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DIATOM COMMUNITY STRUCTURE ALONG PHYSICOCHEMICAL GRADIENTS IN SALINE LAKES¹

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Abstract. Relationships between diatom assemblages and physicochemical factors were examined in 63 saline lakes in western North America. Sodium was the overwhelmingly dominant cation in the lakes examined; lakes above 47° latitude were dominated by SO_4^{-2} , and lakes below 47° were dominated by CO_3^{-2} and Cl^{-1} . This latitudinal gradient for anions was correlated with the distribution and community structure of diatoms. Sixty-two taxa comprised >85% of the total diatom relative abundance in the saline environments. There were strong negative correlations between specific conductance and diversity and species richness, however pH and major cations showed limited predictive value. Cluster analyses identified diatom assemblages along specific conductance and major anion gradients. Indices for specific conductance and major anions were also developed for 62 diatom taxa. These diatom indices provide useful information to interpret past and present physicochemical conditions in lacustrine ecosystems. Greatest diversity was found in habitats with ionic concentrations < seawater and ion composition similar to marine environments. Principal components analyses comparing loadings for major cations and anions, ionic concentration, and diatom community structure suggested that shallow saline lakes may have provided evolutionary pathways for speciation of marine pennate diatoms into athalassic (nonmarine) environments.

Key words: *algal evolution; athalassic; diatoms; indices; latitudinal variation; North America; paleolimnology; periphyton; physicochemical; saline lakes.*

INTRODUCTION

Diatom assemblages have been used as indicators of a variety of environmental conditions in freshwater environments, including nutrient status, alkalinity, and pH (Hustedt 1939, Chloňok 1968, Hecky and Kilham 1973, Patrick 1973, Lowe 1974, Bahls et al. 1984, Charles 1985, Whitmore 1989, Anderson et al. 1990). Additionally, diatom communities have been used to assess long-term changes in lakes due to shifts in climate (Bradbury 1988, Smol 1988, Smol et al. 1991), and human disturbances such as modifications of watershed and acid precipitation (Brugam 1978, Smol and Dickman 1981, Renberg and Hellberg 1982, Battarbee 1984, Battarbee et al. 1986, Kingston et al. 1990).

Only recently have diatoms been postulated to be useful indicators of ionic composition and salinity in athalassic (nonmarine) saline lakes (Hammer et al. 1983, Blinn 1984, Hammer 1986, Bradbury et al. 1989, Blinn 1990, Fritz 1990, Servant-Vildary and Roux 1990, Roux et al. 1991, Tudor et al. 1991). Furthermore, several strains of diatoms isolated from these saline environments produce significant quantities of cellular storage lipids and are being considered for alternative fuel applications (Ben-Amotz et al. 1985).

Although saline lakes are found on every continent, and the total volume of water in these environments

on a global scale nearly equals that in freshwater lakes (Williams 1986), there have been significantly fewer studies on the ecology of organisms in saline lakes compared to freshwater habitats. Furthermore, there is considerably less information on diatoms in saline lakes of North America, especially USA, than similar habitats on other continents, namely Africa, Australia, and South America (Hammer 1986). For example, only the Great Salt Lake (Felix and Rushforth 1979), Utah Lake (Grimes and Rushforth 1982), and Blue Lake Warm Spring (Kaczmarek and Rushforth 1983), all from Utah, have been extensively analyzed for diatoms. Other studies include Castenholz's (1960) study of the attached diatom communities in two saline lakes in the Grand Coulee region of Washington, and phytoplankton surveys by Galat et al. (1981) on Pyramid Lake, Nevada; Sze and Kingsbury (1972) on Onondaga Lake, New York; Verch and Blinn (1971) on Devils Lake, North Dakota, and Blinn (1972) on Stump Lake, North Dakota. More restricted studies on diatoms have been conducted in Mono Lake, California (Mason 1967, Herbst and Bradley 1989), Big Soda Lake, Nevada (Cloern et al. 1983), Abert Lake, Oregon (Herbst and Bradley 1989), and several playa lakes in southern California (Busch and Kubly 1980).

In contrast, Bailey (1922), Kuehne (1941a, b), Hammer et al. (1983), and Hammer (1986) have provided extensive surveys of diatoms in over 50 lakes in the saline lake district of Alberta and Saskatchewan, Canada. However, there have been limited correlations

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between physicochemical parameters and diatom assemblages within these lakes (Hammer et al. 1983, Hammer 1986).

The purposes of this study were (1) to identify those physicochemical factors that influence the community structure of diatom assemblages in saline lake ecosystems of western North America, (2) to determine if regional differences in chemical composition of saline lakes influence regional patterns of diatom community structure, and (3) to develop predictive indices for diatoms, ionic composition, and salinity that could be employed by paleolimnologists and aquatic ecologists to assess and interpret past and present aquatic environments. It is proposed that diatom indicator species not only provide information to help interpret past and present salinity conditions in lacustrine ecosystems, but also yield cues to potential elevated salinities in aquatic environments due to regional and global warming.

MATERIALS AND METHODS

Forty-seven saline aquatic ecosystems were examined for water chemistry and diatom assemblages in western USA and the interior of British Columbia, Canada during June–September 1989 (Table 1). Twenty-one of these habitats were located in the Great Basin Desert and extending into the interior of southern British Columbia, 12 in the semiarid Great Plains, 9 in the Chihuahuan Desert, and 5 in the Sonoran Desert. Water samples were collected (0.2–1 m in depth) from each habitat and filtered through a 0.45- μm membrane filter (Millipore HA). Samples were acidified ($\text{pH} < 3.0$) with concentrated nitric acid and analyzed for major cations (Na^{+1} , K^{+1} , Mg^{+2} , Ca^{+2}) by atomic absorption. Unacidified samples were used to determine SO_4^{-2} , Cl^{-1} , reactive SiO_2 , and total dissolved solids according to standard procedures in APHA (1985). All measurements were completed within 2 mo of collection. Water temperature, pH, specific conductance (at 25°C), and alkalinity (HCO_3^{-1} and CO_3^{-2}) were determined from unfiltered water samples at the time of collection in the field. Diatom assemblages were collected from natural substrata including epipelton (community associated with sediment) and epilithon (community on rock surfaces) from at least five locations near the shoreline (0.1–1 m deep) of each saline habitat. Samples were digested following procedures of Van der Werff (1955), and permanent Hyrax (Auburn, California) slide mounts were prepared for each sample. A minimum of 500 frustules was counted for each slide. Relative abundance values for collections from each saline lake were averaged in the final analyses. A diversity index (H') was calculated for diatom assemblages for each aquatic habitat (Shannon and Weaver 1949).

In addition, water temperature, pH, specific conductance, and diatom collections were taken during 17–20 May in 16 saline habitats in southern Saskatch-

ewan and Alberta. The ionic composition for each habitat was obtained from T. Hammer (*personal communication*, University of Saskatchewan, Saskatoon) and Hammer (1978).

Physicochemical parameters from the 47 aquatic saline habitats in western USA and the southern interior of British Columbia were analyzed using principal components analysis (PCA). The PCA solution was calculated from the Pearson product–moment correlation matrix without rotation using Statview 512+ for the Macintosh computer. For each habitat, factor scores on the first three principal components were calculated as the sum over all physicochemical variables of the observed values of each variable weighted by the factor loading of that variable on each principal component.

Correlations between various paired combinations of diatom taxa and physicochemical variables were also calculated using Pearson's product–moment correlation coefficient on Systat 5.01 (SYSTAT 1984). Significant differences between paired measurements were obtained from Bonferroni values. Equations were developed to identify specific conductance indices (SCI):

$$\text{SCI}_x = \frac{\sum_{i=1}^{N_x} [\log_{10}(\text{RA}_i \cdot 100)] (\text{Specific Conductance})}{N_x}$$

and ion indices (IonI) for Na^{+1} , K^{+1} , Mg^{+2} , Ca^{+2} , HCO_3^{-1} , CO_3^{-2} , Cl^{-1} , and SO_4^{-2} :

$$\text{IonI}_x = \frac{\sum_{i=1}^{N_x} [\log_{10}(\text{RA}_i \cdot 100)](I)}{N_x},$$

where RA_i = relative abundance (percent) of species x in habitat, I = percent composition (based on charge concentration) of specified ion, and N = number of habitats in which species x occurred. These indices (SCI and IonI) provided a relative numeric scale to evaluate various diatom taxa with selected physicochemical variables (see Table 6). Only data from the 47 habitats in western USA and central British Columbia were used to develop these indices because ion data from Saskatchewan lakes were not collected concurrently with diatom samples. Indices were determined for specific conductance and major cations and anions for 62 of the most frequently encountered diatom taxa.

Specific conductance and ionic index values were employed in cluster analyses with 43 representative diatom taxa of the aquatic saline habitats. These taxa made up nearly 75% of the average relative abundance of diatoms in the saline lakes examined. Differences among groups were measured using Euclidean distances.

RESULTS

Chemical characteristics of lakes.—The specific conductance of water in the various saline lakes examined

TABLE 1. Specific conductance (at 25°C), total dissolved solids (TDS) pH, and ion composition, for saline aquatic habitats examined during May–September 1989, in western North America. Lakes are listed in descending order of approximate latitudes.

Habitat	Specific cond. (mS)	TDS (g/L)	pH	Ionic composition (charge concentrations, mmol/L)							
				Na ⁺¹	K ⁺¹	Ca ⁺²	Mg ⁺²	Cl ⁻¹	SO ₄ ⁻²	CO ₃ ⁻²	HCO ₃ ⁻¹
Big Manito Lake, SASK (52°43' N, 109°43' W)*	21.5		9.4	349	6.3	1.1	181	629	449	2.5	13
Reflex Lake, SASK (52°40' N, 109°58' W)*	9.8		9.3	126	1.7	0.3	3	10	50	10.0	13
Wakaw Lake, SASK (52°40' N, 105°35' W)*	2.9		8.4	14	0.8	5.7	15	4	24	0.5	2
Marie Lake, SASK (52°39' N, 105°19' W)*	23.6		8.6	257	6.5	10.7	161	15	304	0.5	7
Arthur Lake, SASK (52°38' N, 105°21' W)*	13.2		8.6	145	10.1	12.9	204	13	271	1.5	9
Basin Lake, SASK (52°38' N, 105°17' W)*	16.8		8.3	96	5.1	6.3	81	18	125	0	12
Muskiki Lake, SASK (52°20' N, 105°45' W)*	256.0		8.3	2704	40.9	3.7	1189	321	2469	0	24
Waldsea Lake, SASK (52°17' N, 105°12' W)*	16.5		8.8	132	7.4	7.9	112	109	132	2	2
Humboldt Lake, SASK (52°09' N, 105°06' W)*	3.9		8.4	11	2.4	3.7	22	3	28	0.5	5
Whiteshire Lake, SASK (52°08' N, 108°17' W)*	131.0		8.9	2191	24.3	76.5	303	282	1340	1.5	12
Patience Lake, SASK (52°07' N, 106°20' W)*	300.0		8.0	4478	1230	18.5	169	5704	365	0	344
Lake Tramping, SASK (52°06' N, 106°47' W)*	13.1		9.1	104	2.8	1.8	6	8	53	1.5	11
Big Quill Lake, SASK (51°55' N, 104°22' W)*	46.5		8.6	350	15.0	9.6	184	629	50	2.5	13
Little Manitou, SASK (51°48' N, 105°30' W)*	90.2		8.3	535	22.8	12.5	390	507	413	3.5	13
Killarney Lake, ALB (52°38' N, 110°45' W)*	11.5		9.3	69	1.8	2.3	2	14	14	9.5	23
Gooseberry Lake, ALB (51°45' N, 105°29' W)*	47.5		9.4	480	8.0	2.8	29	16	166	26.5	40
Wallender Lake, BC (51°39' N, 119°32' W)	43.6	71.2	8.2	550	17.8	6.5	222	64	500	0	25
Alga, BC (50°39' N, 120°32' W)	123.0	182.0	8.5	1817	15.9	6.4	395	87	1290	1.0	4
Bowers Lake, BC (50°39' N, 119°32' W)	23.1	33.5	8.8	162	10.8	8.4	157	30	241	3.5	4
Green Lake, BC (49°17' N, 118°40' W)	3.1	3.3	8.8	14	1.3	0.1	16	4	11	8.0	13
Mahoney Lake, BC (49°17' N, 119°35' W)	23.9	28.9	8.9	253	16.8	0.7	78	39	186	20	5
Fox Lake, ND (48°13' N, 98°34' W)	13.5	13.9	9.2	128	3.6	1.9	34	48	90	6.5	3
Lake 55, ND (48°13' N, 98°33' W)	32.5	31.0	8.5	341	6.6	7.4	58	236	110	1.0	5
Devils Lake, ND (48°00' N, 98°59' W)	4.5	3.5	8.9	31	2.3	2.0	7	10	18	2.5	6
Twin Lake, ND (47°58' N, 99°06' W)	8.5	7.7	8.9	62	2.7	1.6	25	13	46	2.5	3
West Stump Lake, ND (47°55' N, 98°26' W)	26.5	33.5	8.9	306	9.7	2.4	64	74	185	4.0	6
East Stump Lake, ND (47°53' N, 98°22' W)	59.2	85.6	8.5	869	22.3	4.3	165	209	531	3.0	10
Hot Lake, WA (48°58' N, 119°29' W)	29.6	49.6	8.3	127	12.6	7.4	300	23	356	0	5
Lenore Lake, WA (47°29' N, 119°30' W)	2.2	1.9	9.2	19	1.1	0.2	1	6	3	4.5	8
Soap Lake, WA (47°29' N, 119°29' W)	19.5	17.1	9.6	236	13.8	0.1	<1	57	39	56.0	30
Palmer Lake, NB (42°06' N, 102°43' W)	21.3	20.8	9.6	176	93.9	0.3	2	<1	23	104.0	71
Antioch Lake, NB (42°04' N, 102°42' W)	117.0	107.0	9.8	1314	370.8	0.3	<1	204	270	426.0	164
Lakeside, NB (42°04' N, 102°43' W)	69.0	57.0	9.7	593	276	0.3	<1	56	87	289.0	89

TABLE 1. Continued.

