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Environment and phytoplankton relative abundances in a hypersaline lake: 27 years in Great Salt Lake, USA and experiments

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Abstract Over 27 years in Great Salt Lake (GSL: Utah, USA), phytoplankton relative abundances of chlorophytes, diatoms and cyanobacteria varied dramatically (monthly < 10–90% for each). This observed variability within the lake was compared to laboratory experimental results with pure cultures (>>90%) of several of the most common GSL phytoplankton (chlorophyte–*Dunaliella viridis*, diatom–*Nitzschia epithemioides*, cyanobacterium–*Euhalothece* sp.). Maximum abundances and growth rates were measured across ranges of temperature (10–30 °C), salinity (30–150 ppt) and nutrients (nitrogen: 0.0–0.64 mg/L, silica:17–51 mg/L) observed within GSL. Experimental results indicated the abundance and growth rate of *D. viridis* increased as salinity and nitrogen increased and decreased as temperature increased. The abundances and growth rates of *N. epithemioides* and *Euhalothece* decreased as salinity increased, and increased as temperature and nitrogen increased, and *N. epithemioides* increased as silica increased. Observed GSL phytoplankton relative abundances responded to environmental conditions as observed in the experiments, but correlations were weak except for chlorophytes, as diatoms and cyanobacteria relative abundances occasionally increased with unfavorable experimental conditions. The weak correlations between laboratory results and GSL observations could be due to the release of diatoms and cyanobacteria from microbialite biofilms in the lake's benthos with cold stress and high winds, as a 5–10% release can produce diatom and cyanobacteria phytoplankton relative abundances of 24–48%. This suggests a novel potential link between GSL pelagic and benthic zones.

Keywords Great Salt Lake · Hypersaline lake phytoplankton · Chlorophytes · Diatoms · Cyanobacteria · Benthic linkage

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Introduction

Saline lakes represent 44% of the earth's lake water volume (Messager et al. 2016), but they are rapidly disappearing as freshwater inputs are diverted for human use (Wurtsbaugh et al. 2017). These terminal lakes are highly productive for phytoplankton and aquatic invertebrates, which can support large numbers of waterbirds. Nonetheless, these lakes are understudied as their waters are not potable and they have relatively limited biodiversity. Saline lake ecological studies are often short term (one to several years), focus on categorizing biodiversity and its ecological community structure, and assume that salinity drives ecological relationships. This often leads to comparative studies of salinity gradients among lakes within a season(s) (*e.g.,* Kawabata et al. 1997; Golubkov et al. 2007; Salm et al. 2009; Somogyi et al. 2014; Sui et al. 2016; Afonina and Tashlykova 2018, 2019, 2024), or over a few years within a lake (*e.g.,* Esmaelli Dahesht et al. 2010; Muir and Perissinotto 2011; Alfonso et al. 2017; Mohebbi 2020). Oren (2014) points out how little is known about what drives variation in phytoplankton relative abundances in saline lakes. For example, it is unclear whether salinity changes explain variation in a saline lake's phytoplankton abundance and composition among years.

Great Salt Lake (GSL), Utah (USA), is the fourth or fifth largest hypersaline lake in the world, depending on how the areas of other lakes is measured (e.g., inclusion of lower salinity areas), and largest in the western hemisphere (salinity = 60–250 ppt) (Arnow and Stephens 1990; Johnson et al. 2020). Historically, GSL has often been portrayed as a simple pelagic system dominated by the chlorophytes, *Dunaliella viridis* Teodoresco or *D. salina* (Dunal) Teodoresco, that are grazed by brine shrimp (*Artemia franciscana* Kellogg) (*e.g.,* Felix and Rushforth 1980). Construction of a causeway across the lake in the 1960s separated the lake into two main arms, the South Arm, and the North Arm, and with nearly all freshwater inputs entering the South Arm, dramatic differences in salinities between the two arms developed (Felix and Rushforth 1977, 1980; Blinn 1993). Unfortunately, systematic and quantitative phytoplankton sampling was not conducted prior to and after this change, only a qualitative listing of species was provided. The increased salinity of the North Arm eliminated most phytoplankton except the chlorophyte, *Dunaliella salina*, while in the South Arm, the focus of this study, salinity declined.

The salinity decline (still hyhpersaline) in the South Arm has been hypothesized to have changed phytoplankton composition. A diatom increase, based on claims that diatoms were not resident in GSL prior to 1960 due to high salinity unless washed in by streams, has been hypothesized (Felix and Rushforth 1977, 1980; Blinn 1993). Increases in cyanobacteria have also been hypothesized to be due to this change in salinity (Felix and Rushforth 1980). Systematic sampling of South Arm phytoplankton (Belovsky et al. 2011; GSLEP, unpublished data) and laboratory studies with mixed phytoplankton from the South Arm (Larson and Belovsky 2013) sometimes support and sometimes refute these explanations.

Monthly monitoring of phytoplankton communities in the GSL South Arm began in 1994 and early trends were described in Belovsky et al. (2011). The phytoplankton community was found to be composed of a varying set of 60 species, and annual spring maximum phytoplankton abundance varied by ~ 4.7 fold (30–144 μg Chl_a/L), while salinity varied by ~ 2.2 fold (82–176 ppt) (Belovsky et al. 2011). Furthermore, this and other monitoring within GSL found that when diatoms or cyanobacteria increased, South Arm brine shrimp abundance declined, especially when diatoms were abundant (Belovsky et al. 2011). These observations suggest that potential shifts in phytoplankton abundances, namely a decrease in chlorophytes, impact GSL brine shrimp populations. Factorial lab experiments using mixed phytoplankton from the GSL South Arm indicate the potential for salinity, temperature, and nutrients to impact phytoplankton diversity and abundance (Larson and Belovsky 2013), but little is known about how phytoplankton communities in hypersaline systems vary as these factors covary over longer time periods.

Here, we examine experimentally how environmental conditions (salinity, temperature, and nutrients) might affect maximum abundances and growth rates of GSL South Arm phytoplankton and whether these factors may account for variation observed in GSL phytoplankton composition. First, we summarize results from factorial laboratory experiments that were conducted with the most common chlorophyte, *Dunaliella viridis*, a common pelagic diatom (*Nitzschia epithemioides* Grunow), and a common

pelagic cyanophyte (*Euhalothece* sp., formerly listed as *Coccochloris elabens* (Brébisson) F.E. Drouet & W.A. Dailey). Second, we summarize annual trends in pelagic phytoplankton collected from the GSL South Arm over a span of 27 years (1994–2020). Finally, experimental results were used to predict observed monthly phytoplankton relative abundances and total phytoplankton abundances given monthly environmental conditions since 1994. This may lead to a better understanding of how environmental conditions affect the structure of phytoplankton communities in hypersaline lakes.

