Winter phytoplankton communities of Utah Lake, Utah, USA

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Abstract

Phytoplankton samples were collected from ice-covered Utah Lake during February and March, 1979 in order to characterize the winter algal flora. These samples were analyzed for presence and abundance of diatoms and non-diatom algae as well as selected water chemical parameters. A total of 159 diatom taxa and 20 non-diatoms was found in the water column under the ice. The flagellates *Carteria stellifera, Euglena gracilis* and *Chlamydomonas globosa* dominated the winter non-diatom flora while *Stephanodiscus* cf. *dubius, Cyclotella meneghiniana, Navicula minima, Fragilaria construens* var. *venter*, and *Melosira granulata* var. *angustissima* dominated the winter diatom flora. Species richness and abundance were elevated in the major bays of the lake.

Introduction

Phytoplankton ecology of lakes and reservoirs in northern hemisphere temperate zones has been a matter of much study during the past several decades, and the literature is quite extensive. However, the majority of this work has been done during the summer and to a lesser extent during spring and fall. Relatively little phytoplankton work has been performed in the winter, especially on cold temperate and alpine lakes which freeze over. Because of this, a paucity of information exists on phytoplankton populations during cold weather months, especially on populations occurring beneath ice cover.

Even though winter phytoplankton studies are few, some important studies have been performed. Interest in such work was sparked by Rodhe (1955) who reported on plankton communities from ice covered Swedish Lappland Lakes. He found, unexpectedly, that nannoplankton ('μalgae') were extremely abundant beneath the ice. The occurrence of substantial nannoplankton populations in ice covered lakes has since been documented in several other localities including high altitude lakes in Colorado (Pennak, 1968; Keefer & Pennak, 1977; Herrmann, 1978), lakes and ponds of the eastern United States (Wright, 1964; Campbell & Haase, 1981), a mountain lake in Japan (Maeda & Ichimura, 1973), shallow lakes in western Canada (Hickman & Jenkerson, 1978; Hickman, 1979; Moore, 1980), European ice covered lakes (Ferrari, 1976; Pechlaner, 1971; Rodhe *et al.*, 1966) and lakes in Antarctica (Goldman *et al.*, 1967; Light *et al.*, 1981). These authors and others have provided important baseline data for the study of winter phytoplankton communities.

We have recently studied the algal plankton flora beneath the ice of Utah Lake, Utah, USA. The goals of the study were to determine which species dominate the winter phytoplankton community of Utah Lake and to determine if the algal population beneath the ice was homogenous or patchy.

Site description

Utah Lake is a large freshwater lake located in

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central Utah, USA (Fig. 1). The lake occurs at the eastern edge of the Great Basin Geological Province just at the western edge of the Wasatch Mountains which are a major unit of the Rocky Mountain Geological Province. The lake is a remnant of the very large Pleistocene Lake Bonneville which receded to the present Utah Lake and Great Salt Lake some 10 000 years ago. Present day Utah Lake

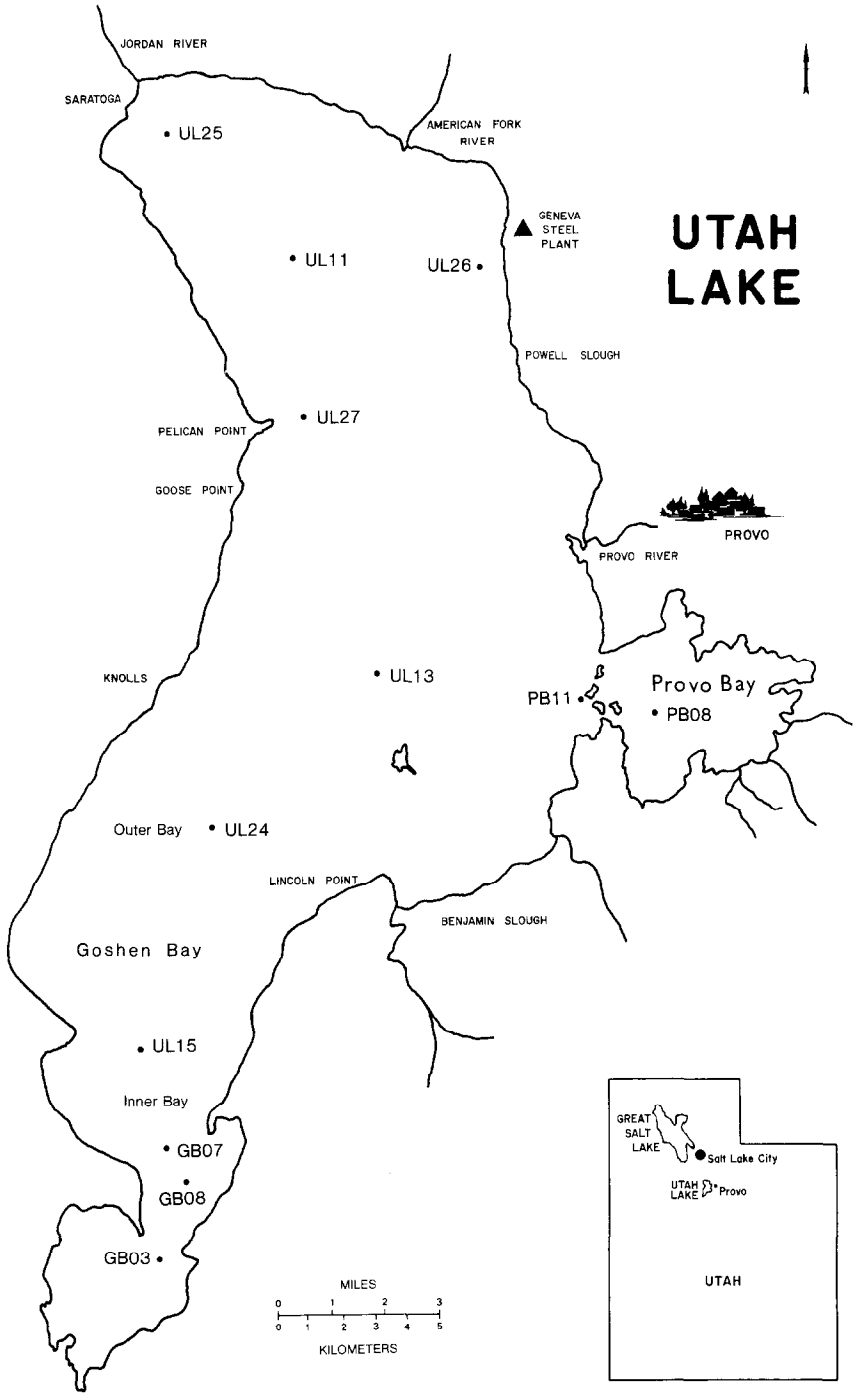

Fig. 1. Reference map of Utah Lake showing prominent geographical features and historical collecting localities.

is approximately 385 km^2 in area with a mean depth of 2.9 m. It is divided naturally into three geographic areas, the main body of the lake, a shallower southern arm known as Goshen Bay, and a large eastern portion, Provo Bay (Fig. 1).

