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Foraminiferal Densities and Pore Water Chemistry in the Indian River, Florida

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and Kenneth P. Severin

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ABSTRACT

Buzas, Martin A., and Kenneth P. Severin. Foraminiferal Densities and Pore Water Chemistry in the Indian River, Florida. *Smithsonian Contributions to the Marine Sciences,* number 36, 38 pages, 32 figures, 29 tables, 6 appendices, 1993.—Two stations were established about 10 m apart at a depth of about 1 m at Link Port, Florida. One consisted of quartz sand and the other of quartz sand with a dense stand of seagrass. At the surface of each station and at a depth of 10 cm at the grass site, four replicate samples consisting of 5 ml each were taken every fortnight from 27 March to 6 November 1978 (17 sampling times, 204 samples). The taxa *Quinqueloculina, Elphidium, Ammonia, Bolivina,* and *Ammobaculites* comprising 98% of the fauna were enumerated. In addition, pore water chemistry was measured for temperature, salinity, oxygen, pH, Eh, NH_3, PO_4, Si, NO_2, and $NO_2 + NO_3$.

General linear models were used to analyze the bare surface-grass surface, and grass surface-grass 10 cm data sets. Foraminiferal densities were evaluated for differences between sites, periodicity, sites × periodicity (interaction), and environmental variables.

Differences in overall density between the bare surface-grass surface sites were not significant for the three most abundant taxa (*Quinqueloculina, Elphidium,* and *Ammonia*). At the grass site the density for all taxa were significantly lower at 10 cm than at the surface (very few individuals were observed at 10 cm).

Hypotheses for periodicity and interaction were significant for all taxa in all comparisons except for *Bolivina* in the bare surface-grass surface analysis. At the bare surface, maximum densities occurred in spring while at the grass surface in summer. Although densities were low at 10 cm, no synchronization between the grass surface and 10 cm was evident.

The environmental variables were significant for all taxa in both comparisons. The environmental variables are, however, highly correlated. To alleviate this difficulty, a principal component analysis was performed on these variables. The first three components included all of the 10 variables. Subsequent multiple regression of foraminiferal densities and the principal components indicated that usually at least two components, accounting for most of the variables, were statistically significant. Thus, no simple relationship between pore water chemistry and density is apparent. The very large difference in density between the grass surface and 10 cm depth is much more strongly related to the pore water chemistry than the smaller differences with time at the surface sites.

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Introduction

A basic variable for ecological studies is density, the number of individuals per volume or area. Densities of foraminiferal species, like those of all organisms, vary in space and time. Geographic changes in foraminiferal species densities have been documented between all marine environments from marshes to the abyss. Large differences in space like those between a marsh and the abyss or the Arctic and the tropics are easily recognized. A general qualitative correlation between observed species densities and the environment is easily accepted as an explanation for these changes. Similarly, differences over vast amounts of geologic time are easily recognized, and explained by the interplay of evolution and the environment. As we decrease the scale of our observations in space and time, however, and, at the same time, increase our effort to achieve quantitative results, differences in species densities and their explanation become much more difficult. Nevertheless, densities do vary over a matter of meters and within a time scale measured in weeks, months, or years. The present study is an analysis of quantitative measurements of species densities and environmental variables observed at two stations about 10 m apart which were sampled every fortnight for 9 months.

During 1978 the chemistry group of the Harbor Branch Oceanographic Institution, Ft. Pierce, Florida monitored 10 pore water chemistry variables on a continual basis at two sites (stations) about 10 m apart at a depth of about 1 m in the Indian River (a shallow lagoon of nearly normal marine salinity on the central east coast of Florida). One station was located on bare quartz sand, the other on quartz sand with a covering of seagrass (mostly *Halodule wrightii* and *Thalassia testidium*). We viewed their study as an ideal opportunity to conduct a study of the foraminifera with an experimental design allowing us to test statistically for differences in density between stations and with time as well as for the statistical significance of 10 environmental variables.

Foraminiferal densities were also enumerated at a depth of 10 cm within the sediment at the grass station. Few living foraminifera were observed at 10 cm and most of the water chemistry variables exhibited a dramatic difference compared to the measurements made at the surface. To test the efficacy of the statistical procedures used in this study, and in others, the same statistical analyses were employed in evaluating the differences between the grass surface and at 10 cm as for the two surface stations.

ACKNOWLEDGMENTS.—We thank the former Chemistry group at the Harbor Branch Oceanographic Insititution, especially J. Montgomery, M. Hucks, G. Peterson, M. Price, and C. Zimmermann. In the field and laboratory K. Carle, D. Mook, and H. Sheng were most helpful. J. Jett prepared the tables, figures, and appendices. L.S. Collins, L.C. Hayek, and B.K. Sen Gupta offered helpful suggestions on the manuscript. We thank J.C. Warren for his careful copy editing. This is contribution No. 319 from the Smithsonian Marine Station at Link Port.

Methods

FIELD.—Two stations were established about 100 m south of the Link Port jetty at a depth of about 1 m. The stations were marked with four poles encompassing an area of about 1 m^2 so that the same area could be re-occupied easily. The sediment at one station consisted of bare quartz sand with a silt-clay content of about 2%. The other was on the same substrate, but had a dense stand of *Halodule wrightii* with some *Thalassia*

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testidium. The sediment was sampled by pushing plastic coring tubes (inner diameter 3.5 cm) into the substrate. At each station four sediment samples were taken indiscriminately (not statistically randomized) at each sampling time which consisted of every fortnight from 27 March until 6 November 1978 (17 sampling times).

The temperature, salinity, oxygen, pH, Eh, NH_3, PO_4, Si, NO_2, $NO_2 + NO_3$ were measured on pore waters by the chemistry group of the Harbor Branch Oceanographic Institution throughout the field experiment (Montgomery et al., 1979).

LABORATORY.—Immediately upon return to the laboratory (within a half-hour), 5 ml of sediment was removed from each core top, and at a depth of 10 cm. Each 5 ml sample was washed over a 63 μm sieve and preserved in 95% ETOH. Prior to examination for foraminifera the sample was stained overnight in rose bengal, dried, floated in a mixture of tetrabromine and acetone (specific gravity 2.3), and re-wet using "photo-flo" as a wetting agent. The foraminifera were enumerated while underwater, a procedure which facilitates the recognition of vividly stained protoplasm. The taxa counted were *Quinqueloculina* (mostly *Q. impressa* and *Q. seminulum*), *Elphidium* (mostly *E. mexicanum* and *E. gunteri*), *Ammonia* (*A. beccarii*), *Bolivina* (*B. striatula*), and *Ammobaculites* (*A. exiguus*). These taxa are sufficiently dissimilar so that they can easily be identified under a binocular microscope and account for 98% of the foraminiferal fauna. The second replicate sample taken at the grass surface on 22 May 1978 was destroyed in a laboratory accident. The mean number of individuals from the other three replicates was used to estimate the missing data (Appendix 2). The systematics of the taxa used here are treated by Buzas and Severin (1982). Enumeration was made by Severin.

STATISTICAL.—We have, then, two stations: one bare sand and the other with a stand of seagrass. For this study, the bare surface, the grass surface, and a depth of 10 cm within the sediment at the grass station were sampled for foraminifera. These three sites were sampled 17 times with four replicates of 5 ml each taken for examination. There are, then, N = 68 replicates or observations at each of the three sites. The number of individuals counted for each of five taxa and the total (the five taxa accounted for over 98% of the total) for each replicate is tabulated for the bare surface in Appendix 1, for the grass surface in Appendix 2, and for grass 10 cm in Appendix 3.

We obtained the measurements made by the chemistry group for 10 water chemistry variables at each of the three sites at each sampling time. These measurements for the bare surface are tabulated in Appendix 4, for the grass surface in Appendix 5, and for the grass 10 cm in Appendix 6.

The data were divided into two sets for statistical analyses, bare surface–grass surface, and grass surface–grass 10 cm. For each analysis we wished to test the following hypotheses; difference between sites (bare surface vs. grass surface or grass surface vs. grass 10 cm), differences with time (periodicity), different periodicities at each site, and the significance of the environmental variables. To accomplish this, we constructed a general linear model (GLM) similar to the one used by Buzas et al. (1977). In matrix notation the GLM is written as

$$\omega : \quad \underset{(n \times 1)}{\mathbf{x}} = \underset{(n \times q)}{\mathbf{Z}'} \; \underset{(q \times 1)}{\hat{\beta}} + \underset{(n \times 1)}{\mathbf{e}}$$

where $\mathbf{x}$, the "dependent" variable is a vector of observed species densities for the $n = 136$ observations ($n_1 = n_2 = 68$), $\mathbf{Z}'$ is a matrix of q "independent" variables, the composition of which will be discussed below, $\hat{\beta}$ is a vector of q parameters "regression coefficients" explaining the observations, and $\mathbf{e}$ is a vector of "errors" or "residuals," assumed to have a normal distribution. The original counts $\mathbf{x}$ were transformed to $\ln(x + 1)$ to make the data more Normal and stabilize the variance.