Methods

Laboratory experiments

From GSL South Arm water, cells of the chlorophyte, *Dunaliella viridis*, the diatom, *Nitzschia epithemioides*, and the cyanobacterium, *Euhalothece* sp., were isolated. *D. viridis* and *Euhalothece* cells were identified microscopically and *N. epithemioides* cells were identified molecularly to genus using DNA metabarcoding of 18S SSU rRNA genes and microscopically to species (Barrett 2020). Monocultures of the cells were developed at 20 °C with *D. viridis* at a salinity of 90 ppt, *Euhalothece* at 25 ppt, and *N. epithemioides* at 30 ppt. Culture saline water was made following the protocol described below. The resulting monocultures were > >90% pure and used in a full factorial experiment to examine maximum abundance and growth rate of each species under different salinity, temperature and nitrogen levels. In addition, the effect of silica on *N. epithemioides* was also examined, as silica can limit diatom frustule construction (Conway and Harrison 1977). These salinity, temperature, nitrogen and silica values were selected given the range of conditions observed in the GSL South Arm when phytoplankton exhibited growth and were grazed by *Artemia* (Belovsky et al. 2011).

Five salinities (30, 60, 90, 120, 150 ppt) were examined, spanning values observed in Farmington Bay, an area of lower salinity maintained by a causeway, and the main South Arm, which is hypersaline and most like the historic lake (Belovsky et al. 2011). Salinity levels determined with a temperature-compensating refractometer (ATAGO PAL-03S) were produced by varying the amounts of Instant Ocean (Spectrum Brands) and Pure and Natural Water Softener Salts (Morton) in a 2:3 ratio in RO water (Larson and Belovsky 2013). The resulting saline mixtures were filtered through a Whatman #4 filter to ensure that they did not contain any *Artemia* cysts that might hatch, because the Morton Salts are mined from the Great Salt Lake.

Three temperatures (10, 20, 30 °C) were employed, which span the range of South Arm water temperatures when most phytoplankton growth is observed (Belovsky et al. 2011). Temperature was maintained in environmental chambers with a light:dark cycle of 16:8 h (Grolux bulbs). Based on previous experiments, light intensities within the chambers were approximately 150 µmol photons s^{-1} m^{-2} (Larson and Belovsky 2013).

Three nitrogen additions were examined (0.01, 0.14, 0.64 mg N/L), as nitrogen is known to limit GSL phytoplankton growth in the South Arm (Stephens and Gillespie 1976; Larson and Belovsky 2013; Belovsky et al. 2011). While phytoplankton can be co-limited by nitrogen and phosphorus, at present there is no evidence for this in GSL South Arm phytoplankton (Ogata et al. 2017) and measures of GSL phosphorus are less available than for measures of nitrogen, which also are limited. The nitrogen values tested are within the range observed in the upper 4 m of the hypersaline region of the South Arm (0.01–1.36 mgN/L) (Belovsky et al. 2011; Naftz 2017). Nitrogen (NH_4NO_3 = 49.6%, $CaNO_3$ = 46.8%, N-NO_3 = 3.5%) and phosphorus (P_2O_5 = 69.6%, KH_2PO_4 = 30.4%) additions provided the Redfield Ratio (16:1 molar N:P, Larson and Belovsky 2013). Finally, three silica additions (17, 34, 51 mg/L), which contain values observed in the South Arm (2–28 mg/L) (Hahl and Handy 1969; Stube et al. 1976; USGS: https://maps.waterdata.usgs.gov/mapper/index.html), were employed for *N. epithemioides.* Silica was provided as $Na_2SiO_3(9\ H_2O)$.

Experiments with *D. viridis* and *Euhalothece* each had three treatment factors producing 45 combinations (3 temperatures × 5 salinities × 3 nitrogen levels). Experiments with *D. viridis* had 3 replicates, for a total of 135 experimental units, and experiments with *Euhalothece* had 5 replicates, for a total of 225 experimental units. Experiments with *N. epithemioides* had four treatment factors producing 135 combinations (3 temperatures × 5 salinities × 3 nitrogen levels × 3 silica levels) with

5 replicates, for a total of 675 experimental units. Experiments were conducted from 2000–2020. This period was required given:

(1) The size of the experiment (1035 experimental units);
(2) Simultaneous studies of brine shrimp (*Artemia franciscana*) feeding (1689 experimental units: Sura et al. 2017; Belovsky et al. 2024a) and population responses (4345 experimental units, Belovsky et al. 2024b) on each phytoplankton species;
(3) Limited environmental chamber space, and.
(4) Experimental logistics.

Experimental units were 50 mL glass tubes with vented caps to allow gas exchange, but minimize evaporation, that contained 40 mL of phytoplankton monoculture solution (Larson 2004; Larson and Belovsky 2013). Tube size was selected in response to difficulties posed by Boyd et al. (2018) for full factorial experiments with phytoplankton (Boyd et al. 2018):

1) necessary replication results in limits due to environmental chamber space and experiment maintenance, which constrains the feasible experimental unit volume;

2) monoculture growth does not address ecological community dynamics (*e.g.,* interspecific competition, grazing, etc.), so that large volumes needed to support food webs are not required;

3) GSL is hypereuthrophic making phytoplankton abundance and growth orders of magnitude greater than in most aquatic systems, so that large volumes are not needed to exhibit large changes;

4) phytoplankton abundance and growth in large volumes requires subsampling for measurement in a fluorometer, which exposes the experimental units to contamination, disturbance and greater effort, while experimental units that can be measured in situ in a fluorometer (*e.g.,* 50 mL tubes) avoids these problems.

Finally, phytoplankton studies have found that smaller volume experimental units can produce reliable results (Owens et al. 1977; Lindström 1983; Moore et al. 1995; Bramucci et al. 2015 Figler et al. 2021; Weisse et al. 2021). Tubes were kept in 8 × 5 racks with adjoining positions vacant to prevent shading.

Tubes were inoculated with either *D. viridis*, *N. epithemioides*, or *Euhalothece* from laboratory monocultures. *N. epithemioides* cultures were first passed through a 54 µm filter to remove cell aggregates. Inoculum of the proper salinity was made to provide a concentration of 5 µg Chl_a/L, as determined using a Turner Design TD-700 fluorometer (sensitivity = 400–600 nm). Fluorescence Signal Unit (FSU) measures were calibrated to chlorophyll abundance (Chl_a, µg/L) using standard methods (Arar and Collins 1997): *D. viridis*: µg/L $Chl_a = 0.55$ FSU-0.54, $r^2 = 0.97$, $N = 10$, $P < 0.00001$; *N. epithemioides*: µg/L $Chl_a = 0.54$ FSU-2.56, $r^2 = 0.99$, $N = 3$, $P < 0.002$; *Euhalothece*: µg/L $Chl_a = 0.21$ FSU-0.33, $r^2 = 0.81$, $N = 9$, $P < 0.005$.

