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A COMPARISON OF EPIPHYTIC DIATOM ASSEMBLAGES ON LIVING AND DEAD STEMS OF THE COMMON GRASS *PHRAGMITES AUSTRALIS*

Judith A. Grimes¹, Larry L. St. Clair¹, and Samuel R. Rushforth¹

ABSTRACT.— Diatoms epiphytic on *Phragmites australis* (Cav.) Trin. ex Steaded stems were collected from a single clone at the southern end of Provo Bay, Utah Lake, Utah. Diatom populations from both living and dead stem sections were analyzed. Species diversity in each sample was high, indicating that the stems provide a relatively stable habitat for diatom epiphytes. Of the 23 genera found, only *Gomphonema* and *Navicula* showed significant trends toward stem preference. The diatoms in this study support the current view that Utah Lake is a slightly saline, eutrophic system.

The occurrence of diatom assemblages as epiphytes on littoral, emergent macrophytes is well documented (Godward 1934, 1937, Knudson 1957, Prowse 1959). Likewise, the impact of such epiphytes on primary productivity and community trophic structure has been examined in several estuarine environments (McIntire et al. 1971, Stowe et al. 1971, and Main et al. 1974), but has been largely ignored in freshwater systems (Wetzel 1964). The epiphytic diatom communities attached to emergents inevitably play a role in the overall productivity of lakes and estuaries. They also contribute to regulation of the overall metabolism of such waters by altering the amount and quality of allochthonous organics entering the lake by acting as physical and metabolic traps or filters. The attached diatom flora also serves as an autochthonous source of particulate organic and dissolved organic matter that is readily available to pelagic animals. The degree of influence of these epiphytic organisms on the productivity of standing waters has rarely been determined. However, Allen (1971) estimated that up to 31.3 percent of the total littoral production could be attributed to epiphytic algae, with up to 21.4 percent of the total lake production being attributable to such attached communities. In addition, a comparison between phytoplankton and epiphyte production demonstrated that the latter was equivalent to 75 percent of the phytoplankton production over the annual period (Allen 1971).

Even though epiphytic communities have been demonstrated to be important, the distribution patterns of such assemblages on the basis of variation in host species and host substrate conditions have received little attention. Likewise, the complex physiological relationship between the host macrophyte and the attached diatom species has received less attention than warranted (Wetzel 1964, 1965, 1969b, Allen 1971, Hough et al. 1975). The impact of this relationship is fundamental to understanding the basic distribution patterns of epiphytes not only on different macrophyte host species but also on members of the same species at different levels of senescence.

The purpose of this study is to illuminate distribution patterns of diatom epiphytes on living and dead specimens of a single macrophyte host (*Phragmites australis* (Cav.) Trin. ex Steaded) in Utah Lake, Utah. The data from this study will be used as a baseline for extended research in Utah Lake on epiphyte distribution patterns and epiphyte impact on lake productivity and trophic structure.

METHODS

Samples were collected 20 September 1978 from a single clone of *Phragmites australis* located at the southern end of the mouth of Provo Bay in Utah Lake. Five samples of living and five of dead *Phragmites australis* stems were collected as cut 10 cm sections, measured from the water level

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down. Samples were prepared according to standard acid-oxidation methods, and permanent diatom slides were made using Naphrax diatom mountant (St. Clair and Rushforth 1977). Slides were examined and diatom species were identified at 1000X with a Zeiss RA research microscope with bright field and Nomarski interference phase-contrast accessories.

Quantitative data on the diatom assemblages were recorded by counting 250–400 diatoms for each sample. Previous studies have shown that a statistically valid count can be obtained within this range (Squires 1977). Each slide was then thoroughly scanned to record the rare species. The results were converted into percent relative density values for all species for each site. Shannon-Wiener diversity indices were calculated for individual samples (Shannon and Wiener 1963).