Habitat	Specific cond. (mS)	TDS (g/L)	pH	Ionic composition (charge concentrations, mmol/L)							
				Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻	SO ₄ ⁻²	CO ₃ ⁻²	HCO ₃ ⁻¹
Border Lake, NB (41°49' N, 102°26' W)	87.6	70.1	9.9	969	162.0	0.5	<1	104	63	475.0	71
Goose Lake, NB (41°48' N, 102°31' W)	7.4	6.5	9.4	63	24.0	0.5	2	7	4	30.0	33
Crescent Lake, NB (41°41' N, 102°24' W)	1.5	2.8	9.0	7	2.1	0.5	2	2	4	4.0	6
Summer Lake, OR (42°50' N, 120°45' W)	22.8	17.1	9.7	275	7.4	0.1	<1	103	9	70.5	26
Lake Abert, OR (42°40' N, 120°15' W)	45.3	39.8	9.6	594	12.7	0.1	<1	363	44	85.5	25
Stateline, OR (42°00' N, 122°00' W)	53.5	57.0	10.0	882	56.3	0.1	<1	106	21	420.0	74
Great Salt Lake, UT (40°42' N, 112°14' W)	109.8	92.5	8.6	1201	48.7	4.6	120	1403	51	0.5	1
Blue Lake, UT (40°20' N, 113°55' W)	15.9	6.5	8.3	83	3.8	3.4	4	100	4	0	3
Goose Lake, CA (42°00' N, 119°19' W)	2.1	1.5	9.0	18	0.8	0.3	<1	6	1	3.5	8
Honey Lake, CA (40°15' N, 120°26' W)	7.7	4.9	9.2	74	1.5	0.3	<1	33	10	11.5	17
Mono Lake, CA (38°00' N, 119°15' W)	77.5	67.2	9.6	1135	30.7	0.3	2	462	94	177.0	148
Owens Lake, CA (36°20' N, 118°10' W)	13.2	10.4	8.7	153	5.0	0.6	3	90	3	11.5	37
Pyramid Lake, NV (40°00' N, 119°35' W)	7.3	4.7	8.8	57	2.8	0.3	5	45	4	5.5	11
Hazen, NV (39°50' N, 119°00' W)	181.0	245.0	9.7	3876	4.3	0.7	2	1397	971	180.0	10
Big Soda Lake, NV (39°31' N, 118°49' W)	26.6	23.5	9.5	323	7.3	0.5	6	172	58	34.5	23
Walker Lake, NV (38°43' N, 118°43' W)	13.4	9.2	9.3	144	4.6	0.3	6	68	26	19.0	22
Chevelon no. 1, AZ (34°55' N, 110°49' W)	3.8	3.1	8.7	48	0.2	3.1	3	33	4	0.5	<1
Chevelon no. 2, AZ (34°55' N, 110°49' W)	9.0	7.8	8.5	106	0.4	6.7	6	83	8	0.5	2
Chevelon no. 3, AZ (34°55' N, 110°49' W)	15.7	13.6	8.4	161	0.2	3.1	3	148	9	0.5	1
Green Pond, AZ (34°51' N, 109°26' W)	56.9	75.0	9.7	1048	3.7	0.4	6	648	9	127.0	81
Red Pond, AZ (34°51' N, 109°26' W)	137.0	192.0	9.4	2535	7.6	0.2	2	1746	1	360.0	170
Zuni Lake, NM (34°27' N, 108°44' W)	170.1	361.0	7.6	5083	57.4	1.5	411	4392	682	0	25
Bitter Lake, NM (33°28' N, 104°24' W)	62.1	63.0	8.9	773	2.5	26.5	103	845	110	0	1
Bitter Lake no. 6, NM (33°27' N, 104°25' W)	17.6	15.8	7.7	114	0.5	22.0	13	133	32	0	1
Figure 8, NM (33°29' N, 104°25' W)	14.8	11.9	8.8	101	0.5	28.0	21	125	30	0	2
Lazy Lagoon, NM (33°29' N, 104°24' W)	40.2	38.2	7.9	437	2.4	24.0	83	440	93	0	3
Lea Lake, NM (33°29' N, 104°25' W)	11.2	9.5	7.6	92	0.4	22.0	7	106	22	0	3
Mirror Lake, NM (33°29' N, 104°27' W)	30.3	29.5	8.3	328	1.3	26.5	50	363	61	0	2
Sink no. 16, NM (33°29' N, 104°25' W)	56.2	43.0	7.8	442	1.1	32.4	66	552	55	0	4
St. Francis Lake, NM (33°29' N, 104°25' W)	14.1	12.4	7.9	122	0.4	26.0	13	138	35	0	2

* Data for ion composition for Saskatchewan and Alberta, Canada, lakes were obtained from U. T. Hammer (*personal communication*) and Hammer (1978).

throughout western North America ranged from 1.5 mS to 300 mS. Lake waters displayed a wide range of values for specific conductance in all the major regions of western North America (Table 1), and therefore there was no significant correlation between latitude and specific conductance ($r = 0.071$, $P > .05$). The most highly concentrated habitat examined was Patience Lake in southern Saskatchewan, Canada (300 mS), while the lake with the lowest ionic concentration was Crescent Lake, Nebraska (1.5 mS).

The dominant cation for the saline lakes examined in North America was Na^+ , i.e., 81% of the lakes were dominated by sodium salts (Fig. 1, Table 1). This pattern was especially true for lakes located below 49° latitude, however aquatic habitats at higher latitudes in the Canadian provinces (Saskatchewan, Alberta, and British Columbia) were dominated by either Na^+ or Mg^{+2} , (Fig. 2, Table 1). Lakes located in the sandhill region of northwestern Nebraska and eastern North Dakota had relatively high concentrations of K^+ , while lakes in the Bottomless Lake district of southeastern New Mexico had relatively high concentrations of Ca^{+2} ions compared to lakes in other regions of North America (Table 1, Fig. 2). Otherwise, both K^+ and Ca^{+2} concentrations were relatively low in the lakes examined throughout western North America.

The anion composition of waters also varied along a latitudinal gradient. Lakes above 47° latitude (i.e., Saskatchewan, Alberta, and British Columbia, Canada, and northern North Dakota), were typically dominated by SO_4^{-2} ions (numbers 29–34 and 15–19 on Fig. 3), while lakes located at lower latitudes in central and southern regions of western USA were dominated by CO_3^{-2} or Cl^{-1} ions (Fig. 2). For example, lakes in the sandhills region of northwestern Nebraska (numbers 21–26 on Fig. 3) were especially high in CO_3^{-2} ions. On the other hand, lakes in the Lahontan Basin of Nevada and the interior of California in the Great Basin Desert (numbers 1–14 on Fig. 3) are positioned intermediately between Cl^{-1} and CO_3^{-2} with respect to dominant anions, and lakes in the arid southwest in Arizona and New Mexico showed high Cl^{-1} concentrations (numbers 35–45 on Fig. 3). Therefore, lakes in the more arid regions of western USA were typically dominated by Cl^{-1} , while the waters in lakes located in regions with moderately arid climates were dominated by CO_3^{-2} and SO_4^{-2} ions.

Concentrations of SiO_2 were relatively high and variable between lakes ($\bar{X} \pm 1 \text{ SD} = 15.3 \pm 17.3 \text{ mg/L}$). Highest average concentrations ($20.4 \pm 21.5 \text{ mg/L}$) were found in the Lahontan Basin of Nevada and the interior of California in the Great Basin Desert, while lowest average concentrations ($4.1 \pm 3.0 \text{ mg/L}$) were found in the southern interior of British Columbia. There was no correlation ($r = 0.063$, $P > .05$) between specific conductance and SiO_2 in the lakes examined.

The hydrogen ion concentration for the saline lakes examined ranged from 10.0 for the Na_2CO_3 lakes in

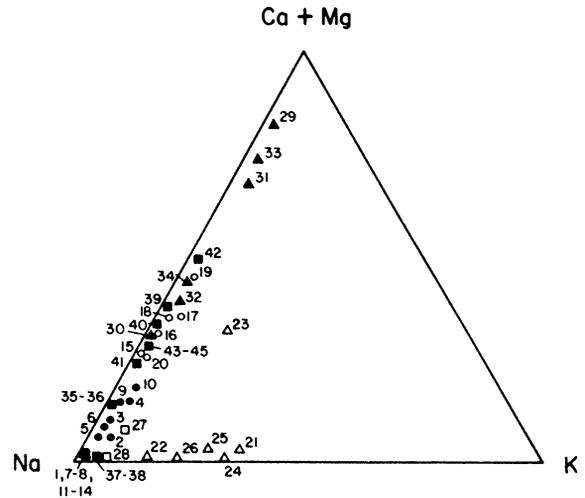


FIG. 1. Relative cation composition of 45 representative saline lakes in western USA and British Columbia, Canada. 1 = Abert, OR; 2 = Goose, CA; 3 = Walker, NV; 4 = Pyramid, NV; 5 = Big Soda, NV; 6 = Owens, CA; 7 = Mono, CA; 8 = Hazen, NV; 9 = Blue, UT; 10 = Great Salt, UT; 11 = Honey, CA; 12 = Stateline number 1, OR; 13 = Stateline number 2, OR; 14 = Summer, OR; 15 = E. Stump, ND; 16 = W. Stump, ND; 17 = Devils, ND; 18 = Fox, ND; 19 = Twin, ND; 20 = Lake 55, ND; 21 = Palmer, NB; 22 = Border, NB; 23 = Crescent, NB; 24 = Lakeside, NB; 25 = Goose, NB; 26 = Antioch, NB; 27 = Lake Lenore, WA; 28 = Soap, WA; 29 = Hot, WA; 30 = Alga, BC; 31 = Green, BC; 32 = Mahoney, BC; 33 = Bowers, BC; 34 = Wallender, BC; 35 = Zuni, NM; 36 = Zuni Drainage, NM; 37 = Green Pond, AZ; 38 = Red Pond, AZ; 39 = St. Francis, NM; 40 = Sink number 16, NM; 41 = Bitter, NM; 42 = Figure 8, NM; 43 = Mirror, NM; 44 = Lea, NM; 45 = Lazy Lagoon, NM. Symbols: ● = Great Basin Desert, ○ = North Dakota, ▲ = British Columbia, △ = Nebraska, ■ = New Mexico, □ = Washington.

California, Nevada, and the sandhills of northwestern Nebraska to 7.6 for the $\text{NaCl}(\text{SO}_4)$ lakes in southeastern New Mexico (Table 1). Carbonate was the only ion that showed a significant correlation ($r = 0.590$, $P < .01$) with pH, and there was no significant relationship between pH and specific conductance (Table 2). Habitats dominated by Na_2CO_3 had the highest average pH ($\bar{X} \pm 1 \text{ SD} = 9.5 \pm 0.3$), while habitats dominated by NaCl had the lowest average pH (8.2 ± 0.5); habitats dominated by $\text{Na}_2(\text{Mg})\text{SO}_4$ had an average pH of 8.7 ± 0.4 .