Restricted Ω models containing s parameters are constructed by equating the appropriate individual or groups of $\hat{\beta}$ to 0. The sum of squares of the residuals, $\mathbf{e}'\mathbf{e}$, for each model is a scalar and is estimated by a least squares solution (Buzas et al., 1977, give the equations). Restricted models can be compared to the general model by the ratio

$$\frac{(\mathbf{e}'\mathbf{e}_{\omega} - \mathbf{e}'\mathbf{e}_{\Omega}) \;/\; (q - s)}{\mathbf{e}'\mathbf{e}_{\Omega} \;/\; (n - q)} = F_{(q - s)(n - q)}$$

The mglh program of "SYSTAT" was used to calculate the sum of squares of the residuals for each model, and these residuals were then used to calculate the F-ratio given above. The results of the analysis are most easily displayed in the standard ANOVA table.

The composition of the matrix $\mathbf{Z}'$ of the ω model is given in Table 1. The vector $\mathbf{z}_1$ is composed of 1's so that $\hat{\beta}_1$ is a constant, $\mathbf{z}_2$ contrasts the difference between sites by assigning +1 to one site and −1 to the other. The vectors $\mathbf{z}_3$ and $\mathbf{z}_4$ are made up of $\sin(m \times \pi/3)$ and $\cos(m \times \pi/3)$, respectively, where $m = 1,\ldots,17$. The vectors $\mathbf{z}_5$ and $\mathbf{z}_6$ are composed of $\sin(m \times \pi/6)$ and $\cos(m \times \pi/6)$, respectively. These vectors are components of a periodic regression (Bliss, 1958) and account for a possible overall periodicity in the observations. Figures 1 and 2 illustrate these vectors over the period of our observations. The possibility exists that the two sites may exhibit periodicity, but that the periodicity differs at the two sites. The interaction vectors $\mathbf{z}_7 = \mathbf{z}_2 \times \mathbf{z}_3$, $\mathbf{z}_8 = \mathbf{z}_2 \times \mathbf{z}_4$, $\mathbf{z}_9 = \mathbf{z}_2 \times \mathbf{z}_5$, and $\mathbf{z}_{10} = \mathbf{z}_2 \times \mathbf{z}_6$ account for this. We have, then, 8 vectors to examine the possible periodicity in our data. Had we constructed instrumental variables to examine the differences between the 17 sampling times and their interaction, we would have required 32 vectors, and made the model much more complicated. Finally, vectors $\mathbf{z}_{11}$ through $\mathbf{z}_{20}$ contain the water chemistry variables completing the $\mathbf{Z}'$ matrix for the GLM.

TABLE 1.—Composition of the $\mathbf{Z}'$ matrix.

$\mathbf{z}_1$ = a vector of units
$\mathbf{z}_2$ = +1 for bare surface, −1 for grass surface
$\mathbf{z}_3$ = $\sin(m \times \pi/3)$, m = 1, . . . ,17
$\mathbf{z}_4$ = $\cos(m \times \pi/3)$, m = 1, . . . ,17
$\mathbf{z}_5$ = $\sin(m \times \pi/6)$, m = 1, . . . ,17
$\mathbf{z}_6$ = $\cos(m \times \pi/6)$, m = 1, . . . ,17
$\mathbf{z}_7$ = $\mathbf{z}_2 \times \mathbf{z}_3$
$\mathbf{z}_8$ = $\mathbf{z}_2 \times \mathbf{z}_4$
$\mathbf{z}_9$ = $\mathbf{z}_2 \times \mathbf{z}_5$
$\mathbf{z}_{10}$ = $\mathbf{z}_2 \times \mathbf{z}_6$
$\mathbf{z}_{11}$ = temperature
$\mathbf{z}_{12}$ = salinity
$\mathbf{z}_{13}$ = oxygen
$\mathbf{z}_{14}$ = pH
$\mathbf{z}_{15}$ = Eh
$\mathbf{z}_{16}$ = NH_3
$\mathbf{z}_{17}$ = PO_4
$\mathbf{z}_{18}$ = Si
$\mathbf{z}_{19}$ = NO_2
$\mathbf{z}_{20}$ = $NO_2 + NO_3$

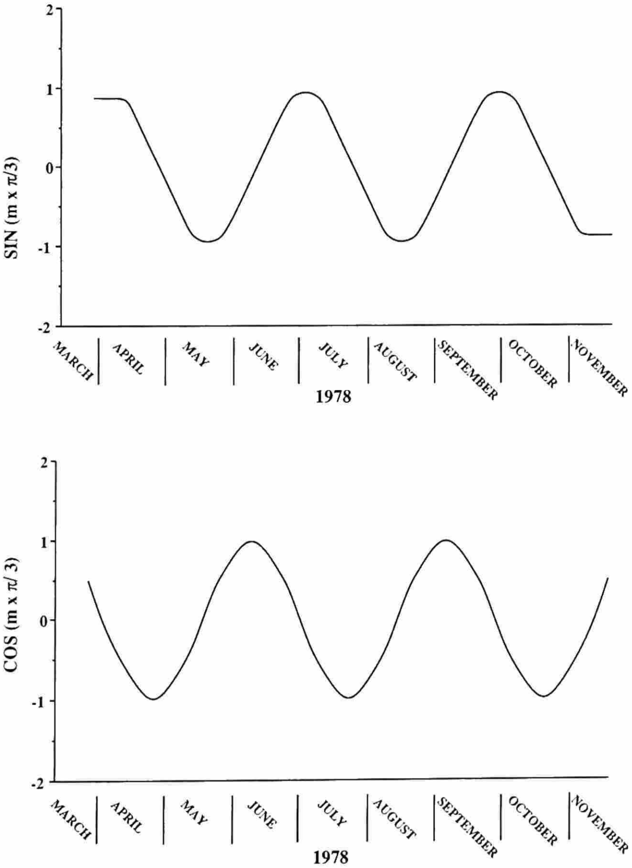

FIGURE 1.—π/3 periodicity.

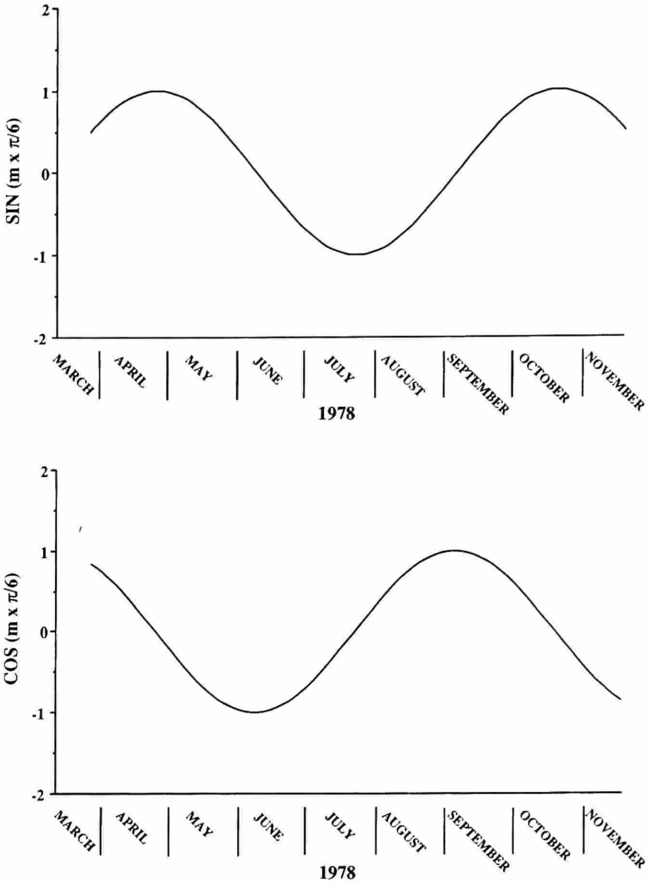

FIGURE 2.—π/6 periodicity.

Bare Surface and Grass Surface

ENVIRONMENTAL VARIABLES.—The recorded temperature values are plotted in Figure 3. The results of a two-way ANOVA with one observation per cell (no replicates were measured for the environmental variables) is shown in Table 2. The hypotheses for differences in mean temperature between stations and with time are both significant at the .05 level, even though the mean temperature at the bare surface is only 1°C higher. The minimum at the bare station was 23°C and at the grass station 22°C. The maximum at each was 32°C and 31°C, respectively. Table 2 shows the mean square for time is higher than for station differences, and, as might be expected, Figure 3 shows summer temperatures were higher than spring and fall.

The recorded salinity values are shown in Figure 4 and the ANOVA results in Table 2. The slightly higher salinities recorded at the bare station were not statistically significant. Differences with time, however, were highly significant with minimum salinities of 20$^0/_{00}$ and 22$^0/_{00}$ recorded at the bare and grass stations, respectively, in August.

Oxygen measurements are plotted in Figure 5 and ANOVA results are presented in Table 2. Differences between stations

TABLE 2.—Analysis of variance for chemical variables on bare surface and grass surface.