Every 3–4 days (*i.e.,* twice a week) during an experimental run, each tube had:

1) its sides scraped to remove phytoplankton that might adhere to the glass and its contents stirred with a sterile glass rod (used only once per tube) to prevent contamination;

2) a fluorometer reading taken to measure phytoplankton abundance (FSUs converted to µg/L Chl_a, see above).

Subsequently, the rack of tubes was returned to the environmental chamber, rotated 180° from its previous orientation and placed in a new position in the chamber to minimize potential differences in light, fan action, etc.

Plots of phytoplankton abundance vs. time were used to assess when a maximum was asymptotically approached (2–3 consecutive measures within 5% of each other) to end the experimental run. This occurred within 5–6 weeks, as previously reported by Larson and Belovsky (2013). Measures of abundance over time in each tube provided three summary values: maximum abundance, time to achieve the maximum, and growth rate ([maximum Chl_a—the initial 5 µg Chl_a/L]/time to achieve the maximum). Finally, to avoid the possible contamination of experiments, all implements (*e.g.*, spatulas, stirring rods, pipettes, etc.) were used in a single tube on a given day and then autoclaved, and then at the end of the experimental run, possible contamination was examined for by sampling phytoplankton in each tube, and the focal species always comprised > > 90%, indicating the absence of contamination.

Lake sampling

Beginning in 1994, phytoplankton in GSL's South Arm (Gilbert, Carrington, and Ogden Bays, except Farmington Bay; Fig. 1) have been monitored monthly (in some years, not all months were sampled) by the Great Salt Lake Ecosystem Project (GSLEP) as part of the Utah Division of Wildlife Resources (UDWR). Detailed descriptions of sampling procedures and phytoplankton enumeration are outlined in Belovsky et al. (2011).

Statistical analysis

Statistical analyses were conducted using SYSTAT 13. Piece-wise linear regression was used to examine when the phytoplankton species asymptotically approached a maximum density over time. The three summary measures for each species (dependent variables: maximum abundance, time to achieve maximum abundance, growth rate) were examined using ANOVA (3-way for the chlorophyte and cyanophyte: treatments = temperature, salinity, nitrogen; 4-way for the bacillariophyte: treatments = temperature, salinity, nitrogen, silica). Maximum Chl_a data were log_{10} transformed to achieve normality. Significant main

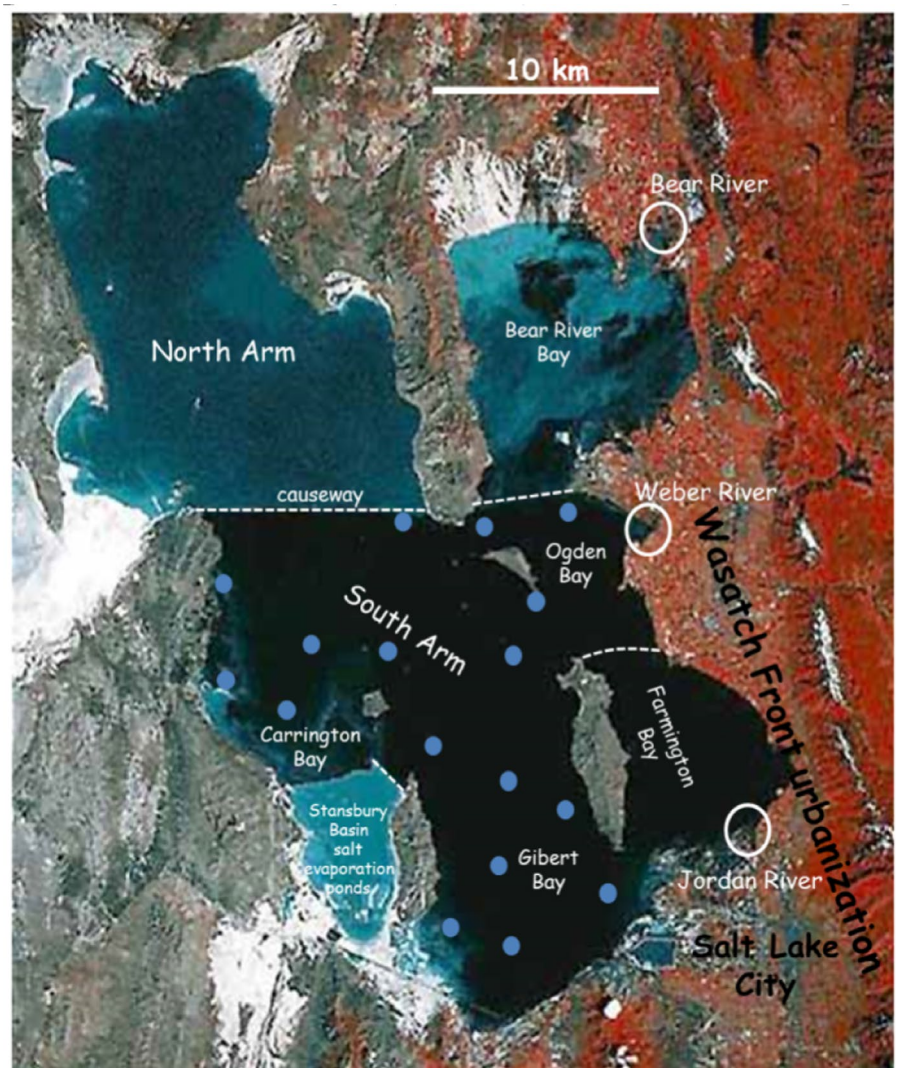

Fig. 1 Image of the Great Salt Lake, Utah, USA (USGS Earth Shots), shows GSLEP sampling locations (blue), river inputs, and causeways (dashed), which create regions that vary in salinity

effects were examined using Tukey's post hoc test to determine which treatment values differed.

GSL South Arm sampling results for the three phytoplankton taxa relative and absolute abundances were examined using regression given observed monthly environmental conditions (*e.g.*, salinity, temperature) from 1994 to 2020. Then our experimental results were compared with the regression results. Finally, we used our experimental results to predict monthly relative abundances of the phytoplankton taxa based on monthly environmental conditions which were then compared with observed monthly phytoplankton relative abundances.

Results

Laboratory experiments

Laboratory data along with treatment means and standard errors are provided in Online Resource 1. Over each 5 to 6-week laboratory experiment, Chl_a linearly approached a maximum asymptote based upon piece-wise regression (example in Fig. 2). This indicates a constant growth rate until carrying capacity was attained, a linear density dependent relationship. All analyses of the experimental responses by each phytoplankton species were based on the maximum asymptote.