The relative density figures for each sample were compared to all other samples and similarity indices were calculated (Ruzicka 1958). These indices were clustered (Sneath and Sokal 1973) to identify unique community associations within and between the living and dead *Phragmites australis* stem sections.

The most prevalent diatoms encountered in the study and the diatoms that significantly differed between the living and the dead specimens of *Phragmites australis* were determined.

RESULTS

Twenty-three genera and 114 diatom species were found on the 10 *Phragmites australis* stem sections (Table 1). The most prevalent diatoms throughout the study were *Navicula graciloides*, *Nitzschia inconspicua*, and *Nitzschia filiformis* (Table 2). *Nitzschia dissipata*, *Stephanodiscus astrea* var. *minutula*, and *Nitzschia palea* were also common. Among the prevalent species, *Amphora veneta* was found to occur only on the living stems, whereas *Navicula schroeteri* var. *escambia* was essentially restricted to the dead stems.

TABLE 1. Alphabetical list of the diatom taxa found on living and dead *Phragmites australis* stem sections from Provo Bay, Utah Lake, and their average relative density.

Species	Living	Dead
<i>Achnanthes hauckiana</i> °°	.07	—
<i>Achnanthes lanceolata</i> var. <i>dubia</i> °	—	P
<i>Achnanthes lewisiana</i>	.26	P
<i>Achnanthes minutissima</i>	2.00	.57
<i>Achnanthes</i> sp.°°	P	—
<i>Amphora ovalis</i>	.31	P
<i>Amphora ovalis</i> var. <i>pediculus</i> °	—	.08
<i>Amphora perpusilla</i>	.76	1.79
<i>Amphora veneta</i>	8.78	1.26
<i>Amphora</i> sp.°°	.19	—
<i>Anomoconeis sphaerophora</i> °°	P	—
<i>Asterionella formosa</i>	.09	.08
<i>Caloneis fenzioides</i> °°	.02	—
<i>Cocconeis placentula</i> var. <i>euglypta</i> °	—	P
<i>Cocconeis placentula</i> var. <i>lineata</i>	.07	.07
<i>Coscinodiscus</i> sp.	.06	.06
<i>Cyclotella kutzingiana</i> °	—	.13
<i>Cyclotella meneghiniana</i>	1.87	1.80
<i>Cymbella affinis</i> °	—	P
<i>Cymbella minuta</i> °	—	.06
<i>Cymbella muelleri</i> °°	.14	—
<i>Cymbella prostrata</i>	.07	.05
<i>Cymbella</i> sp.°°	P	—
<i>Diatoma tenue</i> var. <i>elongatum</i>	.13	.23
<i>Diploneis oblongella</i> °°	.02	—
<i>Epithemia adnata</i> var. <i>porcellus</i>	P	P
<i>Epithemia adnata</i> var. <i>proboscidea</i> °	—	P
<i>Fragilaria brevistriata</i> °	—	P
<i>Fragilaria brevistriata</i> var. <i>inflata</i>	.06	.15
<i>Fragilaria construens</i> °	—	P
<i>Fragilaria construens</i> var. <i>binodis</i>	.06	P
<i>Fragilaria construens</i> var. <i>venter</i>	.65	.11
<i>Fragilaria crotonensis</i> °	—	.17
<i>Fragilaria lapponica</i> °°	.19	—
<i>Fragilaria pinnata</i> °°	.37	—
<i>Fragilaria pinnata</i> var. <i>lancettula</i>	.07	.13
<i>Fragilaria similis</i>	.19	.17
<i>Fragilaria vaucheriae</i>	.90	.63
<i>Fragilaria virescens</i> °°	P	—
<i>Gomphonema affine</i> °°	.13	—
<i>Gomphonema gracile</i> °°	.02	—
<i>Gomphonema intricatum</i> °	—	P
<i>Gomphonema olivaceum</i>	.30	.05
<i>Gomphonema parvulum</i>	.44	.21
<i>Gomphonema subclavatum</i> var. <i>commutatum</i>	.08	P
<i>Gomphonema tenellum</i> °°	.02	—
<i>Gomphonema ventricosum</i> °°	.44	—
<i>Gomphonema</i> sp.°°	.06	—
<i>Melosira granulata</i>	.55	.65
<i>Melosira granulata</i> var. <i>angustissima</i>	1.58	1.05
<i>Melosira italica</i>	.21	P
<i>Navicula arcensis</i> °	—	.15
<i>Navicula arenaria</i> °	—	P
<i>Navicula aurora</i> °°	.02	—
<i>Navicula capitata</i> var. <i>hungarica</i> °	—	.1
<i>Navicula cincta</i> °	—	.59
<i>Navicula circumtexta</i> °	—	.15
<i>Navicula cryptocephala</i>	.29	.35