The watershed area of Utah Lake is composed of a wide array of rock types but with a predominance of sedimentary forms that are easily erodable and rich in nutrients. In addition, the drainage basin supports roughly 250 000 human inhabitants with a significant amount of farming and livestock grazing. Consequently, the lake contains elevated levels of total dissolved solids (TDS) and has been characterized as having poor water quality (Dustin, 1978; Dustin & Merritt, 1980). The lake has been classified as hypereutrophic (Dustin & Merritt, 1980; Fuhriman *et al.*, 1981), but because it has TDS values ranging between 800 and 1700 mg l^{-1} (Rushforth *et al.*, 1981a) it might best be considered as being mildly saline (Hem, 1970) or saline-eutrophic (Squires *et al.*, 1979; Grimes & Rushforth, 1983).

The number of algal species present in the lake is unusually high (Grimes & Rushforth, 1982; Rushforth & Squires, 1985) with a total of more than 500 diatom and 200 non-diatom algae having been identified during the past 50 years. Large blue-green algal blooms occur during summer and fall months (Squires *et al.*, 1979; Whiting *et al.*, 1978) with standing crops as high as 78 000 organisms ml^{-1} reported (Rushforth *et al.*, 1981a).

Methods

Samples for phytoplankton analyses were collected from selected sites established throughout the lake. Samples from the main body of the lake and the two bays were collected during October 1978, and March and April 1979 from 12 long established localities (Fig. 1) known as Historic Sites (Rushforth *et al.*, 1981b). The March samples were collected on March 10, 1979 as ice was just beginning to break up in the lake. To augment the winter data a set of 17 phytoplankton samples was collected during February and the first week of March 1979 from localities throughout Goshen Bay. All of these samples were collected under complete ice cover by chopping or drilling holes through the ice.

All samples for phytoplankton analysis were collected by placing two liters of water from the upper water column directly into jars. In addition, four liters of water were collected from each site for selected chemical analyses. All samples were subsequently returned to the laboratory for study.

Chemical analyses were performed on water samples using standard methods (APHA, 1975) by the Environmental Analysis Laboratory, Department of Civil Engineering, Brigham Young University. A total of 18 analyses was performed on all water samples.

Initial identification of phytoplankton was performed by examining fresh samples on Zeiss RA microscopes. Following identification, organisms were enumerated using Palmer-Maloney counting chambers (Palmer & Maloney, 1954).

Permanent diatom slides were prepared from samples after they had been enumerated. Strewn mounts were prepared following standard nitric acid oxidation techniques and using Naphrax high resolution mounting medium. Diatoms were subsequently examined with Nomarski and bright field objectives, and when present, 400 valves were counted in order to calculate relative density for each species.

Several statistical analyses were performed on the data. An Important Species Index was calculated for each taxon by multiplying its frequency of occurrence by its average percent relative density (Ross & Rushforth, 1980; Kaczmarska & Rushforth, 1983). This method is often superior to using average density or percent presence alone since it takes both the abundance and distribution of each taxon into account. Diversity of each sample was calculated by two methods. The first was species richness, or the total number of taxa encountered in each site. The second was by calculating Shannon-Weaver diversity indices (Shannon & Weaver, 1963; Patten, 1962). We also calculated similarity indices of each site to each other site (Ruzicka, 1958), and clustered these using unweighted pair-group clustering techniques (Sneath & Sokal, 1973) to determine if floristic patterns were evident.

Results

Water chemistry

Average values for 18 water chemical parameters taken over four years during all seasons from 6 of

Table 1. Water chemical parameters for selected Historical Sites in Utah Lake. Means and standard deviations in Part A are for approximately 20 samples collected from 1977 to 1980. Part B contains data for a single set of collections obtained March 10, 1979. Locations of the sites given in this table are shown in Fig. 1.

PART A

Site	Chemical factor – mg/l																	
		SiO2	TURB*	Ca	Mg	Na	K	HCO3	C1	SO4	TDS	COND*	pH	ALK*	HARD*	TKN	NO3	T-P	O-P
GB07	Means	25	56	53	64	194	18	251	259	259	994	1610	8.3	212	397	1.2	0.16	0.07	0.01
(Inner Bay)	S.D.	6	24	9	6	39	2	34	53	33	125	181	0.2	25	35	0.8	0.14	0.04	0.01
UL15	Means	25	60	54	61	181	17	257	236	244	938	1501	8.3	215	386	1.9	0.18	0.06	0.03
(Midbay)	S.D.	6	26	9	5	25	2	30	29	41	81	121	0.3	22	28	2.1	0.18	0.05	0.04
UL24	Means	26	44	54	61	179	18	246	234	245	933	1511	8.4	207	387	1.3	0.18	0.07	0.02
(Outer Bay)	S.D.	5	28	8	5	24	2	30	29	32	76	111	0.2	22	26	0.9	0.18	0.07	0.02
UL13	Means	25	40	54	60	176	17	247	229	242	927	1507	8.4	208	383	0.9	0.19	0.07	0.02
(Main Lake)	S.D.	4	22	7	4	26	2	32	33	37	87	136	0.2	24	20	0.6	0.18	0.05	0.03
UL11	Means	25	55	53	60	173	17	252	222	246	919	1493	8.4	212	381	0.9	0.17	0.08	0.02
(Main Lake)	S.D.	4	31	10	5	22	2	32	31	25	73	91	0.3	24	24	0.5	0.16	0.07	0.02
PB08	Means	16	52	54	43	108	10	234	129	163	649	1091	8.5	204	314	2.1	0.12	0.23	0.05
(Provo Bay)	S.D.	8	34	8	9	32	3	31	45	40	128	203	0.3	26	35	2.0	0.14	0.16	0.04