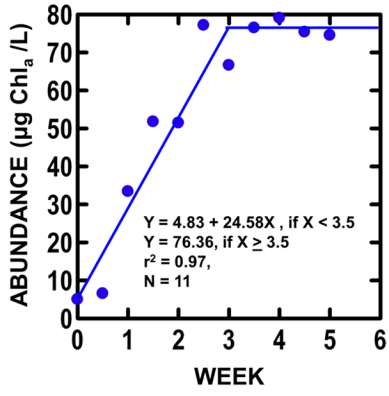

Fig. 2 Example of asymptotic growth to a sustained maximum abundance (Chl_a µg/L: defined by piecewise linear regression) for *Euhalothece*, the cyanobacterium, in laboratory experiments. The results are for temperature = 30 °C, salinity = 30 ppt, and the average of all nitrogen values

D. viridis exhibited the highest average maximum biomass over the experimental treatments (175.6 µg Chl_a/L, SE = 27.4 with *N. epithemiodes* = 118.5 µg Chl_a/L, SE = 8.5 and *Euhalothece* = 99.2 µg Chl_a/L, SE = 13.7). Experimental responses of each phytoplankton species to salinity, temperature, nitrogen, and silica are presented in Fig. 3, along with optimal values and their standard errors (greatest maximum abundance, least time to attain the maximum, and maximum growth rate). ANOVA indicated that all factors and their interactions significantly affected maximum abundance, time to attain the maximum, and growth rate (Fig. 3, Table 1). The combination of factors providing the greatest maximum abundance and growth rate for each species is presented in Table 2.

Performance based on maximum abundance and growth rate for *D. viridis* was greatest at cooler temperatures and higher salinities, while *N. epithemioides* and *Euhalothece* performance was best at higher temperatures and lower salinities. All three species performed better as nitrogen increased. *N. epithemioides* performance also increased with silica (Fig. 3). The proportion of variance explained (measure of effect size) in maximum abundance and growth rate for each species given each treatment is presented in Table 2. For maximum abundance, *D. viridis* was most affected by nitrogen (86.7%), *N. epithemioides* was comparably affected by temperature and nitrogen (47.5 and 40.7%, respectively), and *Euhalothece* was most affected by temperature (64.1%). For growth rate, *D. viridis* was most affected by nitrogen (88.6%) and, *N. epithemioides* and *Euhalothece* were similarly affected by nitrogen and temperature (41.6 and 37.9%; 31.5 and 42.6%, respectively).

Time to attain maximum Chl_a was significantly affected by temperature, salinity, and nitrogen for all three species, and silica for *N. epithemioides* (Fig. 3, Table 1). However, this performance measure was not very instructive, because the time declines as the maximum abundance decreases, *i.e.*, it takes less time to grow less.

Lake sampling

From 1994 to 2020, average annual absolute phytoplankton abundances varied from 8.79–63.33 Chl_a µg/L. Over this period (Online Resource 2: GSLEP database described by Belovsky et al. 2011 and

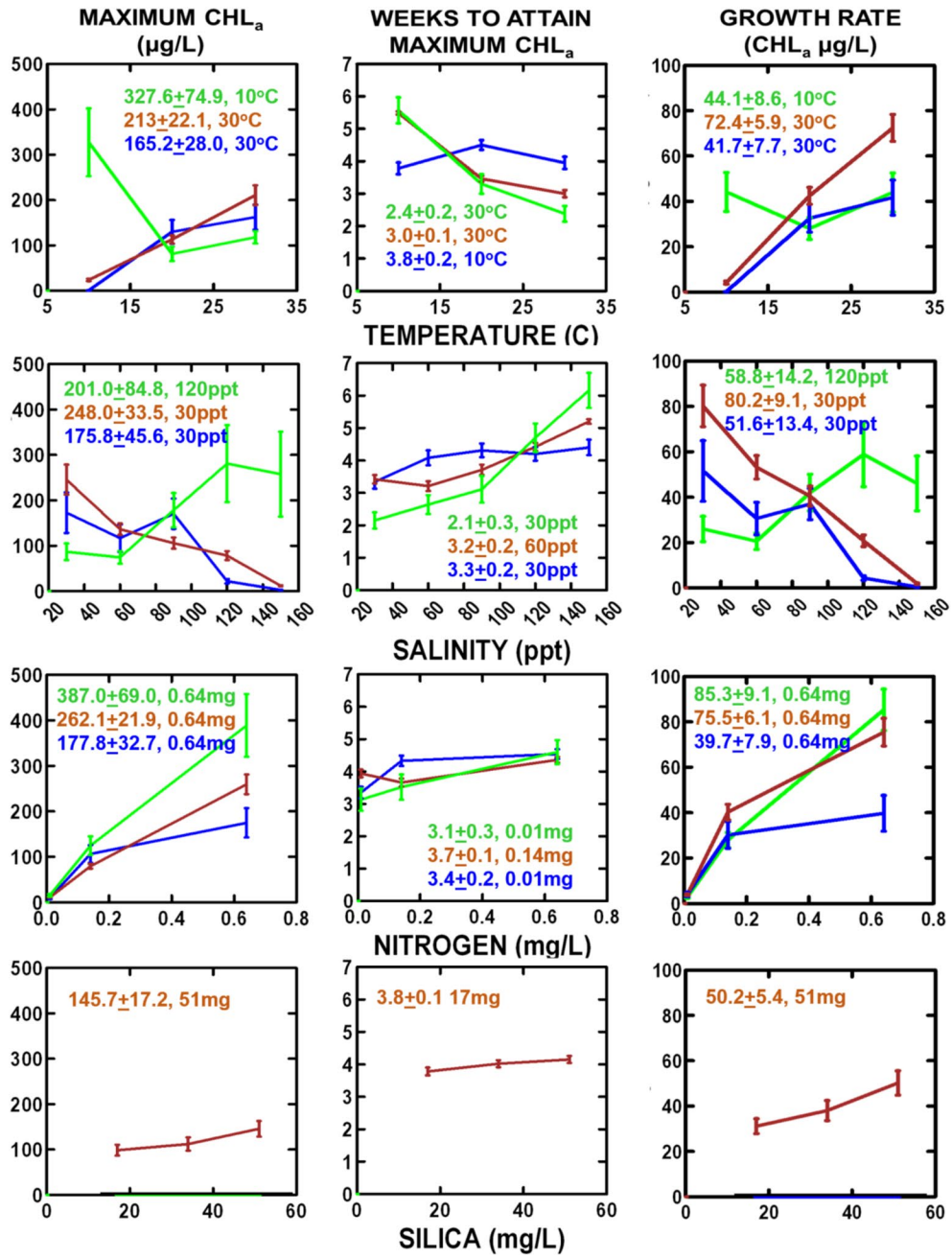

Fig. 3 The ANOVA main effects (rows: temperature, salinity, nitrogen, and silica – only for *Nitzschia epithemioides*), including optimum values and standard errors, from laboratory experiments on phytoplankton responses (columns: maximum Chl$_a$, time to attain maximum Chl$_a$, and growth rate) for the chlorophyte *Dunaliella* viridis (green lines), the diatom *N. epithemioides* (brown lines), and the cyanobacterium *Euhalothece* (blue lines)

several other reports), the chlorophyte, *D. viridis,* dominated in the South Arm as expected, averaging 71.3% (SE = 2.1%, N = 253 months) of annual phytoplankton abundance. However, considerable variation was observed in annual relative and absolute abundances among the three phytoplankton groups