Table I continued.

Species	Living	Dead
<i>Navicula cryptocephala</i> var. <i>veneta</i>	3.45	4.38
<i>Navicula exigua</i> °	—	P
<i>Navicula graciloides</i>	12.35	9.17
<i>Navicula heufferli</i> var. <i>leptocephala</i>	.08	P
<i>Navicula lanceolata</i> °	—	.08
<i>Navicula minima</i>	.07	.84
<i>Navicula oblonga</i>	P	.08
<i>Navicula peregrina</i> °	—	.08
<i>Navicula pupula</i>	P	.08
<i>Navicula radiosa</i> var. <i>tenella</i>	1.13	2.42
<i>Navicula rhyncocephala</i> °	—	P
<i>Navicula salinarum</i> °	—	.13
<i>Navicula salinarum</i> var. <i>intermedia</i>	.08	.05
<i>Navicula schroeteri</i> var. <i>escambia</i>	3.06	6.23
<i>Navicula tenelloides</i>	.15	1.27
<i>Navicula tripunctata</i>	P	.33
<i>Navicula tripunctata</i> var. <i>schizonemoides</i>	.44	1.51
<i>Navicula</i> sp.°	—	.63
<i>Nitzschia acicularis</i>	.51	.66
<i>Nitzschia amphibia</i>	.37	.25
<i>Nitzschia apiculata</i>	.06	.18
<i>Nitzschia dissipata</i>	6.00	4.95
<i>Nitzschia filiformis</i>	7.10	6.83
<i>Nitzschia frustulum</i>	.80	.53
<i>Nitzschia gracilis</i> °	.23	—
<i>Nitzschia hantzschiana</i>	4.94	4.40
<i>Nitzschia holsatica</i>	1.67	2.35
<i>Nitzschia inconspicua</i>	12.40	13.25
<i>Nitzschia linearis</i>	.06	.08
<i>Nitzschia longissima</i> var. <i>closterium</i>	.08	.08
<i>Nitzschia ovalis</i>	.18	.32
<i>Nitzschia palea</i>	6.90	13.50
<i>Nitzschia paleaceae</i>	4.63	3.92
<i>Nitzschia punctata</i> °	—	P
<i>Nitzschia signoidea</i> °	—	P
<i>Nitzschia stagnorum</i> °°	P	—
<i>Nitzschia</i> sp. 1	P	.42
<i>Nitzschia</i> sp. 2°°	.21	—
<i>Ophephora martyi</i> °	—	P
<i>Rhoicosphenia curvata</i>	3.96	6.32
<i>Rhopalodia gibba</i> °	—	.05
<i>Rhopalodia gibberula</i> var. <i>vanheurekii</i>	.10	P
<i>Stephanodiscus astrea</i> °°	.06	—
<i>Stephanodiscus astrea</i> var. <i>minutula</i>	5.15	4.34
<i>Stephanodiscus niagarae</i> °	—	.08
<i>Surirella angustata</i>	P	P
<i>Surirella ovalis</i> var. <i>brightwellii</i> °	—	.15
<i>Surirella ovata</i> °°	.08	—
<i>Synedra acus</i>	.08	1.60
<i>Synedra delicatissima</i> var. <i>angustissima</i>	.15	.02
<i>Synedra fasciculata</i> var. <i>truncata</i> °	—	.08
<i>Synedra mazamaensis</i>	.15	.08
<i>Synedra socia</i>	P	.08
<i>Synedra ulna</i>	P	.11
<i>Synedra ulna</i> var. <i>contracta</i>	.81	.02

°°Species unique to living *Phragmites australis* stems.°Species unique to dead *Phragmites australis* stems.