Based on Pearson product-moment correlation coefficients, all major ions except Ca^{+2} and CO_3^{-2} showed significant correlations with ionic strength for lake waters examined in this study (Table 2). There were strong positive correlations between the monovalent ions of Na^+ , K^+ , Cl^{-1} , and HCO_3^{-1} , as well as Na^+ and the divalent ion of SO_4^{-2} . There was also a strong positive correlation between Mg^{+2} and SO_4^{-2} (Table 2). The equation for the relationship ($r^2 = 0.867$, $P < .001$) between total dissolved solids (TDS) and specific conductance (X) for the 47 saline habitats in western USA and British Columbia was:

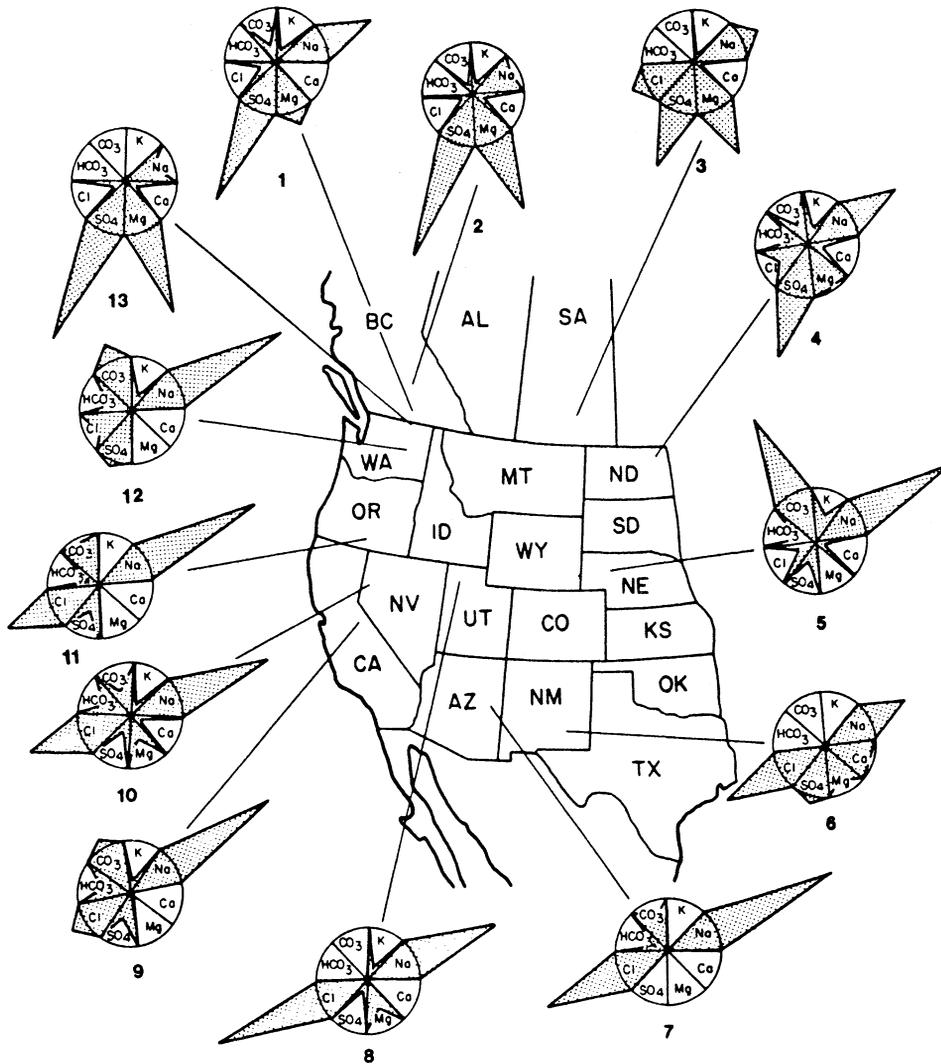


FIG. 2. Maucha diagrams (Maucha 1932) for major ions of representative saline lakes in western North America. 1 = Mahoney, BC; 2 = Bowers, BC; 3 = Little Manito, SASK; 4 = Devils, ND; 5 = Border, NB; 6 = Figure 8, NM; 7 = Green Pond, AZ; 8 = Great Salt, UT; 9 = Mono, CA; 10 = Pyramid, NV; 11 = Abert, OR; 12 = Soap, WA; 13 = Hot, WA. The triangulate coordinate (Cole 1983) was employed to portray relative composition of anions or cations for selected saline habitats, and Maucha (1932) diagrams were constructed to indicate combined anion and cation composition for representative saline habitats.

$$TDS = 11.96 + 0.60X.$$

The principal components analysis (PCA) separated the major ions in the 47 saline aquatic habitats in western USA and British Columbia, Canada into three principal factors (Table 3). The three factors in the PCA accounted for 80% of the variation among major ions in the lakes studied. Factor one explained 36.7% of the variation in chemical composition of the lakes, while factors two and three explained 32.3 and 10.4%, respectively.

The first factor showed significant correlations ($P < .05$) with ions and had a highly significant correlation ($r = -0.907, P < .001$) with specific conductance. There were strong negative loadings for high concentrations

of Na^+ , Cl^- , HCO_3^- , and CO_3^{2-} in factor one. Thus, habitats with high positive factor scores on factor one have low specific conductance, and habitats with high negative scores have high specific conductance.

Factor two also showed significant correlations ($P < .05$) with concentrations of all ions, but there was no significant correlation with specific conductance ($r^2 = -0.281, P > .05$). Factor two had strong positive loadings for concentrations of Mg^{+2} and SO_4^{-2} , strong negative loadings for concentrations of HCO_3^{-1} and CO_3^{-2} , and a significant correlation with pH ($r = -0.672, P < .001$). Thus, habitats with high positive factor scores on factor two have high Mg^{+2} concentrations and low HCO_3^{-1} and CO_3^{-2} concentrations.

Factor three only had significant positive loadings

TABLE 2. Matrix of Pearson correlation coefficients for physicochemical characteristics and biotic indices [Shannon–Wiener diversity (H') and species richness (No. taxa)] for 47 saline aquatic habitats in North America.

	Specific cond.	pH	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻	SO ₄ ⁻²	HCO ₃ ⁻¹	CO ₃ ⁻²
pH	-0.05									
Na ⁺	0.91**	-0.07								
K ⁺	0.61**	-0.03	0.50**							
Ca ²⁺	0.17	-0.43	0.11	0.06						
Mg ²⁺	0.59**	-0.33	0.44*	0.05	0.17					
Cl ⁻	0.73**	-0.21	0.83**	0.69**	0.09	0.20				
SO ₄ ⁻²	0.68**	-0.19	0.58**	0.08	0.25	0.87**	0.17			
HCO ₃ ⁻¹	0.60**	0.22	0.51**	0.83**	-0.07	-0.04	0.61**	0.03		
CO ₃ ⁻²	0.27	0.59**	0.24	0.21	-0.25	-0.21	0.03	-0.07	0.51**	
H'	-0.75**	-0.28	-0.70**	-0.32	0.06	-0.39	-0.49**	-0.47*	-0.39	-0.43*
No. taxa	-0.78**	-0.28	-0.59**	-0.30	-0.02	-0.40	-0.38	-0.47*	-0.39	-0.36

* $P < .05$, ** $P < .01$.

for concentrations of Ca²⁺ and Cl⁻ and a significant negative loading for concentrations of SO₄⁻². Thus, habitats with high positive factor scores on factor three have high Ca²⁺ and Cl⁻ concentrations and low SO₄⁻² concentrations. There was a significant correlation between factor three and pH ($r = -0.672$, $P < .001$), but no significant relationship between factor three and specific conductance ($r = 0.155$, $P > .05$).

Diatom distribution and ecology.—Two hundred and seventy-four diatom taxa were identified from 63 saline aquatic habitats in western North America. Diatoms were present in habitats ranging from 1.5 mS to 300 mS (2.8 to >400 g/L). Members of the Naviculaceae, Nitzschiaceae, Fragilariaceae, and Cymbellaceae were the dominant taxonomic groups, which made up 35.7, 16.4, 10.6, and 9.9% of the total diatom flora, respectively. Sixty-two taxa comprised over 85% of the diatom flora with the most common taxa, *Amphora coffeiformis*, *Nitzschia frustulum* v. *perpusilla*, *Nitzschia*

communis, *Navicula subinflatoidea*, and *Nitzschia palea*, each found in over 63% of the saline lake habitats (Table 4).

There was a strong negative relationship ($r = -0.754$, $P < .01$) between specific conductance and H' diversity (Fig. 4), and specific conductance and species richness ($r = -0.782$, $P < .01$) (Fig. 5). For example, Patience Lake, Saskatchewan (300 mS) had an H' diversity of 1.62 with four taxa, while Wakau Lake, Saskatchewan (2.9 mS) had an H' diversity of 5.54 and 88 taxa. Concentrations of sodium, Cl⁻, SO₄⁻², and CO₃⁻² showed a significant negative correlation with species diversity, while Na⁺ and SO₄⁻² showed a significant negative correlation with species richness (Table 2). Habitats dominated by NaCl salts (specific conductance = 44.7 ± 45.1 mS [$\bar{X} \pm 1$ SD], $n = 14$) had an average H' diversity of 3.22 and a mean of 40 taxa, while habitats dominated by Na₂CO₃ (specific conductance = 38.5 ± 40.9 mS, $n = 19$) had an average H' diversity of 2.78 and a mean of 29 taxa. Habitats dominated by Na₂SO₄ (specific conductance = 40.6 ± 54.6 mS, $n = 28$) had an H' diversity of 3.29 and an average of 28 taxa. There was no significant relationship between pH and species diversity or number of taxa ($r = 0.301$; $P > .05$) and only *Anomoeoneis sphaerophora* ($r = 0.542$; $P = .05$), *Mastogloia smithii* v. *lacustris* ($r = -0.506$; $P < .05$), and *Mastogloia braunii*

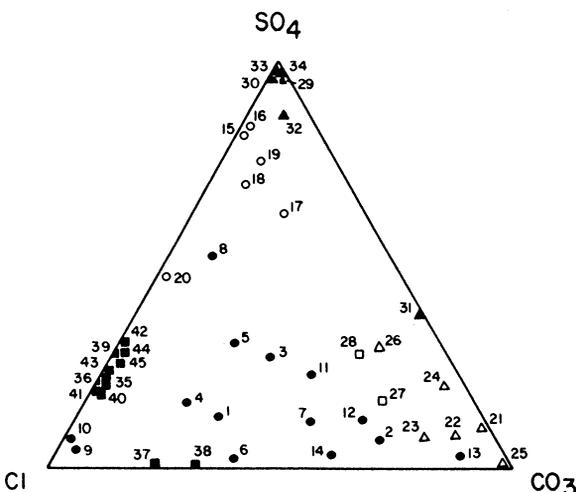


FIG. 3. Relative anion composition of 45 aquatic saline habitats in western USA and British Columbia, Canada. Identification numbers and symbols for lakes are the same as Fig. 1.

TABLE 3. Correlation coefficients for three primary factors from principal components analysis without rotation for major ions in 47 saline aquatic habitats in western USA and British Columbia, Canada.

Ion	Factor 1	Factor 2	Factor 3
Na ⁺	-0.874**	0.367*	0.161
K ⁺	-0.569**	-0.542**	-0.033
Ca ²⁺	0.334*	0.354*	0.710**
Mg ²⁺	-0.394**	0.765**	-0.201
Cl ⁻	-0.677**	0.453**	0.392**
SO ₄ ⁻²	-0.560**	0.605**	-0.360**
HCO ₃ ⁻¹	-0.635**	-0.649**	0.114
CO ₃ ⁻²	-0.639**	-0.671**	0.090

* $P < .05$, ** $P < .01$.

TABLE 4. Relative frequencies in all sampled habitats combined (mean \pm 1 SD), and percent of lakes in which taxa occurred, for dominant diatom taxa collected from 63 saline aquatic habitats in western North America.