Variable	Source	Sum of squares	df	mean square	F	p(F)
Temperature	stations	11.77	1	11.77	22.24	0.00
	time	281.75	16	17.61	33.28	0.00
	residual	8.47	16	0.53		
Salinity	stations	6.62	1	6.62	2.56	0.13
	time	459.62	16	28.73	11.11	0.00
	residual	41.38	16	2.59		
Oxygen	stations	0.39	1	0.39	0.25	0.63
	time	161.39	16	10.09	6.39	0.00
	residual	25.26	16	1.58		
pH	stations	0.06	1	0.06	1.77	0.20
	time	2.98	16	0.19	5.42	0.00
	residual	0.55	16	0.03		
Eh	stations	1823.56	1	1823.56	1.94	0.18
	time	248676.53	16	15542.28	16.52	0.00
	residual	15053.94	16	940.87		
NH_3	stations	597.94	1	597.94	2.84	0.11
	time	9405.39	16	587.84	2.79	0.02
	residual	3368.87	16	210.55		
PO_4	stations	9.52	1	9.52	1.27	0.28
	time	127.32	16	7.96	1.06	0.45
	residual	120.04	16	7.50		
Si	stations	117.23	1	117.23	0.91	0.35
	time	46728.51	16	2920.53	22.78	0.00
	residual	2051.49	16	128.22		
NO_2	stations	0.02	1	0.02	2.25	0.15
	time	0.83	16	0.05	5.53	0.00
	residual	0.15	16	0.01		
$NO_2 + NO_3$	stations	1424.70	1	1424.70	0.62	0.44
	time	36134.21	16	2258.39	0.99	0.51
	residual	36611.80	16	2288.24		

were not statistically significant, but differences with time were. As expected, there is an inverse relationship with temperature, and generally the oxygen values are higher in the spring and fall. Minimum values occurred at the bare station in May, June, and July, and at the grass station in July.

Values for pH are plotted in Figure 6 and ANOVA results are presented in Table 2. Differences between recorded values between stations were small and not statistically significant. Differences with time were significant and, like oxygen, the highest values occurred in spring and fall. Minimum values at both stations were 7.5.

Eh values are plotted in Figure 7 and ANOVA results are presented in Table 2. Although the difference in the mean value between stations was relatively large (Figure 7) it was not statistically significant. On the other hand, differences with time were highly significant, and fluctuated greatly between sampling times. Minimum values at the bare station and grass station were −208 and −128 mV, respectively.

NH_3 values are plotted in Figure 8 and results of the ANOVA are presented in Table 2. No significant difference was observed between stations, but, once again, differences with time were highly significant. Very low to zero values were recorded in the spring and fall with maxima at both stations in the summer.

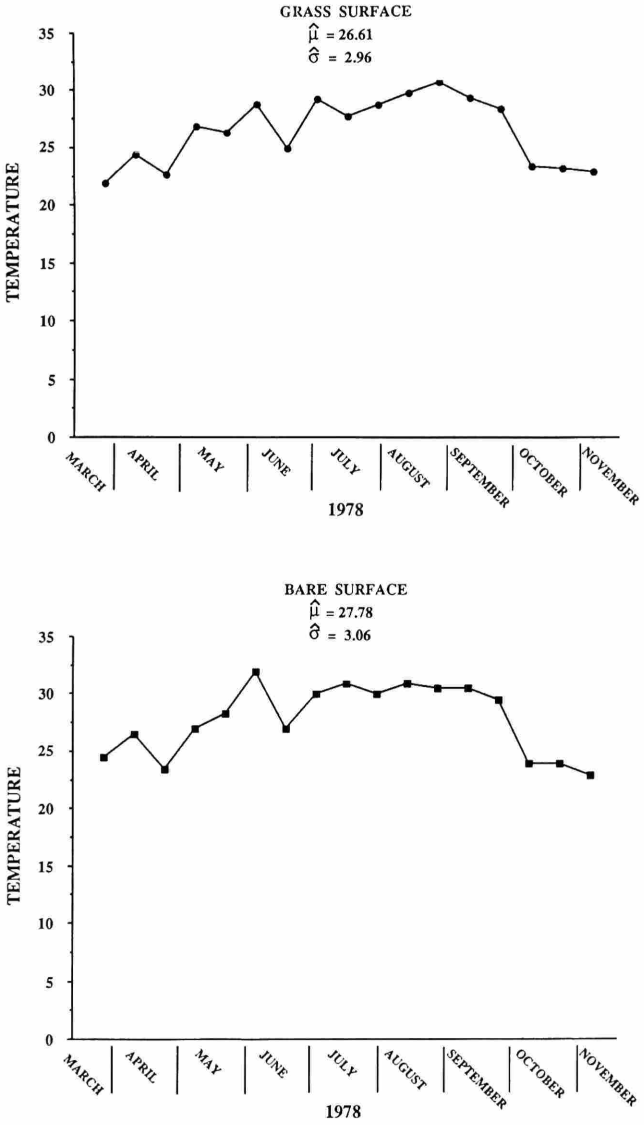

FIGURE 3.—Temperature measurements in °C.

PO_4 values are plotted in Figure 9 and ANOVA results are presented in Table 2. No statistical difference was observed between stations or with time. The measured values were generally very low to zero with the exception of the bare station in September which appears to be an outlier.

The measured Si values are plotted in Figure 10 and the ANOVA results are presented in Table 2. No statistical difference was observed between stations, but differences with time were significant. Zero values were recorded at both stations in

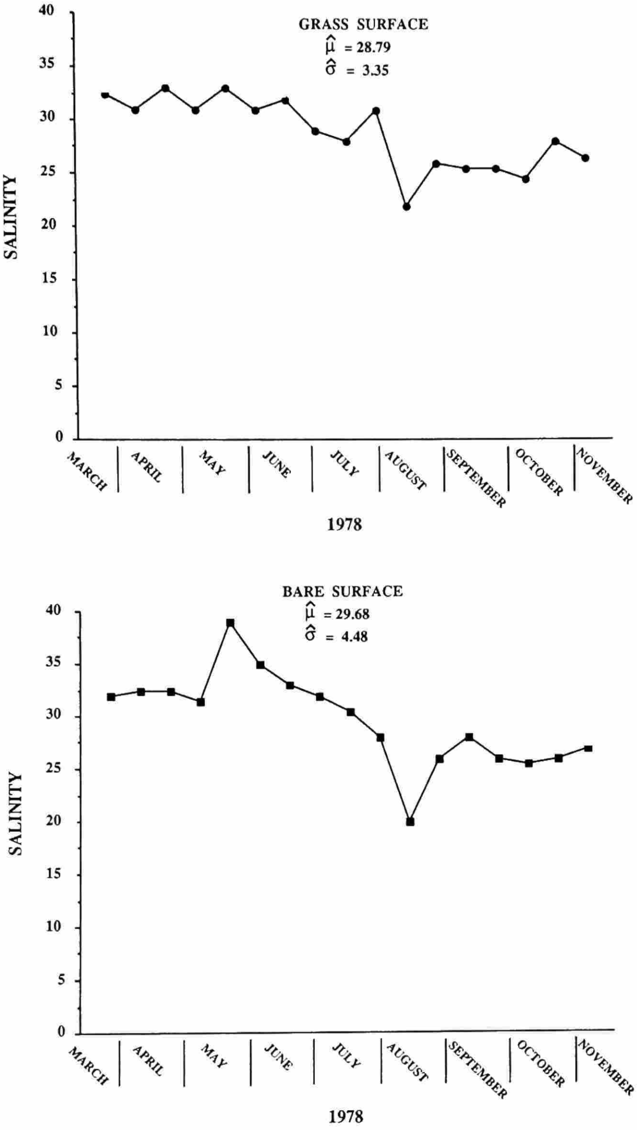

FIGURE 4.—Salinity measurements in ⁰/₀₀.