P Species not recorded on the transects taken for relative density figures but found on other sections of the diatom slide.

Species diversity according to number of species encountered was high, averaging 48 species per sample. However, there were generally 2 to 4 dominant species ranging between 10–18 percent relative density in each sample, which allowed for only moderately high Shannon-Wiener diversity values (Table 3). Forty-nine percent of the diatom species was found in 30 percent of all samples, and 34 percent of the diatom species was found in 50 percent of all samples.

The results of the cluster analysis (Fig. 1) demonstrate the high degree of similarity encountered for all ten samples. Even so, marginal separation into samples from living and dead stems was obtained.

A similarity matrix comparing all 10 samples was constructed.

Means of similarity indices for living stems, dead stems, and between living and dead stems were computed. T-tests were performed and it was determined that there was no significant difference in similarity within or between these samples sets.

DISCUSSION

Each of our 10 samples consistently contained approximately 50 identifiable species. In general, no one species represented more than 18 percent of the total population of any sample. These conditions are indicative of a diverse flora that is further supported by our Shannon-Wiener diversity values and the average number of species per substrate (Table 3). Such conditions indicate that the epiphyte flora in Utah Lake is more diverse than we previously believed. T-tests were computed comparing the means of the Shannon-Wiener diversity indices of both substrates as well as the average number of species from both living and dead stems. No significant differences between the values in either comparison existed.

A total of 23 diatom genera were encountered during this study. The number of species included in these genera was nearly equally distributed between living and dead stems (Table 4). However, substratum preferences were noted in the genera *Navicula* and *Gomphonema* and in individual species within several other genera. Of the 114 species found in the study, 22 were unique to living and 29 were unique to dead stems.

TABLE 2. Important species encountered on *Phragmites australis* stem sections from Provo Bay, Utah Lake, with their percent relative densities. Important species are those species with a percent relative density greater than 3 percent in any one sample.

Species	Living stems					Dead stems				
	1	2	3	4	5	6	7	8	9	10
<i>Achnanthes minutissima</i>					3.1					
<i>Amphora perpusilla</i>						3.3	3.2			
<i>Amphora veneta</i>	17.3		5.6	7.2	11.2					
<i>Cyclotella meneghiniana</i>		3.0								
<i>Melosira granulata</i> var. <i>angustissima</i>					3.9					
<i>Navicula cryptocephala</i> var. <i>veneta</i>	3.4	4.9			4.2	3.7	5.4	3.3	6.1	3.5
<i>Navicula graciloides</i>	9.9	13.2	13.5	14.0	11.2	5.5	13.4	14.9	8.5	13.6
<i>Navicula radiosa</i> var. <i>tenella</i>						3.3	3.2	6.2		
<i>Navicula schroeteri</i> var. <i>escambia</i>					5.7	6.3		6.2	6.2	10.6
<i>Navicula tripunctata</i> var. <i>schizonemoides</i>								3.3		
<i>Nitzschia dissipata</i>	6.5	5.7	3.6	7.5	3.1	4.1	4.6	7.9	3.6	4.7
<i>Nitzschia filiformis</i>	3.1	12.5	5.4	11.1	3.5	6.6	3.2	7.0	5.2	12.2
<i>Nitzschia inconspicua</i>	15.5		23.4	9.5	7.3	12.2	25.7	6.2	12.1	10.1
<i>Nitzschia hantzschiana</i>	3.1		5.7		4.6	5.4		12.3		3.1
<i>Nitzschia holsatica</i>	3.7		3.3					5.4		3.9
<i>Nitzschia palea</i>	5.0	5.7	5.7	7.5	10.4	17.7	9.4	12.4	16.1	12.0
<i>Nitzschia paleacea</i>		10.6	4.5	6.5	5.0			3.3	7.7	7.4
<i>Rhoicosphenia curvata</i>	7.7				6.2	6.6	9.4		12.2	
<i>Stephanodiscus aestrea</i> var. <i>minutula</i>	3.4	5.3		5.2	6.2	5.5	4.6	4.1	3.2	4.3