Species	Relative frequency (%)	% lakes
<i>Amphora coffeiformis</i> (Ag.) Kütz.	10.5 \pm 14.9	92.1
<i>Nitzschia frustulum</i> v. <i>perpusilla</i> (Rabh.) Grun.	10.2 \pm 13.9	95.2
<i>Nitzschia communis</i> Rabh.	9.7 \pm 16.6	93.7
<i>Navicula subinflatooides</i> Hust.	3.4 \pm 11.6	63.5
<i>Nitzschia palea</i> (Kütz.) W. Sm.	3.3 \pm 4.8	81.0
<i>Synedra radians</i> Kütz.	3.2 \pm 9.3	25.2
<i>Nitzschia obtusa</i> W. Sm.	3.0 \pm 12.4	33.3
<i>Navicula cincta</i> (Ehr.) Ralfs.	2.9 \pm 7.9	57.1
<i>Anomoeoneis sphaerophora</i> (Ehr.) Pfitz.	2.7 \pm 6.9	58.7
<i>Cocconeis placentula</i> v. <i>lineata</i> (Ehr.) Van Heurck.	2.2 \pm 6.9	50.8
<i>Mastogloia smithii</i> v. <i>lacustris</i> Grun.	2.0 \pm 4.3	34.9
<i>Brachysira aponica</i> Kütz.	2.0 \pm 6.2	33.3
<i>Cymbella pusilla</i> Grun.	1.8 \pm 2.9	61.9
<i>Fragilaria pinnata</i> v. <i>subsolaris</i> (Grun.) Mayer	1.7 \pm 7.4	17.5
<i>Surirella ovata</i> Kütz.	1.7 \pm 3.3	23.8
<i>Anomoeoneis costata</i> (Kütz.) Hust.	1.6 \pm 5.1	47.6
<i>Mastogloia elliptica</i> v. <i>danseii</i> (Thwaites) Cl.	1.5 \pm 3.3	40.0
<i>Hantzschia amphioxys</i> (Ehr.) Grun.	1.4 \pm 8.4	28.6
<i>Fragilaria vaucheria</i> (Kütz.) Peters	1.4 \pm 6.5	24.4
<i>Navicula cryptocephala</i> v. <i>veneta</i> (Kütz.) Rabh.	1.3 \pm 2.7	57.1
<i>Cyclotella meneghiniana</i> Kütz.	1.2 \pm 3.9	58.7
<i>Amphora arcus</i> v. <i>sulcata</i> (A. Sm.) Cl.	1.2 \pm 4.5	14.3
<i>Eunotia</i> sp.	1.0 \pm 4.2	12.7
<i>Synedra pulchella</i> Ralfs ex Kütz.	1.0 \pm 4.2	42.8
<i>Diatoma tenue</i> Ag.	0.8 \pm 2.9	22.2
<i>Navicula cryptocephala</i> Kütz.	0.8 \pm 1.8	44.4
<i>Campylodiscus clypeus</i> Ehr.	0.8 \pm 3.0	33.3
<i>Nitzschia gandersheimiensis</i> Krasske	0.7 \pm 3.5	17.5
<i>Nitzschia apiculata</i> (Grev.) Grun.	0.7 \pm 2.5	38.1
<i>Denticula elegans</i> Kütz.	0.7 \pm 2.2	33.3
<i>Rhopalodia gibberula</i> (Ehr.) O. Muell.	0.7 \pm 2.3	58.7
<i>Amphora acutiscula</i> Kütz.	0.7 \pm 2.6	31.7
<i>Synedra fasciculata</i> v. <i>truncatum</i> (Grev.) Patr.	0.6 \pm 1.6	11.1
<i>Amphora ovalis</i> v. <i>affinis</i> (Kütz.) V.H. ex deT.	0.5 \pm 1.3	44.4
<i>Fragilaria construens</i> v. <i>venter</i> (Ehr.) Grun.	0.5 \pm 1.3	35.5
<i>Navicula capitata</i> v. <i>hungarica</i> (Grun.) Ross	0.5 \pm 1.8	19.0
<i>Cymbella cymbiformis</i> v. <i>nonpunctata</i> Font.	0.5 \pm 1.3	12.7
<i>Navicula heufleri</i> v. <i>leptocephala</i> (Breb. ex Grun. Patr)	0.5 \pm 1.4	39.6
<i>Rhoicosphenia curvata</i> (Kütz.) Grun. ex Rabh.	0.4 \pm 1.2	20.6
<i>Gomphonema olivaceum</i> (Lyngb.) Kütz.	0.4 \pm 2.1	12.7
<i>Navicula salinarum</i> Grun.	0.4 \pm 1.7	34.9
<i>Navicula pseudocrassirostris</i> Hust.	0.4 \pm 1.4	14.7
<i>Mastogloia braunii</i> Grun.	0.3 \pm 1.0	17.5
<i>Achnanthes haukiana</i> Grun.	0.3 \pm 0.9	36.5
<i>Entomoneis paludosa</i> W. Sm.	0.3 \pm 1.0	30.2
<i>Synedra ulna</i> (Nitz.) Ehr.	0.3 \pm 0.6	38.1
<i>Denticula elegans</i> v. <i>kittomania</i> (Grun.) DeT.	0.2 \pm 1.6	7.9
<i>Nitzschia hungarica</i> Grun.	0.2 \pm 0.7	28.7
<i>Cocconeis placentula</i> v. <i>euglypta</i> (Ehr.) Cl.	0.2 \pm 1.1	19.1
<i>Epithemia argus</i> (Ehr.) Kütz.	0.2 \pm 0.7	28.6
<i>Surirella striatula</i> Turp.	0.2 \pm 0.4	31.7
<i>Amphora ovalis</i> (Kütz.) Kütz.	0.2 \pm 0.4	33.3
<i>Synedra fasciculata</i> (Ag.) Kütz.	0.2 \pm 0.7	20.7
<i>Mastogloia aquilegia</i> Grun.	0.2 \pm 0.8	19.0
<i>Plagiotropis arizonica</i> Czar. & Blinn	0.2 \pm 0.5	20.6
<i>Nitzschia fonticola</i> Grun.	0.2 \pm 0.5	28.6
<i>Entomoneis paludosa</i> v. <i>duplex</i> (Donk.) Reim.	0.1 \pm 0.5	14.3
<i>Cyclotella striata</i> (Kütz.) Grun.	0.1 \pm 0.5	11.1
<i>Diatoma tenue</i> v. <i>elongatum</i> Lyngb.	0.1 \pm 0.4	17.5
<i>Nitzschia tryblionella</i> Hantz.	0.1 \pm 0.3	15.9
<i>Nitzschia amphibia</i> Grun.	0.1 \pm 0.2	20.6
<i>Gomphonema parvulum</i> Kütz.	0.1 \pm 0.3	15.9

($r = -0.762$; $P = .01$) were significantly correlated with pH.

Only a few diatom taxa showed significant Pearson correlations with ions. For example, *Cocconeis placen-*

tula v. *lineata* showed significant correlations ($P < .01$, $n = 29$) with concentrations of K^{+1} ($r = 0.833$), Cl^{-1} ($r = 0.606$), and HCO_3^{-1} ($r = 0.717$), while *Navicula cincta* showed significant correlations ($P < .05$, $n =$

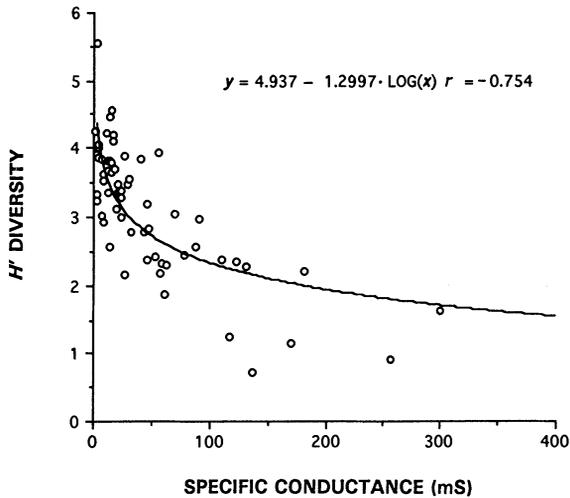


FIG. 4. Relationship between specific conductance and diatom H' diversity for 63 saline lakes in western North America.

27) with Cl^{-1} ($r = 0.521$) and Ca^{+2} ($r = 0.534$), and *Anomoeoneis sphaerophora* showed a significant correlation ($P < .01$, $n = 28$) with concentration of HCO_3^{-1} ($r = 0.610$).

Lakes with high negative loadings for factor one had low species diversity and a low number of taxa (Fig. 6). Factor one loadings explained 63.4% of the variation in H' diversity ($r = -0.889$, $P < .001$) and 51% of the variation in the number of taxa ($r = -0.838$, $P < .001$) in the 47 saline aquatic habitats. *Amphora coffeiformis*, *Anomoeoneis sphaerophora*, *Navicula subinflatooides*, and *Nitzschia communis* showed significant positive relationships to factor one loadings, while *Mastogloia braunii*, *Mastogloia smithii* v. *lacustris*, and *Plagiotropis arizonica* showed significant negative correlations with factor one loadings (Table 5).

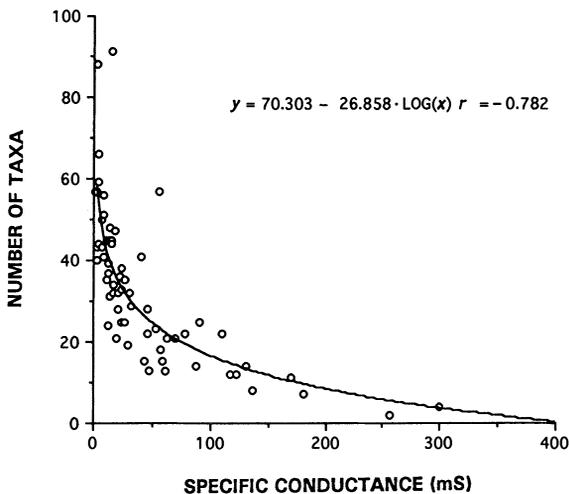


FIG. 5. Relationship between specific conductance and number of diatom taxa for 63 saline lakes in western North America.

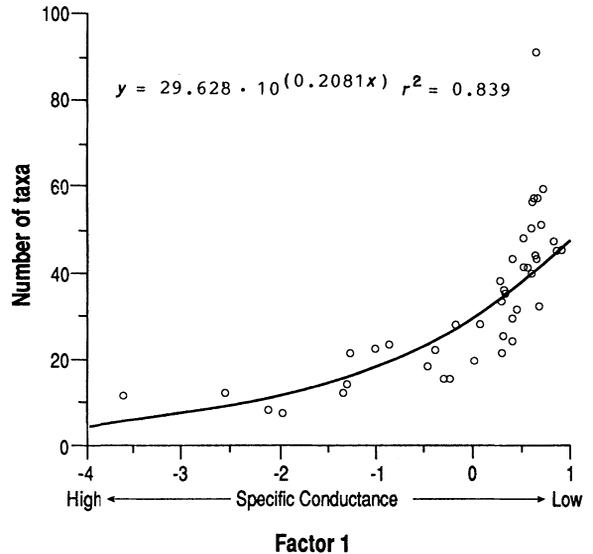


FIG. 6. Relationship between factor one from principal components analysis and number of diatom taxa for 47 saline lakes in western USA. Gradient of specific conductance for factor one is provided along abscissa.

When factor two loadings for each lake are converted into absolute values, there is a significant correlation with number of taxa ($r = 0.740$, $P < .01$) and species diversity ($r = 0.649$, $P < .01$). Both species diversity and number of taxa were highest at intermediate loadings for factor two. Fig. 7 illustrates the relatively narrow tolerance to loadings above and below intermediate concentrations of MgSO_4 as represented by factor scores. *Amphora coffeiformis*, *Synedra fasciculata*, and *Synedra pulchella* showed significant positive correlations with factor two (high tolerance to MgSO_4) while *Anomoeoneis costata*, *Anomoeoneis sphaerophora*, *Nitzschia communis*, *Nitzschia fonticola*, and *Nitzschia palea* showed significant negative correlations (low tolerance to loadings in factor two) (Table 5).

There was no significant correlation between factor three and H' diversity ($r = -0.045$, $P > .05$) or number of taxa ($r = 0.071$, $P > .05$). *Amphora arcus* v. *sulcata*, *Cyclotella meneghiniana*, *Entomoneis paludosa*, *Entomoneis paludosa* v. *duplex*, *Eunotia* sp., *Mastogloia braunii*, *Mastogloia smithii* v. *lacustris*, *Navicula pseudocrassirostris*, *Plagiotropis arizonica*, *Surirella striatula*, and *Synedra radians* had significant positive correlations with factor three. *Nitzschia frustulum* v. *perpusilla*, *Synedra fasciculata*, and *Synedra pulchella* showed significant negative correlations to factor three (Table 5).

The specific conductance (SCI) and ion (IonI) indices ranked various diatom taxa according to their association with ionic strength and major cations and anions (Table 6). Therefore, taxa with the highest SCI values such as *Amphora coffeiformis*, *Navicula subinflatooides*, *Nitzschia communis*, *Nitzschia frustulum* v. *perpusilla*, and *Synedra fasciculata* are considered to be most tol-

TABLE 5. Correlation coefficients for selected diatom taxa and the first three factors from principal components analysis of 47 saline aquatic habitats in western USA and British Columbia, Canada.

