000	0.000	56200.000	48	0.698	2.702	0.8911
LMa716	2	July	161.210	1795.155	19990.0000	0.000	19990.00	1	0.000	0	0
LMb716	3	July	434.194	4834.975	53840.0000	0.000	53840.00	1	0.000	0	0
LMc716	3	July	0.492	5.478	61.0000	0.000	61.000	1	0.000	0	0
LMd716	3	July	39.081	417.810	4846.0000	0.000	4650.00	2	0.244	0.169	0.0776
ULout716	9	July	1.573	17.512	195.0000	0.000	195.000	1	0.000	0	0
PBm716a	5	July	83.121	331.644	10307.0000	0.000	2240.000	23	0.735	2.306	0.8646
LBa717	3	July	848.242	5455.063	105182.0000	0.000	56200.000	16	0.529	1.468	0.6611
GBm716	1	July	206.387	634.211	25592.0000	0.000	2900.000	24	0.838	2.664	0.9164

PBm716b	5	July	354.097	1572.035	43908.0000	0.000	11564.000	19	0.704	2.074	0.8343
SB616	8	July	416.871	2030.843	51692.0000	0.000	15000.000	15	0.672	1.82	0.8021
GBNs716	1	July	26.073	184.146	3233.0000	0.000	2000.000	20	0.498	1.492	0.5929
LM716	3	July	50.290	191.519	6236.0000	0.000	1280.000	18	0.780	2.254	0.8759
SB716	8	July	318.968	2380.121	39552.0000	0.000	26152.000	16	0.492	1.364	0.5465
PLb816a	6	Aug	32.968	221.799	4088.0000	0.000	1736.00	5	0.684	1.101	0.6299
PLa816a	6	Aug	9.540	47.776	1183.0000	0.000	390.000	9	0.790	1.735	0.7913
PLc816a	6	Aug	24.016	217.436	2978.0000	0.000	2400.00	6	0.391	0.7	0.3362
LM816	3	Aug	4.145	29.117	514.0000	0.000	310.000	10	0.593	1.366	0.5972
PBm816	5	Aug	279.081	1822.220	34606.0000	0.000	19152.000	14	0.568	1.499	0.6509
PBc816	5	Aug	249.411	2323.215	30927.0000	0.000	25830.000	13	0.299	0.766	0.2979
PM816	7	Aug	1016.484	6757.843	126044.0000	0.000	69900.000	22	0.468	1.446	0.6384
PLb816b	6	Aug	25.008	156.296	3101.0000	0.000	1600.000	11	0.632	1.515	0.6795
PLa816b	6	Aug	111.823	763.981	13866.0000	0.000	6160.00	9	0.544	1.196	0.6185
PLc816b	6	Aug	30.629	240.518	3798.0000	0.000	2550.00	5	0.564	0.907	0.4987
GB816	1	Aug	318.758	1775.374	39526.0000	0.000	16800.000	19	0.590	1.738	0.7438
LMS816	3	Aug	52.871	371.611	6556.0000	0.000	3780.000	17	0.455	1.29	0.5967
PBc816b	5	Aug	608.798	3820.437	75491.0000	0.000	29600.000	13	0.497	1.274	0.6769
AmF816	3	Aug	90.565	765.186	11230.0000	0.000	8450.000	10	0.430	0.991	0.4209
LB816	3	Aug	499.710	4351.166	61964.0000	0.000	48160.000	12	0.369	0.917	0.3854
LM816b	3	Aug	727.726	7470.247	90238.0000	0.000	83160.000	15	0.151	0.409	0.149
SB816	8	Aug	111.258	738.431	13796.0000	0.000	6048.00	7	0.602	1.172	0.6395
ULSP816	3	Aug	43.129	358.849	5348.0000	0.000	3892.00	5	0.533	0.858	0.4381
PLb816c	6	Aug	28.194	258.680	3496.0000	0.000	2856.00	6	0.385	0.689	0.3185
PLa816c	6	Aug	3.032	22.053	376.0000	0.000	224.000	4	0.753	1.044	0.5688
PLc816c	6	Aug	253.871	2783.717	31480.0000	0.000	31000.00	4	0.065	0.09	0.0301
PBc816e	5	Aug	30.952	290.041	3838.0000	0.000	3190.00	3	0.488	0.536	0.2895
GBn816c	1	Aug	337.710	1623.990	41876.0000	0.000	11872.000	13	0.730	1.871	0.8069