Table 1 ANOVA results (*df* = degrees of freedom, F = F-statistics, *P* = probability) for each of the three phytoplankton species' experimental studies

Independent variables		Max. Chl_a		Time		Growth rate	
	df	F	P	F	P	F	P
Taxa	2, 885	935.19[a]	0.000001	5.64[b]	0.003	25.61[c]	0.000001
Temperature (Temp)	2, 885	975.01	0.000001	259.78	0.000001	99.79	0.000001
Salinity (Sal)	4, 885	297.34	0.000001	146.90	0.000001	35.73	0.000001
Nitrogen (N)	2, 885	1332.64	0.000001	79.16	0.000001	30.50	0.000001
Taxa X Temp	4, 885	321.81	0.000001	98.87	0.000001	38.12	0.000001
Taxa X Sal	8, 885	87.12	0.000001	24.87	0.000001	29.72	0.000001
Taxa X N	4, 885	38.50	0.000001	19.49	0.000001	19.22	0.000001
Temp. X Sal	8, 885	39.28	0.000001	8.95	0.000001	22.03	0.000001
Temp X N	4, 885	14.76	0.000001	12.07	0.000001	21.19	0.000001
Sal. X N	8, 885	3.75	0.0002	5.19	0.000002	8.71	0.000001
Taxa X Temp X Sal	16, 885	10.72	0.000001	12.29	0.000001	6.03	0.000001
Taxa X Temp X N	8, 885	36.50	0.000001	8.89	0.000001	12.43	0.000001
Taxa X Sal X N	16, 885	30.06	0.000001	4.29	0.000001	15.16	0.000001
Temp X Sal X N	16, 885	8.66	0.000001	5.49	0.000001	7.14	0.000001
Taxa X Temp X Sal X N	32, 885	5.93	0.000001	4.00	0.000001	3.13	0.000001

[a]All three species different ($P < 0.000001$)

[b]*Nitzschia epithemioides* and *Euhalothece* not different ($P < 0.68$)

[c]*Dunaliella viridis* and *Nitzschia epithemioides* not different ($P < 0.97$)

Table 2 Observed optimum (maximum) value for each of the three phytoplankton species and the associated temperature, salinity, nitrogen and silica value are listed. In addition, the proportion of variance explained by ANOVA (relative effect) that can be attributed to each factor in experiments is presented

	Maximum values	Relative effect			
		Temperature	Salinity	Nitrogen	Silica
Max Chl_a					
Dunaliella viridis	1526.3 ± 144.7 µg Chl_a/L 10 °C, 150ppt, 0.64 mg N/L	9.8%	3.6%	86.7%	–
Nitzschia epithemioides	1405.8 ± 169.0 µg Chl_a/L 30 °C, 30ppt, 0.64 mg N/L, 51 mg Si/L	47.5%	10.4%	40.7%	1.5%
Euhalothece	554.9 ± 46.2 µg Chl_a/L 30 °C, 90ppt, 0.64 mg N/L	64.1%	17.6%	18.3%	–
Time					
Dunaliella viridis		54.8%	33.4%	11.8%	–
Nitzschia epithemioides		76.2%	17.1%	5.4%	1.3%
Euhalothece		21.5%	15.1%	63.4%	-
Growth rate					
Dunaliella viridis	187.5 ± 7.4 µg Chl_a/L 10 °C, 120ppt, 0.64 mg N/L	4.2%	7.1%	88.6%	–
Nitzschia epithemioides	352.8 ± 25.5 µg Chl_a/L 30 °C, 30ppt 0.64 mg N/L, 51 mg Si/L	37.9%	17.2%	41.6%	3.3%
Euhalothece	139.5 ± 78.6 µg Chl_a/L 30 °C, 30ppt, 0.64 mg N/L	42.6%	25.9%	31.5%	–

–Not included in experiments

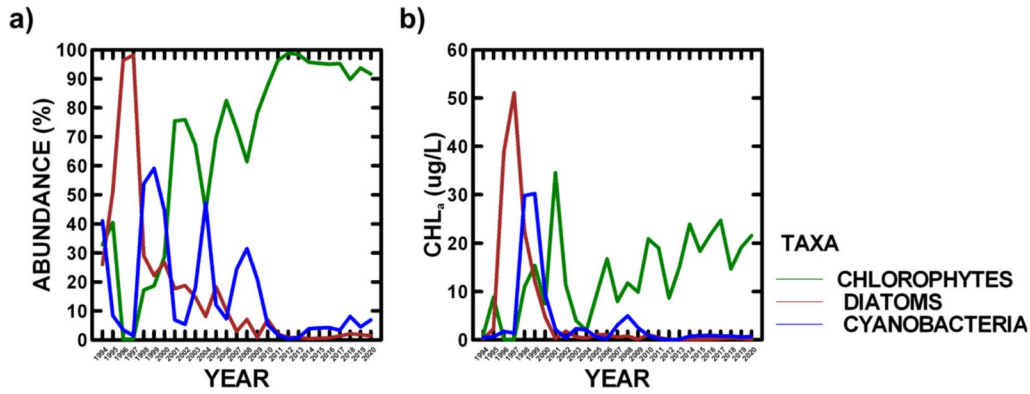

Fig. 4 **a** Annual average phytoplankton relative and **b** absolute abundances (Chl$_a$ µg/L) since 1994 for chlorophytes (green line), diatoms (brown line) and cyanobacteria (blue line). The data sources are provided in Online Resource 2

(chlorophytes, diatoms and cyanobacteria; Fig. 4). Over this 27 year period, annual relative abundance of chlorophytes averaged < 50% in only 8 years with only 4 years < 20%; diatoms averaged > 40% in only 3 years and < 10% in 16 years; and cyanobacteria averaged > 40% in only 5 years and < 10% in 17 years. Annual relative abundance values were significantly correlated with the previous year's relative abundance ($P < 0.000001$– 0.04), but never with annual temperature and salinity values ($P < 0.35$–0.50).

Annual GSL South Arm values do not convey how variable abundances for each taxa can be, as monthly relative values can vary from ~ 0–100% and absolute abundances from 0–135 µg Chl$_a$/L. This may reflect the highly variable monthly changes in temperature and salinity (nitrogen was not considered, because measurements were limited and methodologies changed over the period). Using stepwise regression, monthly temperatures and salinities were compared to monthly relative and absolute abundances (Online Resource 2) with and without including the previous month's relative and absolute abundance (Table 3). The previous month's relative or absolute abundance examines the influence of past conditions.

