PLANKTON BIOMASS, DIETS, PRODUCTION- BIOMASS RATIOS, AND ECOTROPHIC EFFICIENCY ESTIMATES FOR UTAH LAKE FOODWEB MODEL DEVELOPMENT IS IT RAINING ALGAE ON THE BENTHOS IN THE SUMMER?

Technical Report · December 2021

1 author:

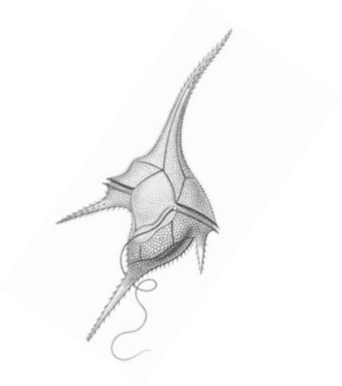
David Richards
OreoHelix Ecological

OreoHelix Ecological “Dedicated to Evaluating and Protecting the World’s Ecological Health, Integrity, and Well Being…. One Snail at a Time”

Filename: Plankton Biomass Estimates for Utah Lake Foodweb Models
Version 1.0

PLANKTON BIOMASS, DIETS, PRODUCTION-BIOMASS RATIOS, AND ECOTROPHIC EFFICIENCY ESTIMATES FOR UTAH LAKE FOODWEB MODEL DEVELOPMENT

IS IT RAINING ALGAE ON THE BENTHOS IN THE SUMMER?



To
Wasatch Front Water Quality Council, Salt Lake City, UT

By
David C. Richards, Ph.D.

OreoHelix Ecological, Vineyard UT 84059
Phone: 406.580.7816
Email: oreohelix@icloud.com

December 28, 2021

Cover images: left, *Ceratium hirundinella* (dinoflagellate) one of the most dominant phytoplankton taxa in Utah Lake; right, *Daphnia* sp. one of the most common zooplankton taxa in the lake. *Ceratium hirundinella* are also one of the larger sized phytoplankton species in the lake that have defensive spines preventing even large sized *Daphnia* sp. from feeding on them. Drawings not to scale.

Table of Contents

List of Figures

List of Tables

List of Appendices

INTRODUCTION

Development of a quantitative and predictive food web model is of critical importance if we are to scientifically manage Utah Lake’s ecosystem into the future. Water quality chemistry models are being developed for Utah Lake by Utah Division of Water Quality and University of Utah however, they are only half of the equation. Much of the lake’s ecosystem function is governed by its food web including algal blooms and State designated beneficial uses are directed at its foodweb including its warm water fishery, waterfowl and shorebirds, and the aquatic life they depend on. Even though Utah Lake’s ecosystem has been subject to human induced hysteresis and is presently in a much simpler, less resistant, and potentially unstable state than that which existed < 200 years ago, its food web interactions are several orders of magnitude greater than water quality chemical interactions (Richards et al 2019).

No attempts have been made to fully model Utah Lake’s food web from water column plankton - to microbial loop -to benthic production- to fisheries, even though as a shallow lake ecosystem, interactions between the benthos and water column are inseparable. Subsequently, very little data has been compiled and analyzed, particularly concerning water column plankton, microbial loop components, and benthic invertebrate contributions to the food web. This report is the summary of the first step in food web model development for Utah Lake.

Food web models including the model being developed for Utah Lake require broad literature reviews, analysis of empirical data, and collaborative contributions by experts. Food web models need to be an accounting system where disparate information from various sources is standardized and rendered compatible (Mackinson and Daskalov 2007). Thoroughness and thoughtfulness in representing Utah Lake’s ecosystem are crucial, as the models produced will be the foundation for subsequent analyses using dynamic simulation tools. Like all models, the food web model being developed for Utah Lake is not final because our knowledge about the lake’s ecosystem can never be complete (Okey et al., 2002). However, because this model will identify knowledge and data gaps, even preliminary runs of the model can be useful, and indeed their usefulness will increase as the model is further refined (Mackinson and Daskalov 2007).

ECOPATH WITH ECOSIM, EWE

After close examination of many models, the most appropriate and useful food web model for Utah Lake selected was Ecopath with Ecosim, EwE and add on models (https://ecopath.org). EwE is designed for straightforward construction, parameterization, and analysis of mass-balance trophic models of aquatic ecosystems and is one of the most widely used aquatic food web models in the world (https://ecopath.org). A brief introduction to EwE is from the Ecopath with Ecosim 6.6.6 free software Introduction is as follows:

> “The Ecopath mass-balance modelling system is built on an approach initially presented by J.J. Polovina for estimating biomass and food consumption of the elements (species or groups of species). The model was then combined with various approaches from theoretical ecology, notably those proposed by R.E. Ulanowicz, for the analysis of flows between the elements of ecosystems. However, the system has been optimized for direct use in fisheries assessment as well as for addressing environmental questions through the inclusion of the temporal dynamic model, Ecosim, and the spatial dynamic model, Ecospace.

> Since its initial development in the early 1980s, the mass-balance approach incorporated in the Ecopath software has been widely used for constructing food web models of marine and other ecosystems. This has led to a number of generalizations on the structure and functioning of such ecosystems, relevant to the issue of fisheries impacts. Some of these generalizations have revisited older themes, while others were new. Both sets of generalizations have impacted on the development of the Ecopath approach itself. Herein, the description of the average state of an ecosystem, using Ecopath proper, also serves to parameterize systems of coupled difference and differential equations, used to depict changes in biomasses and trophic interactions in time (Ecosim) and space (Ecospace).
>
> The results of these simulations can then be used to modify the initial Ecopath parameterization, and the simulations rerun until external validation is achieved. This reconceptualization of the Ecopath approach as an iterative process, which helps address issues of structural uncertainty, does not, however, markedly increase its input requirements. Rather, it has become possible, through a semi-Bayesian resampling routine to explicitly consider the numerical uncertainty associated with these inputs.
>
> Real ecosystems are more complicated than the mass-balance fluxes of biomass in Ecopath, however large the number of functional groups we include in our models. Real ecosystems also have dynamics far more complex than represented in Ecosim. The issue to consider, when evaluating the realism of simulation software, is, however, not how complex the software and the processes are that are represented therein. Rather, the question is which structure allows a representation of the basic features of an ecosystem, given a limited amount of inputs. On such criterion, it was obvious that a major deficiency of the Ecopath with Ecosim approach was its assumption of homogenous spatial behaviour. This has been remedied through the development of Ecospace (Note that in Walters et al., 1999 Eq. 13, the sign for the T' factor was reversed by mistake.), a dynamic, spatial version of Ecopath, incorporating all key elements of Ecosim.
>
> The Ecopath with Ecosim software has been distributed to more than 3000 registered users in 124 countries, and more than 200 publications utilizing it have appeared in the scientific literature. See www.ecopath.org for an update."

Because this is the first step in modeling Utah Lakes food web and the lack of standardization and compatibility of data, and the infancy of collaboration with State and university biologists, only phytoplankton and zooplankton components of the food web are fully discussed in this report.

PHYTOPLANKTON

INTRODUCTION

Water column phytoplankton are the most important primary producers in Utah Lake because of its turbidity induced light limitation and the loss of littoral zone rooted aquatic plants (Richards 2021). Fortunately, expert phytoplankton assemblage data has been collected over the past few years on the lake and those data were available for model development.

METHODS

11,496 records were evaluated from a Utah Division of Water Quality, Utah State University, and Wasatch Front Water Quality Council combined dataset of Utah Lake phytoplankton samples collected from 1995 to 2018. All phytoplankton and benthic algal taxonomy were performed by Rushforth Phycology, the leading algal taxonomy experts for Utah Lake and surrounding aquatic ecosystems. Data were filtered to remove entries that were surface grab samples and were not representative of phytoplankton assemblages. Remaining taxa data from each sample date and location were combined into phytoplankton divisions resulting in 2360 datapoints. Cell volume (µm^3 mL^{-1}) was converted directly to biovolume (µg mL^{-1}). Geometric means for each phytoplankton division were generated by month and annual. Geometric means are more appropriate than arithmetic mean when data are not independent. In this case, plankton biomasses were assumed to be temporal and spatial autocorrelated and therefore, not independent. Very few data were collected from November through March consequently, best fit linear and quadratic regressions on natural log (ln) transformed data were made to estimate biovolumes from January through March using marginal means predictions on back transformed data using Stata 16.1 (StataCorp 2021) (Figure 1). December biovolumes were assumed to be the same as January estimates and November estimates were made by subtracting December estimates from October means and then dividing by 2 (roughly exponential decay from October to December).

Utah Lake has a surface area of about 392.55 km^2 and most phytoplankton were collected and occurs at 1 m depth as the lake is highly turbid with Secchi depths rarely exceeding 25 cm (2x Secchi = 0.5 m). This equated to an estimated 358,943,219,898 L of water. Phytoplankton division monthly and annual biovolumes were then calculated as metric tonnes and tonnes km^{-2} for food web model use.

RESULTS

Best fit quadratic regression equations for estimating early season biomass were the most appropriate for all phytoplankton divisions except Chlorophyta where a liner model fit best. Regressions models had very good fits, $R^2 > 0.85$ except for Cryptophyta and Euglenophyta (Figure 1).