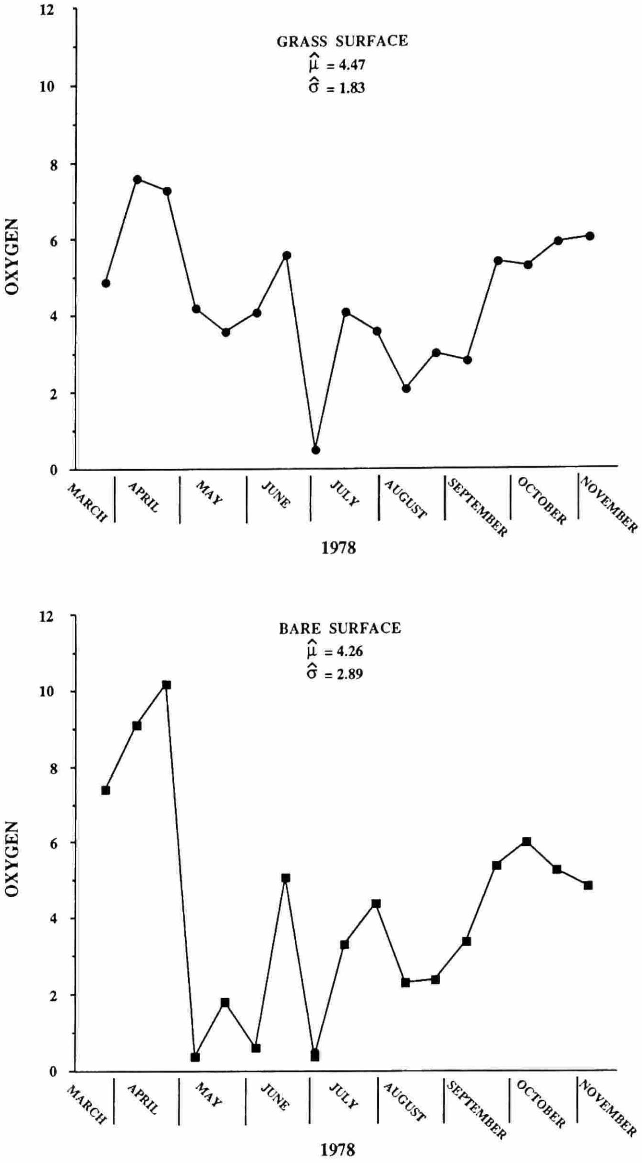

FIGURE 5.—Oxygen measurements in mg-at/l.

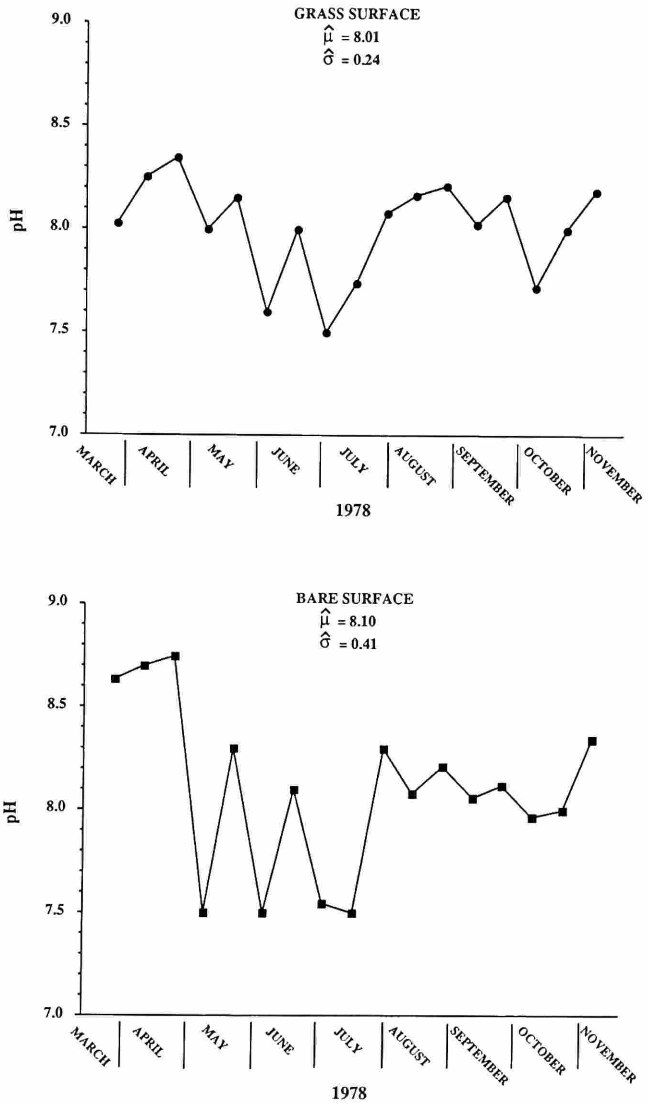

FIGURE 6.—pH measurements.

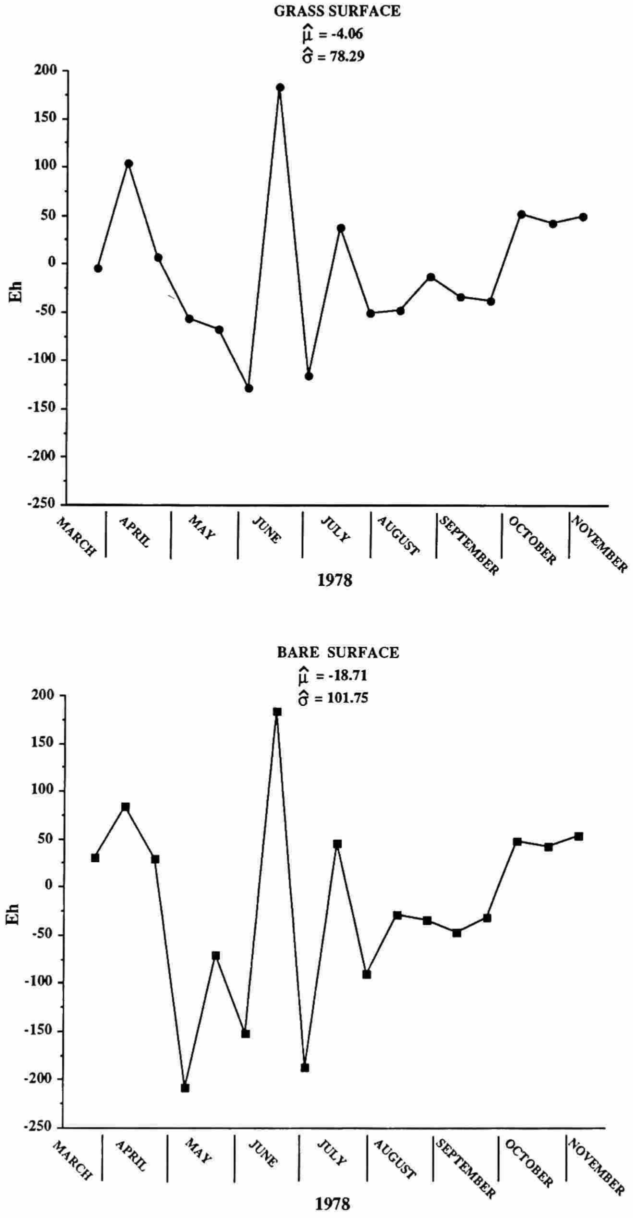

FIGURE 7.—Eh measurements in mV.

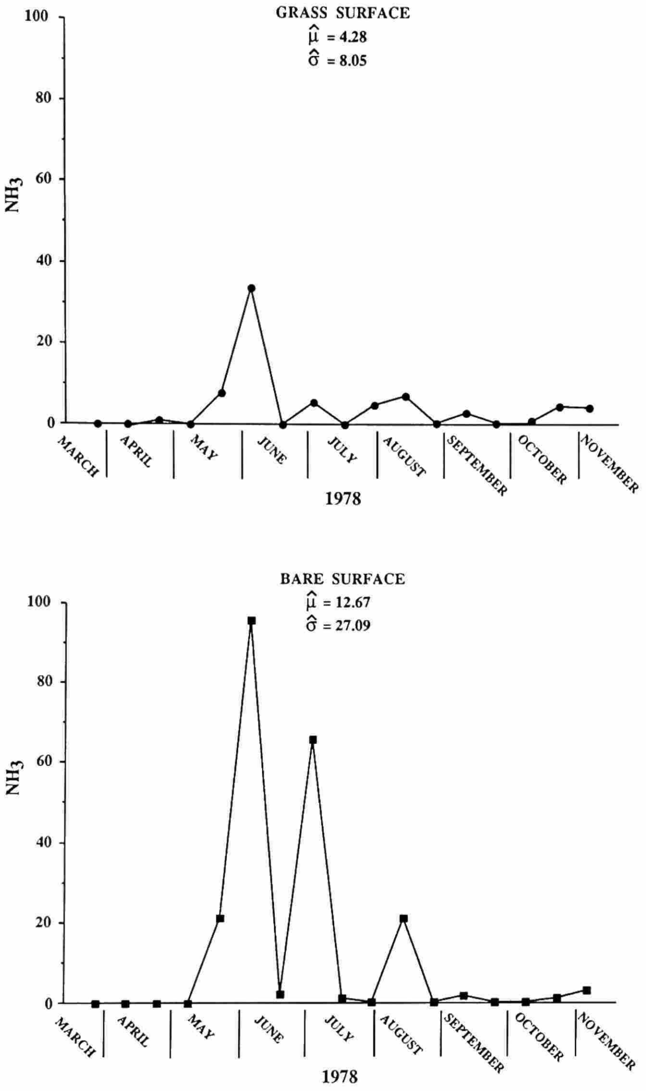

FIGURE 8.—NH_3 measurements in µg-at/l.