Species	Factor 1	Factor 2	Factor 3
<i>Amphora coffeiformis</i>	0.422**		
<i>Anomoeoneis sphaerophora</i>	0.347*		
<i>Mastogloia braunii</i>	-0.287*		
<i>Mastogloia smithii</i> v. <i>lacustris</i>	-0.341*		
<i>Navicula subinflatooides</i>	0.418**		
<i>Nitzschia communis</i>	0.345*		
<i>Plagiotropis arizonica</i>	-0.313*		
<i>Amphora coffeiformis</i>		0.675**	
<i>Anomoeoneis costata</i>		-0.324*	
<i>Anomoeoneis sphaerophora</i>		-0.543**	
<i>Nitzschia communis</i>		-0.496**	
<i>Nitzschia fonticola</i>		-0.289*	
<i>Nitzschia palea</i>		-0.338*	
<i>Synedra fasciculata</i>		0.427**	
<i>Synedra pulchella</i>		0.409**	
<i>Amphora arcus</i> v. <i>sulcata</i>			0.303*
<i>Cyclotella meneghiniana</i>			0.378**
<i>Entomoneis paludosa</i>			0.361*
<i>Entomoneis paludosa</i> v. <i>duplex</i>			0.412**
<i>Eunotia</i> sp.			0.494**
<i>Mastogloia braunii</i>			0.382**
<i>Mastogloia smithii</i> v. <i>lacustris</i>			0.412**
<i>Navicula pseudocrassirostris</i>			0.500**
<i>Nitzschia frustulum</i> v. <i>perpusilla</i>			-0.322*
<i>Plagiotropis arizonica</i>			0.347*
<i>Surirella striatula</i>			0.375**
<i>Synedra fasciculata</i>			-0.428**
<i>Synedra pulchella</i>			-0.434**
<i>Synedra radians</i>			0.526**

erant of habitats with high ionic strength because the index is a function of the normalized frequency of occurrence and ionic concentration (See *Materials and methods*). In contrast, species with the lowest SCI values such as *Cocconeis placentula* v. *euglypta*, *Fragilaria*

vaucheria, *Gomphonema parvulum*, *Nitzschia amphibia*, and *Nitzschia tryblionella*, are considered to be less tolerant of elevated ion concentrations.

Cluster analysis of specific conductance indices (SCI) for selected diatom taxa illustrated two major groups. Group one included taxa with SCI values <85, and formed five subgroups of diatom assemblages along a specific conductance gradient (Fig. 8). The diatom taxa in the first subgroup (I₁) had SCI values <20 and were considered least tolerant to elevated ion concentrations. This assemblage occurred in habitats with specific conductance values <10 mS ($\bar{X} \pm 1 \text{ SD} = 7.5 \pm 6.5 \text{ mS}$) and was represented by *Cocconeis placentula* v. *euglypta*, *Fragilaria vaucheria*, *Gomphonema palea*, and *Nitzschia amphibia*. The diatom assemblage in subgroup two (I₂) had SCI values of 20–30 and included *Diatoma tenue*, *Entomoneis paludosa*, *Gomphonema olivaceum*, *Surirella striatula*, and *Synedra ulna*. This assemblage occurred in habitats with specific conductance values <30 mS ($16.7 \pm 18.1 \text{ mS}$). *Achnanthes haukiana*, *Amphora ovalis* v. *affinis*, *Denticula elegans*, *Fragilaria construens* v. *venter*, *Navicula salinarum*, *Nitzschia obtusa*, *Rhoicosphenia curvata*, and *Rhopalodia gibberula* are representative taxa within subgroup three (I₃). These taxa typically occurred in habitats with specific conductance values <50 mS ($24.6 \pm 28.2 \text{ mS}$). The diatom assemblage in subgroup four (I₄) had SCI values of 50–60 and was represented by *Brachysira aponina*, *Cocconeis placentula* v. *lineata*, *Mastogloia*

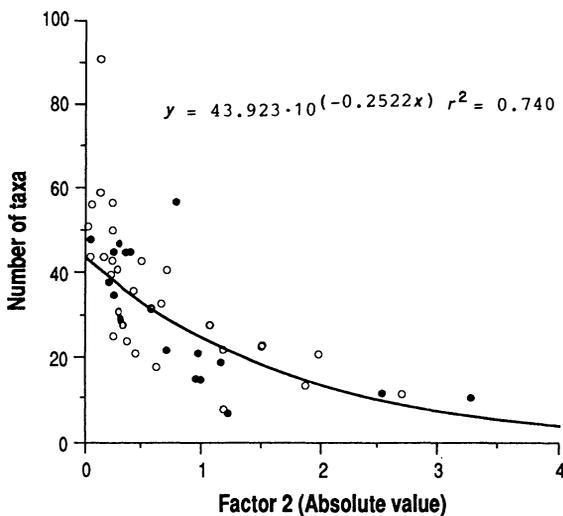


FIG. 7. Relationship between absolute values for factor two from principal components analysis and number of diatom taxa for 47 saline lakes in western USA. Closed circles represent positive factor scores and open circles represent negative factor scores.

TABLE 6. Specific conductance indices (SCI) and ion indices (IonI) for selected diatom taxa collected from saline aquatic habitats in western North America. Diatom taxa are arranged according to their occurrence from highest to lowest specific conductance index. Values in boldface indicate highest anion and cation values for each taxon.

Species	SCI	IonI							
		Cations				Anions			
		Mg ⁺²	Ca ⁺²	Na ⁺¹	K ⁺¹	CO ₃ ⁻²	HCO ₃ ⁻¹	SO ₄ ⁻²	Cl ⁻¹
<i>Navicula subinflatoides</i>	125.2	32.5	7.3	157.6	11.5	40.1	10.2	71.9	108.0
<i>Amphora coffeiformis</i>	112.9	51.3	14.6	184.3	10.8	34.2	15.9	102.2	105.7
<i>Nitzschia communis</i>	98.8	40.7	10.9	175.4	11.7	42.5	16.5	87.4	93.5
<i>Synedra fasciculata</i>	91.4	52.7	5.8	116.6	2.9	2.1	2.2	103.8	68.8
<i>Nitzschia frustulum</i> v. <i>perpusilla</i>	89.4	43.9	9.7	181.3	11.7	42.5	20.1	93.0	89.6
<i>Synedra radians</i>	82.1	32.6	35.4	176.3	1.7	9.4	5.9	49.2	175.7
<i>Nitzschia palea</i>	82.0	37.3	9.3	161.0	12.1	43.1	17.7	77.2	75.9
<i>Synedra pulchella</i>	77.1	83.9	4.2	101.7	3.9	6.7	5.8	158.2	23.8
<i>Eunotia</i> sp.	72.3	43.1	48.7	165.5	0.6	4.1	2.8	66.3	180.0
<i>Anomooneis sphaerophora</i>	70.4	20.7	4.2	147.2	15.9	58.4	20.5	56.0	51.6
<i>Cymbella pusilla</i>	66.5	52.9	17.0	150.0	4.3	16.3	8.9	92.5	98.0
<i>Anomooneis costata</i>	66.1	35.3	5.1	136.6	19.1	56.9	21.0	68.6	49.5
<i>Amphora arcus</i> v. <i>sulcata</i>	60.9	45.9	43.7	158.4	2.1	0.0	2.3	70.4	177.0
<i>Hantzschia amphioxys</i>	58.1	17.7	4.4	133.2	9.9	38.5	23.9	50.2	52.6
<i>Cocconeis placentula</i> v. <i>lineata</i>	55.7	23.6	10.3	115.6	9.8	27.9	11.4	56.0	69.0
<i>Brachysira aponina</i>	55.6	41.4	19.2	149.2	3.8	20.7	10.4	70.3	110.5
<i>Nitzschia gandersheimiensis</i>	55.6	23.4	27.6	155.5	0.6	10.5	4.2	46.5	150.4
<i>Navicula cryptocephala</i>	54.1	32.8	8.7	131.9	9.8	33.8	19.3	63.8	59.7
<i>Mastogloia smithii</i> v. <i>lacustris</i>	53.9	48.5	29.9	160.5	2.8	10.3	7.0	80.2	137.5
<i>Navicula pseudocrassirostris</i>	51.9	32.5	39.3	134.1	1.1	2.8	2.5	51.2	145.9
<i>Fragilaria pinnata</i> v. <i>subsolitaria</i>	51.7	60.1	6.4	151.9	20.9	37.3	16.0	133.2	52.4
<i>Denticula elegans</i>	47.1	35.2	10.3	129.9	9.8	32.5	18.3	56.6	77.7
<i>Denticula elegans</i> v. <i>kittoniana</i>	46.6	31.9	8.9	152.6	8.3	15.9	17.1	48.1	120.4
<i>Navicula cryptocephala</i> v. <i>veneta</i>	46.4	43.9	5.3	154.6	9.7	37.8	20.2	97.9	60.1
<i>Amphora acutiscula</i>	46.0	52.3	16.8	122.5	6.9	16.5	7.5	91.9	79.5
<i>Nitzschia fonticola</i>	45.6	13.4	0.8	100.7	16.2	49.5	12.6	40.2	25.4
<i>Rhoicosphenia curvata</i>	43.9	34.6	5.0	137.2	20.2	55.4	19.1	74.2	48.2
<i>Navicula cincta</i>	43.8	40.9	4.9	120.4	7.7	24.2	12.3	86.7	46.6
<i>Surirella ovata</i>	42.9	11.7	10.5	118.7	6.3	36.1	17.4	23.1	60.9
<i>Mastogloia braunii</i>	41.5	27.4	33.9	147.7	0.9	0.1	1.1	46.9	154.2
<i>Fragilaria construens</i> v. <i>venter</i>	39.9	29.3	13.6	108.4	3.5	11.9	7.3	57.8	75.9
<i>Campylodiscus clypeus</i>	39.1	46.7	4.3	112.6	14.0	73.5	19.5	74.9	41.9
<i>Amphora ovalis</i> v. <i>affinis</i>	38.3	31.5	10.9	130.0	16.0	40.3	22.5	69.6	54.3
<i>Navicula salinarum</i>	38.3	24.4	7.5	97.1	2.9	17.5	6.7	42.2	65.0
<i>Achnanthes haukiana</i>	37.1	29.9	9.8	111.9	6.6	15.3	6.8	67.3	66.8
<i>Nitzschia obtusa</i>	36.5	48.4	21.3	141.0	2.9	11.1	7.4	82.5	107.4
<i>Navicula heufleri</i> v. <i>leptocephala</i>	36.1	35.4	14.9	113.1	4.5	11.9	7.3	65.9	71.6
<i>Nitzschia punctata</i>	35.9	47.9	8.8	114.4	3.5	5.2	4.7	101.7	61.4
<i>Rhopalodia gibberula</i>	35.4	21.0	7.4	115.6	8.7	30.3	16.7	39.3	65.2
<i>Entomoneis paludosa</i> v. <i>duplex</i>	33.9	31.3	37.8	94.9	0.9	1.3	1.4	57.0	91.8
<i>Mastogloia elliptica</i> v. <i>danseii</i>	33.3	56.9	22.5	126.6	4.2	12.1	7.5	95.8	90.2
<i>Cyclotella meneghiniana</i>	31.6	22.1	15.1	124.2	5.2	19.5	11.6	43.7	102.8
<i>Plagiotropis arizonica</i>	31.6	26.9	29.9	122.9	1.6	1.5	2.7	48.5	123.7
<i>Nitzschia apiculata</i>	30.7	40.8	7.9	106.2	4.6	13.8	9.4	80.7	54.2
<i>Mastogloia smithii</i>	29.7	23.0	30.2	124.4	0.6	0.1	0.8	43.4	126.2
<i>Synedra fasciculata</i> v. <i>truncatum</i>	29.1	42.2	1.5	103.3	10.7	22.2	8.8	96.8	30.2
<i>Diatoma tenue</i>	27.6	41.0	1.7	164.0	6.2	37.3	23.9	90.3	62.1
<i>Cyclotella striata</i>	27.5	50.2	5.8	101.3	4.4	5.7	6.5	115.0	33.3
<i>Amphora ovalis</i>	27.2	25.8	10.3	75.9	3.7	18.6	10.4	52.7	45.0
<i>Epithemia argus</i>	27.4	22.4	15.6	105.4	4.8	17.5	11.7	35.6	81.0
<i>Synedra ulna</i>	26.1	31.5	4.9	101.4	10.5	30.6	19.1	51.1	46.7
<i>Entomoneis paludosa</i>	25.8	34.2	21.7	113.3	5.1	15.3	12.9	50.5	88.4
<i>Surirella striatula</i>	24.9	17.4	12.9	98.5	1.8	12.2	7.5	29.8	79.4
<i>Navicula capitata</i> v. <i>hungarica</i>	22.9	38.3	2.6	110.9	14.6	30.7	17.2	82.1	35.2
<i>Gomphonema olivaceum</i>	23.5	45.9	1.2	144.4	7.0	40.5	27.7	77.1	52.5
<i>Nitzschia hungarica</i>	22.8	20.9	7.9	106.7	3.4	18.4	14.5	41.7	63.9
<i>Diatoma tenue</i> v. <i>elongatum</i>	19.2	29.4	8.6	93.9	3.8	9.9	8.9	65.4	56.3
<i>Fragilaria vaucheria</i>	16.5	24.9	4.4	141.6	12.2	44.5	36.8	102.5	49.2
<i>Nitzschia amphibia</i>	15.4	33.2	20.1	134.9	14.0	41.2	34.1	66.7	56.8
<i>Nitzschia tryblionella</i>	14.9	46.7	4.2	122.0	4.7	23.3	22.3	97.3	33.6
<i>Gomphonema parvulum</i>	11.0	12.3	3.7	93.6	7.7	24.0	17.5	28.5	45.5
<i>Cocconeis placentula</i> v. <i>euglypta</i>	9.8	23.5	15.9	92.5	5.7	13.4	11.8	44.2	57.3