The most important species in each sample are indicated by boldface type.

TABLE 3. Shannon-Wiener diversity values for the five living and five dead *Phragmites australis* stem sections from Provo Bay, Utah Lake.

Sample No.	Living	Dead	S°	
			Living	Dead
1	2.96	3.12	48	52
2	2.96	2.95	50	47
3	2.86	3.09	33	50
4	2.96	2.55	44	38
5	3.07	3.15	47	51
\bar{x}	2.962	3.035	44.4	47.6

*Average number of species/substrate.

An analysis of the diatom types unique to the living stems reveals that most were periphytic stalk formers, whereas those unique to the dead stems were mostly periphytic mobile forms.

The distribution of species of *Gomphonema* and *Navicula* on *Phragmites* stems showed significant deviation from random. Thus, of a total of nine *Gomphonema* species encountered during this study, eight of these occurred on living stems, five of which were restricted to living stems. Conversely, of four species that occurred on dead stems, only one was restricted to that habitat. These data sug-

gest that the living stems provide a more suitable substrate for several *Gomphonema* species. Such species tend to be strictly epiphytic in distribution, usually being attached by a gelatinous jelly stipe (Patrick and Reimer 1966). Whether the preference of these species for living stems is relative to the availability of nutrients or the physical condition of the substrate is yet to be determined.

Some interesting distribution patterns were also observed in the 26 species of *Navicula*. Twenty-five of these were found on the dead stems, of which 11 were restricted to that substrate. On the other hand, only 15 *Nav-*