LM816c	3	Aug	96.032	919.979	11908.0000	0.000	10190.00	7	0.293	0.57	0.2578
PM816c	3	Aug	261.371	2503.935	32410.0000	0.000	27664.00	7	0.267	0.519	0.2578
PLb816d	6	Aug	9.524	95.482	1181.0000	0.000	1057.00	2	0.485	0.336	0.1879
PLc816d	6	Aug	9.202	99.607	1141.0000	0.000	1109.00	3	0.120	0.132	0.0546
GBn816e	1	Aug	269.863	1756.728	33463.0000	0.000	16630.000	13	0.497	1.276	0.6529
LH816e	3	Aug	349.371	2603.058	43322.0000	0.000	23545.000	10	0.422	0.971	0.5479
LM816d	3	Aug	80.105	782.554	9933.0000	0.000	8680.00	6	0.283	0.507	0.2285
PM816d	3	Aug	3.790	33.716	470.0000	0.000	372.000	4	0.534	0.741	0.359
PBc816d	5	Aug	823.831	8481.504	102155.0000	0.000	94245.00	9	0.143	0.313	0.1441
PLa816d	6	Aug	295.782	3232.744	36677.0000	0.000	36000.00	3	0.094	0.103	0.0364
PLb916a	6	Sept	376.306	3419.369	46662.0000	0.000	37640.00	7	0.341	0.663	0.3314
PLa916a	6	Sept	188.694	1277.178	23398.0000	0.000	11757.00	5	0.677	1.09	0.6255
LM916a	3	Sept	40.597	226.892	5034.0000	0.000	2290.000	15	0.643	1.742	0.7421
PLc916a	6	Sept	363.540	3592.256	45079.0000	0.000	39900.00	7	0.249	0.485	0.2109
GBn916a	1	Sept	0.565	3.895	70.0000	0.000	40.000	5	0.742	1.194	0.611
PBm916a	5	Sept	239.976	2233.674	29757.0000	0.000	24500.000	13	0.228	0.586	0.2989
PBn916a	5	Sept	34.774	282.423	4312.0000	0.000	2803.00	5	0.446	0.719	0.4643
PM916a	7	Sept	29.065	254.569	3604.0000	0.000	2741.00	3	0.590	0.649	0.3782
PBc916a	5	Sept	1247.250	10688.709	154659.0000	0.000	113000.000	10	0.302	0.696	0.4044
GBn916b	1	Sept	401.403	2499.995	49774.0000	0.000	24600.000	11	0.613	1.469	0.6816
LB916b	3	Sept	508.073	2064.882	63001.0000	0.000	16500.000	24	0.726	2.309	0.8598
LMs916b	3	Sept	1726.677	9715.735	214108.0000	0.000	98500.000	21	0.578	1.761	0.7387
PA916b	3	Sept	276.306	1198.115	34262.0000	0.000	8320.000	17	0.713	2.02	0.8415
SB916b	3	Sept	322.895	2870.690	40039.0000	0.000	31400.000	13	0.292	0.75	0.3597
GBns916c	1	Sept	249.565	2362.184	30946.0000	0.000	26000.00	9	0.238	0.522	0.2753
LBn916c	3	Sept	12.218	76.886	1515.0000	0.000	712.000	8	0.645	1.341	0.6751
LM916c	3	Sept	102.919	981.469	12762.0000	0.000	10900.000	13	0.245	0.63	0.2645
PA916c	4	Sept	6.266	44.441	777.0000	0.000	355.000	9	0.500	1.099	0.5896

SB916c	8	Sept	38.935	251.707	4828.0000	0.000	2500.000	10	0.580	1.335	0.6576
GBns916d	1	Sept	73.290	680.268	9088.0000	0.000	7420.00	8	0.252	0.524	0.3028
LB916d	3	Sept	242.323	2532.052	30048.0000	0.000	28200.000	12	0.138	0.343	0.1185
PA916d	4	Sept	22.677	151.632	2812.0000	0.000	1592.000	14	0.544	1.435	0.6343
SB916d	3	Sept	14.823	161.627	1838.0000	0.000	1800.00	5	0.079	0.127	0.0408
GBn1016a	1	Oct	526.516	3855.265	65288.0000	0.000	35000.000	19	0.350	1.031	0.563
LB1016a	3	Oct	86.290	626.845	10700.0000	0.000	6625.000	11	0.485	1.163	0.5698
SB1016a	8	Oct	39.871	256.201	4944.0000	0.000	2100.000	10	0.528	1.215	0.6616
PLb1016a	6	Oct	33.153	159.697	4111.0000	0.000	1014.00	8	0.824	1.713	0.8063
PLa1016a	6	Oct	16.242	110.581	2014.0000	0.000	1120.00	9	0.577	1.268	0.6211
PLc1016a	6	Oct	37.992	327.854	4711.0000	0.000	3570.00	5	0.467	0.751	0.3962
LM1016a	3	Oct	105.460	1010.835	13077.0000	0.000	11200.00	8	0.260	0.541	0.257
PM1016a	7	Oct	271.581	2873.812	33676.0000	0.000	32000.000	11	0.111	0.267	0.0962
PBc1016a	5	Oct	83.427	717.551	10345.0000	0.000	7900.000	11	0.362	0.869	0.4002
PBm1016a	5	Oct	25.653	167.571	3181.0000	0.000	1750.000	14	0.561	1.481	0.6506
GBn1016b	1	Oct	28.290	148.804	3508.0000	0.000	1243.000	10	0.708	1.63	0.7706
SB1016b	8	Oct	423.177	4606.304	52474.0000	0.000	51300.000	13	0.056	0.143	0.0441
PLb1016b	6	Oct	11.960	104.101	1483.0000	0.000	1100.00	3	0.544	0.597	0.3859
PLa1016b	6	Oct	67.476	396.214	8367.0000	0.000	3600.000	12	0.644	1.601	0.7161
PLc1016b	6	Oct	141.194	1482.111	17508.0000	0.000	16500.00	6	0.156	0.28	0.1105
LM1016b	3	Oct	3.065	18.838	380.0000	0.000	143.000	6	0.708	1.268	0.6897
PM1016b	7	Oct	132.798	1126.847	16467.0000	0.000	12200.00	5	0.468	0.753	0.416
PBc1016b	5	Oct	27.306	273.160	3386.0000	0.000	3036.00	8	0.216	0.449	0.1914
GBns1116a	1	Nov	49.097	338.434	6088.0000	0.000	3640.000	11	0.574	1.377	0.6118
LB1116a	3	Nov	55.726	322.166	6910.0000	0.000	2200.000	14	0.543	1.434	0.7246
SB1116a	8	Nov	12.387	90.900	1536.0000	0.000	900.000	7	0.524	1.019	0.5612
PLb1116a	6	Nov	36.548	292.038	4532.0000	0.000	3190.00	8	0.499	1.037	0.4812
PLa1116a	6	Nov	23.960	141.434	2971.0000	0.000	1160.000	10	0.619	1.424	0.7132