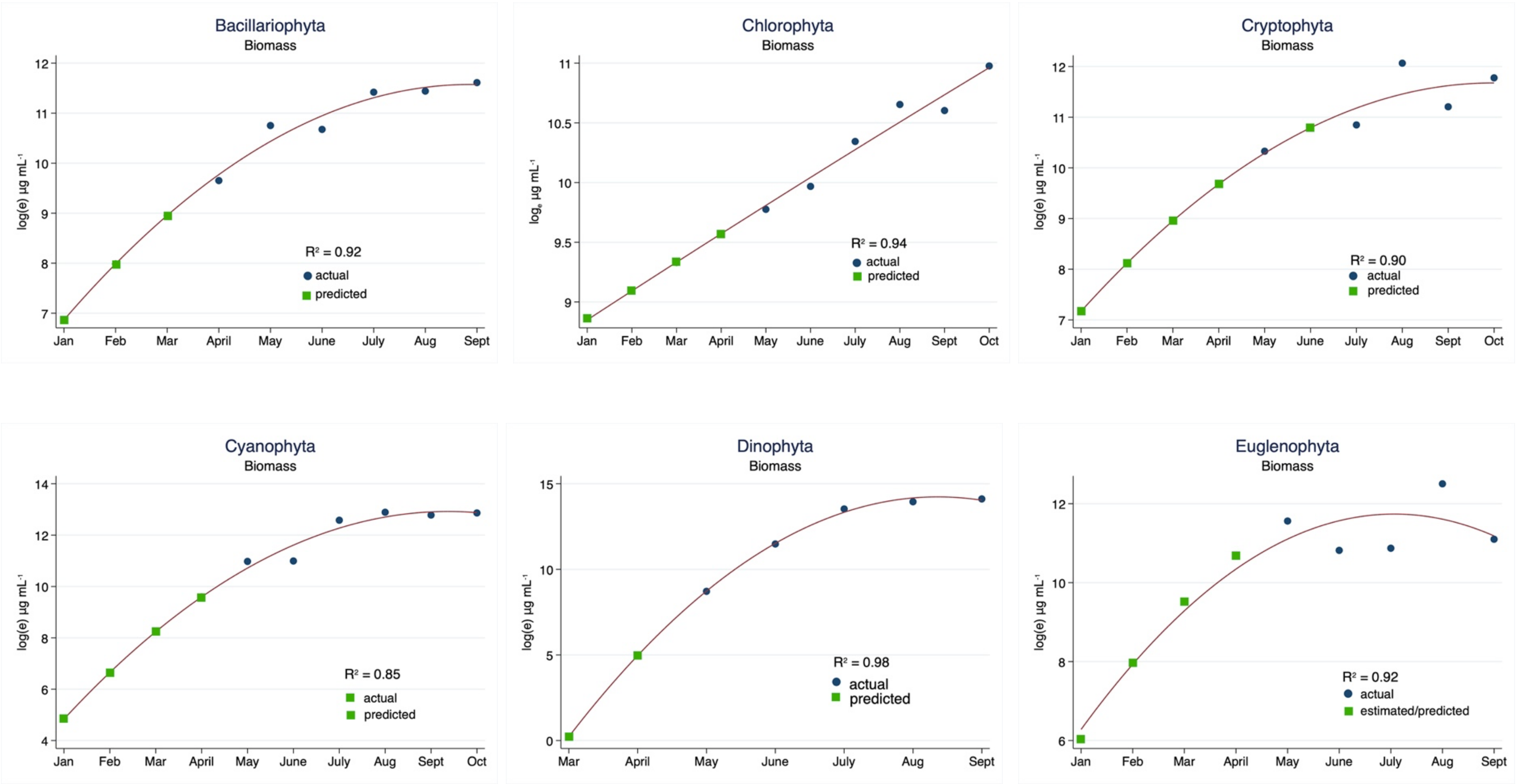


Figure 1. Best fit regressions for estimating early season (January to April) phytoplankton division biomass in Utah Lake. R^2 are pre-predicted values except for Cryptophyta and Euglenophyta, which were estimated and then predicted from regression equations.

Estimated phytoplankton division biomass (µg mL^{-1}) showed a seasonal pattern with low biomasses in winter and high biomasses in summer (Figure 2).

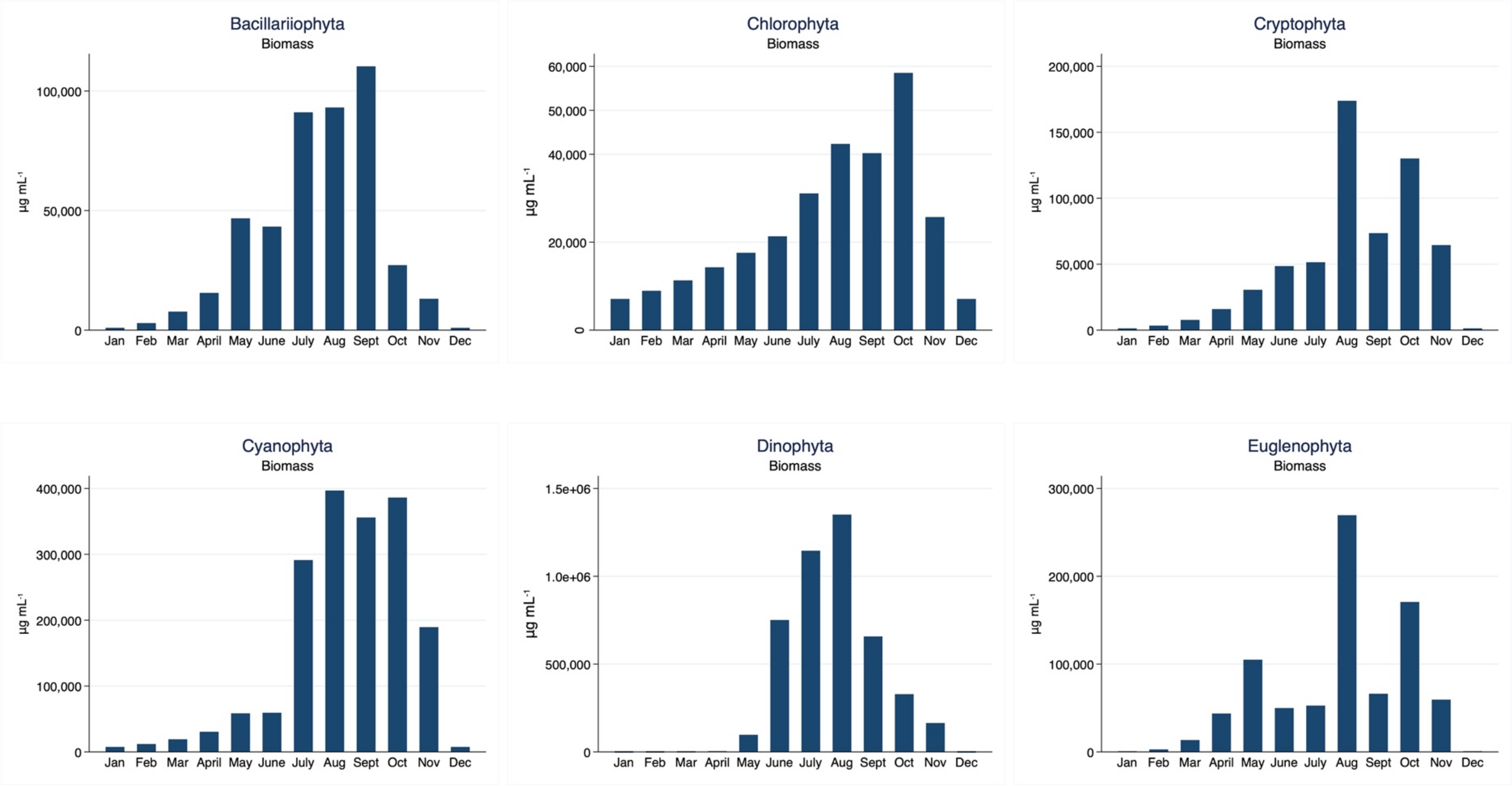


Figure 2. phytoplankton division estimated biomass (μg mL^{-1}) by month in Utah Lake. Note: scales are different for each division.

Estimated phytoplankton division mean monthly biovolume (µg mL^{-1}) are in Table 1 and estimated monthly biomass (tonnes) and biomass (tonnes) km^{-2} are in Table 2.

Table 1. Estimated mean monthly biovolume (μg mL^{-1})) of phytoplankton divisions in Utah Lake. Values in black font are geometric means of actual data. Values in red are predicted and estimated values from regressions.

	Bacillariophyta	Chlorophyta	Cryptophyta	Cyanophyta	Dinophyta	Euglenophyta
Jan	959	7,055	1,301	7,537	81	416
Feb	2,941	8,923	3,355	12,005	307	2,865
March	7,747	11,285	7,737	19,120	1,156	13,516
April	15,552	14,271	15,957	30,452	4,357	43,700
May	46,761	17,603	30,592	58,506	97,153	104,962
June	43,275	21,332	48,555	59,441	750,911	49,906
July	91,088	31,078	51,406	291,251	1,145,145	52,670
Aug	93,094	42,351	173,882	396,728	1,350,914	269,445
Sept	110,326	40,261	73,538	355,901	657,140	66,128
Oct	27,161	58,492	130,128	386,072	328,529	170,717
Nov	13,101	25,707	64,413	189,267	164,224	59,486
Dec	959	7,078	1,301	7,537	81	416
mean	**37,747**	**23,786**	**50,180**	**151,151**	**375,000**	**69,519**

Table 2. Estimated monthly biomass (tonnes) and biomass (tonnes) km^{-2} in Utah Lake

Month	Tonnes	tonnes km^{-2}
Jan	623	0.17
Feb	1,091	0.30
March	2,174	0.60
April	4,461	1.22
May	12,763	3.50
June	34,940	9.59

July	59,679	16.39
Aug	83,505	22.93
Sept	46,781	12.84
Oct	39,523	10.85
Nov	18,529	5.09
Dec	624	0.17

Estimated mean annual phytoplankton division biovolume (µg mL^{-1}), biomass (tonnes), and tonnes km^{-2} are in Table 3.

Table 3. Estimated mean annual phytoplankton division biovolume (μg mL^{-1}), biomass (tonnes), and tonnes km^{-2} in Utah Lake.

Division	μg mL^{-1}	Tonnes	Tonnes km^{-2}
Bacillariophyta	37,747	1,355	0.372
Chlorophyta	23,786	854	0.234
Cryptophyta	50,180	1,801	0.495
Cyanophyta	151,151	5,425	1.490
Dinophyta	375,000	13,460	3.696
Euglenophyta	69,519	2,495	0.685
Total	**707,384**	**25,391**	**6.971**

Phytoplankton Cell Size

Phytoplankton cell size is important regulator of diets of zooplankton that are limited by gape size. Phytoplankton taxa in Utah Lake vary in size, some are single celled, multicell, coenobial, aggregated, filamentous, or colonial (Richards 2021). Therefore, the best metric available to predict zooplankton diet was ‘cumulated biovolumes of cells in a colony (µm^{3})’, which was derived from Rimet and Druart (2018) and applied to Utah Lake phytoplankton taxa summed to division level. Bacillariophyta were the smallest sized with a median of 272 µm^{3} and ranged up to an extremely large size of 39,250 µm^{3} for Dinophyta, over 144 times larger (Table 4, Figure 3). Dinophyta in Utah Lake are dominated by one species, *Ceratium hirudinella*, which also have spines further preventing zooplankton grazing.