PART B

GB07	28	50	67	78	310	25	294	430	280	1370	2100	8.4	241	490	0.4	0.07	0.04	0.01
UL15	30	20	61	70	220	19	272	280	280	1100	1700	8.5	232	440	0.3	0.05	0.014	0.003
UL24	31	6	62	73	220	19	268	280	280	1110	1700	8.4	228	460	0.3	0.03	0.015	0.003
UL13	30	7	62	63	200	18	266	260	260	1040	1600	8.5	230	420	0.5	0.13	0.015	0.018
UL11	30	4	62	66	200	19	259	260	240	1040	1600	8.4	221	420	0.5	0.09	0.03	0.025
PB08	16	16	72	32	64	6	270	60	112	501	820	8.4	228	310	0.9	0.48	0.35	0.14

*Turbidity is in Formazin turbidity units, conductivity in umhos/cm, alkalinity and hardness as mg/l CaCO3.

the historic sites in Utah Lake are presented in Table 1, Part A. The results of these analyses demonstrated that the lake was turbid, high in several dissolved salts and generally nutrient rich. These results for the most part confirm those reported in previous studies (Dustin & Merritt, 1980; Fuhriman *et al.*, 1981). The lake was essentially homogenous except for Provo Bay and inner Goshen Bay. Provo Bay had elevated nutrients and lowered TDS while inner Goshen Bay showed elevated TDS levels.

The results of chemical analyses performed March 10, 1979 are presented in Table 1, Part B. The winter sites in Goshen Bay had higher levels of several dissolved salts than main lake sites with inner Goshen Bay being notably higher. Provo Bay was much lower in several salts and had higher nutrient levels than occurred at other sites. The two bays were more turbid than the main body of the lake during the winter, but still generally less turbid than the four year all season averages.

General description of the winter flora

The winter phytoplankton flora in Utah Lake was composed predominantly of the unicellular flagellates, *Carteria stellifera, Chlamydomonas globosa,* and *Euglena gracilis.* In the main body of the lake, the actual occurrence of these taxa was patchy and some sites had only one or two of the three species. Considerable variability in abundance from site to site was also observed. Only three other species of non-diatom algae were collected in any of the sites from the main body of the lake. These were *Ankistrodesmus convolutus, Euglena proxima* and *Micratinium pusillum.* Many additional non-diatom taxa were collected in the bays together with the dominant flagellates. For instance, a total of 30 taxa was collected in Provo Bay, and 26 taxa occurred in Goshen Bay.

Diatom occurrence and abundance in the winter flora of Utah Lake was variable, ranging from extremely rare or absent in some samples to more than 200 cells ml in others. The most important taxon in the diatom flora was a small species of *Stephanodiscus* which we have tentatively identified as *Stephanodiscus dubius* (Fricke) Hust. This alga dominated the flora in almost every stand where diatoms occurred in high numbers, usually comprising between 20 and 40% of the frustules in a sample. The other species contributing a major portion of the flora throughout the lake were *Cyclotella meneghiniana, Melosira granulata* var. *angustissima, Navicula minima* and *Stephanodiscus astrea* var. *minutula.* These five taxa contributed between 50 and 70% of the total diatom population in sites throughout the study area except for those in Provo Bay and inner Goshen Bay. In Provo Bay *Stephanodiscus* cf. *dubius* was especially dominant, and the five abundant species made up 87% of the flora. In inner Goshen Bay the relative importance of these major species was lower than in the rest of the lake.

Table 2. Alphabetical list of non-diatom algae collected under the ice in Goshen Bay during the winter of 1979.

Ankistrodesmus convolutus Corda
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus falcatus var. *mirabilis* (West & West) G. S. West

Anabaena spiroides var. *crassa* Lemm.

Aphanizomenon flos-aquae (Lemm.) Ralfs

Carteria stellifera Nyg.
Carteria species

Chlamydomonas altera Skuja
Chlamydomonas globosa Snow
Chlamydomonas polypyrenoideum Pres.
Chlamydomonas species

Closteriopsis longissima var. *tropica* West & West

Coelastrum microporum Naeg.

Dictyosphaerium ehrenbergianum Naeg.

Euglena gracilis Kleb.
Euglena oxyuris Schmarda
Euglena proxima Dang.

Kirchneriella lunaris (Kirch.) Moeb.
Microcystis incerta Lemm.

Oocystis gloeocystiformis Borge

Phacus chloroplastes Pres.

Scenedesmus bijuga var. *alterans* (Rein.) Hansg.
Scenedesmus quadricauda (Turp.) Breb.

Schroederia setigera (Schroed.) Lemm.

Trachelomonas crebea (Kill.) Defl.

Wislouchiella planktonica Skv.

Goshen Bay flora

Table 2 presents a list of 26 non-diatom algal taxa collected from under the ice at the Goshen Bay Winter Sites. Three of these were Cyanophyta, 18 were Chlorophyta and five were Euglenophyta. In addition a total of 159 diatom taxa was present in the ice covered waters (Table 3). The genera *Navicula* and *Nitzschia* contained a disproportionate number of these taxa just as they do during the entire year (Rushforth & Squires, 1985).

Table 3. Alphabetical list of diatoms collected under the ice in Goshen Bay during the winter of 1979.

Achnanthes affinis Grun.
Achnanthes lanceolata (Breb.) Grun.
Achnanthes lanceolata var. *dubia* Grun.
Achnanthes linearis (W. Sm.) Grun.
Achnanthes minutissima Kuetz.
Achnanthes pinnata Hust.
Achnanthes sublaevis var. *crassa* Reim.

Amphipleura pellucida Kuetz.

Amphora ovalis (Kuetz.) Kuetz.
Amphora ovalis var. *affinis* (Kuetz.) V.H. ex DeT.
Amphora perpusilla (Grun.) Grun.
Amphora veneta Kuetz.