PLc1116a	3	Nov	19.000	137.396	2356.0000	0.000	1430.00	8	0.547	1.137	0.5736
LM1116a	3	Nov	29.540	271.924	3663.0000	0.000	3000.00	6	0.352	0.63	0.3141
PM1116a	7	Nov	111.008	996.984	13765.0000	0.000	11000.00	9	0.348	0.764	0.3467
PBe1116a	5	Nov	46.694	345.886	5790.0000	0.000	3540.00	9	0.483	1.061	0.553
PBm1116a	5	Nov	22.492	157.447	2789.0000	0.000	1500.00	8	0.557	1.158	0.5999
GBns1216	1	Dec	506.766	4184.039	62839.0000	0.000	43000.00	5	0.453	0.729	0.4466
LBs1216	3	Dec	4.952	22.932	614.0000	0.000	126.000	7	0.915	1.78	0.8204
LMs1216	3	Dec	26.774	188.183	3320.0000	0.000	1800.00	9	0.487	1.07	0.5968
SB1216	8	Dec	16.121	97.859	1999.0000	0.000	800.000	10	0.591	1.361	0.6972
AVERAGES:			211.1	1491.	0.2617E+05	0	0.1513E+05	11.3	0.500	1.191	0.5294

Appendix 5. Pairwise comparisons of adjusted predictions of phytoplankton taxa richness by site. VCE =robust; linear prediction

Sites	Contrast	Std.Err.	t	P > t	95% Lower CI	95% Upper CI
LM vs LB	-0.190	2.436	-0.080	0.938	-5.018	4.637
PA vs LB	-0.524	2.708	-0.190	0.847	-5.891	4.843
PB vs LB	-0.752	2.300	-0.330	0.744	-5.311	3.807
P-L vs LB	-5.504	2.036	-2.700	0.008	-9.539	-1.470
PM vs LB	-4.302	2.723	-1.580	0.117	-9.698	1.095
SB vs LB	-3.190	2.236	-1.430	0.156	-7.622	1.241
ULout vs LB	2.143	4.868	0.440	0.661	-7.505	11.791
PA vs LM	-0.333	2.528	-0.130	0.895	-5.344	4.678
PB vs LM	-0.561	2.086	-0.270	0.788	-4.696	3.573
P-L vs LM	-5.314	1.790	-2.970	0.004	-8.861	-1.766
PM vs LM	-4.111	2.545	-1.620	0.109	-9.154	0.932
SB vs LM	-3.000	2.015	-1.490	0.139	-6.994	0.994
ULout vs LM	2.333	4.770	0.490	0.626	-7.121	11.788
PB vs PA	-0.228	2.398	-0.100	0.924	-4.981	4.525
P-L vs PA	-4.980	2.146	-2.320	0.022	-9.233	-0.728
PM vs PA	-3.778	2.806	-1.350	0.181	-9.339	1.784
SB vs PA	-2.667	2.337	-1.140	0.256	-7.298	1.964
ULout vs PA	2.667	4.915	0.540	0.589	-7.075	12.408
P-L vs PB	-4.752	1.601	-2.970	0.004	-7.925	-1.580
PM vs PB	-3.550	2.415	-1.470	0.145	-8.337	1.237
SB vs PB	-2.439	1.849	-1.320	0.190	-6.103	1.226
ULout vs PB	2.895	4.703	0.620	0.539	-6.426	12.215
PM vs P-L	1.203	2.165	0.560	0.580	-3.088	5.493
SB vs P-L	2.314	1.507	1.540	0.128	-0.673	5.301
ULout vs P-L	7.647	4.579	1.670	0.098	-1.428	16.723
SB vs PM	1.111	2.354	0.470	0.638	-3.555	5.777
ULout vs PM	6.444	4.923	1.310	0.193	-3.313	16.202
ULout vs SB	5.333	4.672	1.140	0.256	-3.926	14.592

Appendix 6. Pairwise comparisons of adjusted predictions for phytoplankton taxa richness by month. VCE =robust; linear prediction.