Chlorophyte relative and absolute abundances were positively affected by increasing salinity with or without the previous month's relative or absolute abundances, and were also negatively affected by

Table 3 Statistically significant stepwise regression results (correlation sign, P = probability, r^2 = coefficient of determination, and N = number of months) for the observed monthly relative and absolute abundances of the three GSL phytoplankton taxa since 1994 (Online Resource 2), as a function of monthly GSL temperature (T) and salinity (S) with and without the previous month's relative or absolute abundance included. Prior month's relative and absolute abundances are always statistically significant

Taxa	Relative					Absolute				
	S	T	r^2	N	P	S	T	r^2	N	P
Chlorophytes										
Without chlorophytes from prior month	+		0.11	250	0.00001	+	–	0.33	226	0.00001
With chlorophytes from prior month	+	–	0.67	223	0.00001	+	–	0.53	201	0.00001
Diatoms										
Without diatoms from prior month	–		0.04	250	0.001	–	–	0.09	226	0.00004
With diatoms from prior month	–		0.43	223	0.00001	–		0.51	201	0.00001
Cyanobacteria										
Without cyanobacteria from prior month	–		0.07	250	0.00003	–	–	0.17	226	0.00001
With cyanobacteria from prior month	–		0.34	223	0.00001	–		0.46	201	0.00001

increasing temperature for all but relative abundance without the previous month's relative abundance (Table 3). This meets our laboratory expectations. Both diatom and cyanobacteria relative and absolute abundances were negatively affected by increasing salinity with or without the previous month's relative or absolute abundances, but temperature had no effect or a negative effect (Table 3). This meets the laboratory expectation for salinity, but not for temperature (positive response expected). Finally, regressions including the prior month's relative or absolute abundances improved the fit (Table 3: $r^2 = 0.04–0.33$ vs. $r^2 = 0.34–0.67$), which indicates the importance of previous conditions.

While GSL chlorophyte relative abundances were well described by experimental expectations, diatom and cyanobacteria were not (Table 3). This can be visualized in Fig. 5. The observed (1994–2020) GSL South Arm monthly temperatures and salinities are shown as a gray region. Pie diagrams at the corners of the gray region are laboratory projected relative abundances of the three phytoplankton taxa, given the observed extreme temperatures and salinities. The stippled region within the gray area denotes favorable conditions for the taxa (relative abundance ≥ 20%) based on laboratory projections. Finally, points are the GSL monthly conditions when the taxa were observed to be ≥ 20%. When chlorophytes are ≥ 20%, they fall within the stippled region 98.7% of the time (228/231). When diatoms are ≥ 20%, they fall within the stippled region only 23% of the time (11/47) and cyanobacteria only 16% of the time (9/56). This suggests that additional factors other than salinity and temperature must be affecting diatom and cyanobacteria relative abundances when they are abundant.

Discussion

It is thought that variability in phytoplankton relative and absolute abundances must be largely due to environmental factors in hypersaline lakes, especially salinity (*e.g.*, Blinn 1993, Padisák and Naselli-Flores 2021). Many studies examine how environmental factors affect hypersaline phytoplankton using spatial and temporal variability in the field, but these results can be misleading compared to laboratory experiments (Niyatbekov and Barinova 2018). This limitation arises because field environmental factors (*e.g.*, temperature, salinity, etc.) may not vary sufficiently and may covary, which makes identification of their impacts difficult to assess via correlation. Therefore, we conducted laboratory experiments growing some of the most common GSL phytoplankton at different salinities, temperatures, and nitrogen availabilities.

The most common GSL South Arm chlorophyte *D. viridis* performed better at lower temperatures and higher salinities, while the common diatom *N. epithemioides* and the common cyanobacterium *Euhalothece* performed better at lower salinities and

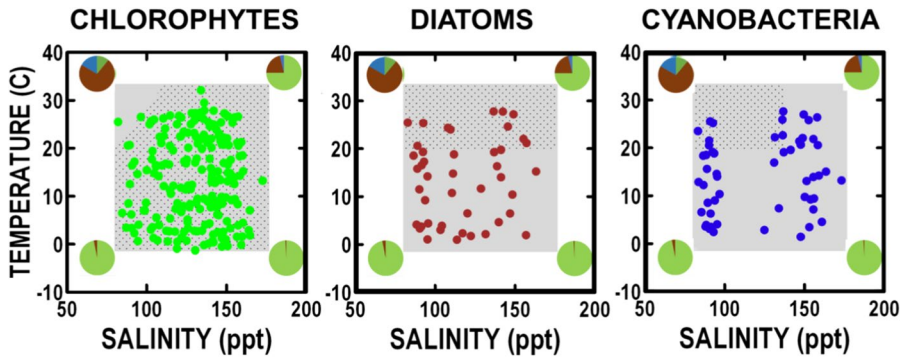

Fig. 5 Monthly chlorophyte, diatom and cyanobacteria relative abundances ≥ 20% since 1994 are plotted (circles) within the range of observed GSL temperatures and salinities (grey region). Pie charts present expected relative abundances of these taxa at extreme temperatures and salinities (corners of grey region) based on maximum abundance of a taxon's representative species in the laboratory divided by the sum of all three representative species' maximum abundances (linear interpolation if temperature and salinity values fall between experimental treatments). The stippled area within the grey region is the range of temperatures and salinities that are expected to produce relative abundances ≥ 20% based on laboratory experiments

higher temperatures. Unlike our laboratory studies, most studies in the literature are short term (days vs. our 5–6 weeks), and only report growth (increase in cell density for biotech culturing), not maximum abundance (carrying capacity). These studies with *D. viridis* find better performance as salinity increases (Gibor 1956; Johnson et al. 1968; Brock 1975; Jiménez and Niell 1991a, b; Garcia et al. 2007; Oren 2014), which agree with our findings. Unlike our result, some of these studies report better performance at higher temperatures (Gibor 1956; Jiménez and Niell 1991a, b; Garcia et al. 2007). The few studies with *Nitzschia* spp. indicate better performance at lower salinities (Nübel et al. 2000; Clavero et al. 2008; Kelly et al. 2014), and studies with other closely related diatoms find better performance as temperature increases, which agree with our findings (Montagnes and Franklin 2001; Adenan et al. 2013; Sugie et al. 2020). Some of the few studies with *Euhalothece* spp. find better performance as salinity declines (Bhatt et al. 2016), as we do, while others find better performance as salinity increases (Mogany et al. 2018), and all observe better performance as temperature increases, as we do (Bhatt et al. 2016; Mogany et al. 2018). Finally, our laboratory studies with *D. viridis*, *N. epithemioides, and Euhalothece* sp. found better performance with increased nitrogen; however, *Euhalothece* was less responsive to nitrogen, which is consistent with their ability to fix nitrogen (Mogany et al. 2018).