Anomoeoneis sphaerophora (Ehr.) Pfitz.
Anomoeoneis vitrea (Grun.) Ross

Asterionella formosa Hassall

Bacillaria paradoxa Gmelin

Caloneis amphisbaena (Bory) Cl.
Caloneis bacillum (Grun.) Cl.
Caloneis fenzlioides Cl.-Eul.
Caloneis limosa (Kuetz.) Patr.
Caloneis oregonica (Ehr.) Patr.

Cocconeis diminuta Pant.
Cocconeis disculus (Schum.) Cl.
Cocconeis pediculus Ehr.
Cocconeis placentula Ehr.
Cocconeis placentula var. *euglypta* (Ehr.) Cl.
Cocconeis placentual var. *lineata* (Ehr.) V.H.

Cyclotella bodanica Eulen.
Cyclotella kuetzingiana Thwaites
Cyclotella meneghiniana Kuetz.
Cyclotella ocellata Pant.
Cyclotella striata var. *ambigua* Grun.

Cymatopleura elliptica (Breb.) W. Sm.
Cymatopleura solea (Breb.) W. Sm.

Cymbella affinis Kuetz.
Cymbella cymbiformis Ag.
Cymbella inaequalis (Ehr.) Rabh.
Cymbella mexicana (Ehr.) Cl.
Cymbella minuta Hilse ex Rabh.
Cymbella muelleri Hust.

Denticula subtilis Grun.
Denticula tenuis Kuetz.

Diatoma hiemale (Roth) Heib.
Diatoma tenue var. *elongatum* Lyngb.
Diatoma vulgare Bory

Diploneis elliptica (Kuetz.) Cl.
Diploneis marginestriata Hust.
Diploneis pseudovalis Hust.

Entomoneis alata (Ehr.) Ehr.

Epithemia argus var. *protracta* A. Mayer
Epithemia ocellata (Ehr.) Kuetz.
Epithemia turgida (Ehr.) Kuetz.

Fragilaria brevistriata Grun.
Fragilaria brevistriata var. *inflata* (Pant.) Hust.
Fragilaria construens (Ehr.) Grun.
Fragilaria construens var. *binodis* (Ehr.) Grun.
Fragilaria construens var. *pumila* Grun.
Fragilaria construens var. *venter* (Ehr.) Grun.
Fragilaria similis Krasske
Fragilaria vaucheriae (Kuetz.) Peters.

Frustulia vulgaris (Thwaites) DeT.

Gomphonema intricatum var. *vibrio* (Ehr.) Cl.
Gomphonema olivaceum (Lyngb.) Kuetz.
Gomphonema parvulum Kuetz.
Gomphonema tenellum Kuetz.
Gomphonema ventricosum Greg.

Gyrosigma acuminatum (Kuetz.) Rabh.
Gyrosigma spencerii (Quek.) Griff. & Henfr.

Hantzschia amphioxys (Ehr.) Grun.

Mastogloia elliptica var. *danseii* (Thwaites) Cl.

Melosira granulata (Ehr.) Ralfs
Melosira granulata var. *angustissima* O. Muell.
Melosira italica (Ehr.) Kuetz.

Navicula capitata var. *hungarica* (Grun.) Ross
Navicula cincta (Ehr.) Ralfs
Navicula circumtexta Meist. ex Hust.
Navicula cryptocephala Kuetz.
Navicula cryptocephala var. *veneta* (Kuetz.) Rabh.
Navicula cuspidata (Kuetz.) Kuetz.
Navicula heufleri Grun.
Navicula heufleri var. *leptocephala* (Breb. ex Grun.) Perag.
Navicula lanceolata (Ag.) Kuetz.

Table 3. (Continued).

Navicula minima Grun.
Navicula mutica Kuetz.
Navicula oblonga (Kuetz.) Kuetz.
Navicula pelliculosa (Breb. ex Kuetz.) Hilse
Navicula peregrina (Ehr.) Kuetz.
Navicula pygmaea Kuetz.
Navicula radiosa Kuetz.
Navicula radiosa var. *tenella* (Breb. ex Kuetz.) Grun.
Navicula reinhardtii var. *elliptica* Herib.
Navicula rhynchocephala Kuetz.
Navicula rhynchocephala var. *amphiceros* (Kuetz.) Grun.
Navicula rhynchocephala var. *germainii* (Wall.) Patr.
Navicula salinarum Grun.
Navicula salinarum var. *intermedia* (Grun.) Cl.
Navicula scutelloides W. Sm. ex Greg.
Navicula secreta var. *apiculata* Patr.
Navicula tripunctata (O. F. Muell.) Bory
Navicula species

Neidium iridis (Ehr.) Cl.

Nitzschia acicularis W. Sm.
Nitzschia acuta Hantz.
Nitzschia amphibia Grun.
Nitzschia apiculata (Greg.) Grun.
Nitzschia denticula Grun.
Nitzschia dissipata (Kuetz.) Grun.
Nitzschia filiformis (W. Sm.) Hust.
Nitzschia fonticola Grun.
Nitzschia frustulum (Kuetz.) Grun.
Nitzschia gracilis Hantz.
Nitzschia granulata Grun.
Nitzschia hantzschiana Rabh.
Nitzschia hungarica Grun.
Nitzschia inconspicua Grun.
Nitzschia intermedia Hantz. ex Cl. & Grun.
Nitzschia linearis (Ag.) W. Sm.
Nitzschia ovalis Arnott
Nitzschia palea (Kuetz.) W. Sm.
Nitzschia paleacea Grun.
Nitzschia punctata (W. Sm.) Grun.
Nitzschia pusilla (Kuetz.) Grun. em. Lange-Bert.
Nitzschia sigmoidea (Ehr.) W. Sm.
Nitzschia subacicularis Hust.
Nitzschia tryblionella Hantz.
Nitzschia tryblionella var. *debilis* (Arnott) A. Mayer
Nitzschia tryblionella var. *levidensis* (W. Sm.) Grun.
Nitzschia tryblionella var. *victoriae* Grun.
Nitzschia species

Opephora martyi Herib.

Pinnularia acrosphaeria W. Sm.
Pinnularia maior (Kuetz.) Rabh.
Pinnularia microstauron (Ehr.) Cl.
Pinnularia viridis (Nitz.) Ehr.
Pinnularia viridis var. *minor* Cl.
Pinnularia species

Plagiotropis arizonica Czar. & Blinn

Pleurosigma australe Grun.
Pleurosigma delicatulum W. Sm.