Sites	Contrast	Std.Err.	t	P > t	95% Lower CI	95% Upper CI
May vs April	8.400	2.391	3.510	0.001	3.660	13.140
June vs April	4.500	1.838	2.450	0.016	0.858	8.142
July vs April	5.889	2.187	2.690	0.008	1.555	10.223
Aug vs April	-1.935	0.931	-2.080	0.040	-3.781	-0.090
Sept vs April	-0.391	1.110	-0.350	0.725	-2.592	1.809
Oct vs April	-1.611	0.911	-1.770	0.080	-3.416	0.194
Nov vs April	-2.000	0.703	-2.850	0.005	-3.393	-0.607
June vs May	-3.900	3.016	-1.290	0.199	-9.877	2.077
July vs May	-2.511	3.241	-0.770	0.440	-8.934	3.912
Aug vs May	-10.335	2.566	-4.030	0.000	-15.422	-5.249
Sept vs May	-8.791	2.637	-3.330	0.001	-14.017	-3.566
Oct vs May	-10.011	2.559	-3.910	0.000	-15.083	-4.939
Nov vs May	-10.400	2.493	-4.170	0.000	-15.340	-5.460
July vs June	1.389	2.856	0.490	0.628	-4.272	7.050
Aug vs June	-6.435	2.060	-3.120	0.002	-10.518	-2.353
Sept vs June	-4.891	2.147	-2.280	0.025	-9.146	-0.636
Oct vs June	-6.111	2.051	-2.980	0.004	-10.176	-2.046
Nov vs June	-6.500	1.967	-3.300	0.001	-10.399	-2.601
Aug vs July	-7.824	2.377	-3.290	0.001	-12.535	-3.114
Sept vs July	-6.280	2.453	-2.560	0.012	-11.141	-1.419
Oct vs July	-7.500	2.369	-3.170	0.002	-12.195	-2.805
Nov vs July	-7.889	2.297	-3.430	0.001	-12.441	-3.336
Sept vs Aug	1.544	1.449	1.070	0.289	-1.327	4.416
Oct vs Aug	0.324	1.302	0.250	0.804	-2.257	2.905
Nov vs Aug	-0.065	1.166	-0.060	0.956	-2.376	2.247
Oct vs Sept	-1.220	1.436	-0.850	0.397	-4.066	1.626
Nov vs Sept	-1.609	1.314	-1.220	0.223	-4.213	0.995
Nov vs Oct	-0.389	1.150	-0.340	0.736	-2.669	1.891

Appendix 7. Pairwise comparisons of adjusted predictions for phytoplankton abundance by month. VCE =robust; linear prediction

	Contrast	Std. Err.	t	P > t	95% CIs	
April vs March	0.12	0.37	0.33	0.74	-0.62	0.87
May vs March	0.53	0.54	0.98	0.33	-0.54	1.59
June vs March	0.36	0.46	0.79	0.43	-0.55	1.28
July vs March	-0.09	0.73	-0.12	0.91	-1.54	1.37
Aug vs March	-0.36	0.49	-0.73	0.47	-1.32	0.61
Sept vs March	-0.18	0.55	-0.33	0.74	-1.26	0.90
Oct vs March	-0.69	0.49	-1.43	0.16	-1.66	0.27
Nov vs March	-1.21	0.42	-2.86	0.01	-2.05	-0.37
May vs April	0.40	0.39	1.04	0.30	-0.36	1.17
June vs April	0.24	0.27	0.91	0.37	-0.29	0.77
July vs April	-0.21	0.63	-0.33	0.74	-1.46	1.04
Aug vs April	-0.48	0.31	-1.54	0.13	-1.10	0.14
Sept vs April	-0.31	0.40	-0.77	0.44	-1.09	0.48
Oct vs April	-0.82	0.31	-2.65	0.01	-1.43	-0.21
Nov vs April	-1.33	0.20	-6.78	0.00	-1.72	-0.94
June vs May	-0.16	0.47	-0.34	0.73	-1.09	0.77
July vs May	-0.61	0.74	-0.83	0.41	-2.08	0.85
Aug vs May	-0.88	0.50	-1.78	0.08	-1.87	0.10
Sept vs May	-0.71	0.55	-1.28	0.20	-1.81	0.39
Oct vs May	-1.22	0.49	-2.47	0.02	-2.20	-0.24
Nov vs May	-1.73	0.43	-4.00	0.00	-2.59	-0.88
July vs June	-0.45	0.68	-0.66	0.51	-1.81	0.91
Aug vs June	-0.72	0.41	-1.76	0.08	-1.54	0.09
Sept vs June	-0.55	0.48	-1.14	0.26	-1.50	0.40
Oct vs June	-1.06	0.41	-2.59	0.01	-1.87	-0.25
Nov vs June	-1.57	0.33	-4.74	0.00	-2.23	-0.92
Aug vs July	-0.27	0.70	-0.39	0.70	-1.66	1.12
Sept vs July	-0.10	0.74	-0.13	0.90	-1.57	1.38
Oct vs July	-0.61	0.70	-0.87	0.39	-2.00	0.78
Nov vs July	-1.12	0.66	-1.70	0.09	-2.43	0.18
Sept vs Aug	0.17	0.50	0.35	0.73	-0.83	1.18
Oct vs Aug	-0.34	0.44	-0.77	0.44	-1.21	0.53
Nov vs Aug	-0.85	0.37	-2.31	0.02	-1.58	-0.12
Oct vs Sept	-0.51	0.50	-1.02	0.31	-1.51	0.48
Nov vs Sept	-1.03	0.44	-2.32	0.02	-1.90	-0.15
Nov vs Oct	-0.51	0.37	-1.41	0.16	-1.24	0.21

Appendix 8. Pairwise comparisons of adjusted predictions for zooplankton abundance by month. VCE = robust; truncated negative binomial prediction.