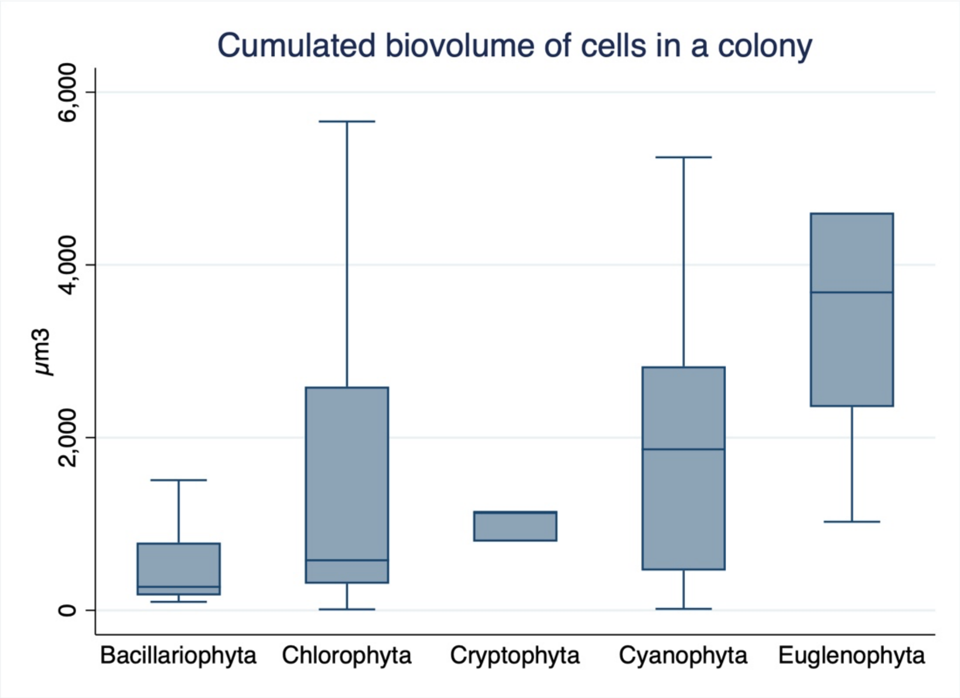
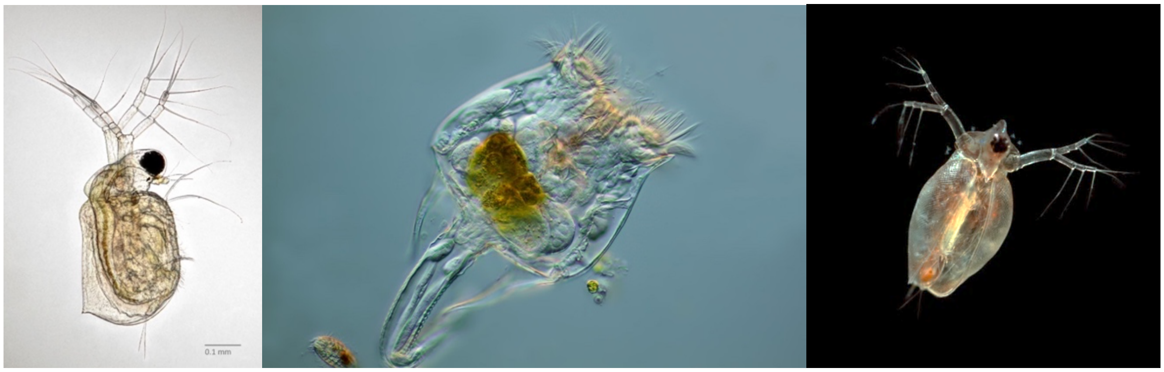


Figure 3. Median, 25th, 75th, and ranges of cumulated biovolume of cells in phytoplankton division colonies in Utah Lake. Dinophyta = 39,250 μm^3.

Table 4. Summary statistics of cumulated biovolume of cells in phytoplankton division colonies in Utah Lake. Dinophyta = 39,250 μm^3.

algaldivision	mean	sd	p50	p25	p75
Bacillariophyta	1108.485	1912.316	271.75	172.8	784
Chlorophyta	3106.625	6826.049	579.59	307.72	2590.5
Cryptophyta	910.8616	415.7939	1139.82	795.99	1139.82
Cyanophyta	2805.835	4448.702	1864.375	461.2	2825.72
Euglenophyta	12404.63	26110.78	3681.65	2353.69	4605.33

ZOOPLANKTON



INTRODUCTION

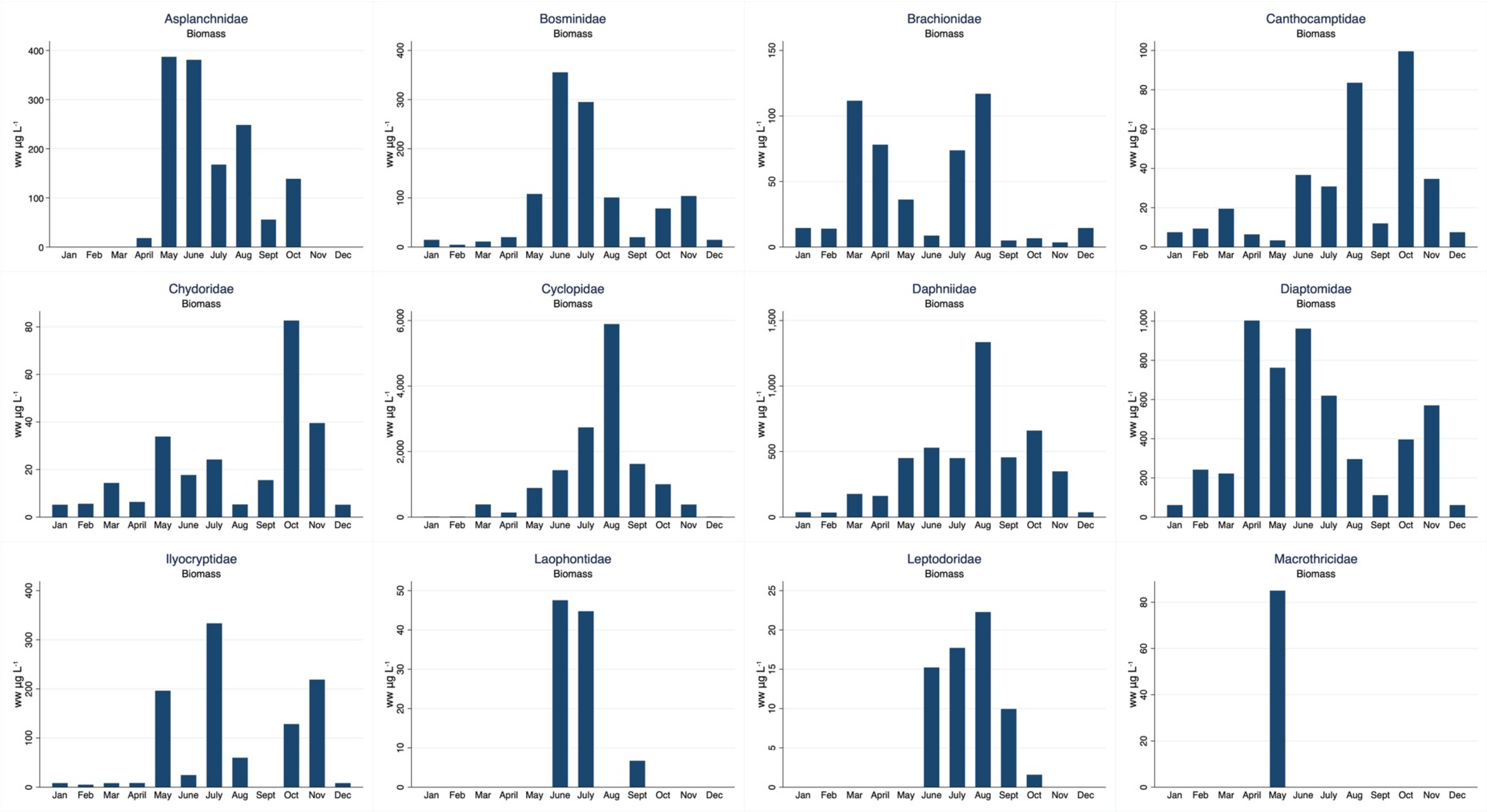
Zooplankton are the main consumers of phytoplankton and are in turn consumed by small fish, including all juvenile fishes and all juvenile and adult June Suckers in Utah Lake (Richards et al. 2019They are the chief intermediaries between primary production and higher trophic levels, and thus play a critical role in Utah Lake food web dynamics (Richards et al. 2019).

METHODS

Zooplankton data for Utah Lake for the years 2015 to 2018 were obtained from Richards (year). Biomass estimates for zooplankton were similar to those used for phytoplankton biomass estimates with a few exceptions. Zooplankton family level densities were relativized by lengths following Richards (2019a, b), lengths were converted to dry weight by a factor of 16.78 µg (dry weight of *Daphnia pulex* Richards (2019a, b) standardized value = 1), and then divided by 0.15 conversion from dry weight to wet weight (USEPA method citation).

RESULTS

Estimated mean monthly wet weight biomass (µg L^{-1}) of zooplankton families in Utah Lake are in Figure 4. Zooplankton biomass (Figure 4) generally followed the phytoplankton monthly biomass with greater biomasses in summer months (Figure 2).


Asplanchnidae Biomass

Bosminidae Biomass

Brachionidae Biomass

Canthocamptidae Biomass

Chydoridae Biomass

Cyclopidae Biomass

Daphniidae Biomass

Diaptomidae Biomass

Ilyocryptidae Biomass

Laophontidae Biomass

Leptodoridae Biomass

Macrothricidae Biomass

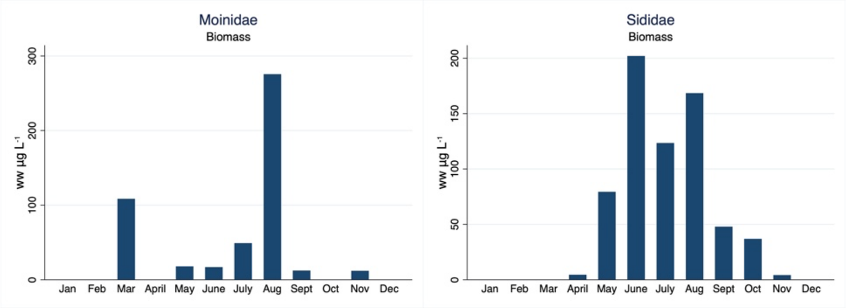


Figure 4. Estimated mean monthly wet weight biomass (μg L^{-1}) of zooplankton families in Utah Lake (data from Richards 2019a, 2019b). Based on density values from Table 7, dry weight = 16.78 (μg L^{-1}) and dry weight = 0.15 wet weight. Insufficient data from December, therefore estimated to be the same as January values. Values are in Appendix 2.

Estimated monthly and mean annual zooplankton family biomass (tonnes) and tonnes km^{-2} in Utah Lake are in Table 5 and Table 6.

Table 5. Estimated monthly and mean annual zooplankton family biomass (tonnes) in Utah Lake.