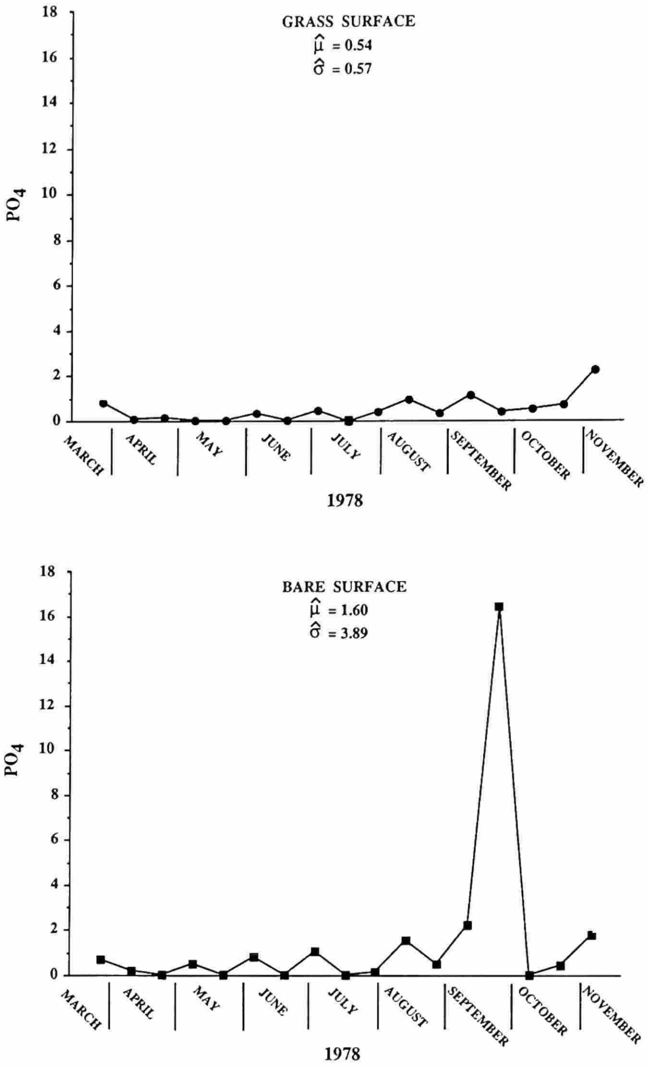

FIGURE 9.—PO_4 measurements in µg-at/l.

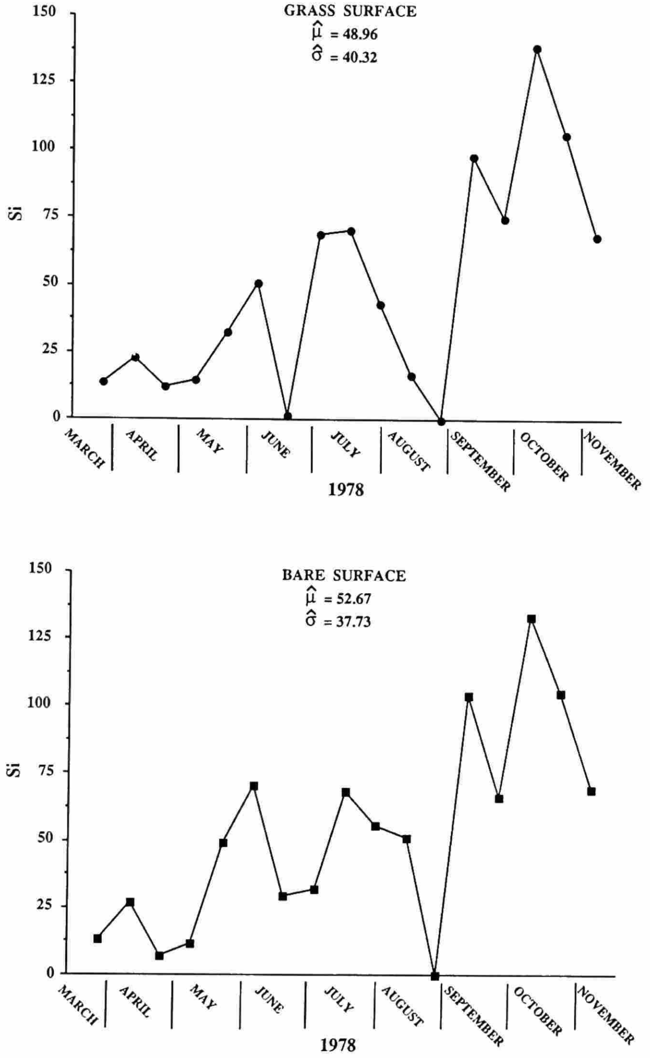

FIGURE 10.—Si measurements in µg-at/l.

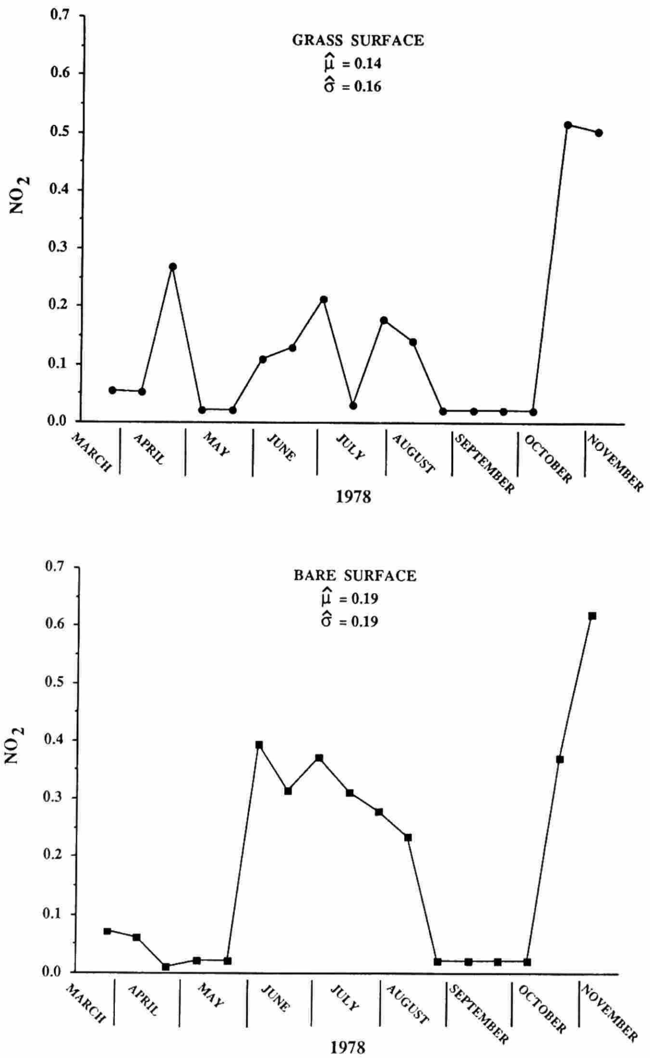

FIGURE 11.—NO_2 measurements in µg-at/l.

August; however, values generally increase from March to November.

NO_2 values are plotted in Figure 11 and the ANOVA results are presented in Table 2. Significant differences were again noted only with time. In general, values are low with maxima in summer and fall at the bare station and spring, summer, and fall at the grass station. Both stations had minima values from late August until early October.

$NO_2 + NO_3$ values are plotted in Figure 12, and ANOVA results are presented in Table 2. No significant differences were observed between stations or with time. An unexplainably high value was recorded in April at the grass station.

Table 3 shows the correlation coefficients between the environmental variables. Temperature and NH_3 are positively correlated with one another and negatively with oxygen, pH, and Eh which are all positively correlated with one another. Consequently, any hypothesis concerning the significance of a particular variable on species density is not independent of the others.

A way to avoid this difficulty is to transform the original variables to principal components. Principal component analysis is a technique which produces a succinct parsimonious summarization of many correlated (non-zero covariance) variables by transforming the original variables to independent (zero covariance) variables called principal components. An additional advantage of the technique is that the first principal component will account for most of the variability in the data, the second less, and so on (Seal, 1964). Eigenvalues were calculated from the correlation matrix (Table 3) using the SYSTAT statistical package. The first three eigenvectors account for 63.43% of the variability. The factor score coefficients (standardized vectors which when multiplied by the original standardized variables produce the principal components) indicate that all the environmental variables contribute substantially to the first three principal components (Table 4). The coefficients (Table 4) indicate that the first principal component (PC1) accounting for 31% of the variability contrasts