Pairwise comparisons of adjusted predictions

Model VCE : **Robust**

Expression : **Predicted number of events, predict()**

monthcode	Delta-method		Unadjusted		Unadjusted	
	Contrast	Std. Err.	z	P> z	[95% Conf. Interval]	
April vs March	2.8909	11.9941	0.24	0.81	-20.6172	26.3989
May vs March	8.9589	15.3777	0.58	0.56	-21.1808	39.0987
June vs March	38.0633	26.8767	1.42	0.16	-14.6141	90.7406
July vs March	102.2394	58.3082	1.75	0.08	-12.0426	216.5213
Aug vs March	106.0825	32.7334	3.24	0.00	41.9262	170.2387
Sept vs March	12.7865	16.5004	0.77	0.44	-19.5538	45.1268
Oct vs March	73.1965	66.7146	1.10	0.27	-57.5617	203.9546
Nov vs March	-13.3809	12.9421	-1.03	0.30	-38.7470	11.9852
May vs April	6.0680	9.6263	0.63	0.53	-12.7992	24.9353
June vs April	35.1724	24.0516	1.46	0.14	-11.9678	82.3126
July vs April	99.3485	57.0623	1.74	0.08	-12.4916	211.1886
Aug vs April	103.1916	30.4723	3.39	0.00	43.4669	162.9162
Sept vs April	9.8956	11.3408	0.87	0.38	-12.3320	32.1233
Oct vs April	70.3056	65.6541	1.07	0.28	-58.3740	198.9852
Nov vs April	-16.2718	4.8460	-3.36	0.00	-25.7697	-6.7738
June vs May	29.1044	25.8953	1.12	0.26	-21.6495	79.8582
July vs May	93.2805	57.8601	1.61	0.11	-20.1233	206.6843
Aug vs May	97.1235	31.9661	3.04	0.00	34.4711	159.7760
Sept vs May	3.8276	14.8835	0.26	0.80	-25.3435	32.9987
Oct vs May	64.2375	66.4004	0.97	0.33	-65.9049	194.3800
Nov vs May	-22.3398	10.7795	-2.07	0.04	-43.4672	-1.2124
July vs June	64.1761	61.8369	1.04	0.30	-57.0219	185.3741
Aug vs June	68.0192	38.7802	1.75	0.08	-7.9887	144.0270
Sept vs June	-25.2768	26.5974	-0.95	0.34	-77.4067	26.8531
Oct vs June	35.1332	70.0962	0.50	0.62	-102.2528	172.5191
Nov vs June	-51.4442	24.5750	-2.09	0.04	-99.6103	-3.2781
Aug vs July	3.8431	64.6636	0.06	0.95	-122.8952	130.5814
Sept vs July	-89.4529	58.1892	-1.54	0.12	-203.5017	24.5959
Oct vs July	-29.0429	87.3212	-0.33	0.74	-200.1892	142.1034
Nov vs July	-115.6203	57.2972	-2.02	0.04	-227.9207	-3.3198
Sept vs Aug	-93.2960	32.5736	-2.86	0.00	-157.1390	-29.4529
Oct vs Aug	-32.8860	72.8902	-0.45	0.65	-175.7482	109.9762
Nov vs Aug	-119.4634	30.8265	-3.88	0.00	-179.8822	-59.0445
Oct vs Sept	60.4100	66.7130	0.91	0.37	-70.3450	191.1650
Nov vs Sept	-26.1674	12.3026	-2.13	0.03	-50.2800	-2.0548
Nov vs Oct	-86.5774	65.6878	-1.32	0.19	-215.3231	42.1684

Appendix 9. Pairwise comparisons of adjusted predictions for zooplankton abundance by sites. VCE =robust; truncated negative binomial prediction.