Family	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Mean
Asplanchnidae	0	0	0	7	139	137	60	89	20	50	0	46
Bosminidae	5	2	4	7	39	128	106	36	7	28	37	36
Brachionidae	5	5	40	28	13	3	26	42	2	2	1	15
Canthocamptidae	3	3	7	2	1	13	11	30	4	36	12	11
Chydoridae	2	2	5	2	12	6	9	2	6	30	14	8
Cyclopidae	4	2	139	50	319	514	983	2115	582	360	138	473
Daphniidae	13	12	63	58	162	190	161	479	164	237	125	151
Diaptomidae	22	87	80	360	274	345	222	106	40	142	205	171
Ilyocryptidae	3	2	3	3	70	9	120	21	0	46	79	32
Laophontidae	0	0	0	0	0	17	16	0	2	0	0	3
Leptodoridae	0	0	0	0	0	5	6	8	4	1	0	2
Macrothricidae	0	0	0	0	31	0	0	0	0	0	0	3
Moinidae	0	0	39	0	6	6	18	99	4	0	4	16
Sididae	0	0	0	2	28	73	44	60	17	13	2	22
Total	**57**	**115**	**380**	**519**	**1094**	**1446**	**1783**	**3088**	**852**	**945**	**617**	**990**

Table 6. Estimated monthly and mean annual zooplankton family biomass (tonnes) km^{-2} in Utah Lake

Family	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Mean
Asplanchnidae	0.000	0.000	0.000	0.002	0.038	0.038	0.017	0.024	0.005	0.014	0.000	0.013
Bosminidae	0.001	0.000	0.001	0.002	0.011	0.035	0.029	0.010	0.002	0.008	0.010	0.010
Brachionidae	0.001	0.001	0.011	0.008	0.004	0.001	0.007	0.012	0.000	0.001	0.000	0.004
Canthocamptidae	0.001	0.001	0.002	0.001	0.000	0.004	0.003	0.008	0.001	0.010	0.003	0.003
Chydoridae	0.001	0.001	0.001	0.001	0.003	0.002	0.002	0.001	0.002	0.008	0.004	0.002
Cyclopidae	0.001	0.001	0.038	0.014	0.087	0.141	0.270	0.581	0.160	0.099	0.038	0.130
Daphniidae	0.004	0.003	0.017	0.016	0.044	0.052	0.044	0.132	0.045	0.065	0.034	0.042

Diaptomidae	0.006	0.024	0.022	0.099	0.075	0.095	0.061	0.029	0.011	0.039	0.056	0.047
Ilyocryptidae	0.001	0.000	0.001	0.001	0.019	0.002	0.033	0.006	0.000	0.013	0.022	0.009
Laophontidae	0.000	0.000	0.000	0.000	0.000	0.005	0.004	0.000	0.001	0.000	0.000	0.001
Leptodoridae	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.001	0.000	0.000	0.001
Macrothricidae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Moinidae	0.000	0.000	0.011	0.000	0.002	0.002	0.005	0.027	0.001	0.000	0.001	0.004
Sididae	0.000	0.000	0.000	0.000	0.008	0.020	0.012	0.017	0.005	0.004	0.000	0.006
Total	**0.016**	**0.032**	**0.104**	**0.142**	**0.300**	**0.397**	**0.489**	**0.848**	**0.234**	**0.259**	**0.169**	**0.272**

Estimated geometric mean monthly densities (animals l^{-1}) of zooplankton families are in Table 7.

TABLE 7. ESTIMATED GEOMETRIC MEAN MONTHLY DENSITIES (ANIMALS L^{-1}) OF ZOOPLANKTON FAMILIES IN UTAH LAKE (DATA FROM RICHARDS 2019A, 2019B). INSUFFICIENT DATA FROM DECEMBER, THEREFORE ESTIMATED TO BE THE SAME AS JANUARY VALUES.

Family	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Asplanchnidae	0.00	0.00	0.00	0.16	3.46	3.40	1.50	2.22	0.50	1.24	0.00	0.00
Bosminidae	0.13	0.04	0.10	0.18	0.96	3.18	2.64	0.90	0.18	0.70	0.93	0.13
Brachionidae	0.13	0.12	1.00	0.70	0.32	0.08	0.66	1.05	0.04	0.06	0.03	0.13
Canthocamptidae	0.07	0.08	0.17	0.06	0.03	0.33	0.28	0.75	0.11	0.89	0.31	0.07
Chydoridae	0.05	0.05	0.13	0.06	0.30	0.16	0.22	0.05	0.14	0.74	0.35	0.05
Cyclopidae	0.09	0.06	3.45	1.24	7.93	12.80	24.47	52.67	14.49	8.96	3.42	0.09
Daphniidae	0.32	0.31	1.58	1.45	4.02	4.73	4.02	11.93	4.08	5.90	3.12	0.32
Diaptomidae	0.55	2.17	1.99	8.97	6.81	8.60	5.54	2.64	1.00	3.54	5.10	0.55
Ilyocryptidae	0.07	0.04	0.07	0.08	1.75	0.22	2.98	0.53	0.00	1.15	1.96	0.07
Laophontidae	0.00	0.00	0.00	0.00	0.00	0.42	0.40	0.00	0.06	0.00	0.00	0.00
Leptodoridae	0.00	0.00	0.00	0.00	0.00	0.14	0.16	0.20	0.09	0.01	0.00	0.00
Macrothricidae	0.00	0.00	0.00	0.00	0.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Moinidae	0.00	0.00	0.97	0.00	0.16	0.15	0.44	2.46	0.11	0.00	0.11	0.00
Sididae	0.00	0.00	0.00	0.04	0.71	1.81	1.10	1.51	0.43	0.33	0.04	0.00
Total	**1.41**	**2.88**	**9.46**	**12.92**	**27.24**	**36.01**	**44.40**	**76.91**	**21.22**	**23.53**	**15.36**	**1.41**

ZOOPLANKTON GROUPS

More simplified, easier to understand, and commonly used groupings than family level is by groups Cladocera, Copepoda, and Rotifera, although much important ecological information is lost. The following results are based on these groups.

Copepods had greater monthly biomass every month and was greatest in summer months (Figure 5, Figure 6). Cladocera had the second greatest biomass and followed similar monthly patterns (Figure 5, 5). Rotifers had the lowest biomass seasonally but may have been underreported due to sampling method bias (see Discussion). Monthly biomass values are in Appendix 3.

FIGURE 5. ESTIMATED MONTHLY BIOMASS OF THREE ZOOPLANKTON GROUPS, CLADOCERA, COPEPODA, AND ROTIFERA IN UTAH LAKE.

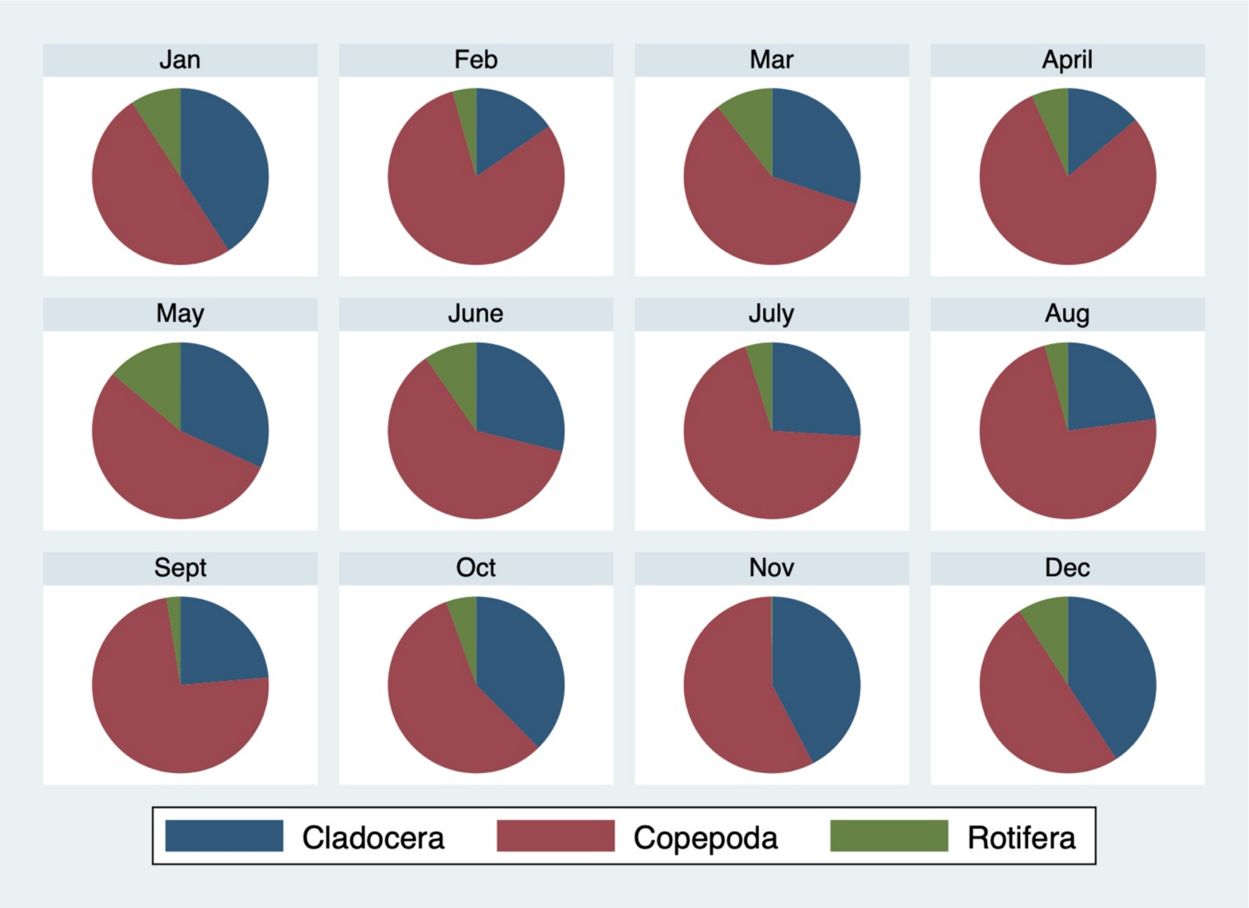


FIGURE 6. MONTHLY RELATIVE BIOMASS ABUNDANCES OF THREE ZOOPLANKTON GROUPS, CLADOCERA, COPEPODA, AND ROTIFERA IN UTAH LAKE.

ZOOPLANKTON DIETS AS A FUNCTION OF SIZE

All the zooplankton families analyzed in this report are considered phytoplankton filter feeding grazers, except Leptodoridae which are predators. In general, phytoplankton < 30 um (along major axis of cell or colony) is often considered edible by zooplankton but is also dependent on gape size of zooplankton (Lampert and Sommer 2007, Kazama et al. 2022) citations). For example, Rotifera are small zooplankton and have corresponding small gape sizes. Length estimates of zooplankton based on values from literature and used to estimate biomasses are in Table 8.

TABLE 8. LENGTH ESTIMATES OF ZOOPLANKTON BASED ON VALUES FROM LITERATURE. LENGTH ESTIMATE SOURCES: CENTRAL MICHIGAN UNIVERSITY WEBSITE (ACCESSED MARCH 12, 2019), CULVER ET AL. (1985), AND NOAA GREAT LAKES ENVIRONMENTAL RESEARCH LABORATORY WEBSITE (ACCESSED MARCH 12, 2019), CENTER FOR FRESHWATER BIOLOGY (ACCESSED MARCH 20, 2019). USGS (ACCESSED MARCH 20, 2019).