Rhoicosphenia curvata (Kuetz.) Grun. ex Rabh.

Rhopalodia gibba (Ehr.) O. Muell.
Rhopalodia gibberula (Ehr.) Muell.
Rhopalodia gibberula (var. *vanheurckii* O. Muell.
Rhopalodia musculus (Kuetz.) O. Muell.

Scoliopleura peisonis Grun.

Stephanodiscus astraea var. *minutula* (Kuetz.) Grun.
Stephanodiscus cf. *dubius*
Stephanodiscus invisitatus Hohn & Heller.
Stephanodiscus niagarae Ehr.

Surirella linearis W. Sm.
Surirella ovalis Breb.
Surirella ovata Kuetz.
Surirella striatula Turp.

Synedra acus Kuetz.
Synedra delicatissima var. *angustissima* Grun.
Synedra ulna (Nitz.) Ehr.

Algal assemblages from the Goshen Bay sites were quite variable especially those collected from different geographical portions of the bay. The outer bay was the most similar to the main lake in total algal density and composition of the non-diatom flora. However, diatom abundance and diversity in the outer bay were lower than in the main lake. The inner bay had higher phytoplankton abundance, a greater number of taxa, higher species diversity and a more complex community structure than the outer bay and main lake (Fig. 4). Midbay sites were intermediate showing similarities to the main lake in the diatom flora and similarities to the inner bay in the non-diatom flora.

The similarity of sites within the three regions of Goshen Bay is illustrated by Fig. 2 which is a cluster diagram of similarity indices based on non-diatom species occurrence at each site. Three cluster groups are evident. Group I is composed of sites in the outer bay which were species poor, comprised entirely of one or more of the three unicellular flagellates *Carteria stellifera, Chlamydomonas globosa* and *Euglena gracilis*. Group II, with the exception of outer bay site NO09 and inner bay site GB08, is composed of sites from the middle portion of the bay. The algal assemblages in the mid-

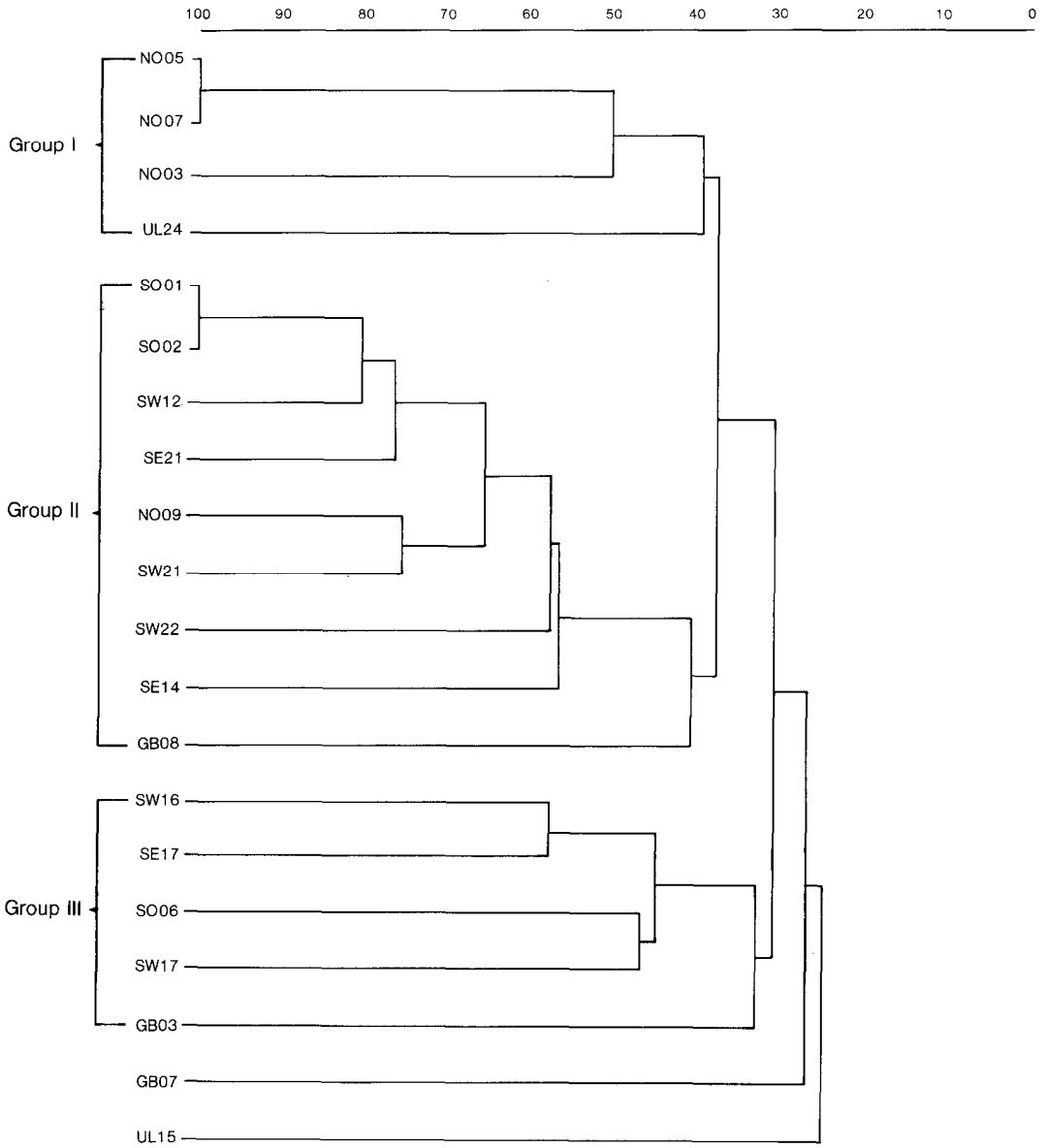

Fig. 2. Cluster diagram of nondiatom algal samples collected from Goshen Bay in Utah Lake during February and March, 1979. Group I includes outer bay sites, Group II middle bay sites and Group III inner bay sites.

bay consistently had the three flagellates *C. stellifera, C. globosa* and *E. gracilis* dominating the individual floras. In addition, the frequent occurrence of *Aphanizomenon flos-aquae, Ankistrodesmus falcatus* and *A. convolutus* plus the occasional occurrence of other green and bluegreen algal taxa increased the species richness of these sites.