Pairwise comparisons of adjusted predictions

Model VCE : **Robust**

Expression : **Predicted number of events, predict()**

	Delta-method		Unadjusted		Unadjusted	
	Contrast	Std. Err.	z	P> z	[95% Conf. Interval]	
sitecodelocation						
LB vs GB	139.93	127.24	1.10	0.27	-109.46	389.33
LM vs GB	10.08	39.03	0.26	0.80	-66.41	86.58
PA vs GB	-52.25	30.53	-1.71	0.09	-112.10	7.59
PB vs GB	-70.36	26.35	-2.67	0.01	-122.01	-18.71
P-L vs GB	-21.82	27.43	-0.80	0.43	-75.58	31.94
PM vs GB	4.72	37.64	0.13	0.90	-69.06	78.51
SB vs GB	107.01	129.12	0.83	0.41	-146.07	360.08
ULout vs GB	-53.33	29.47	-1.81	0.07	-111.08	4.42
LM vs LB	-129.85	128.02	-1.01	0.31	-380.77	121.06
PA vs LB	-192.19	125.71	-1.53	0.13	-438.58	54.20
PB vs LB	-210.29	124.77	-1.69	0.09	-454.84	34.25
P-L vs LB	-161.75	124.99	-1.29	0.20	-406.73	83.22
PM vs LB	-135.21	127.60	-1.06	0.29	-385.31	114.88
SB vs LB	-32.93	177.68	-0.19	0.85	-381.17	315.31
ULout vs LB	-193.26	125.46	-1.54	0.12	-439.15	52.63
PA vs LM	-62.34	33.71	-1.85	0.06	-128.40	3.73
PB vs LM	-80.44	30.00	-2.68	0.01	-139.24	-21.65
P-L vs LM	-31.90	30.90	-1.03	0.30	-92.47	28.66
PM vs LM	-5.36	40.23	-0.13	0.89	-84.21	73.49
SB vs LM	96.92	129.90	0.75	0.46	-157.68	351.52
ULout vs LM	-63.41	32.74	-1.94	0.05	-127.59	0.77
PB vs PA	-18.11	17.41	-1.04	0.30	-52.23	16.02
P-L vs PA	30.44	19.04	1.60	0.11	-6.89	67.76
PM vs PA	56.98	32.10	1.77	0.08	-5.94	119.90
SB vs PA	159.26	127.53	1.25	0.21	-90.70	409.22
ULout vs PA	-1.07	21.86	-0.05	0.96	-43.92	41.78
P-L vs PB	48.54	11.16	4.35	0.00	26.67	70.41
PM vs PB	75.08	28.19	2.66	0.01	19.84	130.32
SB vs PB	177.37	126.56	1.40	0.16	-70.68	425.41
ULout vs PB	17.03	15.47	1.10	0.27	-13.29	47.35
PM vs P-L	26.54	29.14	0.91	0.36	-30.56	83.65
SB vs P-L	128.82	126.87	1.02	0.31	-119.84	377.49
ULout vs P-L	-31.51	17.28	-1.82	0.07	-65.38	2.36
SB vs PM	102.28	129.48	0.79	0.43	-151.50	356.06
ULout vs PM	-58.05	31.09	-1.87	0.06	-118.99	2.88
ULout vs SB	-160.33	127.28	-1.26	0.21	-409.79	89.12

Appendix 10. Pairwise comparisons of adjusted predictions for phytoplankton evenness by site. VCE =robust; fractional probit prediction

SiteCode	Delta-method		Unadjusted	
	Contrast	Std. Err.	[95% Conf. Interval]	
LB vs GB	-0.07	0.08	-0.23	0.09
LM vs GB	-0.06	0.08	-0.20	0.09
P-L vs GB	-0.05	0.06	-0.17	0.07
PA vs GB	0.02	0.07	-0.12	0.16
PB vs GB	-0.08	0.06	-0.20	0.05
PL vs GB	0.22	0.05	0.13	0.32
PM vs GB	-0.13	0.07	-0.27	0.02
SB vs GB	-0.14	0.09	-0.31	0.03
ULout vs GB	0.02	0.18	-0.32	0.37
LM vs LB	0.02	0.09	-0.16	0.19
P-L vs LB	0.02	0.08	-0.13	0.17
PA vs LB	0.09	0.09	-0.08	0.26
PB vs LB	-0.00	0.08	-0.16	0.15
PL vs LB	0.30	0.07	0.16	0.43
PM vs LB	-0.05	0.09	-0.23	0.12
SB vs LB	-0.07	0.10	-0.26	0.12
ULout vs LB	0.09	0.18	-0.27	0.45
P-L vs LM	0.01	0.07	-0.13	0.14
PA vs LM	0.07	0.08	-0.08	0.23
PB vs LM	-0.02	0.07	-0.16	0.12
PL vs LM	0.28	0.06	0.17	0.40
PM vs LM	-0.07	0.08	-0.23	0.09
SB vs LM	-0.08	0.09	-0.27	0.10
ULout vs LM	0.08	0.18	-0.28	0.43
PA vs P-L	0.07	0.06	-0.06	0.19
PB vs P-L	-0.02	0.06	-0.14	0.09
PL vs P-L	0.28	0.04	0.20	0.35
PM vs P-L	-0.07	0.07	-0.21	0.06
SB vs P-L	-0.09	0.08	-0.25	0.07
ULout vs P-L	0.07	0.17	-0.27	0.41
PB vs PA	-0.09	0.07	-0.23	0.04
PL vs PA	0.21	0.05	0.10	0.31
PM vs PA	-0.14	0.08	-0.30	0.01
SB vs PA	-0.16	0.09	-0.33	0.02
ULout vs PA	0.00	0.18	-0.35	0.35
PL vs PB	0.30	0.04	0.22	0.38
PM vs PB	-0.05	0.07	-0.19	0.09
SB vs PB	-0.07	0.08	-0.23	0.10
ULout vs PB	0.10	0.18	-0.25	0.44
PM vs PL	-0.35	0.06	-0.46	-0.24
SB vs PL	-0.37	0.07	-0.51	-0.23
ULout vs PL	-0.20	0.17	-0.54	0.13
SB vs PM	-0.02	0.09	-0.20	0.16
ULout vs PM	0.15	0.18	-0.21	0.50
ULout vs SB	0.16	0.19	-0.20	0.53