Taxon	mean length (mm)

Acanthocyclops americanus	1.13
Alona setulosa	0.71
Asplanchna sp.	0.80
Attheyella sp.	0.75
Bosmina longirostris complex	0.41
Brachionus calyciflorus	0.38
Brachionus sp. Almenara	0.18
Brachionus variabilis	0.28
Ceriodaphnia dubia	0.85
Ceriodaphnia sp.	0.75
Chydoridae sp.	0.48
Daphnia ambigua	0.80
Daphnia magna	4.00
Daphnia mendotae	2.15
Daphnia pulex	1.00
Daphnia retrocurva	1.14
Daphnia sp.	1.50
Diaphanosoma cf. Heberti	0.56
Ilyocryptus sp.	0.73
Leptodiaptomus sicilis female	1.25
Leptodiaptomus sicilis male	1.25
Leptodora kindti	1.00
Leydigia louisi	0.56
Macrothrix sp.	0.71
Microcyclops rubellus	0.64
Moina micrura	0.50
Onychocamptus mohammed	0.55
Ostracoda	0.70

Platyias quadricornis	0.23
Scapholeberis mucronata	0.70
Simocephalus sp.	3.50

ZOOPLANKTON/PHYTOPLANKTON BIOMASS RATIOS, *Z*/*P*

The zooplankton to phytoplankton ratio, *Z*/*P* is often used as a metric evaluating trophic status of a water body and ecosystem functioning, and as a component of food web models. *Z*/*P* typically decreases with increased eutrophication (Gulati, 1983; Andronikova, 1996; Jeppesen et al., 1999, 2000, 2005; Haberman & Laugaste, 2003, Blank et al. 2010).

Utah Lake *Z*/*P* varied seasonally with higher values in winter vs. summer and the highest *Z*/*P* in March = 0.18 and a mean = 0.07 (Figure 7). *Z*/*P* shows that zooplankton grazing was much less efficient from June through November (Figure 7).

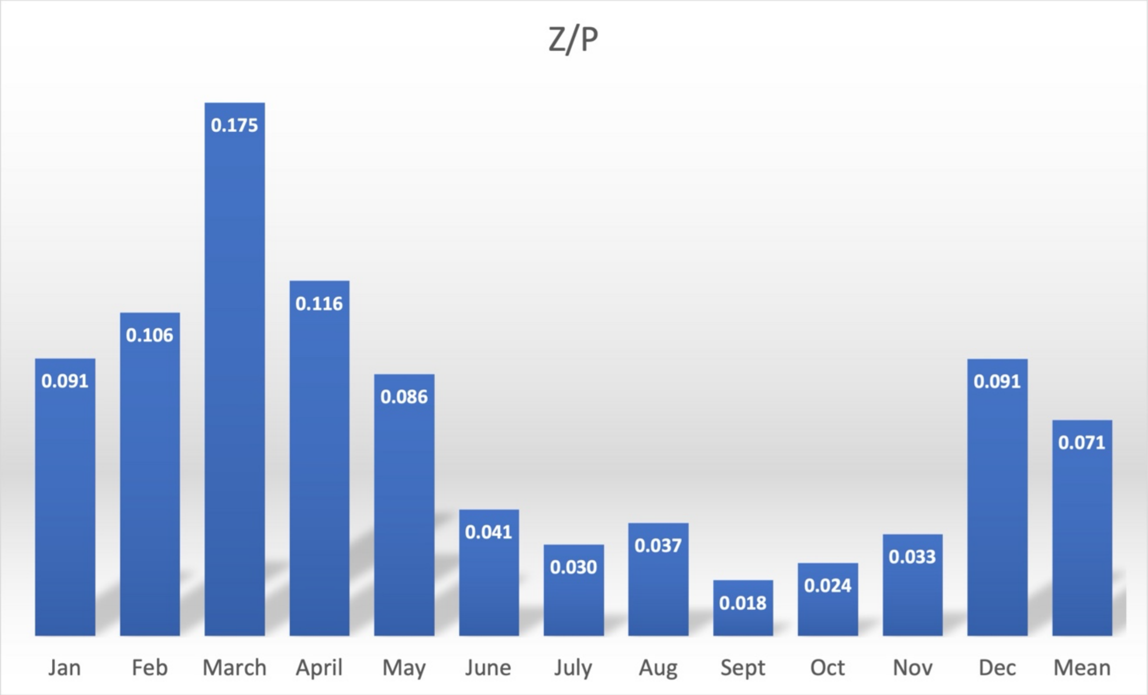


FIGURE 7. UTAH LAKE MONTHLY ZOOPLANKTON TO PHYTOPLANKTON BIOMASS RATIO, *Z*/*P*.

PRODUCTION TO BIOMASS RATIO, P/B

The production to biomass ratio, P/B is the turnover rate for each plankton group and is one of the basic inputs of food web models. Basically, it is the instantaneous rate of total mortality, Z which is the sum of predation loss, net migration, biomass change, and other mortality (Heymans et al. 2016, Pauly et al. 2000). However, it was not possible to estimate the annual mean production of plankton groups in Utah Lake from available data. Preliminary literature estimates of P/B for phytoplankton range from 100 to 300, and zooplankton from about 7 to 15 (Mackinson and Daskalov 2007, Heymans et al. 2016). More intensive literature review is needed to improve P/B estimates.

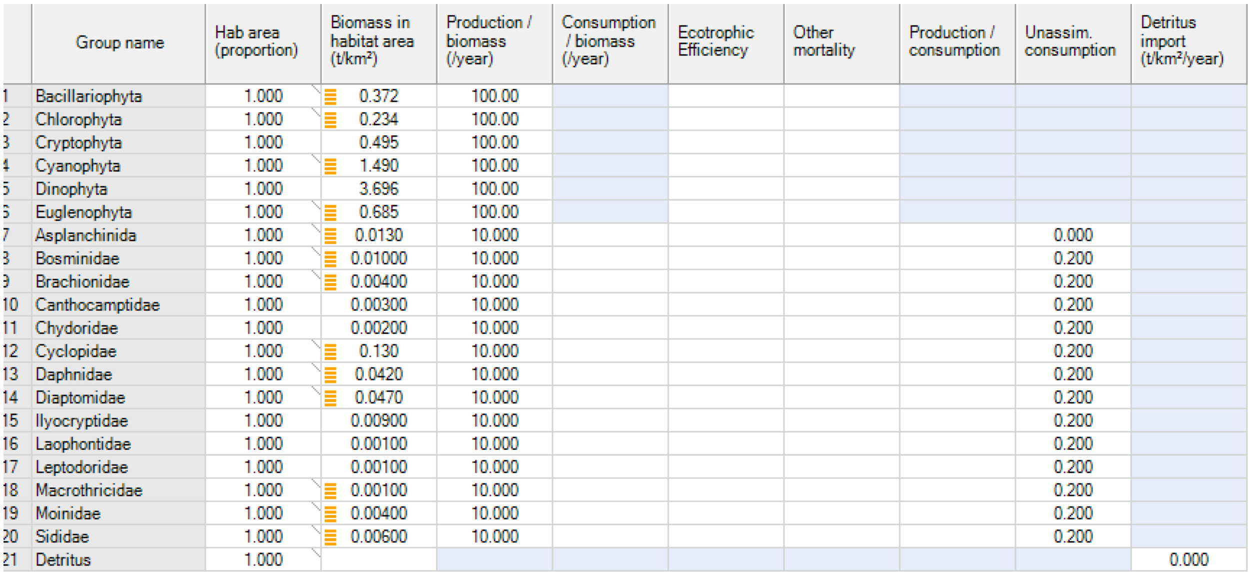
EXCRETION/EGESTION RATES

Excretion/egestion rates are unknown for Utah Lake zooplankton and will have to be estimated from literature values. Zooplankton excretion is invariably rapidly utilized by phytoplankton or incorporated into the 'microbial loop' as DOM (see Nanoplankton and the Microbial Loop). Fecal pellets excreted by larger zooplankton are likely 1) utilized by smaller zooplankton, especially Rotifera, 2) quickly incorporated into the microbial loop or 3) sink to the benthos and become part of the benthic component of the lake's food web (see Benthic Functional Groups). Heymans et al. (2016) suggested that excretion/egestion rates are typically higher for functional groups that feed on phytoplankton and a rate of 40% is realistic for zooplankton grazers. Initial models will use this rate and will be refined as more information is obtained.

PLANKTON FOOD WEB MODEL DEVELOPMENT

Values generated for the plankton section of the food web were loaded into Ecopath to begin balancing the model and exploring the food web. Basic input values are in Table 9. Phytoplankton and zooplankton groups were modeled to occupy all of the lake (Hab area proportion = 1.00), biomass input for each group was from data in Table 3 and Table 6 [(Biomass in habitat area (t/km^2)] and production to biomass ratio, P/B [Production/biomass(/year)]was arbitrarily modelled as 100 for phytoplankton and 10 for zooplankton loosely based on literature values for illustrative purposes only.

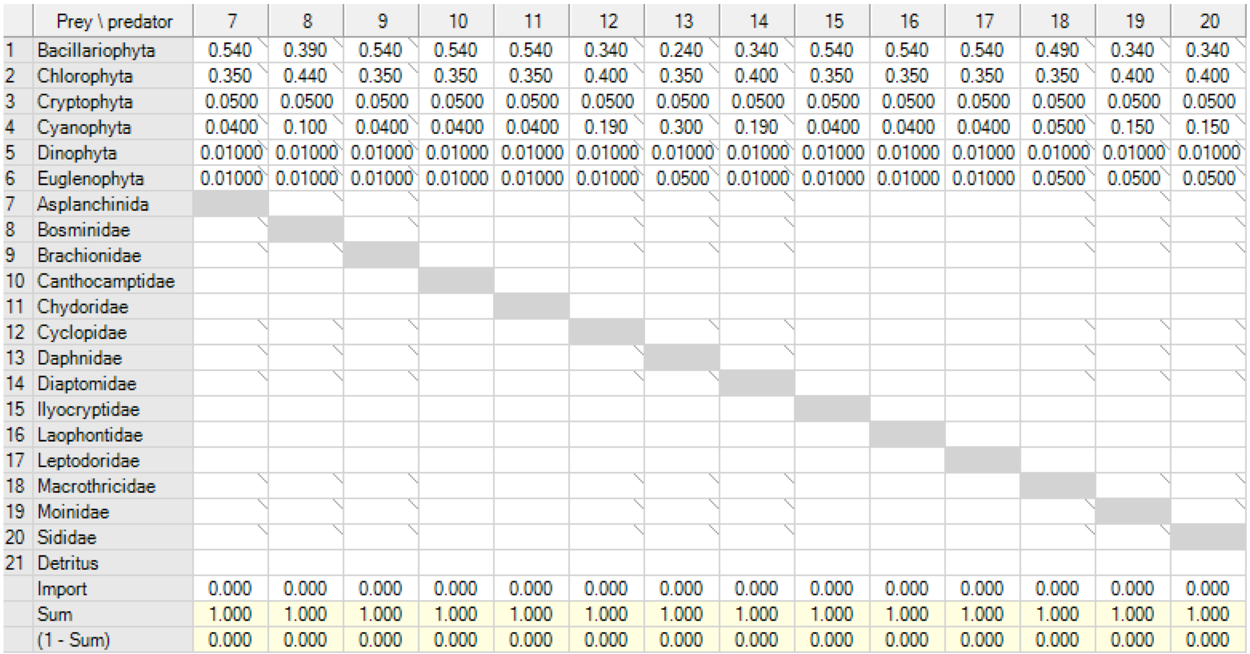
TABLE 9. BASIC INPUT COMPONENT OF INITIAL STAGES OF ECOPATH FOOD WEB MODEL.