The sites from inner Goshen Bay (Group III) were richer in species than either the outer bay or midbay sites containing up to 12 species of nondiatom algae per site. Fourteen of the 26 nondiatom taxa collected in Goshen Bay were collected only from this region.

Aphanizomenon flos-aquae, Ankistrodesmus convolutus and *Ankistrodesmus falcatus* were major constituents in these inner bay sites, and the

Table 4. Population density, species richness and Shannon Weaver diversity for nondiatom and diatom populations collected from various parts of Utah Lake during the winter of 1979. The numbers represent within group means.

Lake Area	Nondiatoms			Diatoms		
Total	Total Plankton (per ml)	Total Species	S-W Diversity	Total Diatoms (per ml)	Total Species	S-W Diversity
Main Lake and Outer Goshen Bay	51	3	0.9	15	22	3.1
Mid Goshen Bay	248	5	1.6	20	30	4.0
Inner Goshen Bay	734	8	1.5	185	48	4.1
Provo Bay	665	21	3.1	96	31	1.9

three aforementioned flagellates, although still abundant, were not as dominant as in the midbay and outer bay sites. Furthermore, many of the additional non-diatom taxa were other species of flagellate algae. The cluster of inner bay sites is not as distinct as in other areas of the bay since the occurrence of rare species varied considerably among these samples thus lowering site similarity.

Diatoms were an important component of the algal flora in Goshen Bay. The highest densities and number of species occurred in the inner bay, and trends of increasing species richness, species diversity and abundance were all evident moving from the outer bay to the inner bay region (Table 4).

Diatom community composition also differed among the various parts of the bay. Table 5 presents importance values for the major diatom species occurring in Utah Lake and Goshen Bay

Table 5. List of species in the Utah Lake winter flora with importance values greater than 1.0. Importance values were determined by multiplying percent frequency by relative density (Ross and Rushforth, 1980).

Species	Site					
	All Stands	Main Lake	Outer Goshen Bay	Mid Goshen Bay	Inner Goshen Bay	Provo Bay
Stephanodiscus cf. *dubius*	19.73	34.03	13.34	18.21	8.24	69.45
Cyclotella meneghiniana	5.99	7.55	0.44	7.34	11.04	6.85
Navicula minima	2.70	5.58	1.71	5.92	0.85	0.57
Fragilaria construens var. *venter*	2.40	0.86	0.70	3.93	4.48	0.03
Melosira granulata var. *angustissima*	2.24	8.35	0.08	3.74	0.96	3.90
Surirella ovalis	2.23	0.03	3.54	1.21	5.17	0.35
Stephanodiscus astrea var. *minutula*	2.11	4.35	0.31	3.42	1.29	4.95
Nitzschia palea	1.55	0.54	0.04	0.31	7.98	0.95
Navicula rhynchocephala	1.46	0.19	0.12	0.17	9.23	0.03
Pleurosigma delicatula	1.09	0.09	0.16	1.41	3.88	0.03
Amphora ovalis var. *affinis*	0.83	2.00	0.82	0.87	0.78	0.03
Navicula cryptocephala var. *veneta*	0.66	2.35	0.21	0.16	0.93	0.30
Achnanthes minutissima	0.62	1.99	0.00	0.22	0.05	0.13
Amphora ovalis	0.51	0.00	0.00	1.24	1.42	0.03
Amphora perpusilla	0.46	3.60	0.00	0.55	0.07	0.17
Nitzschia acicularis	0.31	0.09	0.00	0.16	1.13	3.10
Synedra ulna	0.28	0.01	0.04	0.14	1.46	0.13
Navicula capitata var. *hungarica*	0.27	1.97	0.00	0.22	0.05	0.05
Navicula cryptocephala	0.22	1.07	0.08	0.03	0.16	0.13
Stephanodiscus invisitatus	0.17	0.44	0.00	0.14	0.00	2.65

during February and March in 1979. The importance of *Stephanodiscus* cf. *dubius* in the lake during the sampling period is evident from this analysis. It was the most important diatom in all localities except inner Goshen Bay where its relative importance was markedly lower. *Cyclotella meneghiniana, Navicula rhynchocephala, Nitzschia palea, Surirella ovalis, Pleurosigma delicatula, Nitzschia acicularis* and *Synedra ulna* all reached their maximum importance value in inner Goshen Bay. *Fragilaria construens* var. *venter* and *Amphora ovalis* were also highest here but showed a corresponding increase in midbay sites. Three additional taxa which were major constituents of the winter flora elsewhere in the lake showed noteworthy decreases in importance values in inner Goshen Bay. These were *Navicula minima, Melosira granulata* var. *angustissima* and *Stephanodiscus astrea* var. *minutula*. Several taxa were similar between the lake sites and the midbay sites, reflecting an overall similarity between these two areas. The outer bay sites showed a noteworthy decrease in importance of many of the major species in the flora. The reasons for this are not clear, but probably are due to local environmental conditions in this area of the lake. A few taxa occurred in elevated numbers in the main lake sites versus the Goshen Bay sites. The most noteworthy of these was *Melosira granulata* var. *angustissima* which occurred in moderate to high numbers in all of these sites.

It is interesting that rapid and significant changes in the algal flora of Goshen Bay, both spatially and temporally, occurred during our sampling period. Spatial variability among sites in one area of the bay such as between non-diatoms in the inner bay and diatoms in the outer bay has been noted above. Temporal differences occurred between samples collected in inner Goshen Bay on March 3 and on March 10, 1984. The early samples showed high abundance of *Navicula rhynchocephala* and *Nitzschia palea* whereas samples collected a week later contained much lower numbers of these organisms. Conversely, numbers of *Stephanodiscus* cf. *dubius, Cyclotella meneghiniana, Pleurosigma delicatulum, Surirella ovalis* and *Synedra ulna* increased considerably between March 3 and March 10. All of these taxa with the exception of *Surirella ovalis* continued to increase during April in this part of the lake.