Appendix 11. Pairwise comparisons of adjusted predictions for phytoplankton evenness by month. VCE =robust; fractional probit prediction

monthcode	Delta-method		Unadjusted	
	Contrast	Std. Err.	[95% Conf. Interval]	
April vs March	0.12	0.04	0.03	0.20
May vs March	0.18	0.05	0.08	0.28
June vs March	0.04	0.07	-0.10	0.18
July vs March	-0.02	0.09	-0.20	0.16
Aug vs March	-0.16	0.06	-0.27	-0.05
Sept vs March	-0.15	0.06	-0.27	-0.03
Oct vs March	-0.16	0.07	-0.29	-0.03
Nov vs March	-0.10	0.05	-0.20	0.00
May vs April	0.06	0.03	0.01	0.11
June vs April	-0.08	0.06	-0.19	0.04
July vs April	-0.14	0.08	-0.29	0.02
Aug vs April	-0.28	0.04	-0.34	-0.21
Sept vs April	-0.27	0.04	-0.35	-0.19
Oct vs April	-0.27	0.05	-0.37	-0.17
Nov vs April	-0.22	0.03	-0.27	-0.16
June vs May	-0.14	0.06	-0.26	-0.02
July vs May	-0.20	0.08	-0.36	-0.04
Aug vs May	-0.34	0.04	-0.43	-0.26
Sept vs May	-0.33	0.05	-0.43	-0.24
Oct vs May	-0.34	0.06	-0.45	-0.23
Nov vs May	-0.28	0.04	-0.35	-0.21
July vs June	-0.06	0.10	-0.25	0.13
Aug vs June	-0.20	0.07	-0.33	-0.07
Sept vs June	-0.19	0.07	-0.33	-0.05
Oct vs June	-0.20	0.08	-0.35	-0.05
Nov vs June	-0.14	0.06	-0.26	-0.02
Aug vs July	-0.14	0.09	-0.31	0.03
Sept vs July	-0.13	0.09	-0.31	0.04
Oct vs July	-0.14	0.09	-0.32	0.05
Nov vs July	-0.08	0.08	-0.24	0.09
Sept vs Aug	0.01	0.06	-0.10	0.12
Oct vs Aug	0.00	0.06	-0.12	0.12
Nov vs Aug	0.06	0.04	-0.03	0.15
Oct vs Sept	-0.00	0.07	-0.13	0.13
Nov vs Sept	0.05	0.05	-0.05	0.15
Nov vs Oct	0.06	0.06	-0.05	0.17

Appendix 12. Pairwise comparisons of adjusted predictions for phytoplankton diversity by site. VCE =robust; linear regression prediction

SiteCode	Delta-method		Unadjusted		Unadjusted	
	Contrast	Std. Err.	t	P> t	[95% Conf. Interval]	
LB vs GB	-0.14	0.26	-0.55	0.59	-0.67	0.38
LM vs GB	-0.09	0.25	-0.37	0.71	-0.59	0.40
P-L vs GB	-0.37	0.18	-2.04	0.04	-0.73	-0.01
PA vs GB	0.09	0.27	0.34	0.73	-0.45	0.64
PB vs GB	-0.19	0.21	-0.90	0.37	-0.61	0.23
PL vs GB	0.90	0.15	6.08	0.00	0.61	1.20
PM vs GB	-0.52	0.23	-2.26	0.03	-0.98	-0.06
SB vs GB	-0.43	0.24	-1.81	0.07	-0.90	0.04
ULout vs GB	0.36	0.56	0.64	0.52	-0.75	1.48
LM vs LB	0.05	0.30	0.17	0.87	-0.54	0.64
P-L vs LB	-0.23	0.24	-0.93	0.35	-0.71	0.25
PA vs LB	0.24	0.32	0.75	0.45	-0.39	0.87
PB vs LB	-0.05	0.27	-0.17	0.86	-0.57	0.48
PL vs LB	1.05	0.22	4.79	0.00	0.61	1.48
PM vs LB	-0.38	0.28	-1.34	0.18	-0.93	0.18
SB vs LB	-0.29	0.29	-1.00	0.32	-0.86	0.28
ULout vs LB	0.51	0.58	0.87	0.39	-0.65	1.66
P-L vs LM	-0.28	0.23	-1.22	0.23	-0.73	0.17
PA vs LM	0.19	0.31	0.61	0.54	-0.42	0.79
PB vs LM	-0.10	0.25	-0.38	0.70	-0.60	0.40
PL vs LM	1.00	0.20	4.92	0.00	0.60	1.40
PM vs LM	-0.43	0.27	-1.59	0.11	-0.96	0.11
SB vs LM	-0.34	0.28	-1.23	0.22	-0.88	0.21
ULout vs LM	0.46	0.58	0.79	0.43	-0.69	1.60
PA vs P-L	0.47	0.25	1.85	0.07	-0.03	0.96
PB vs P-L	0.18	0.18	0.98	0.33	-0.18	0.54
PL vs P-L	1.28	0.10	12.24	0.00	1.07	1.48
PM vs P-L	-0.15	0.20	-0.73	0.46	-0.56	0.26
SB vs P-L	-0.06	0.21	-0.28	0.78	-0.48	0.36
ULout vs P-L	0.73	0.55	1.33	0.19	-0.36	1.83
PB vs PA	-0.28	0.27	-1.04	0.30	-0.83	0.26
PL vs PA	0.81	0.23	3.53	0.00	0.36	1.26
PM vs PA	-0.62	0.29	-2.13	0.04	-1.19	-0.04
SB vs PA	-0.53	0.30	-1.78	0.08	-1.11	0.06
ULout vs PA	0.27	0.59	0.45	0.65	-0.90	1.43
PL vs PB	1.09	0.15	7.24	0.00	0.80	1.39
PM vs PB	-0.33	0.23	-1.43	0.16	-0.79	0.13
SB vs PB	-0.24	0.24	-1.01	0.32	-0.72	0.23
ULout vs PB	0.55	0.56	0.98	0.33	-0.56	1.67
PM vs PL	-1.43	0.18	-8.09	0.00	-1.77	-1.08
SB vs PL	-1.34	0.19	-7.19	0.00	-1.70	-0.97
ULout vs PL	-0.54	0.54	-1.00	0.32	-1.62	0.53
SB vs PM	0.09	0.26	0.35	0.73	-0.42	0.60
ULout vs PM	0.88	0.57	1.55	0.12	-0.25	2.01
ULout vs SB	0.79	0.57	1.38	0.17	-0.34	1.93