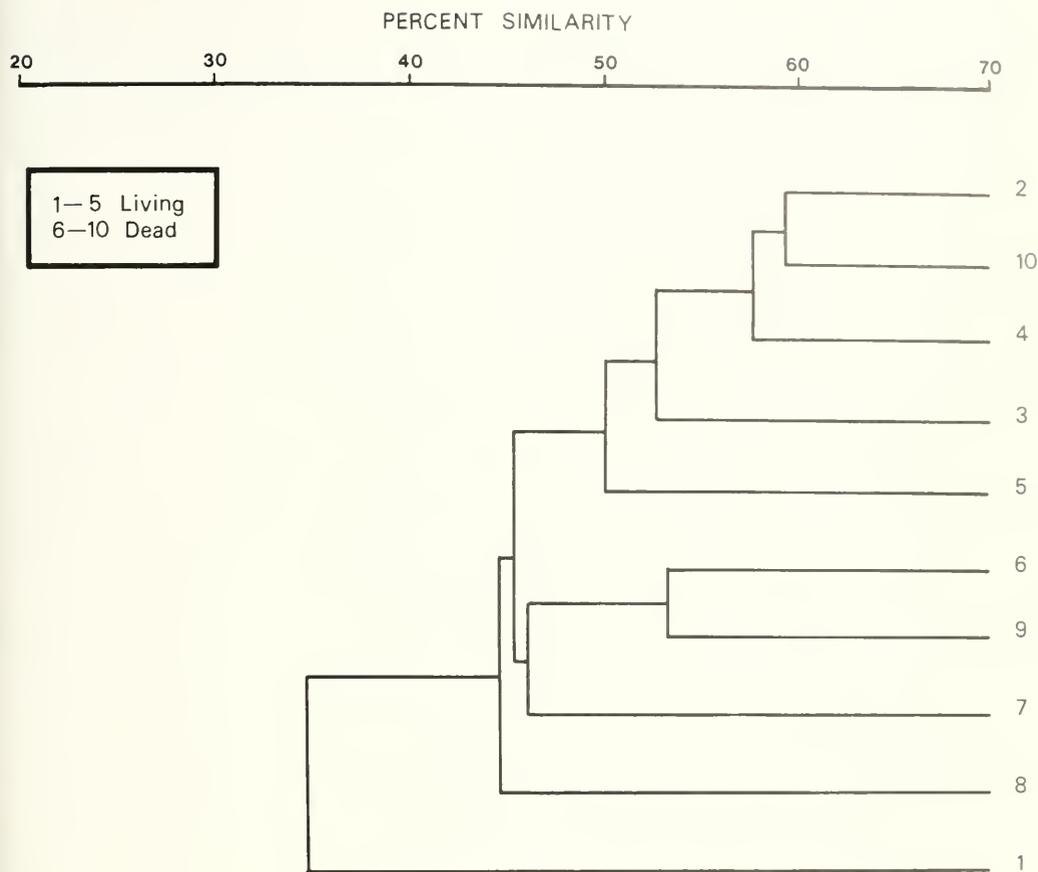


Fig. 1. Cluster dendrogram showing similarities of diatoms on living and dead *Phragmites australis* stem sections from Provo Bay, Utah Lake.

icula species were observed on the living stems and only one taxon was restricted to living stems.

We believe the high number of *Navicula* species in our samples can be accounted for, at least in part, by the fact that many are opportunistic, occurring on a wide variety of substrates. These opportunistic *Navicula* species occurred primarily on dead *Phragmites* stems except for one or two species that dominated both living and dead stems. The reason for this is open to speculation, but it is probably related to nutrient interaction, the physical condition of the substrate, or reduced competition on the dead stems.

The hypothesis that condition of the *Phragmites* stems had no effect on the presence or absence of *Gomphonema* and *Navicula* was tested by chi-square analysis using a 2 X 2 contingency table. The results departed sig-

nificantly from random. This supported the concept that *Gomphonema* and *Navicula* were separated on the basis of habitat type.

Consistent with other Utah Lake studies, the diatoms in this study reflect the condition of the lake waters. Most of the prevalent diatoms were either alkaphilous or alkabiontic forms and also indicators of eutrophy. Additionally, many are known to have the ability to withstand elevated levels of dissolved salts. These data, together with the elevated diversity found at Utah Lake, support the current view that Utah Lake is a saline-eutrophic ecosystem.

We recognize the preliminary nature of the present study. Even so, we believe the differences shown in communities on the living versus the dead stems are significant. Future studies are planned to expand our data

TABLE 4. Alphabetical list of diatom genera found on *Phragmites australis* stem sections from Provo Bay, Utah Lake and the occurrence of species from those genera on living and dead substrates.

Genus	Living	Dead
<i>Ammanthia</i>	4	3
<i>Amphora</i>	4	5
<i>Ammonia</i>	1	0
<i>Asterionella</i>	1	1
<i>Caloneis</i>	1	0
<i>Cocconeis</i>	1	2
<i>Coscinodiscus</i>	1	1
<i>Cyclotella</i>	1	2
<i>Cymbella</i>	3	3
<i>Diatoma</i>	1	1
<i>Diploneis</i>	1	0
<i>Epithemia</i>	1	2
<i>Fragilaria</i>	9	9
<i>Gomphonema</i>	5	4
<i>Melosira</i>	3	3
<i>Nacella</i>	15	25
<i>Nitzschia</i>	15	17
<i>Ophraphora</i>	0	1
<i>Rhodosphenia</i>	1	1
<i>Rhoopalodia</i>	1	2
<i>Stephanodiscus</i>	2	2
<i>Surirella</i>	2	2
<i>Synedra</i>	6	7

base to the other species of emergent macrophytes in Utah Lake. Furthermore, we plan studies to answer the following questions: (1) Are some epiphytes host specific? (2) What patterns of seasonal succession are evident in the epiphytic flora? (3) What impact does the epiphytic flora have on productivity and trophic structure of the lake? These questions take on added significance for future resource management in light of proposed large-scale changes in Utah Lake, such as the diking of Provo and Goshen bays.