Seasonal changes in the flora

Figure 3 shows the winter season phytoplankton in the perspective of fall and early spring plankton

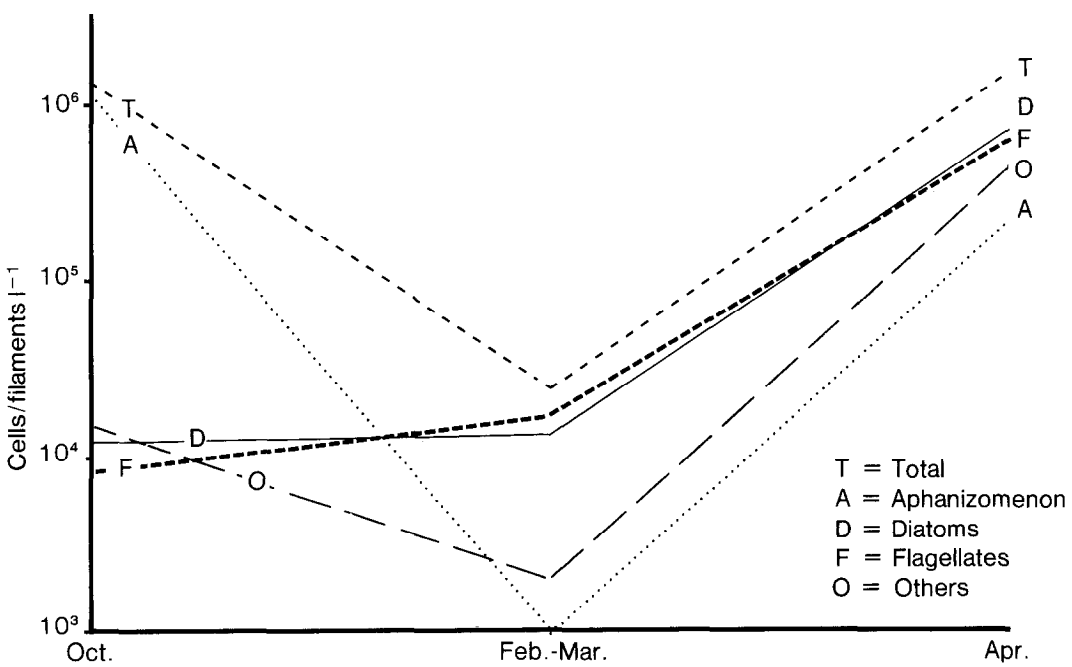

Fig. 3. Number of cells/filaments per liter of four algal groups plotted against time for the fall, winter and early spring of 1978–1979.

populations. This graph was compiled from data collected from Historic Sites during all three periods. Data from Historical Sites in Provo Bay and inner Goshen Bay were excluded from these averages because of the distinctiveness of these habitats. The fall flora was dominated by *Aphanizomenon flos-aquae* which comprised from 96–99% of the total in all sites. This alga disappeared from most of the lake during the winter, occurring only in sites collected from middle and inner Goshen Bay. After the disappearance of this taxon, other groups increased in relative importance. The absolute densities of diatoms during winter remained about the same as during the fall while flagellate densities increased. At ice off, the populations of all groups increased significantly, with several taxa reaching higher total abundance than during the previous fall. Two of the most prominent non-diatom algae increasing in the early spring were *Ankistrodesmus convolutus* and *Ankistrodesmus falcatus*. The two major diatoms increasing during the spring period were *Stephanodiscus* cf. *dubius* and *Cyclotella meneghiniana*.

Discussion

Winter phytoplankton populations in many lakes examined throughout the world appear to be quite similar. Such floras tend to be dominated by small organisms including unicellular flagellates of the genera *Chlamydomonas, Cryptomonas, Ochromonas* and *Rhodomonas* (Wright, 1964; Maeda & Ichimura, 1973). In addition, coccoid bluegreen and green algae are often abundant, particularly in alpine (Pennak, 1968; Keefer & Pennak, 1977) and Antarctic lakes (Goldman *et al.*, 1967). Small cell size and the motile habit have been suggested as being important in determining what species may dominate an under-ice flora where turbulence is generally low (Rodhe, 1955; Goldman, 1967). Hickman & Jenkerson (1978) noted that their early under-ice flora in Hastings Lake, Alberta, Canada, was dominated by small non-motile algae. However, as the non-turbulent period increased in length, these algae were replaced by flagellates which could maintain their position in the water column.

The Utah Lake algal assemblage is quite similar to others that have been studied in the dominance of flagellates during winter months. However, some important differences exist. For instance, in addition to *Chlamydomonas* which is a common winter plankter, Utah Lake flagellate assemblages include the green alga *Carteria* and several euglenoids. Euglenoids are apparently rather rare in winter floras but have been occasionally reported (Pennak, 1968). Furthermore, cryptomonads were absent from the Utah Lake winter flora as were coccoid bluegreen and green algae.

The winter diatom flora of Utah Lake is dominated by species of *Stephanodiscus* and *Cyclotella*. *Stephanodiscus* dominance has been previously reported for Swedish Lappland lakes by Rodhe (1955). However, many winter floras are dominated by a variety of other taxa such as *Asterionella* (Campbell & Hasse, 1981; Ferrari, 1976; Maeda & Ichimura, 1973), *Chaetoceros* (Hickman, 1979), *Eunotia* (Wright, 1964), *Fragilaria* (Campbell & Haase, 1981; Wright, 1964), *Melosira* (Campbell & Haase, 1981) *Meridion* (Ferrari, 1976; Wright, 1964), *Nitzschia* (Ferrari, 1976), *Rhizosolenia* (Campbell & Haase, 1981), *Synedra* (Hickman, 1979; Maeda & Ichimura, 1973; Wright, 1964) and *Tabellaria* (Wright, 1964). It appears from our data and from some of the reports cited above that the diatoms which dominate the winter floras are the same taxa which dominate the flora throughout the rest of the year. This phenomenon has been noted by other workers (Hickman, 1979), and seems to be a more important factor than small size in determining which diatom taxa will be present in high numbers in the winter algal assemblage.