We also report here trends in annual and monthly phytoplankton relative and absolute abundances of the most dominant phytoplankton groups (chlorophytes, diatoms, and cyanobacteria) within the GSL South Arm over a 27-year period as reported by various researchers (Figs. 2 and 5; Online Resource 2). The abundance values varied dramatically. Variation in chlorophyte abundance was explained by our experimental results for *D. viridis*, given monthly changes in temperature and salinity (Table 3; Fig. 5). While decreasing salinity has been proposed to increase cyanobacteria and especially diatom abundances (Felix and Rushforth 1977, 1980; Blinn 1993; Larson and Belovsky 2013), their variability was not explained very well by our experimental results for *Euhalothece* and *N. epithemioides*, given monthly changes in salinity and temperature (Table 3; Fig. 5). In fact, diatom and cyanophyte abundances generally were greater at higher salinities and lower temperatures than predicted by our laboratory studies (Fig. 5). These results suggest that something in addition to salinity and temperature is important to diatom and cyanophyte relative abundances in the lake.

Grazing on the phytoplankton might be an additional factor that affects relative abundances. There are protozoan grazers in the lake, but they are not abundant in the pelagic zone (194.7 #/mL ± 124.5 SE: Belovsky et al. 2011) and are more associated with the benthos. However, brine shrimp (*Artemia franciscana*) are dominant grazers, that can seasonally reduce phytoplankton abundance (Stephens and Gillespie 1976; Wurtsbaugh and Gliwicz 2001; Belovsky et al. 2011). For example, average phytoplankton abundance declines from 46.0 ± 7.8 (SE) μg Chl_a/L in April to 9.9 ± 2.0 (SE) μg Chl_a/L from June–September (Belovsky et al 2011), when brine shrimp are most abundant. This grazing would not affect phytoplankton relative abundances if brine shrimp do not feed selectively (Reeve 1963), but brine shrimp preferentially feed on *D. viridis* (Belovsky et al. 2024a), which should further increase diatom and cyanobacteria relative abundance during these warmer summer months above our experimental expectations, which was not observed. Therefore, we discount grazing of the phytoplankton as an additional factor.

Competition among phytoplankton might be an additional factor affecting relative abundances, but this is often discounted as a single species overwhelmingly dominates phytoplankton communities in most hypersaline lakes (Padisák and Naselli-Flores 2021). However, Brock (1975) suggests that GSL *Dunaliella* may be more abundant at higher salinities, because they are restricted to high salinities by competition with cyanobacteria at lower salinities. However, competition does not explain this, because we found that *D. viridis* monocultures performed best at higher salinities, and *Euhalothece* monocultures performed best at lower salinities. Larson (2004) found *D. viridis* and *Carteria* sp. from GSL exhibit competition in laboratory experiments over a range of salinities, but this was of minor importance relative to their salinity tolerances. Therefore, performance at different salinities for each taxa does not depend on the presence or absence of another taxa, which discounts competition as an additional factor.

Influxes of cyanobacteria and especially diatoms from freshwater inputs, such as surrounding wetlands

and hypereutrophic Farmington Bay might be an additional factor (Felix and Rushforth 1977, 1980; Blinn 1993), as increases in diatom and cyanobacteria relative abundances appear as occasional spikes (≥ 20%: Fig. 4). These areas have phytoplankton and periphyton abundances that are ~ 5% of the South Arm's phytoplankton abundance (Table 4); therefore, even a release of all this biomass to the South Arm is unlikely to produce the observed spikes in diatom and cyanobacteria relative abundances. Furthermore, species of diatoms and cyanobacteria in these areas of fresher waters are not those observed in the South Arm (Marcarelli et al. 2006; Wurtsbaugh and Marcarelli 2005, 2006; Wurtsbaugh et al. 2008, 2012). Therefore, we discount outside influxes of fresher waters, as an additional factor.

Release of cyanobacteria and diatoms into the GSL South Arm phytoplankton from the benthos might be an additional factor. Microbialites cover 34% of the benthos, the world's greatest abundance (700 km^2: Baskin 2014), and are carbonate structures created by a productive biofilm with periphyton composed of approximately 22% diatoms and 74% cyanobacteria (Lindsay et al. 2019; Anderson et al. 2020; Barrett 2020). The average periphyton abundance is 470% greater than South Arm phytoplankton abundance (Table 4). A release of only 5–10% of the biomass from this periphyton can increase diatoms and cyanobacteria in the phytoplankton to 24–48% relative abundances. Interestingly, the periphyton annually can decline by as much as 50% from its peak (Barrett 2020), which is more than sufficient to increase diatom and cyanobacteria abundances within the phytoplankton. Furthermore, species from two diatom genera, *Nitzschia* and *Navicula* and the cyanobacterium *Euhalothece*, which are common in the phytoplankton of the South Arm, are dominant within the periphyton (Lindsay et al. 2019; Barrett 2020). Therefore, microbialite proximity to the pelagic zone, its periphyton abundance and its species composition could be the source of diatom and cyanobacteria spikes in the phytoplankton (Fig. 4 and 5).

Release from the microbialite periphyton might occur with grazing by benthic brine fly larvae (*Ephydra cinerea* Packard 1871 and *Cirrula hians* Say, 1830) on microbialite periphyton (Collins 1980). Brine fly larvae preferentially consume diatoms, so their scraping releases cyanobacteria into the water column (Cato, Chambers and Belovsky unpubl.). As for brine shrimp grazing, this cannot be the explanation of diatom and cyanobacteria spikes, because this should further increase diatom and cyanobacteria relative abundance during the warmer summer months when brine fly larvae are most abundant, which is opposite of when spikes occur.

Release from the microbialite periphyton might occur if the periphyton is stressed. Microbialite periphyton laboratory studies (Anderson et al. 2020) find a negative response to cool temperatures and increasing salinity, and a positive response to nitrogen, similar to our responses observed for *N. epithemioides* and *Euhalothece* (Fig. 3). Furthermore,

Table 4 Pelagic and benthic primary producer abundance in Great Salt Lake

	Area[a]	Depth[a]	Total	Density	Pimary producer abundance
Pelagic					
	2056 km^2	4.5 m	9.3 X 10^{12} L	24.9 µg Chl_a/L[b]	2.30 X 10^{14} µg Chl_a
Farmington					
	140 km^2	0.76 m	1.1 X 10^{11}L	110 µg Chl_a/L[c,d]	1.17 X 10^{13} µg Chl_a
Wetlands					
	1460 km^2	0.3 m	4.4 X 10^{11}L	27 µg Chl_a/L[e]	1.19 X 10^{13} µg Chl_a
Microbialite					
	700 km^2		7 X 10^8 m^2	155.2 X 10^4 µg Chl_a/m^2[f]	1.09 X 10^{15} µg Chl_a

[a]Baskin, 2005

[b]GSLEP database

[c]McCulley et al. 2015

[d]Wurtsbaugh et al. 2008

[e]Pendleton et al. 2020

temperature is far more important to the microbialite diatom-cyanobacteria periphyton (Anderson et al. 2020) and phytoplankton laboratory abundances than salinity (Table 2). Therefore, cold temperatures may stress microbialite periphyton and cause a release of diatoms and cyanobacteria; this hypothesis is supported as 30/36 ($\chi^2_{1\text{-sided}} = 16$, $P < 0.000001$) diatom and 29/47 ($\chi^2_{1\text{-sided}} = 2.6$, $P < 0.05$) cyanobacteria monthly spikes occur in September–February when temperatures decrease.