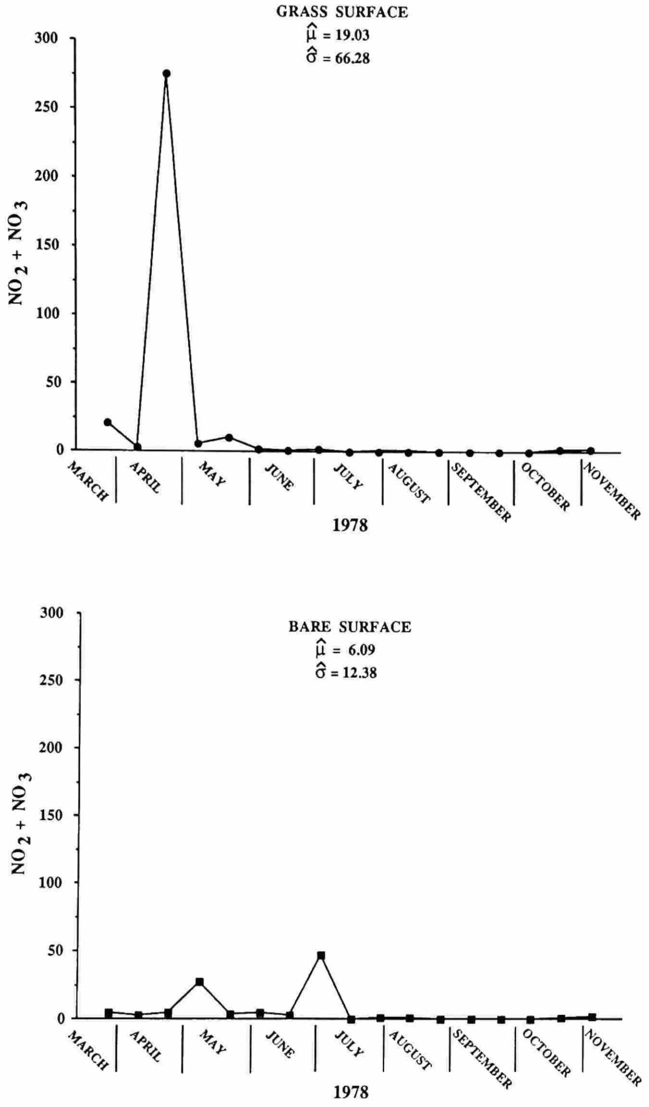

FIGURE 12.—$NO_2 + NO_3$ measurements in μg-at/l.

TABLE 3.—Correlation matrix for chemical variables for bare surface and grass surface. 0.05 level is underlined.

	Temperature	Salinity	Oxygen	pH	Eh	NH_3	PO_4	Si	NO_2	$NO_2 + NO_3$
Temperature	1.00									
Salinity	–0.14	1.00								
Oxygen	–0.68	0.07	1.00							
pH	–0.36	0.03	0.69	1.00						
Eh	–0.52	–0.08	0.69	0.44	1.00					
NH_3	0.40	0.29	–0.48	–0.44	–0.52	1.00				
PO_4	0.14	–0.24	0.03	0.03	–0.07	–0.03	1.00			
Si	–0.06	–0.39	–0.05	–0.33	0.04	0.04	0.13	1.00		
NO_2	–0.15	–0.04	–0.08	–0.14	0.09	0.32	–0.05	0.21	1.00	
$NO_2 + NO_3$	–0.26	0.24	0.15	0.10	–0.06	0.02	–0.07	–0.23	0.12	1.00

TABLE 4.—Factor score coeffecients for chemical variables for bare surface and grass surface.

Chemical variable	Factor		
	PC1(31%)	PC2(18%)	PC3(14%)
Temperature	–0.24	0.05	–0.30
Salinity	0.01	–0.45	0.04
Oxygen	0.29	0.00	0.04
pH	0.24	–0.07	–0.19
Eh	0.25	0.12	0.13
NH_3	–0.22	–0.18	0.22
PO_4	–0.02	0.24	–0.16
Si	–0.05	0.39	0.34
NO_2	–0.03	0.01	0.59
$NO_2 + NO_3$	0.06	–0.31	–0.17

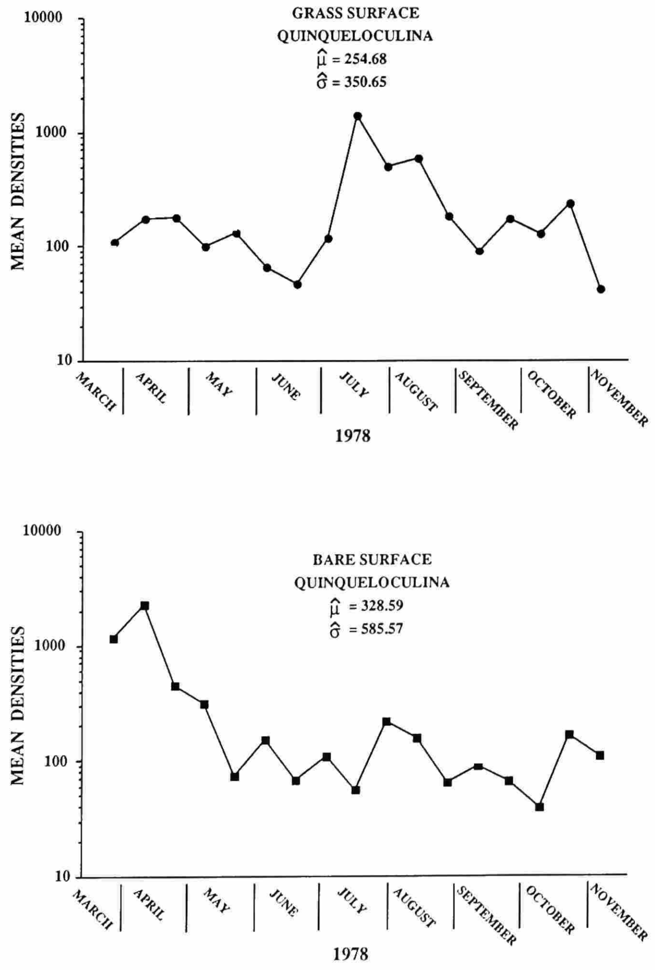

FIGURE 13.—Mean number of individuals of *Quinqueloculina* per 5 ml of sediment (density).

temperature and NH_3 with oxygen, pH, and Eh. The second principal component (PC2) accounting for 18% of the variability consists mainly of salinity, Si, and $NO_2 + NO_3$, although PO_4, NH_3, and Eh also contribute and a line of demarkation is not as clear cut as for PC1. The coefficients (Table 4) indicate that the third principal component (PC3) accounting for 14% of the variability consists mainly of NO_2, Si, and temperature, but again there is no dramatic demarkation. The most highly correlated variables (Table 3) are all concentrated on PC1.

SPECIES DENSITIES, STATION DIFFERENCES, PERIODICITY, AND ENVIRONMENTAL VARIABLES.—*Quinqueloculina: Quinqueloculina* was the most abundant taxon making up about 75% of the total living foraminifera at the surface stations. A plot of the mean densities observed at the bare and grass surface at the two stations is shown in Figure 13. The ANOVA table for six hypotheses is shown in Table 5. We recall that each hypothesis is formulated by equating the desired $\hat{\beta}$ to zero. For example, the Ω model used to test for station differences deletes $\hat{\beta}_2$, for $\pi/3$ periodicity and interaction $\hat{\beta}_3 = \hat{\beta}_4 = \hat{\beta}_7 = \hat{\beta}_8 = 0$, and so on. Table 5 indicates that all hypotheses except for station differences are significant. The overall mean density at the bare station is higher than at the grass station, but is not statistically significant at the chosen 0.05 level. Figure 13 shows that the bare station had high densities in spring while the grass station had high densities in summer. The environmental variables are significant as a group. Because they are not independent, testing for the significance of each individually is risky. Nevertheless, using the standard errors of the $\hat{\beta}$'s from the ω model for calculating confidence limits indicates oxygen, Eh, PO_4, Si, and $NO_2 + NO_3$ are significant. Again, emphasizing that the variables are not independent, the ease of calculation using "SYSTAT" made the calculation of simple regressions for each of the variables vs. density irresistible. The results shown in Table 6 indicate the regressions for oxygen, pH, PO_4, Si, and NO_2 are significant. A way of avoiding the correlations between variables is to calculate a multiple regression using principal components instead of the original variables. Because the

TABLE 5.—Statistical analysis of GLM for *Quinqueloculina* for bare surface and grass surface.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Stations	1.86	1	1.86	3.64	0.06
$\pi/3$ periodicity and interaction	22.53	4	5.63	11.04	0.00
$\pi/6$ periodicity and interaction	27.50	4	6.88	13.38	0.00
$\pi/3$ interaction	9.88	2	4.94	9.68	0.00
$\pi/6$ interaction	20.45	2	10.23	20.05	0.00
Environmental variables	37.34	10	3.73	7.32	0.00
Residual	59.17	116	0.51		

TABLE 6.—Values of F-ratio's for simple regressions on species densities and environmental variables at bare surface and grass surface. (+ indicates signficant (.05 level) positive value of β; – significant negative value of β.)