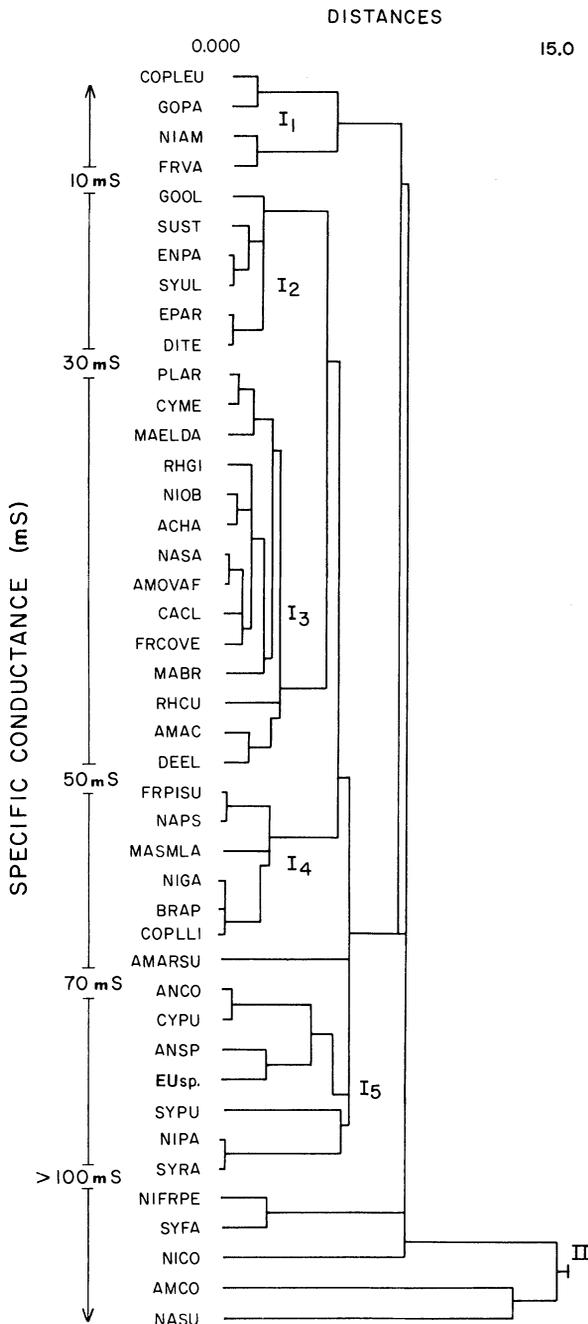


FIG. 8. Cluster analysis of 43 diatom taxa along a specific conductance gradient. Taxa used in this cluster comprised >75% of the diatom species in saline lakes in western USA. COPLEU = *Cocconeis placentula* v. *euglypta*, GOPA = *Gomphonema parvulum*, NIAM = *Nitzschia amphibia*, FRVA = *Fragilaria vaucheria*, GOOL = *Gomphonema olivaceum*, SUST = *Surirella striatula*, ENPA = *Entomoneis paludosa*, SYUL = *Synedra ulna*, EPAR = *Epithemia argus*, DITE = *Diatoma tenue*, PLAR = *Plagiotropis arizonica*, CYME = *Cymbella meneghiniana*, MAELDA = *Mastogloia elliptica* v. *danseii*, RHGI = *Rhopalodia gibberula*, NIOB = *Nitzschia obtusa*, ACHA = *Achnanthes haukiana*, NASA = *Navicula salinarum*, AMOVAF = *Amphora ovalis* v. *affinis*, CACL = *Campylodiscus clypeus*, FRCOVE = *Fragilaria construens* v. *venter*, MABR = *Mastogloia braunii*, RHCU = *Rhoicosphenia*

smithii v. *lacustris*, *Navicula pseudocrassirostris*, and *Nitzschia gandersheimiensis*. This diatom assemblage occurred in habitats with specific conductance values <70 mS (30.4 ± 31.9 mS). The diatom assemblage in subgroup 5 (I₅) had SCI values of 60–85 and was represented by *Anomoeoneis costata*, *Anomoeoneis sphaerophora*, *Cymbella pusilla*, *Eunotia* sp., *Nitzschia palea*, *Synedra pulchella*, and *Synedra radians*. Taxa within this assemblage typically occurred in habitats with specific conductance values <100 mS (35.3 ± 32.9 mS). The specific conductance values given for each subgroup represent the upper limits for that diatom assemblage because, in all cases, taxa within any one subgroup occurred throughout the entire range of specific conductance values below these values (Fig. 8).

The diatom assemblage in group two (II) included taxa with SCI values >85.0 and was represented by *Amphora coffeiformis*, *Navicula subinflatoides*, *Nitzschia communis*, *Nitzschia frustulum* v. *perpusilla*, and *Synedra fasciculata*. This diatom assemblage is characterized as most indicative of habitats with high specific conductance and the most euryhaline because taxa within this assemblage occurred over the full range of ionic concentrations (1.5–300 mS).

The ion (IonI) indices provided instructive information on indicator taxa for selected ions (Table 6). Sodium had the highest average ion index (IonI = 128.6 ± 25.3 [$\bar{X} \pm 1$ SD]) for all 62 taxa examined. This reflects the dominance of Na⁺ in the saline lakes in North America and may suggest that cations have limited influence on the distribution of diatom taxa in these habitats. However, there were several taxa (e.g., *Anomoeoneis* spp., *Fragilaria pinnata* v. *subsolutarius*) that showed relatively high IonI values for K⁺, while other taxa (*Mastogloia* spp., *Nitzschia gandersheimiensis*) showed relatively low IonI values for this ion, and therefore may reflect differences in tolerance to K⁺ (Table 6). Similar patterns are also shown for Ca²⁺ and Mg²⁺ (Table 6).

Diatom taxa showed distinct associations with anions based on ion indices. For example, *Diatoma tenue*, *Fragilaria pinnata* v. *subsolutarius*, *Fragilaria vaucheria*, *Navicula capitata* v. *hungarica*, *Nitzschia apiculata*, *Nitzschia punctata*, *Rhoicosphenia curvata*, *Synedra*

curvata, AMAC = *Amphora acutiscula*, DEEL = *Denticula elegans*, FRPISU = *Fragilaria pinnata* v. *subsolutarius*, NAPS = *Navicula pseudocrassirostris*, MASMLA = *Mastogloia smithii* v. *lacustris*, NIGA = *Nitzschia gandersheimiensis*, BRAP = *Brachysira aponina*, COPLLI = *Cocconeis placentula* v. *lineata*, AMARSU = *Amphora arcus* v. *sulcata*, ANCO = *Anomoeoneis costata*, CYPU = *Cymbella pusilla*, ANSP = *Anomoeoneis sphaerophora*, EUsp = *Eunotia* sp., SYPU = *Synedra pulchella*, NIPA = *Nitzschia palea*, SYRA = *Synedra radians*, NIFRPE = *Nitzschia frustulum* v. *perpusilla*, SYFA = *Synedra fasciculata*, NICO = *Nitzschia communis*, AMCO = *Amphora coffeiformis*, NASU = *Navicula subinflatoides*.

fasciculata, and *Synedra pulchella* showed high IonI values for SO_4^{-2} -dominated habitats (Table 6). In contrast, *Amphora arcus* v. *sulcata*, *Entomoneis paludosa*, *Eunotia* sp., *Mastogloia braunii*, *Mastogloia smithii* v. *lacustris*, *Navicula pseudocrassirostris*, *Navicula subinflatoides*, *Nitzschia gandersheimiensis*, *Nitzschia obtusa*, *Plagiotropis arizonica*, and *Synedra radians* are representative species of high IonI values for Cl^{-1} -dominated habitats. Finally, *Anomoeoneis costata*, *Anomoeoneis sphaerophora*, *Campylodiscus clypeus*, and *Nitzschia fonticola* showed relatively high IonI values for CO_3^{-2} habitats. Each taxon within these three diatom assemblages showed a strong association with a particular anion, and therefore may have utility as an indicator species.

Other taxa (e.g., *Amphora arcus* v. *sulcata*, *Eunotia* sp., *Mastogloia* spp., and *Navicula pseudocrassirostris*) showed relatively low IonI values for CO_3^{-2} , which suggests an antagonistic response to the CO_3^{-2} ion. Still other taxa (e.g., *Amphora coffeiformis*, *Cocconeis placentula* v. *lineata*, *Nitzschia communis*, *Nitzschia frustulum* v. *perpusilla*) showed similarly high IonI values for several anions and therefore are considered eurytolerant to anions or ubiquitous in their distribution (Table 6).

Cluster analysis of specific conductance and anions (CO_3^{-2} , SO_4^{-2} , Cl^{-1}) showed close associations between diatom taxa and anions (Fig. 9). Taxa near the top of the dendrogram showed a strong association to SO_4^{-2} with *Synedra pulchella* being the most indicative of SO_4^{-2} -dominated habitats (Fig. 9, Table 6). In contrast, taxa near the bottom of the dendrogram showed a strong association to Cl^{-1} , with *Synedra radians* the best indicator of Cl^{-1} -dominated habitats. The mid-portion of the dendrogram consisted of taxa (*Anomoeoneis sphaerophora*, *A. costata*, and *Campylodiscus clypeus*) that were associated with relatively high concentrations of CO_3^{-2} . The progression of taxa above this midpoint toward the top of the diagram showed an increased association with SO_4^{-2} , while the taxa below the midpoint showed an increased association with Cl^{-1} (Fig. 9, Table 6). Those taxa (*Amphora arcus* v. *sulcata*, *Eunotia* sp., *Mastogloia* spp., and *Synedra radians*) that were least associated with CO_3^{-2} are clustered near the bottom of the tree. Typically taxa at both ends of the dendrogram have higher SCI values than taxa near the middle of the dendrogram.