LITERATURE CITED

- ALLEN, H. L. 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecol. Monogr.* 41:97-127.
- GODWARD, M. B. 1934. An investigation of the causal distribution of algal epiphytes. *Beih. Bot. Centralbl.* 52A:506-539.
- . 1937. An ecological and taxonomic investigation of the littoral algal flora of Lake Windermere. *J. Ecol.* 25:496-565.
- HOOVER, R. A., AND R. G. WETZEL. 1975. The release of dissolved organic carbon from submersed aquatic macrophytes: diel, seasonal, and community relationships. *Verh. Int. Ver. Limnol.* 19:939-948.
- KNUDSON, B. M. 1957. Ecology of the epiphytic diatom *Tabellaria flocculosa* (Roth) Kutz. var. *flocculosa* in three English lakes. *J. Ecology* 45:93-112.
- MAIN, S. P., AND C. D. MCINTIRE. 1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon. *Bot. Mar.* 17:88-99.
- MCINTIRE, C. D., AND W. S. OVERTON. 1971. Distributional patterns of assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecology* 52:758-777.
- PATRICK, R., AND C. REIMER. 1966. The diatoms of the United States. *Acad. Nat. Sci. Phil., Monograph* 13, v. 1. 688 pp.
- PROWSE, G. A. 1959. Relationship between epiphytic algal species and their macrophytic hosts. *Nature* 183:1204-1205.
- RUSHFORTH, S. R., L. L. ST. CLAIR, J. A. GRIMES, J. R. JOHANSEN, AND M. WHITING. The phytoplankton of Utah Lake. *Great Basin Nat. Mem.* 5. In press.
- RUZICKA, M. 1955. Anwendung mathematisch-statistischer methoden in der geobotanik (Synthetische bearbeitung von aufnahmen). *Biologia Bratislav.* 13:647-661.
- SHANNON, C. E., AND W. WIENER. 1963. The mathematical theory of communication. University of Illinois Press, Urbana.
- SNEATH, R. H. A., AND R. R. SOKAL. 1963. Numerical taxonomy: principles and practice of numerical classification. W. H. Freeman Co., San Francisco. 573 pp.
- SNEDECOR, G. W., AND W. COCHRAN. 1965. Statistical methods. Iowa State Press. 593 pp.
- SQUIRES, L. E., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1979. Algal response to a thermal effluent: study of a power station on the Provo River, Utah, U.S.A. *Hydrobiologia* 63:11:17-32.
- ST. CLAIR, L. L., AND S. R. RUSHFORTH. 1977. The diatom flora of the Goshen Warm Springs ponds and wet meadows, Goshen, Utah, U.S.A. *Nova Hedwigia* 25:353-425.
- STOWE, W. C., AND J. C. GOSSELINK. 1971. Community structure and production of the epiphytic algae in the Barataria Bay area of Louisiana. Paper read at the 34th annual meeting of the American Society of Limnology and Oceanography, Winnipeg, June 14-17.
- WETZEL, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. *Int. Rev. Ges. Hydrobiol.* 49:1-61.
- . 1965a. Techniques and problems of primary productivity measurements in higher aquatic plants and periphyton. *Mem. Ist. Ital. Idrobiol., Suppl.* 15:147-165.
- . 1969b. Factors influencing photosynthesis and excretion of dissolved organic matter by aquatic macrophytes in hardwater lakes. *Verh. Int. Ver. Limnol.* 17:72-85.