	Group name	Hab area (proportion)	Biomass in habitat area (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic Efficiency	Other mortality	Production / consumption	Unassim. consumption	Detritus import (t/km²/year)
1	Bacillariophyta	1.000	0.372	100.00						
2	Chlorophyta	1.000	0.234	100.00						
3	Cryptophyta	1.000	0.495	100.00						
4	Cyanophyta	1.000	1.490	100.00						
5	Dinophyta	1.000	3.696	100.00						
6	Euglenophyta	1.000	0.685	100.00						
7	Asplanchinida	1.000	0.0130	10.000					0.000	
8	Bosminidae	1.000	0.01000	10.000					0.200	
9	Brachionidae	1.000	0.00400	10.000					0.200	
10	Canthocamptidae	1.000	0.00300	10.000					0.200	
11	Chydoridae	1.000	0.00200	10.000					0.200	
12	Cyclopidae	1.000	0.130	10.000					0.200	
13	Daphnidae	1.000	0.0420	10.000					0.200	
14	Diaptomidae	1.000	0.0470	10.000					0.200	
15	Ilyocryptidae	1.000	0.00900	10.000					0.200	
16	Laophontidae	1.000	0.00100	10.000					0.200	
17	Leptodoridae	1.000	0.00100	10.000					0.200	
18	Macrothricidae	1.000	0.00100	10.000					0.200	
19	Moinidae	1.000	0.00400	10.000					0.200	
20	Sididae	1.000	0.00600	10.000					0.200	
21	Detritus	1.000								0.000

Diet composition values are in Table 10. Proportion of phytoplankton groups in the diets of each zooplankton group were best guess estimates that needed to sum to 1.00. The general assumption was that phytoplankton groups in zooplankton diets were mostly inversely proportional to size of phytoplankton cells (Figure 3).

TABLE 10. DIET COMPOSITION COMPONENT OF INITIAL STAGES OF ECOPATH FOOD WEB MODEL.



	Prey \ predator	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Bacillariophyta	0.540	0.390	0.540	0.540	0.540	0.340	0.240	0.340	0.540	0.540	0.540	0.490	0.340	0.340
2	Chlorophyta	0.350	0.440	0.350	0.350	0.350	0.400	0.350	0.400	0.350	0.350	0.350	0.350	0.400	0.400
3	Cryptophyta	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500
4	Cyanophyta	0.0400	0.100	0.0400	0.0400	0.0400	0.190	0.300	0.190	0.0400	0.0400	0.0400	0.0500	0.150	0.150
5	Dinophyta	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000
6	Euglenophyta	0.01000	0.01000	0.01000	0.01000	0.01000	0.01000	0.0500	0.01000	0.01000	0.01000	0.01000	0.0500	0.0500	0.0500
7	Asplanchinida														
8	Bosminidae														
9	Brachionidae														
10	Canthocamptidae														
11	Chydoridae														
12	Cyclopidae														
13	Daphnidae														
14	Diaptomidae														
15	Ilyocryptidae														
16	Laophontidae														
17	Leptodoridae														
18	Macrothricidae														
19	Moinidae														
20	Sididae														
21	Detritus														
	Import	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(1 - Sum)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

An initial food web flow diagram was then produced to illustrate relationships between primary producers (phytoplankton) (trophic level 1) and consumers (zooplankton grazers) (trophic level 2). The flow diagram is presented in Figure 8.

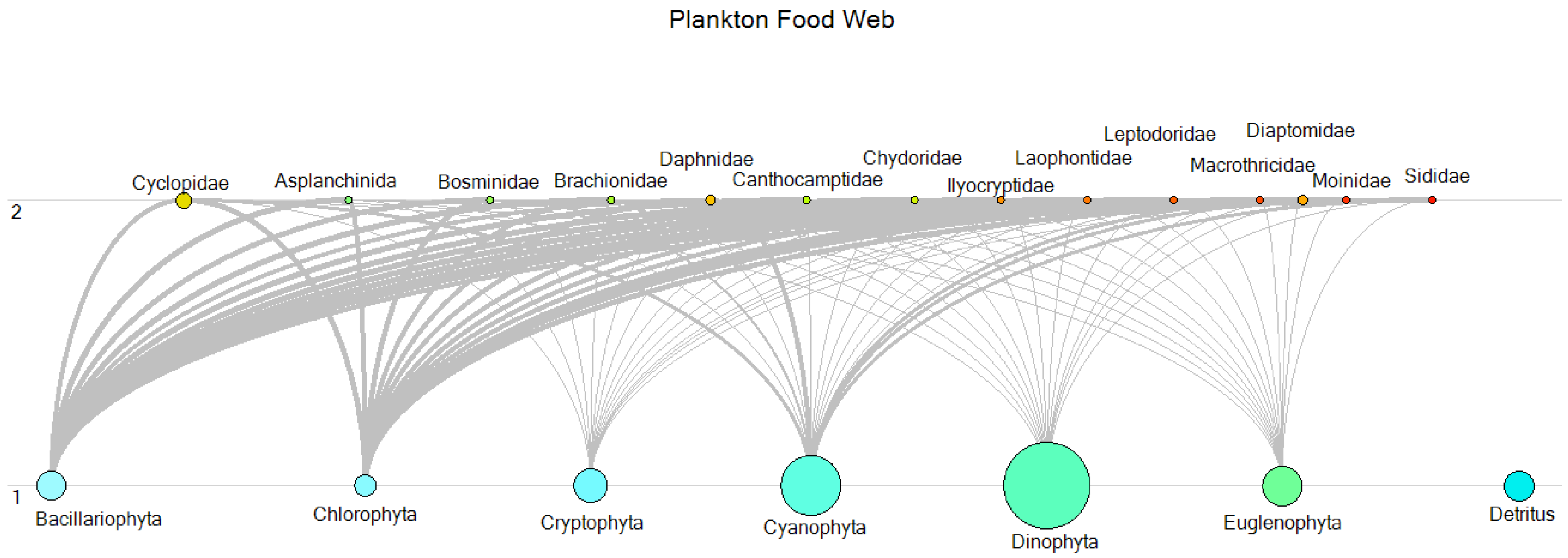


Figure 8. Ecopath flow diagram of plankton component of food web. Phytoplankton are trophic level 1, zooplankton, trophic level 2. Sizes of spheres are relative annual biomasses for each group (tonnes km-2), connection lines are relative proportions of diets for each group. This figure is for illustrative purposes only. strengths of connections and size of groups are based on data available at this time.

ADDITIONAL FOOD WEB FACTIONS

At this time only phytoplankton and zooplankton water column portion of Utah Lake's food web has been evaluated and preliminary values generated. Two other compartments that interact with plankton water column portion are benthic and fish functional groups.

BENTHIC FUNCTIONAL GROUPS

The benthos' are a critical component of Utah Lake's food web (Figure 9, Figure 10) (Richards et al. 2019, Richards and Miller 2019a, b, Richards 2019a, b, Richards 2018, Richards and Miller 2017). Benthic functional groups that will be part of the model include two chironomid taxa, *Chironomus* sp. and *Tanypus* sp., one bivalve, *Corbicula* sp., and oligochaete worms. Other benthic invertebrate taxa occur in the lake, but these four taxa dominate the biomass. Future models may include other benthic invertebrate taxa when aquatic plants and littoral zones are modeled.

FISH FUNCTIONAL GROUPS

Several fish functional groups will be included in the models including carp, white bass, largemouth bass, crappie, walleye, northern pike, channel catfish, bullhead catfish, Utah sucker, and June sucker. Almost all the groups undergo ontological diet shifts, and several stanzas (age/size classes) will be modeled to account for diet shifts. In addition, all these taxa have different diets from benthivory, planktivory, piscivory, to omnivory that will be modeled.

DISCUSSION

WATER COLUMN FOOD WEB INTERACTIONS

The food web models that are being developed can be as simple or complicated as needed to answer research and management questions. In simplified models, several important components are left out either because of unknown values or a focus on higher trophic level fisheries questions. Several components that will be addressed in Utah Lake food web models that are often overlooked by other models include cell lysis, turbulence fragmentation of phytoplankton cells, sloppy feeding by zooplankton, egestion, the microbial loop and sinking from water column to benthic portion of the food web (see Benthic Functional Groups).

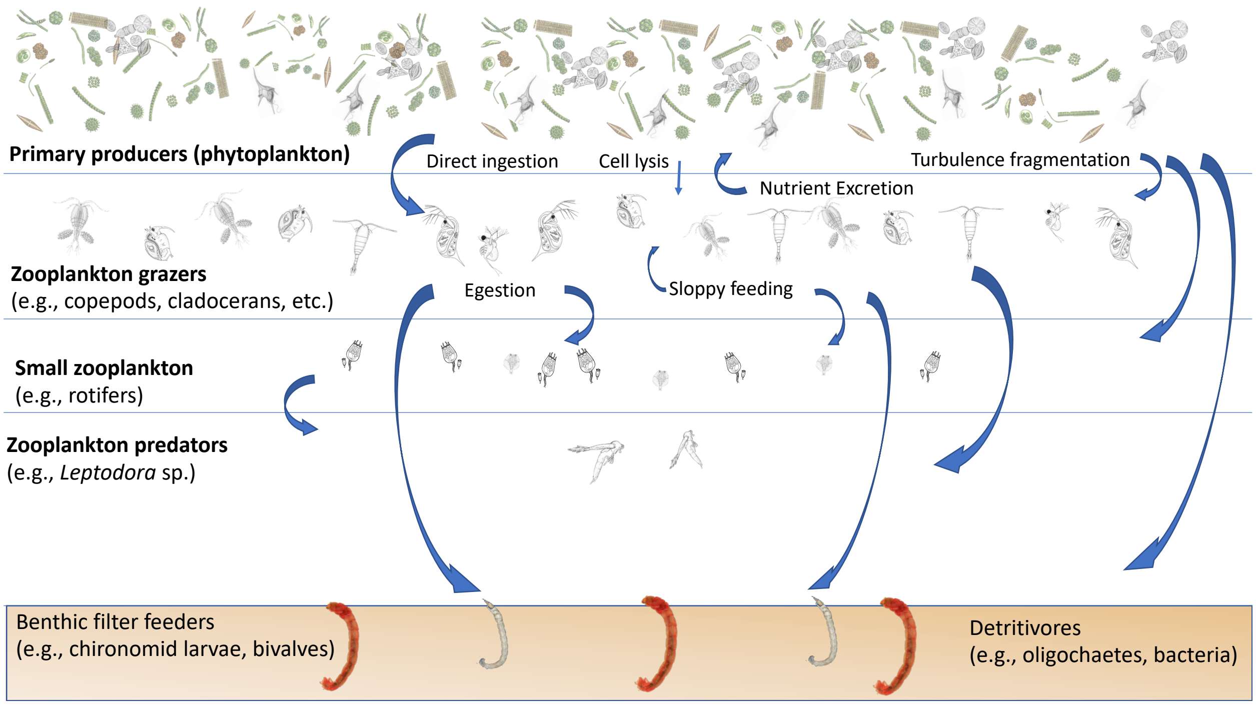


FIGURE 9. WATER COLUMN FOOD WEB INTERACTIONS THAT WILL BE INCORPORATED INTO UTAH LAKE FOOD WEB MODELS.