DISCUSSION

Chemical features of lakes.—The chemical composition of saline lakes in the interior regions of western North America shows a strong relationship to latitude, with lakes at higher latitudes (above 47°) dominated by Na_2SO_4 and MgSO_4 , and lakes at intermediate and low latitudes dominated by Na_2CO_3 and NaCl (Fig. 2). The distribution of dissolved salts along the latitudinal gradient implies differential interactions between cli-

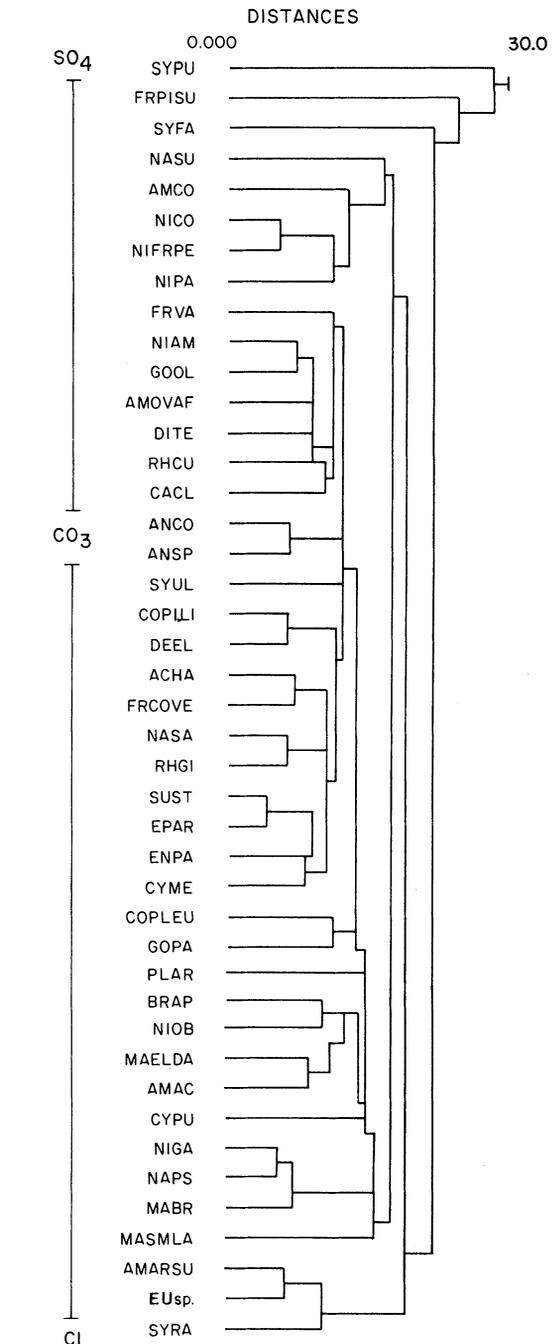


FIG. 9. Cluster analysis of 43 diatom taxa along an anion gradient. Taxa used in this cluster comprised >75% of the diatom species in saline lakes in western USA. Codes for diatom taxa are given in the legend of Fig. 8.

mate and geological processing (Gibbs 1970, Eugster and Hardie 1978, Drever 1988). For example, a potential source of SO_4^{-2} is the ubiquitous Cretaceous black shale in western Canada. Through weathering processes, combined with moderate levels of precipitation and evaporation (Hammer 1986), this shale could transfer relatively high concentrations of SO_4^{-2} to

TABLE 7. Summary of Pearson correlations between diatom community structure (H' diversity and number of taxa) and specific conductance and various ion compositions for saline lakes in western North America.

Lake types	Correlation (R^2)	
	H' diversity	Number of taxa
All lake types ($n = 63$)	-0.569**	-0.630**
Lakes with specific conductance > 100 mS ($n = 9$)	-0.079	-0.643**
Lakes with specific conductance > 75 mS ($n = 12$)	-0.322*	-0.70**
Lakes with specific conductance > 50 mS ($n = 19$)	-0.361**	-0.414**
Lakes with specific conductance > 25 mS ($n = 30$)	-0.500**	-0.381**
NaCl lakes (all concentrations) ($n = 20$)	-0.569**	-0.607**
Na ₂ SO ₄ lakes (all concentrations) ($n = 24$)	-0.551**	-0.750**
Na ₂ CO ₃ lakes (all concentrations) ($n = 19$)	-0.510**	-0.828**

* $P < .05$, ** $P < .01$.

aquatic ecosystems. In contrast, the high concentrations of CO₃⁻² and Cl⁻¹ at the lower latitudes of western USA result from interactions of weathering of sedimentary deposits and high evaporation rates that differentially precipitate CO₃⁻² and SO₄⁻² over Cl⁻¹ salts.

The divergence in relative ion proportions (especially anions) of saline lakes from those of freshwater environments suggests that climatic conditions override geochemical influences in determining the ionic composition of waters in saline lakes. The lakes examined are located between 33° N and 53° N latitude and 99° W and 122° W longitude (Table 1, Fig. 2), and experience varied and relatively high ratios of evaporation to precipitation. For example, saline lakes between 33° N and 40° N latitude experience relatively high evaporation-to-precipitation ratios. The relative proportions of anions for saline lakes in this region are the same as seawater (Cl⁻¹ > SO₄⁻² > CO₃⁻²). On the other hand, the anion proportions for saline lakes above 47° N, with relatively lower evaporation-to-precipitation ratios, are SO₄⁻² > Cl⁻¹ > CO₃⁻² (Fig. 2). Anion proportions for freshwater lakes are CO₃⁻² > SO₄⁻² > Cl⁻¹ (Cole 1983).

The relative proportion of cations in athalassic saline lakes are Na⁺¹ > or < Mg⁺² > K⁺¹ > Ca⁺², with Na⁺¹ the dominant ion in 81% of the habitats, compared to Ca⁺² > Mg⁺² > Na⁺¹ > K⁺¹ for freshwater environments (Drever 1988). The proportions of cations in saline lakes are, to a large part, the same as those in seawater.

Therefore, the wide range of relative ion proportions (especially anions) in saline lakes throughout North America results, in large part, from the differential precipitation of ions due to differences in ratios of evaporation to precipitation (Drever 1988). Clarke (1924) states that under high evaporation rates, CaCO₃ precipitates first, allowing SO₄⁻² and Cl⁻¹ to concentrate. As erosion of sedimentary deposits increases dissolved Ca⁺² levels, CaSO₄ precipitates, while Cl⁻¹ remains in solution.

The average specific conductance (47.3 ± 60.0 mS [$\bar{X} \pm 1$ SD], $n = 63$) in athalassic (nonmarine) saline

lakes of western North America is similar to that of thalassic (marine) environments. The average specific conductance for water in marine environments is 48.0 mS.

Diatom ecology.—Specific conductance (total dissolved solids) and major anions are important predictors of the distribution and community structure of diatoms in saline lakes in western North America, while pH and major cations show no relationship to diatom community structure in these highly concentrated aquatic ecosystems. Diatom species diversity and number of taxa show an inverse relationship to specific conductance, and selected diatom taxa reveal strong associations with specific anions as well as ranges of specific conductance.

Recently, Williams et al. (1990) argue that biotic communities in saline lakes show a rapid decline in species number in low range (0–10 g/L) saline systems, but a less dramatic decline at intermediate (10–30 g/L) and high (> 100 g/L) salinity ranges. In contrast, I report a significant negative relationship for saline lakes in western North America between specific conductance and diatom community structure at several ranges of specific conductance and for several ionic compositions (i.e., NaCl, Na₂SO₄, Na₂CO₃).

Table 7 summarizes Pearson correlations for diatom community structure and various levels of specific conductance and ion composition. All levels of specific conductance show a significant negative relationship with H' diversity except for those lakes > 100 mS. It should be noted, however, that the relationship between specific conductance and H' diversity is strongest at low ranges of specific conductance, because correlation values progressively decrease with an increase in specific conductance (Table 7).

In addition to physiological constraints, low species diversity in saline lakes may be influenced by the fact that there are significantly fewer highly saline lakes than freshwater ponds and lakes throughout North America. Less than 27% of the saline lakes examined had specific conductance values ≥ 50 mS; approximate conductance above which species number remains low (Fig. 5). It is well established that numbers of species

increase as colonization area increases (Begon et al. 1990). Perhaps saline lakes provide models to further test hypotheses on colonization, community structure, extinction, and island biogeography.

The lack of significant correlations between pH and H' diversity and number of taxa, and the fact that only two species (*Anomoeoneis sphaerophora* and *Mastogloia braunii*) show a significant correlation with pH suggests that specific conductance and/or ionic composition overrides any effect of pH on diatom community structure in saline lakes. The saline lakes in this study were typically well buffered: concentration of $\text{CaCO}_3 = 124.2 \pm 254$ meq/L (mean \pm SD), with an average pH of 8.9 ± 0.6 ranging from 7.6 to 10.0. Servant-Vildary and Roux (1990) also reported that ionic elements were more important than pH for diatom community structure in saline lakes in southern Bolivia.

The lack of correlation between pH and distribution of diatoms in saline lakes may suggest that diatoms are more sensitive to variation in pH from neutral to acid, rather than near-neutral to basic. Charles (1985) reported that diatom distributions in the dilute lake waters (pH ranged from 4.5 to 7.8; mean specific conductance = $24.8 \mu\text{S}/\text{cm}$) of the Adirondacks in northern New York were strongly correlated with pH-related factors. Consequently, diatoms have been successfully used to infer pH from dilute lakewater (Charles 1985), and for paleolimnological reconstructions in freshwater lakes (Whitmore 1989, Kingston et al. 1990, Scruton et al. 1990), but may have limited predictive value in saline lakes where pH values are typically >8.3 .

Specific conductance index (SCI) values for diatom taxa may provide information on the upper tolerance limits of diatom taxa to ionic concentrations (Table 6, Fig. 8). Diatom taxa with high SCI values (*Navicula subinflatooides*, *Amphora coffeiformis*, *Nitzschia communis*, *Synedra fasciculata*, *Nitzschia frustulum* v. *perpusilla*) are strongly associated with elevated concentrations of ions (>100 mS), in contrast to other taxa (*Fragilaria vaucheria*, *Nitzschia amphibia*, *Gomphonema parvulum*, *Cocconeis placentula* v. *euglypta*) that show weak associations with elevated ion concentrations (>10 mS). Each taxon in the assemblage with high SCI values has standard deviations greater than their means, indicating a wide tolerance range to specific conductance (eurytolerant), while each taxon in the assemblage with low SCI values has SD values less than their means, indicating a more restricted association with elevated concentrations of ions (stenotolerant).

Specific anions influenced the relative frequency and distribution of individual diatom taxa in saline lakes. For example, principal components and cluster analyses, and ion index (IonI) values show that certain diatom taxa (*Synedra radians*, *Mastogloia* spp.) associate with Cl^- -dominated habitats, while other taxa (*Synedra pulchella*, *Synedra fasciculata*, *Fragilaria pin-*

nata v. *subsolitaria*, *Navicula subinflatooides*) commonly associate with SO_4^{2-} -dominated habitats. Still other taxa (*Anomoeoneis costata*, *Anomoeoneis sphaerophora*, *Campylodiscus clypeus*) tend to be common in CO_3^{2-} -dominated habitats.

Therefore, diatom taxa provide useful indicators of specific anions. As outlined in Table 6, diatom taxa with high anion index (IonI) values indicate a strong association with that particular anion or combination of anions. The IonI values for diatoms can be used for interpreting the origin of deposits, and for assessing past and present water chemistry in lacustrine ecosystems.

The absence of a correlation between diatoms and major cations may result from the overwhelming dominance of sodium in the saline lakes throughout western North America. It may also suggest that the differential negative charges of anions have a stronger influence on diatom physiology than positively charged cations. The influence of cation and anion chemistry on diatom distribution needs further investigation.

The summarizing statistics for principal components analyses provide evidence that athalassic saline lakes were the evolutionary pathways for the rapid speciation of pennate diatoms from marine habitats into freshwater environments. This hypothesis is supported by the striking increase in number of diatom taxa at specific conductance loadings <45 mS (0.0 in Fig. 6), or the approximate specific conductance of seawater (48 mS). This pattern suggests that osmotic adjustments to low ion concentrations are easier than adjustments to higher concentrations of ions, and speciation at concentrations above that of seawater were limited. Furthermore, the average proportions of major ions in saline lakes at the point (factor one = 0.5) of increased species number most nearly approximate the proportion of ions in seawater, with the exception that Na^+ and Cl^- are reversed in order of relative proportions. In addition, factor two loadings show that intermediate concentrations of MgSO_4 ($\text{Mg}^{+2} = 44.8$ meq/L and $\text{SO}_4^{2-} = 103.1$ meq/L) have the highest number of taxa, with dramatic decreases in the number of species above and below this intermediate concentration (Fig. 7). These data indicate that diatoms are sensitive to MgSO_4 concentration, and that speciation in habitats that deviated from these intermediate concentrations was limited.

Ion index (IonI) values further suggest that salt lake diatom assemblages are a result of invasions from marine environments. Ion indices for diatoms (Table 6) indicate that nearly 73% of the 62 diatom taxa that were important in saline lakes show a strong association with Cl^- , while only 56 and 6.5% show strong associations with SO_4^{2-} and CO_3^{2-} , respectively. Carbonate ions, the anion of lowest proportion (0.6%) in seawater, appear to be the most restraining to diatom community structure. Finally, lakes dominated by NaCl have a higher average number of taxa (40) compared

to lakes dominated by Na_2CO_3 (29 taxa) and Na_2SO_4 (28 taxa).

Therefore, marine and estuarine diatom taxa may have been most successful in the invasion of shallow saline environments dominated by NaCl , while speciation was more limited in those environments that deviated from the ionic proportions of seawater, i.e., MgSO_4 and Na_2CO_3 . The abundance of shallow saline habitats during the Cretaceous and Tertiary Periods provided a progression of ion concentrations, from seawater to relatively dilute waters, for the adaptive radiation of species into freshwaters. It is important to note that the geologic time frame for the appearance of pennate diatoms during the early Tertiary or late Cretaceous Period (60–100 million years ago, Simonsen 1972), and the expansion of freshwater-type diatoms during the Oligocene (25–40 million years ago) is consistent with the proposed hypothesis.