With cold stress, physical disturbances may release weakened periphyton into the phytoplankton. A likely disturbance is wind created waves, seiches, turbulence and upwelling, which are powerful forces in shallow playa lakes with a large surface area like GSL (MacIntyre and Melack 1995; Hamilton and Mitchell 1996; Pannard et al. 2011; Zhou et al. 2015; Smith et al. 2024). Furthermore, microbialites are particularly vulnerable as they are typically found on average < 1 m below the surface. Diatom and cyanobacteria abundances ≥ 20% are positively correlated (Table 5) with average monthly wind speed squared (correlate of shear-force: Talley et al. 2011), and negatively correlated with temperature, which supports the hypothesis of stress and disturbance (Table 5). Abundances < 20% are not correlated with wind and positively correlated with temperature (Table 5), as expected from our laboratory experiments. Therefore, we suggest that increased winds may scour microbialites, which releases diatoms and cyanobacteria into the phytoplankton from cold stressed periphyton.

Several observations question the above hypothesis for microbialite periphyton release. First, the spikes in diatom and cyanobacteria relative abundances are not similar to microbialite periphyton composition. This may be due to differential responses of diatoms and cyanobacteria in the periphyton to temperature and the physical structure of microbialites which may result in differential release. We know that temperature responses of the periphyton and planktonic cyanobacteria and diatoms differ slightly (Fig. 3, Anderson et al. 2020), and microbialite periphyton structure has cyanobacteria producing a sticky matrix and diatoms, with their silica frustule, providing rigidity (Winsborough and Golubic 1987; Reid et al. 2000). Second, microbialites were abundant before salinity declined in the South Arm with causeway construction (Collins 1980; Baskin 2014; Anderson et al. 2020), but prior diatom and cyanobacteria spikes in the phytoplankton were not reported. Unfortunately, as pointed out above, phytoplankton sampling was neither frequent nor quantitative.

The potential linkage between the benthic microbialite periphyton and the pelagic phytoplankton needs to be investigated further. A future avenue might attempt to distinguish benthic and pelagic produced diatoms and cyanobacteria of the same species found in the microbialite periphyton and phytoplankton using a combination of molecular (Baxter 2018; Brown et al. 2022) and stable isotope techniques (Naftz et al. 2008), as recently employed in other GSL studies. If the source of diatoms and cyanobacteria can be distinguished, absolute abundance of each must be quantified, which requires qPCR of 16S and 18S RNA (Yeh et al. 2021), not just simple PCR (Baxter 2018; Brown et al. 2022).

Nonetheless, the possible large release of microbialite periphyton into the phytoplankton may represent a novel linkage between the pelagic and benthic zones that can be important to aquatic ecosystems (Vadeboncoeur et al. 2002; Vadeboncoeur and Power 2017). This link may be important to the GSL South Arm food web. First, pelagic feeding brine shrimp abundance declines when diatoms are abundant (Belovsky et al. 2011) and their production of commercially harvested overwintering cysts is dramatically reduced (Belovsky and Perschon 2019). Second whether periphyton release affects fly larvae abundance that relies on it for food and pupal attachment is unknown. Finally, brine shrimp and brine fly larvae

Table 5 Multiple regression results (positive or negative, P = probability, r = correlation coefficient, and N = number of months) for diatoms and cyanobacteria relative abundances ≥ 20% expected to be > 20% (Fig. 5), and < 20% in the phytoplankton when expected to be < 20% (Fig. 5), given wind shear (wind^2), temperature, salinity, and taxa. Blank cells are not statistically significant ($P < 0.15$)

Data	N, r	Wind^2	Temperature	Salinity	Taxa
Abundance ≥ 20%	102, 0.39	+, $P < 0.0002$	−, $P < 0.05$		$P < 0.10$
Abundance < 20%	400, 0.20		+, $P < 0.03$		$P < 0.0001$

are abundant food sources that attract the migration of many species of waterbirds to GSL. Therefore, this potential link between the benthos and phytoplankton has important conservation and economic impacts.

Conclusion

Common Great Salt Lake chlorophyte, diatom and cyanobacteria phytoplankton responses to temperature, salinity and nitrogen in laboratory monocultures were compared to their observed monthly relative abundances in the lake from 1994 to 2020, given monthly temperatures and salinities. Chlorophyte relative abundance was highly correlated with temperatures and salinities favorable for growth in the laboratory, but correlations for diatoms and cyanobacteria were weak. Rather, Great Salt Lake diatoms and cyanobacteria relative abundances occasionally spiked at temperatures and salinities unfavorable for their growth in the laboratory. Possible explanations (brine shrimp grazing, phytoplankton competition, and freshwater inflow sources) for these spikes were examined and discounted. One endogenous source, the benthic microbialite periphyton appears to be a promising explanation for these spikes.

Microbialite periphyton is very abundant and almost entirely composed of the diatom and cyanobacteria species observed in the phytoplankton. Laboratory studies by Anderson et al. (2020) indicate that winter cold temperatures should stress this periphyton, and we suggest that wind disturbances may dislodge stressed periphyton into the phytoplankton. Therefore, a benthic-pelagic linkage may exist, which needs to be more thoroughly investigated. However, our observations of this possible linkage may be expected given the growing list of linkages between benthic and pelagic zones in freshwater lakes (Genkai-Kato et al. 2012; Brothers et al. 2016), marine areas (Christianen et al. 2017; Griffiths et al. 2017) and hypersaline lakes (MacIntyre and Jellison 2001; MacIntyre and Melack 1995).

When relative abundances of diatoms and cyanobacteria periodically spike, the pelagic filter-feeding brine shrimp (*Artemia franciscana*) tend to decrease in abundance (Belovsky et al. 2011). Release of microbialite periphyton may reduce food and pupation sites for brine fly larvae (*Ephydra cinerea* and *Cirrula hians*) that live on microbialites. Fewer brine shrimp and brine fly larvae result in less food for waterbirds, and fewer brine shrimp may lead to lower production of their overwintering cysts that can be commercially harvested for the aquaculture industry (Belovsky and Perschon 2019). Therefore, the microbialite-phytoplankton linkage has important food web, conservation, and economic consequences. Finally, in these times of increasing Great Salt Lake salinities and temperatures (Barrett and Belovsky 2020) with anthropogenic diversion of water from Great Salt Lake inflows and climate change, impacts on phytoplankton and the benthic-pelagic linkage need to be a concern for management to conserve these ecological and economic values of the lake.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

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