Environmental variables	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
Temperature	0.05	5.20^-	0.29	2.37	4.09^-
Salinity	0.20	21.10^+	5.77^+	49.23^+	6.79^-
Oxygen	7.66^+	13.22^+	0.08	0.54	4.37^+
pH	15.44^+	16.99^+	0.10	0.83	3.10
Eh	0.15	0.08	0.08	0.41	0.19
NH_3	1.64	0.00	1.98	1.22	7.09^-
PO_4	4.00^-	2.03	1.19	11.21^+	1.59
Si	7.23^-	7.60^-	0.25	17.88^-	3.36
NO_2	4.38^-	0.05	9.60^+	0.67	1.95
$NO_2 + NO_3$	0.07	1.02	0.22	6.64^+	0.27

principal components are orthogonal, each hypothesis is independent and the analysis is similar to a one-way ANOVA. The results of an analysis on the log densities of *Quinqueloculina* and the first three PC's of the environmental variables are shown in Table 7. The overall F-ratio is significant and the test for the significance of each PC, which are independent, indicates that PC1 and PC3 are significant at the 0.05 level while PC2 is nearly so. We recall from Table 4 that temperature, oxygen, pH, Eh, and NH_3 all contribute nearly equally to the first PC, and the third PC is weighed heavily on temperature, Si, and NO_2. Thus, the analysis using principal components requires seven of the 10 environmental variables for two PC's and 10 for three to explain the results. All of the above analyses indicate that the identification of one or two variables as solely significant for the observed densities is impossible.

Elphidium: *Elphidium* constitutes about 14% of the total living population and mean densities at the bare and grass stations are plotted in Figure 14 and the results of the GLM analysis is presented in Table 8. Although the mean density at the bare station is again higher than at the grass station, it is not statistically significant. The $\pi/3$ periodicity and interaction hypotheses are significant, but the $\pi/6$'s are not. Figure 14 indicates a spring high at the bare station, but no pronounced summer high at the grass station as was observed with *Quinqueloculina.* The group of environmental variables are significant, and the $\hat{\beta}$'s for Eh, PO_4, NO_2, and $NO_2 + NO_3$ were significant. Regressions of density vs. each individual environmental variable yielded a significant F-ratio for temperature, salinity, oxygen, pH, and Si (Table 6). The results of multiple-regression of *Elphidium* densities and the first three PC's of the environmental variables are shown in Table 9. The first two PC's are significant and these account for all of the environmental variables except NO_2. Here, we note that individual tests of the $\hat{\beta}$'s from the ω model and individual $\hat{\beta}$'s from simple regressions do not agree testifying to the difficulty encountered when variables are highly correlated.

Ammonia: *Ammonia* makes up about 8% of the total living population and mean densities at the bare and grass stations are plotted in Figure 15. The results of the GLM analysis are presented in Table 10. The overall mean density is slightly higher at the bare station, but not significantly so. The $\pi/3$ periodicity and interaction hypotheses are significant and Figure 15 indicates an early spring maximum at the bare station while both stations have summer and fall maxima. Environmental variables are significant as a group and the $\hat{\beta}$'s for Eh, NO_2, and $NO_2 + NO_3$ were significant. Individual simple regressions on density vs. environmental variables yielded significant F-ratios for salinity and NO_2 (Table 6). The results of the multiple regression on densities of *Ammonia* and the PC's of the environmental variables are shown in Table 11. The results present us with a small dilemma because the F-ratio for the overall analysis has a probability of 0.06 which is slightly above our chosen level, and, therefore, is not significant. On the other hand, PC3 is significant (Table 11). If we choose to regard the third principal component as significant, then temperature, Si, and NO_2 are the major contributors, especially NO_2 (Table 4). The F-ratio for environmental variables in the ω model, while significant, is the smallest encountered for any of the five taxa analyzed. *Ammonia* appears, then, to be the least influenced by the 10 variables measured in this study.

Bolivina: *Bolivina* constitutes about 1% of the total living population and mean densities at the bare and grass stations are plotted in Figure 16. The results of the GLM analysis are shown in Table 12. Although the differences in densities between stations are small, they are, nevertheless, statistically significant, and the highest density is at the grass station. None of the hypotheses for periodicity are significant. There does appear to be a decrease in density over the course of sampling, but the fluctuations in density shown in Figure 16 are small compared to those considered previously (note the difference in the scale of the ordinate). The environmental variables are significant as

TABLE 7.—Regression of *Quinqueloculina* and principal components for bare surface and grass surface.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.11$
Constant	5.00	0.09	57.41	0.00	
PC1	0.20	0.09	2.28	0.02	
PC2	−0.17	0.09	−1.94	0.06	
PC3	−0.24	0.09	−2.69	0.01	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	16.68	3	5.56	5.39	0.00
Residual	136.13	132	1.03		

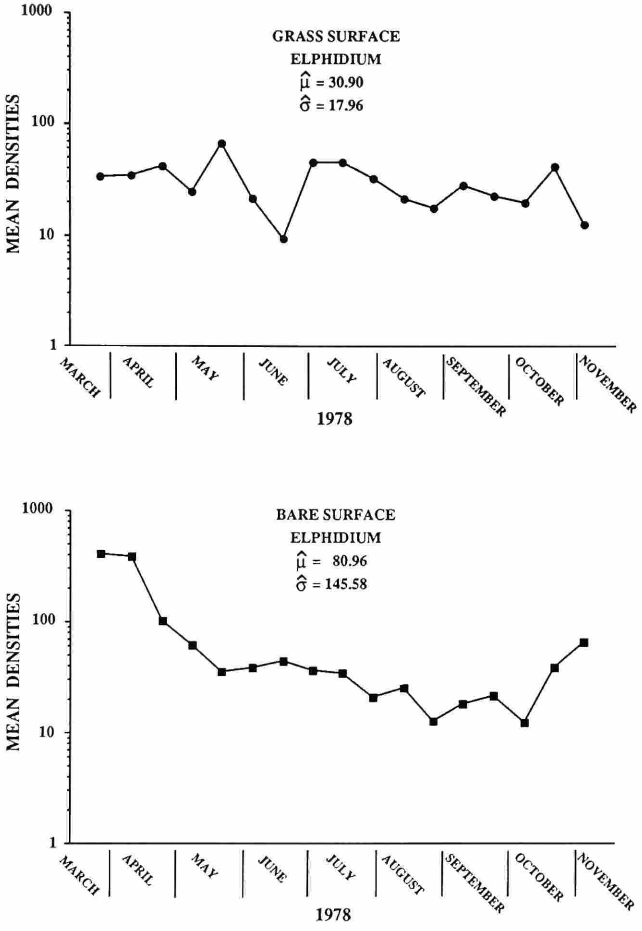

FIGURE 14.—Mean number of individuals of *Elphidium* per 5 ml of sediment (density).

TABLE 8.—Statistical analysis of GLM for *Elphidium* for bare surface and grass surface.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Stations	0.88	1	0.88	1.78	0.18
$\pi/3$ periodicity and interaction	8.28	4	2.07	4.21	0.00
$\pi/6$ periodicity and interaction	2.94	4	0.74	1.49	0.21
$\pi/3$ interaction	3.73	2	1.87	3.79	0.03
$\pi/6$ interaction	2.91	2	1.45	2.95	0.06
Environmental variables	28.43	10	2.84	5.78	0.00
Residual	57.04	116	0.49		

TABLE 9.—Regression of *Elphidium* and principal components for bare surface and grass surface.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.18$
Constant	3.50	0.07	50.73	0.00	
PC1	0.21	0.07	3.05	0.00	
PC2	−0.30	0.07	−4.32	0.00	
PC3	−0.03	0.07	−0.40	0.69	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	18.25	3	6.08	9.39	0.00
Residual	85.54	132	0.65		

a group, and the $\hat{\beta}$'s for salinity and Si were significant. F-ratios for simple regressions are significant for salinity, PO_4, Si, and NO_2 + NO_3 (Table 6). Multiple regression on densities of *Bolivina* and the first three PC's of the environmental variables are shown in Table 13. Only PC2 consisting mostly of salinity, Si, and NO_2 + NO_3 (Table 4) is significant. The relationship with salinity and to a lesser extent with Si are notable for this species.

Ammobaculites: *Ammobaculites* also constitutes about 1% of the total living population and mean densities for the bare and grass stations are plotted in Figure 17. The results of the GLM analysis are shown in Table 14. The hypothesis for station differences is significant with the highest densities occurring at the grass surface. The $\pi/3$ periodicity and interaction hypotheses are significant, and Figure 17 indicates the now familiar spring maximum was observed at the bare station after which time the densities remained very low (Appendix 1). At the grass surface the densities increased overall during the sampling duration (Appendix 2). The hypothesis for the environmental variables is significant. The $\hat{\beta}$'s of the ω model for the variables pH, PO_4, Si, NO_2, and NO_2 + NO_3 were significant. The F-ratios for temperature, salinity, oxygen, and NH_3 were significant for simple regressions on density and environmental variables (Table 6). The results of a multiple regression on the densities of *Ammobaculites* and the first three PC's of the environmental variables are shown in Table 15. The first two PC's are significant indicating that all the variables except for NO_2 (Table 4) are important contributors. Again, we note the inconsistencies obtained by testing the environmental variables individually.