The Utah Lake flora is similar in many respects to that of two Canadian lakes, Lake Ministik (Hickman, 1979) and Lake Hastings (Hickman & Jenkerson, 1978). As with Utah Lake, these two lakes are shallow, eutrophic, alkaline and covered with ice in the winter. Hastings Lake was dominated by colonial bluegreen algae during the autumn. During the winter, the populations of these algae decreased similar to our population decrease of *Aphanizomenon* in Utah Lake. Even so, small populations of *Gomphosphaeria* and *Microcystis* remained in the water column under the ice in the Canadian lakes while *Aphanizomenon* in Utah Lake was absent in winter months except for a few Goshen Bay and Provo Bay sites. As mentioned by Fallon & Brock (1981), this is probably due at least in part to life cycle strategies of these organisms.

Aphanizomenon forms akinetes and therefore does not remain in the winter flora as vegetative filaments. *Microcystis* and *Gomphosphaeria* do not form akinetes and hence overwinter in the vegetative condition either in the water column (Hickman & Jenkerson, 1978) or on the substratum (Fallon & Brock, 1981). The abundance of small green chlorococcine algae including *Kirchneriella, Selenastrum, Actinastrum, Ankistrodesmus, Dictyosphaeria* and *Oocystis* in the Canadian lakes is also similar to the situation in Utah Lake although in Utah Lake these algae were much more abundant in the bays than in the main lake. It is also noteworthy that winter diatom population dynamics and early growth at ice off of a series of green and bluegreen algae were similar between the Canadian lakes and Utah Lake.

In general, the Utah Lake winter phase of the yearly phytoplankton cycle is similar to that recorded for other temperate lakes and reservoirs. With the onset of cold weather and short days, a drastic population decrease of several of the important summer and fall taxa occurs. However, this decrease does not occur in all groups equally. Generally the flagellates are least affected and may actually increase in number. Likewise, diatoms generally show a winter decrease, although not as extensive as some of the other groups. Diatoms dominant in the winter are often those important during the fall, although generally present in diminished numbers.

The actual abundance of algae present in winter floras in lakes that freeze over appears to depend upon the degree of ice and snow cover due to their effect upon light penetration. Furthermore, snow cover seems to be more important in suppression of algal growth than ice thickness. Wright (1964) reported values of 30–40% light transmission for 31–41 cm of ice, but transmission dropped significantly when ice was snow covered, reaching a low of 0.19% with 29 cm of snow cover. Phytoplankton productivity dropped accordingly. When ice is thin and transparent, high algal densities have been recorded (Maeda & Ichimura, 1973). When ice is thick and/or snow cover is added, authors have reported reduced phytoplankton productivity (Campbell & Hasse, 1981; Hickman & Jenkerson, 1978; Willen, 1961; Ferarri, 1976). Often, however, spring phytoplankton increases are observed under the ice and continue to their maxima after ice breakup. This is undoubtedly related to longer insolation periods, melting snow and thinning ice which occur as the season progresses. While the present study did not monitor weekly changes during the winter period, it is likely that the high densities of some flagellates and diatoms such as *Stephanodiscus* cf. *dubius* and *Cyclotella meneghiana* which occurred in March and continued to rise in April were examples of this phenomenon.

The distribution of phytoplankton in the water column is another phenomenon which has been investigated during winter phytoplankton studies. Maeda & Ichimura (1973) reported that microflagellates were abundant in the whole water column during the ice-covered period, but occurred deeper in the water column during the summer. Some authors have reported a concentration of winter phytoplankters in the upper portion of the water column, especially when light penetration is reduced (Wright, 1964; Hickman & Jenkerson, 1978; Hickman, 1979). Phototactic responses by flagellate algae has been associated with this phenomenon, and it is likely that the ability to swim to the top of the water column as light availability decreases is one reason for the success of flagellates during the winter. Physiological adaptation to low light intensity and facultative heterotrophy are also possible factors contributing to the survival of various algal taxa in ice-covered lakes (Rodhe, 1955; Rodhe *et al.*, 1966; Goldman, 1967; Wright, 1964).

The prevalence of diatoms in the winter in Utah Lake is similar to the condition noted for other Utah waters. Deer Creek Reservoir, which is in the same drainage basin as Utah Lake, has been reported to contain high populations of *Stephanodiscus* and *Cyclotella* as well as *Fragilaria* and *Asterionella* beneath the ice (McDonald, 1962; Chatwin, 1956; Gaufin & McDonald, 1965). The winter flora of Flaming Gorge Reservoir which is located in northeastern Utah, has been reported to be dominated by diatom plankters *Tabellaria fenestrata, Asterionella formosa* and species of *Synedra* (Varley, 1967). *Stephanodiscus hantzschii* increased during the late winter until it became quite important.

The winter diatom flora of Utah Lake, particularly in the bays, is richer in species than that reported in the literature for other waters. The large

number of taxa in the water column is unusual, but has been reported for Utah Lake during other seasons as well (Rushforth *et al.*, 1981a). However, during periods when the lake was not covered with ice, it has been assumed that the diatoms in the water column were present due to shallow water and wind caused turbulence. This assumption may need to be reassessed due to the continued presence of a high number of taxa during winter when ice cover should eliminate such turbulence.

From our data, it can be seen that the separate parts of Utah Lake function differently. Specifically, the bays are species rich and contain green and bluegreen algae which are rare or absent from the remainder of the lake. This is likely important in the development of the early spring flora since those species which overwinter in the bays may act as inoculum. We have observed this directly in samples taken from the mouth of Provo Bay which show the influence of migration of species from the bay to the lake. Likewise, the fact that middle Goshen Bay is intermediate in species number between the inner bay and main body of the lake may reflect this phenomenon. Rapid and thorough mixing of water in the lake due to wind and water currents facilitates this distribution of species. This is especially demonstrated by the major early blooms of *Ankistrodesmus falcatus* and *Ankistrodesmus convolutus* in the spring flora of the lake.

Both diatom and non-diatom standing crops are higher in the bays than in the main body of the lake. This is the case in Goshen Bay even though salinity increases somewhat in comparison to the main lake. This increase in salinity does not appear to influence the non-diatom flora appreciably, although the diatom flora is somewhat different due to the occurrence of a number of brackish water taxa.

The results of our study have demonstrated that under-ice conditions in Utah Lake are complex. More study is necessary to illuminate all of the factors responsible for floral and standing crop difference as well as seasonal population dynamics. Likewise, the reasons for the presence of so many diatoms in the water column of the lake are not clear. We hope to study these problems in the future.

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