Although there is some overlap between periphytic diatom taxa in marine estuaries (Main and McIntire 1974, Amspoker and McIntire 1978, Sullivan and Moncreiff 1988) and those in lacustrine ecosystems, the taxa are typically quite distinct for each system. Furthermore, many of the taxa in estuarine environments are in the Naviculaceae, Nitzschiaceae, and Cymbellaceae, as are taxa in athalassic saline lakes. Pennate diatoms, which include those taxa that developed mechanisms for locomotion on substrata to adjust to higher levels of ultraviolet light and sediment deposition, may have been the most successful taxa invading these shallow saline environments. The importance of athalassic environments in the adaptive radiation of diatoms into lacustrine ecosystems needs extensive laboratory studies to further develop the hypothesis.

Synedra shows the greatest divergence in habitat occupation in the saline lakes because different taxa represent extremes in their association with anions. *Synedra fasciculata*, and especially *Synedra pulchella*, show a close association with SO_4^{-2} -dominated habitats, while *Synedra radians* shows a close association with Cl^{-1} -dominated habitats (Fig. 9). The physiological adjustments by *Synedra* to monovalent and divalent anions needs laboratory experimentation.

The occurrence of *Eunotia* sp. in the New Mexico habitats (Table 1) with relatively high specific conductance ($\bar{X} = 30.8$ mS) and Ca^{+2} concentrations ($\bar{X} = 51.6$ meq/L) is unexplainable at this time. Typically, populations of *Eunotia* occur in habitats with acid-to-circumneutral pH, and low mineral and Ca^{+2} concentrations (Patrick and Reimer 1966, Round et al. 1990).

In summary, this study correlates diatom community assemblages with ionic composition in 63 saline lakes in western North America. The resulting specific conductance and ion indices should prove useful for interpreting the origin of geological deposits, and for assessing past and present water chemistry in lacustrine environments. Furthermore, this data set will provide

comparative baseline information to help establish the extent of dispersion of microalgae between isolated continents.

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LITERATURE CITED

- Amspoker, M. C., and C. D. McIntire. 1978. Distribution of intertidal diatoms associated with sediments in Yaquina Estuary, Oregon. *Journal of Phycology* **14**:387–395.
- Anderson, N. J., B. Rippey, and A. C. Stevenson. 1990. Change to a diatom assemblage in a eutrophic lake following point source nutrient re-direction: a palaeolimnological approach. *Freshwater Biology* **23**:205–217.
- APHA. 1985. Standard methods for the examination of water and wastewater. Sixteenth edition. American Public Health Association, Washington, D.C., USA.
- Bahls, L. L., E. E. Weber, and J. O. Jarvie. 1984. Ecology and distribution of major diatom ecotypes in the southern Fort Union Coal Region of Montana. Geological Survey Professional Paper **1289**.
- Bailey, L. W. 1922. Diatoms from the Quill Lakes, Saskatchewan and from Airdairie, Alberta. *Contributions of the Canadian Biologist* **11**:157–183.
- Battarbee, R. W. 1984. Diatom analysis and the acidification of lakes. *Philosophical Transactions of the Royal Society of London* **B 305**:451–477.
- Battarbee, R. W., R. B. Davis, and J. Merilainen, editors. 1986. Diatoms and lake acidity. Dr. W. Junk, Dordrecht, The Netherlands.
- Begon, M., J. L. Harper, and C. R. Townsend. 1990. Pages 786–815 in *Ecology, individuals, populations, and communities*. Second edition. Blackwell Scientific, Boston, Massachusetts, USA.
- Ben-Amotz, A., T. G. Tornabene, and W. H. Thomas. 1985. Chemical profiles of selected species of microalgae with emphasis on lipids. *Journal of Phycology* **21**:72–81.
- Blinn, D. W. 1972. Seasonal notes on plankton algae of East Stump Lake, North Dakota. *Prairie Naturalist* **4**:17–21.
- . 1984. Growth responses to variations in temperature and specific conductance by *Chaetoceros muelleri* (Bacillariophyceae). *British Phycological Journal* **19**:31–35.
- . 1990. The diatom flora of Lake Eyre South; a large episodically filled salt lake in South Australia. *Hydrobiologia* **210**:101–104.
- Bradbury, J. P. 1988. A climatic-limnologic model of diatom succession for paleolimnological interpretation of varved sediments at Elk Lake, Minnesota. *Journal of Paleolimnology* **1**:115–131.

- Bradbury, J. P., R. M. Forester, and R. S. Thompson. 1989. Late Quaternary paleolimnology of Walker Lake, Nevada. *Journal of Paleolimnology* 1:249–267.
- Brugam, R. B. 1978. Human disturbance and the historical development of Linsley pond. *Ecology* 59:19–36.
- Busch, D. E., and D. M. Kubly. 1980. Diatoms from desert playas in southern California. *Journal of Arid Environments* 3:55–62.
- Castenholz, R. W. 1960. Seasonal changes in the attached algae of freshwater and saline lakes in the Lower Grand Coulee, Washington. *Limnology and Oceanography* 5:1–28.
- Charles, D. F. 1985. Relationships between surface sediment diatom assemblages and lakewater characteristics in Adirondack lakes. *Ecology* 66:994–1011.
- Cholnoky, B. J. 1968. Die ökologie der Diatomeen in Binnengewässer. H. Cramer, Lehre, Germany.
- Clarke, F. W. 1924. The data of geochemistry. Fifth edition. United States Geological Survey Bulletin 770.
- Cloern, J. E., B. E. Cole, and R. S. Oremland. 1983. Seasonal changes in the chemistry and biology of a meromictic lake (Big Soda Lake, Nevada, U.S.A.). *Hydrobiologia* 105:195–206.
- Cole, G. A. 1983. Textbook of limnology. Third edition. Waveland Press, Prospect Heights, Illinois, USA.
- Drever, J. I. 1988. The geochemistry of natural waters. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Eugster, H. P., and L. A. Hardie. 1978. Saline lakes. Pages 237–293 in A. Lerman, editor. *Lakes: chemistry, geology, physics*. Springer-Verlag, New York, New York, USA.
- Felix, E. A., and S. R. Rushforth. 1979. The algal flora of the Great Salt Lake, Utah, USA. *Nova Hedwigia* 31:163–195.
- Fritz, S. C. 1990. Twentieth-century salinity and water-level fluctuations in Devils Lake: test of a diatom-based transfer function. *Limnology and Oceanography* 35:1771–1781.
- Galat, D. L., E. L. Lider, S. Vigg, and S. R. Robertson. 1981. Limnology of a large, deep, North American terminal lake, Pyramid Lake, Nevada, U.S.A. *Hydrobiologia* 82:281–317.
- Gibbs, R. J. 1970. Mechanisms controlling world water chemistry. *Science* 170:1088–1090.
- Grimes, J. A., and S. R. Rushforth. 1982. Diatoms of recent bottom sediments of Utah Lake, Utah, U.S.A. *Bibliotheca Phycologica* 55.
- Hammer, U. T. 1978. The saline lakes of Saskatchewan. III. Chemical characterization. *Internationale revue der gesamten Hydrobiologie* 63:311–335.
- . 1986. Saline lake ecosystems of the world. *Monographiae Biologicae* 59.
- Hammer, U. T., J. Shames, and R. C. Haynes. 1983. The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. *Hydrobiologia* 105:1–26.
- Hecky, R. E., and P. Kilham. 1973. Diatoms in alkaline saline lakes: ecology and geochemical implications. *Limnology and Oceanography* 18:53–71.
- Herbst, D. B., and T. J. Bradley. 1989. Salinity and nutrient limitations on growth of benthic algae from two alkaline salt lakes of the Western Great Basin (USA). *Journal of Phycology* 25:673–678.
- Hustedt, F. 1939. Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali, und Sumatra nach dem Material der Deutschen Limnologischen Sunda-Expedition III. Die ökologischen Faktoren und ihr Einfluss auf die Diatomeenflora. *Archiv für Hydrobiologie (Supplement)* 16:274–394.
- Kaczmarek, I., and S. R. Rushforth. 1983. The diatom flora of Blue Lake Warm Spring, Utah, U.S.A. *Bibliotheca Diatomologica* 2.
- Kingston, J. C., R. B. Cook, R. G. Kreis, Jr., K. E. Camburn, S. C. Schindler, L. C. K. Shane, and G. A. King. 1990. Paleocological investigation of recent lake acidification in the northern Great Lakes states. *Journal of Paleolimnology* 4:153–201.
- Kuehne, P. E. 1941a. The phytoplankton of southern and central Saskatchewan. Part I. *Canadian Journal of Research C* 19:292–311.
- . 1941b. The phytoplankton of southern and central Saskatchewan. Part II. *Canadian Journal of Research C* 19:313–322.
- Lowe, R. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. Environmental Protection Agency EPA-670/4-74-05.
- Main, S. P., and C. D. McIntire. 1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon (U.S.A.). *Botanica Marina* 17:88–99.
- Mason, D. T. 1967. Limnology of Mono Lake, California. University of California Press, Berkeley, California, USA.
- Maucha, R. 1932. Hydrochemische methoden in der limnologie. Die Binnengewässer, 12. Schweizerbartsche erlagsbuchhandlung, Stuttgart, Germany.
- Patrick, R. 1973. Use of algae, especially diatoms, in the assessment of water quality. Biological methods for the assessment of water quality. American Society for Testing Materials ASTM STP 528.
- Patrick, R., and C. W. Reimer. 1966. The diatoms of the United States. Number 13. Monographs of the Academy of Natural Sciences of Philadelphia 1.
- Renberg, I., and R. Hellberg. 1982. The pH history of lakes in southwestern Sweden, as calculated from the subfossil diatom flora of the sediments. *Ambio* 11:30–33.
- Round, F. E., R. M. Crawford, and D. G. Mann. 1990. The diatoms: biology and morphology of the genera. Cambridge University Press, New York, New York, USA.
- Roux, M., S. Servant-Vildary, and M. Servant. 1991. Inferred ionic and salinity of a Bolivian Quaternary lake, as estimated from fossil diatoms in the sediments. *Hydrobiologia* 210:3–18.
- Scruton, D. A., J. K. Elnor, and S. N. Ray. 1990. Fossil diatom inferred reconstruction of the pH history of two acidic, clear water lakes from insular Newfoundland, Canada. *Hydrobiologia* 214:259–266.
- Servant-Vildary, S., and M. Roux. 1990. Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes. *Hydrobiologia* 197:267–290.
- Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Urbana, University of Illinois Press, Urbana, Illinois, USA.
- Simonson, R. 1972. Ideas for a more natural system of the centric diatoms. *Nova Hedwigia* 39:37–54.
- Smol, J. P. 1988. Paleoclimate proxy data from freshwater arctic diatoms. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 23:837–844.
- Smol, J. P., and M. D. Dickman. 1981. The recent histories of three Canadian Shield lakes: a paleolimnological experiment. *Archiv für Hydrobiologie* 93:83–108.
- Smol, J. P., I. R. Walker, and P. R. Leavitt. 1991. Paleolimnology and hindcasting climatic trends. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 24:1240–1246.
- Sullivan, M. J., and C. A. Moncreiff. 1988. A multivariate analysis of diatom community structure and distribution in a Mississippi salt marsh. *Botanica Marina* 31:93–99.
- SYSTAT. 1984. SYSTAT, the system for statistics. SYSTAT, Evanston, Illinois, USA.
- Sze, P., and J. M. Kingsbury. 1972. Distribution of phytoplankton in a polluted saline lake, Onondaga Lake, New York. *Journal of Phycology* 8:25–37.
- Tudor, E. R., D. W. Blinn, and D. M. Churchill. 1991. Distribution of diatoms in the northern Kimberley region,

- Western Australia in relation to water chemistry. *Journal of the Royal Society of Western Australia* 73:93-99.
- Van der Werff, A. 1955. A new method of concentrating and cleaning diatoms and other organisms. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 12:276-277.
- Verch, R., and D. W. Blinn. 1971. Seasonal investigations of algae from Devils Lake, North Dakota. *Prairie Naturalist* 3:67-79.
- Whitmore, T. J. 1989. Florida diatom assemblages as indicators of trophic state and pH. *Limnology and Oceanography* 34:882-895.
- Williams, W. D. 1986. Limnology, the study of inland waters: a comment on perceptions of studies of salt lakes, past and present. Pages 471-484 *in* P. DeDecker and W. D. Williams, editors. *Limnology in Australia. Monographiae Biologicae* 61.
- Williams, W. D., A. J. Boulton, and R. G. Taaffe. 1990. Salinity as a determinant of salt lake fauna: a question of scale. *Hydrobiologia* 197:257-266.