ROTIFERA UNDERREPRESENTED

Even though Rotifera family biomasses were comparatively high, it appears that Rotifera were underrepresented in the data because of the size mesh used in the zooplankton net (≈100 μm). This is unfortunate and additional sampling may need to be conducted using smaller mesh size to allow for regression-based estimates of the present data and updating models.

NANOPLANKTON AND THE MICROBIAL LOOP

It is widely recognized that a large portion of primary production flows through the water column pool of dissolved organic matter (DOM), either after excretion by phytoplankton or by lysis of ungrazed cells. This component of primary production is not directly available to zooplankton grazers. It is mainly used by bacteria and auto/ heterotrophic nanoflagellates (Mackinson and Daskalov 2007). Bacteria and nanoflagellates can utilize anywhere from 5 to 50% of primary production in some aquatic systems (van Es and Meyer-Reil 1982, Mackinson and Daskalov 2007) that is then converted into bacteria and nanoflagellate biomass which then becomes available to zooplankton grazers via the 'microbial loop' (Azam et al. 1983) (Figure 10). Cole et al. (1989) reported that heterotrophic bacterial production can be twice as large as the production of zooplankton production and planktonic bacterial production can range from 20%–30% of total planktonic primary production (Mackinson and Daskalov 2007). Kirman (2000) classified microflora (bacteria and nanoflagellates) as those organisms smaller than phytoplankton (microplankton = 20 to 200 μm, nano = 2 to 20 μm, picoplankton = 0.2 to 2 μm).

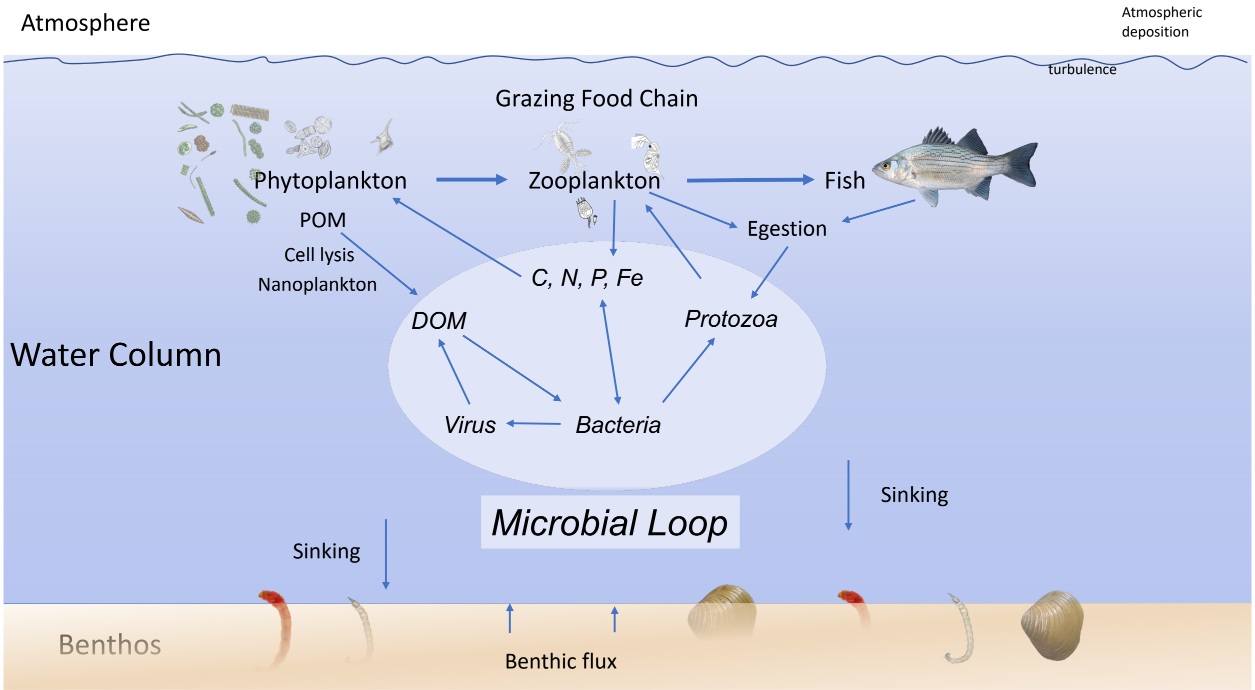


FIGURE 10. SIMPLIFIED VERSION OF THE MICROBIAL LOOP IN UTAH LAKE. MODIFIED FROM AZAM (1998). THE IMPORTANCE OF THE MICROBIAL LOOP IN UTAH LAKE'S FOOD WEB IS LIKELY VASTLY UNDERESTIMATED AND WHICH WILL BE INCORPORATED INTO ONGOING FOOD WEB MODELS.

Given the hypereutrophic condition and the dominance of water column food web components of Utah Lake, the microbial loop (Figure 10) is expected to be a significant if not dominant contributor to the lake's food web. At this time, the microbial loop will be modeled as part of the detritus component and then depending on relevant literature findings incorporated into separate groups similar to phytoplankton divisions and zooplankton families used in the initial model.

IS IT RAINING ALGAE ON THE BENTHOS IN THE SUMMER?

An important finding of this initial food web model development was that zooplankton grazers did not appear to be able to utilize a large portion of the phytoplankton biomass during summer months, i.e., low ecotrophic efficiency. Several factors likely contributed to this underutilization, 1) large size of phytoplankton cells particularly Cyanophyta and Dinophyta, 2) extreme fast growth rates of phytoplankton [(many cyanophytes can have doubling times of < 1 day (Richards 2021)], and 3) inedibility of phytoplankton, especially Cyanophyta, Dinophyta, and Euglenophyta (Richards 2021). Dinophyta, Cyanophyta, and Euglenophyta accounted for 84% of phytoplankton biomass and are less susceptible to feeding from zooplankton. Zooplankton grazers may have been able to shred some of the large sized phytoplankton however, much of it was either incorporated into the microbial loop or sank to the benthos.

Benthic invertebrates in Utah Lake are very efficient filter feeders and their biomass can be quite high, particularly chironomid larvae and Corbicula bivalves (Richards et al 2019, etc.). This consistent raining of smaller sized phytoplankton from the water column can help maintain benthic invertebrate secondary production that can then be utilized by the many tons of benthivorous fishes that inhabit the lake. This phenomenon will be central to Utah Lake food web models.

LITERATURE CITED

Andronikova, I. N. 1996. Structural and Functional Organization of Zooplankton in Lake Ecosystems of Different Trophic Status. Nauka, St. Petersburg (in Russian).

Azam, F. 1988. Microbial control of oceanic carbon flux: the plot thickens. Science. Vol. 280: 694-696.

Blank. K, Laugaste,R., and J. Haberman. 2010. Temporal and spatial variation in the zooplankton:phytoplankton biomass ratio in a large shallow lake. Estonian Journal of Ecology, 2010, 59, 2, 99ñ115 doi: 10.3176/eco.2010.2.02

Cole, J.J., Finlay, S., and Pace, M.L., 1989. Bacterial production in fresh and saltwater ecosystems: a cross system overview. Mar. Ecol. Prog. Ser., 43: 1-10.

Gulati, R. D. 1983. Zooplankton and its grazing as indicators of trophic status in Dutch lakes. Environ. Monit. Assess., 3, 343-354.

Haberman, J. & Laugaste, R. 2003. On characteristics reflecting the trophic state of large and shallow Estonian lakes (L. Peipsi, L. Vırtsj‰rv). Hydrobiologia, 506/509, 737ñ744.

Heymans, J.J. et al. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecological Modelling 331 (2016) 173–184.

Jeppesen, E., Jensen, J. P., S¯ndergaard, M. & Lauridsen, W. T. 1999. Trophic dynamics in turbid and clear water lakes with special emphasis on the role of zooplankton for water clarity. Hydrobiologia, 408/409, 217ñ231.

Jeppesen, E., Jensen, J. P., S¯ndergaard, M., Lauridsen, T. & Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along phosphorus gradient. Freshwater Biol., 45, 201ñ218.

Jeppesen, E., S¯ndergaard, M., Jensen, J. P. et al. 2005. Lake responses to reduced nutrient loading ñ an analysis of contemporary long-term data from 35 case studies. Freshwater Biol., 50, 1747-1771.

Kazama T, Urabe J, Yamamichi M, Tokita K, Yin X, Katano I, Doi H, Yoshida T, Hairston NG Jr (2021) A unified framework for herbivore-to-producer biomass ratio reveals the relative influence of four ecological factors. Communications Biology 4: 49 DOI: 10.1038/s42003-020-01587-9 [Supplement] [Dryad] (Authorea DOI: 10.22541/au.159121368.85843146)Lampert, W. & U. Sommer, 2007. Limnoecology. Oxford University Press, New York: 152–180.

Mackinson, S. and Daskalov, G., 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterization. Sci. Ser. Tech Rep., Cefas Lowestoft, 142: 196pp.

Okey,T., Vargo, G., Mackinson, S., Vasconcellos, M., Mahmoudi, B. and Meyer, C., 2002. Simulating community effects of sea floor shading by plankton blooms over the West Florida shelf. pp55-56. In: (V. Christensen, G. Reck and J.L. Maclean (Eds.)). Proceedings of the INCO-DC Conference Placing Fisheries in their Ecosystem Context, Galápagos Islands, Ecuador, 4-8 December 2000. ACP-EU. Fish. Res. Rep., (12).

Pauly, Daniel & Christensen, Villy & Walters, Carl. (2000). Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science. 57. 697-706. 10.1006/jmsc.2000.0726.

Polovina, J.J., 1984. Model of a coral reef ecosystem I. The ECOPATH model and its applications to French Frigate Shoals. Coral Reefs, 3: 1-11.

Richards, D.C. 2021. Seasonal patterns of phytoplankton assemblage densities and functional traits in Utah Lake: A foodweb model prerequisite. Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Ecological, Vineyard, UT.

Richards, D. C. 2018. Relationships between Phytoplankton Richness and Diversity, Zooplankton Abundance, and cyanoHAB Dominance in Utah Lake, 2016. Draft Technical Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Consulting. 67pp.

Richards, D. C. and T. Miller. 2017. A preliminary analysis of Utah Lake's unique foodweb with a focus on the role of nutrients, phytoplankton, zooplankton, and benthic invertebrates on HABs. Utah Lake Research 2016. Progress Report. Wasatch Front Water Quality Council, Salt Lake City, UT.

Richards, D. C. and T. Miller. 2019a. A Provisional Multi-Metric Index of Biological Integrity (MIBI) to Assess Water Quality in Utah Lake centered on Regulatory Directives. Draft Technical Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Ecological, Vineyard, UT.