Appendix 13. Pairwise comparisons of adjusted predictions for phytoplankton diversity by month. VCE =robust; linear regression prediction

monthcode	Delta-method		Unadjusted		Unadjusted	
	Contrast	Std. Err.	t	P> t	[95% Conf. Interval]	
April vs March	0.14	0.17	0.83	0.41	-0.20	0.48
May vs March	0.70	0.21	3.25	0.00	0.27	1.12
June vs March	0.16	0.27	0.58	0.56	-0.38	0.70
July vs March	0.13	0.31	0.41	0.68	-0.48	0.73
Aug vs March	-0.66	0.19	-3.40	0.00	-1.05	-0.28
Sept vs March	-0.57	0.21	-2.71	0.01	-0.98	-0.15
Oct vs March	-0.64	0.21	-3.09	0.00	-1.06	-0.23
Nov vs March	-0.48	0.19	-2.55	0.01	-0.86	-0.11
May vs April	0.55	0.13	4.29	0.00	0.30	0.81
June vs April	0.02	0.21	0.08	0.93	-0.40	0.44
July vs April	-0.02	0.25	-0.06	0.95	-0.52	0.49
Aug vs April	-0.80	0.09	-8.60	0.00	-0.99	-0.62
Sept vs April	-0.71	0.12	-5.81	0.00	-0.95	-0.47
Oct vs April	-0.78	0.12	-6.57	0.00	-1.02	-0.55
Nov vs April	-0.63	0.08	-7.50	0.00	-0.79	-0.46
June vs May	-0.54	0.25	-2.16	0.03	-1.03	-0.04
July vs May	-0.57	0.29	-2.00	0.05	-1.14	-0.00
Aug vs May	-1.36	0.16	-8.52	0.00	-1.67	-1.04
Sept vs May	-1.26	0.18	-7.11	0.00	-1.61	-0.91
Oct vs May	-1.34	0.18	-7.61	0.00	-1.69	-0.99
Nov vs May	-1.18	0.15	-7.68	0.00	-1.48	-0.88
July vs June	-0.03	0.33	-0.10	0.92	-0.69	0.62
Aug vs June	-0.82	0.23	-3.53	0.00	-1.28	-0.36
Sept vs June	-0.73	0.24	-2.97	0.00	-1.21	-0.24
Oct vs June	-0.80	0.24	-3.29	0.00	-1.28	-0.32
Nov vs June	-0.64	0.23	-2.82	0.01	-1.10	-0.19
Aug vs July	-0.79	0.27	-2.90	0.00	-1.32	-0.25
Sept vs July	-0.69	0.28	-2.45	0.02	-1.25	-0.13
Oct vs July	-0.77	0.28	-2.73	0.01	-1.33	-0.21
Nov vs July	-0.61	0.27	-2.28	0.02	-1.14	-0.08
Sept vs Aug	0.09	0.15	0.61	0.54	-0.21	0.40
Oct vs Aug	0.02	0.15	0.11	0.91	-0.28	0.32
Nov vs Aug	0.18	0.13	1.40	0.16	-0.07	0.42
Oct vs Sept	-0.08	0.17	-0.45	0.66	-0.41	0.26
Nov vs Sept	0.08	0.15	0.56	0.58	-0.21	0.38
Nov vs Oct	0.16	0.15	1.09	0.28	-0.13	0.45