Richards, D. C. and T. Miller. 2019b. Utah Lake Research 2017-2018: Progress Report: Continued analysis of Utah Lake's unique foodweb with a focus on the role of nutrients, phytoplankton, zooplankton, and benthic invertebrates on cyanoHABs. Chapter 1: Phytoplankton Assemblages. Submitted to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Consulting, Vineyard, UT.

Richards, D.C. 2019a. Zooplankton assemblages in highly regulated Utah Lake: 2015-2018. Progress Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Consulting, Vineyard, UT.

Richards, D.C. 2019b. Spatial and Temporal Variability of Zooplankton Body Lengths in Utah Lake. Technical Memo to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Consulting, Vineyard, UT.

Richards, D.C. 2019c. Spatial and Temporal Variability in Zooplankton Assemblages in Utah Lake 2015 to 2019. Progress Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Consulting, Vineyard, UT.

Richards, D.C. et al. 2019. Factors Effecting the Ecological Health and Integrity of Utah Lake with a Focus on the Relationships between Water Column Regulators, Benthic Ecosystem Engineers, and CyanoHABs. Progress Report 2020. Version 2.3. Report to Wasatch Front Water Quality Council, Salt Lake City, UT. OreoHelix Ecological, Vineyard, UT.

Rimet, F and J-C, Druart. 2018. A trait database for Phytoplankton of temperate lakes: numerical file. https://zenodo.org/record/1164834#.XRNrPXvgrOR.

StataCorp. 2021. Stata/IC 16.1 for Mac (Intel 64-bit). College Station, TX.

Van Es and L. Meyer-Reil (1982) Biomass and metabolic activity of heterotrophic marine bacteria. Advances in Microbial Ecology 6: 111–170.

APPENDICES

APPENDIX 1. REGRESSION EQUATIONS

Bacillariophyta

				Number of obs	6
Source	SS	df	MS	F (2, 3)	17.87
Model	2.49	2	1.24	Prob > F	0.02
Residual	0.21	3	0.07	R-squared	0.92
Total |	2.69	5	0.54	Adj R-squared	0.87
				Root MSE	0.26

Log_e Bacillariophyta	Coef.	Std. Err.	t	P>|t|	[95% Conf. Interval]	
Month*Month	-0.08	0.04	-1.76	0.18	-0.21	0.06
Month	1.35	0.56	2.39	0.10	-0.45	3.15
Constant	5.59	1.75	3.2	0.05	0.02	11.16

Chlorophyta

Number of obs = 6	
Prob > F	0.001
R-squared	0.9494
Adj R-squared	0.9367
Root MSE	0.11341

Source	SS	df	MS
Model	0.96505508	1	0.96505508
Residual	0.05144877	4	0.01286219
Total	1.01650385	5	0.20330077

logeChloro |	Coef.	Std. Err.	t	P>|t|	[95% Conf.	Interval]
Month	0.23	0.03	8.66	0.001	0.16	0.31
Constant	8.62	0.21	41.36	0	8.05	9.20

Cryptophyta

```
      Source |       SS           df       MS      Number of obs   =        10
-------------+----------------------------------   F(2, 7)         =    117.15
       Model |   22.317682         2   11.158841   Prob > F        =    0.0000
    Residual |  .666754443         7  .095250635   R-squared       =    0.9710
-------------+----------------------------------   Adj R-squared   =    0.9627
       Total |  22.9844365         9  2.55382627   Root MSE        =    .30863
```

```
------------------------------------------------------------------------------------
      logeCryptoph_01 |      Coef.   Std. Err.       t    P>|t|     [95% Conf. Interval]
----------------------+-------------------------------------------------------------
             var20_01 |       1.11        0.15     7.35    0.00         0.76        1.47
                      |
c.var20_01#c.var20_01 |      -0.06        0.01    -4.16    0.00        -0.09       -0.02
                      |
                _cons |       6.11        0.36    16.84    0.00         5.25        6.97
------------------------------------------------------------------------------------
```

Cyanophyta

```
      Source |       SS           df       MS      Number of obs   =         9
-------------+----------------------------------   F(1, 7)         =    102.63
       Model |  12.3806067         1  12.3806067   Prob > F        =    0.0000
    Residual |  .844469958         7  .120638565   R-squared       =    0.9361
-------------+----------------------------------   Adj R-squared   =    0.9270
       Total |  13.2250766         8  1.65313458   Root MSE        =    .34733
```

```
-------------------------------------------------------------------------------
      logeCyano |      Coef.   Std. Err.       t    P>|t|     [95% Conf. Interval]
----------------+--------------------------------------------------------------
c.var24#c.var24 |       0.04        0.00    10.13    0.00         0.03        0.05
                |
          _cons |       9.39        0.18    52.00    0.00         8.96        9.81
-------------------------------------------------------------------------------
```

Revised Cyanophyta with > 10 million biovolumes

```
      Source |       SS           df       MS      Number of obs   =         6
-------------+----------------------------------   F(2, 3)         =      9.49
       Model |  3.76008256         2  1.88004128   Prob > F        =    0.0504
    Residual |  .594532312         3  .198177437   R-squared       =    0.8635
-------------+----------------------------------   Adj R-squared   =    0.7725
       Total |  4.35461487         5  .870922974   Root MSE        =    .44517

------------------------------------------------------------------------------
logeCyanoph~a |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
        var9 |       2.16       1.10     1.97    0.14        -1.33        5.66
             |
c.var9#c.var9 |     -0.12       0.07    -1.58    0.21        -0.35        0.12
             |
       _cons |       2.79       3.97     0.70    0.53        -9.85       15.42
------------------------------------------------------------------------------
```

Dinophyta

```
      Source |       SS           df       MS      Number of obs   =         7
-------------+----------------------------------   F(2, 4)         =   3540.75
       Model |  168.344758         2   84.172379   Prob > F        =    0.0000
    Residual |  .095089784         4  .023772446   R-squared       =    0.9994
-------------+----------------------------------   Adj R-squared   =    0.9992
       Total |  168.439848         6   28.073308   Root MSE        =    .15418

------------------------------------------------------------------------------
        logeDino |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-----------------+----------------------------------------------------------------
           var13 |       8.15       0.20    39.98    0.00         7.59        8.72
                 |
c.var13#c.var13 |      -0.49       0.02   -28.99    0.00        -0.53       -0.44
                 |
           _cons |     -19.85       0.57   -34.88    0.00       -21.43      -18.27
------------------------------------------------------------------------------
```

Euglenophyta

```
      Source |       SS           df       MS      Number of obs   =         9
-------------+----------------------------------   F(2, 6)         =     34.29
       Model |  29.2867655         2  14.6433828   Prob > F        =    0.0005
    Residual |  2.56196947         6  .426994912   R-squared       =    0.9196
-------------+----------------------------------   Adj R-squared   =    0.8927
       Total |   31.848735         8  3.98109188   Root MSE        =    .65345

------------------------------------------------------------------------------
   logeEugleno |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
---------------+----------------------------------------------------------------
         var29 |       2.09       0.38     5.49    0.00         1.16         3.03
               |
c.var29#c.var29 |      -0.15       0.04    -3.98    0.01        -0.24        -0.06
               |
         _cons |       4.34       0.83     5.21    0.00         2.30         6.37
------------------------------------------------------------------------------
```

Appendix 2. Estimated mean monthly wet weight biomass (μg L^{-1}) of zooplankton families in Utah Lake (Richards). Based on density values from Table 7, dry weight = 16.78 (μg L^{-1}), and dry weight = 0.15 wet weight Insufficient data from December, therefore estimated to be the same as January values.

Family	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Asplanchnidae	0.00	0.00	0.00	18.16	387.06	380.83	167.63	248.41	55.78	138.71	0.00	0.00
Bosminidae	14.54	4.47	11.08	19.97	107.92	355.46	295.08	100.75	19.90	78.44	103.74	14.54
Brachionidae	14.54	13.97	111.63	78.06	36.23	8.72	73.78	116.95	4.95	6.65	3.50	14.54
Canthocamptidae	7.50	9.36	19.46	6.42	3.36	36.67	30.79	83.56	11.99	99.54	34.63	7.50
Chydoridae	5.19	5.59	14.36	6.38	33.87	17.69	24.21	5.33	15.54	82.66	39.54	5.19
Cyclopidae	10.01	6.65	385.89	138.22	887.65	1431.67	2737.38	5891.87	1621.38	1002.53	383.11	10.01
Daphniidae	36.34	34.46	176.42	161.72	450.15	529.28	449.83	1335.01	455.90	660.21	348.93	36.34
Diaptomidae	61.29	242.20	222.20	1003.02	762.15	961.88	619.38	295.81	111.78	396.12	570.02	61.29
Ilyocryptidae	8.24	5.00	8.18	8.46	196.27	24.61	333.36	59.83	0.00	128.41	218.87	8.24
Laophontidae	0.00	0.00	0.00	0.00	0.00	47.54	44.75	0.00	6.71	0.00	0.00	0.00
Leptodoridae	0.00	0.00	0.00	0.00	0.00	15.22	17.71	22.27	9.95	1.58	0.00	0.00
Macrothricidae	0.00	0.00	0.00	0.00	85.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Moinidae	0.00	0.00	108.51	0.00	17.88	16.89	49.00	275.55	12.31	0.00	11.94	0.00
Sididae	0.00	0.00	0.00	4.47	79.36	202.01	123.42	168.47	47.95	36.90	4.19	0.00
Total	157.66	321.71	1057.73	1444.89	3046.91	4028.48	4966.33	8603.80	2374.15	2631.75	1718.48	157.66

Appendix 3. Estimated monthly zooplankton GROUP BIOMASS (tonnes) and tonnes m^{-2} in Utah Lake.

Month	Zooplankton Group	metric tons (tonnes)	tonnes/km
Jan	Cladocera	23.086	0.006
	Copepoda	28.286	0.008
	Rotifera	5.220	0.001
Feb	Cladocera	17.777	0.005
	Copepoda	92.682	0.025
	Rotifera	5.015	0.001
March	Cladocera	114.341	0.031
	Copepoda	225.255	0.062
	Rotifera	40.069	0.011
April	Cladocera	72.147	0.020
	Copepoda	411.948	0.113
	Rotifera	34.538	0.009
May	Cladocera	348.344	0.096
	Copepoda	593.389	0.163
	Rotifera	151.936	0.042
June	Cladocera	416.791	0.114
	Copepoda	889.375	0.244
	Rotifera	139.829	0.038
July	Cladocera	463.975	0.127
	Copepoda	1232.002	0.338
	Rotifera	86.652	0.024
Aug	Cladocera	706.116	0.194

	Copepoda	2251.017	0.618
	Rotifera	131.144	0.036
Sept	Cladocera	201.568	0.055
	Copepoda	628.821	0.173
	Rotifera	21.796	0.006
Oct	Cladocera	354.707	0.097
	Copepoda	537.763	0.148
	Rotifera	52.177	0.014
Nov	Cladocera	261.028	0.072
	Copepoda	354.552	0.097
	Rotifera	1.257	0.000
Dec	Cladocera	23.086	0.006
	Copepoda	28.286	0.008
	Rotifera	5.220	0.001