In summary, we recognize no station differences for the three most abundant taxa. For the rare species *Bolivina* and *Ammobaculites* which together constitute only about 2% of the total living population, densities are higher at the grass station. All of the taxa except for *Bolivina* exhibited periodicity. *Quinqueloculina, Elphidium,* and *Ammonia* all showed high densities in spring at the bare surface station and in summer at the grass surface. *Bolivina* exhibited an overall decreasing density from spring onward at both stations while *Ammobaculites* increased at the grass surface station and decreased at the

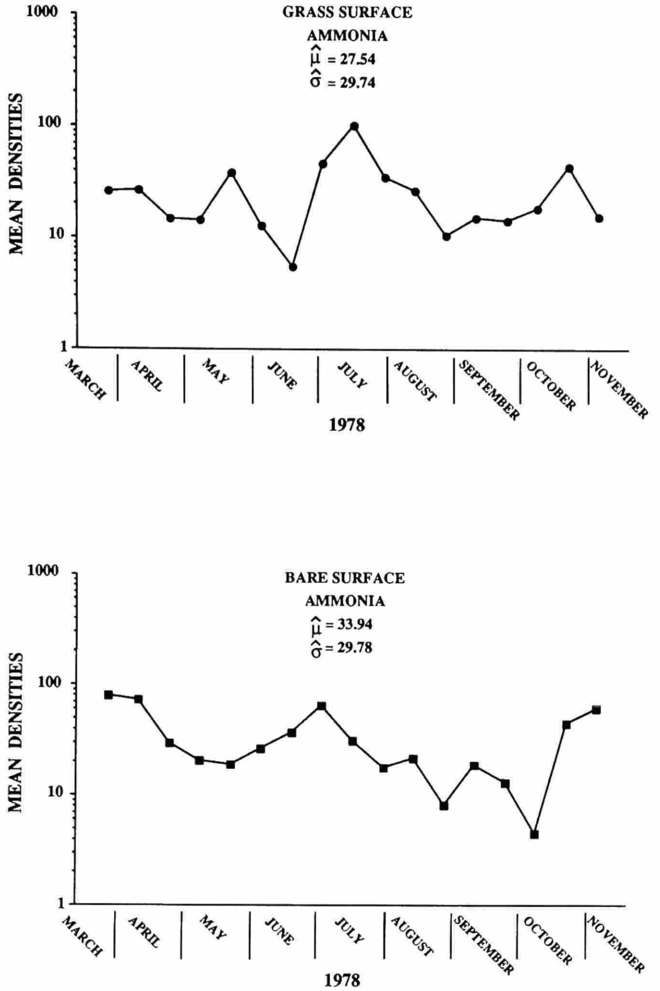

FIGURE 15.—Mean number of individuals of *Ammonia* per 5 ml of sediment (density).

TABLE 10.—Statistical analysis of GLM for *Ammonia* for bare surface and grass surface.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Stations	0.06	1	0.06	0.13	0.72
$\pi/3$ periodicity and interaction	11.29	4	2.82	5.98	0.00
$\pi/6$ periodicity and interaction	4.24	4	1.06	2.24	0.07
$\pi/3$ interaction	6.38	2	3.19	6.76	0.00
$\pi/6$ interaction	1.94	2	0.97	2.05	0.13
Environmental variables	16.60	10	1.66	3.52	0.00
Residual	54.70	116	0.47		

TABLE 11.—Regression of *Ammonia* and principal components for bare surface and grass surface.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.06$
Constant	3.14	0.07	45.92	0.00	
PC1	−0.01	0.07	−0.16	0.87	
PC2	−0.12	0.07	−1.72	0.09	
PC3	0.15	0.07	2.18	0.03	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	4.92	3	1.64	2.58	0.06
Residual	83.81	132	0.64		

bare surface. The environmental variables were significant as a group for all taxa, however, individual variables cannot be evaluated with confidence.

Grass Surface and Grass 10 cm

ENVIRONMENTAL VARIABLES.—The recorded temperature values are plotted in Figure 18, and the results of a two-way ANOVA testing for differences between surface and 10 cm and with time are shown for temperature and all the other environmental variables in Table 16. The hypothesis testing for differences in mean temperature between the surface and 10 cm depth is not significant, however, the hypothesis testing for time is. As everyone knows, the water is warmer in the summer and cooler in spring and fall. A very high temperature was recorded in June and a very low one in August at 10 cm.

The measured salinity values are shown in Figure 19. Only the hypothesis for time is significant. Salinities were highest in spring except for the first observation in March at 10 cm. Both stations experienced a dip in salinity in August.

The recorded oxygen values are shown in Figure 20. The mean square for differences between surface and 10 cm is large and highly significant, and the mean square for time, although relatively much smaller, is nearly significant. Figure 20 illustrates and Appendix 6 tabulates zero recordings for oxygen during spring and summer at 10 cm making the difference between the surface and 10 cm (depth hypothesis) so dramatic.

The measured pH values are plotted in Figure 21. The depth hypothesis is significant, and the pH is always lower at 10 cm (Figure 21, Appendix 5, 6). Even at 10 cm, however, only one reading (November) recorded a value below 7.

Eh values are plotted in Figure 22. The depth hypothesis is significant. Values of Eh at 10 cm are always negative, and usually highly so, while the values at the surface fluctuate from positive to negative with a slightly negative mean (Figure 22, Appendix 5, 6).

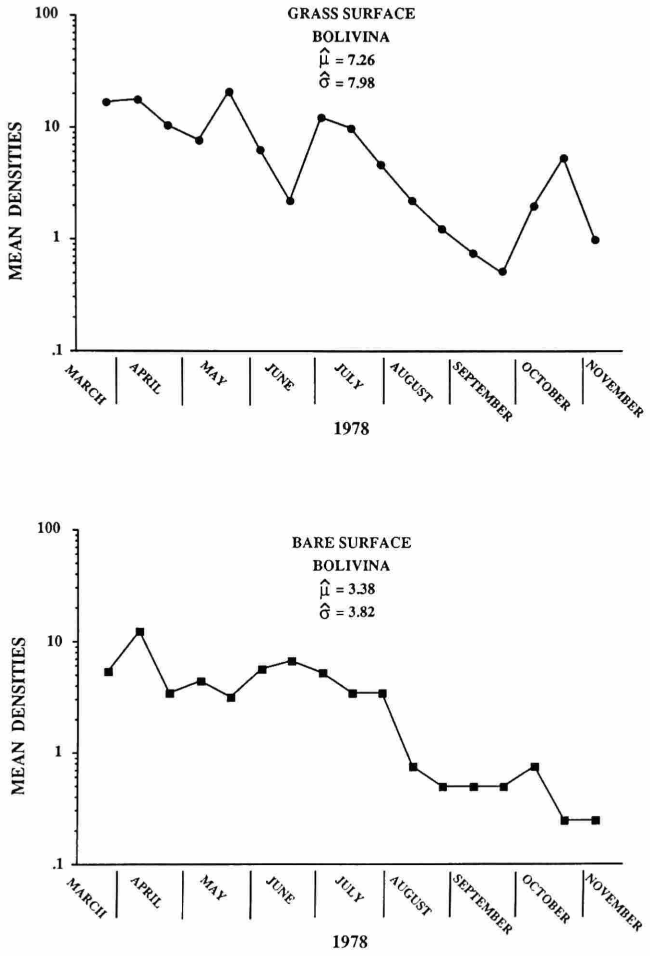

FIGURE 16.—Mean number of individuals of *Bolivina* per 5 ml of sediment (density).

TABLE 12.—Statistical analysis of GLM for *Bolivina* for bare surface and grass surface.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Stations	4.03	1	4.03	7.45	0.01
π/3 periodicity and interaction	4.38	4	1.09	2.02	0.10
π/6 periodicity and interaction	3.33	4	0.83	1.54	0.20
π/3 interaction	1.25	2	0.62	1.15	0.32
π/6 interaction	0.36	2	0.18	0.33	0.72
Environmental variables	42.21	10	4.22	7.80	0.00
Residual	62.77	116	0.54		

TABLE 13.—Regression of *Bolivina* and principal components for bare surface and grass surface.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.28$
Constant	1.38	0.07	19.10	0.00	
PC1	0.04	0.07	0.47	0.64	
PC2	−0.52	0.07	−7.14	0.00	
PC3	0.01	0.07	0.19	0.85	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	36.34	3	12.11	17.07	0.00
Residual	93.66	132	0.71		

NH_3 values are plotted in Figure 23. The depth hypothesis is significant. The values at 10 cm are usually two orders of magnitude greater than at the surface (Appendix 5, 6). Two zero values were recorded at 10 cm, one in April and one in October. We suspect these anomalies are due to problems with instrumentation.

PO_4 values are plotted in Figure 24. The hypothesis for depth is significant. The values for PO_4 were very low at the surface, and one or two orders of magnitude higher at 10 cm (Appendix 5, 6). A very high value was recorded at 10 cm in June.

Si values are plotted in Figure 25 and the hypothesis for depth is significant. The values for Si at the surface are an order of magnitude smaller than at 10 cm (Appendix 5, 6). At 10 cm zero values were recorded in April, August, and October. Except for the zero value in August, the pattern is very similar to that observed for NH_3 at 10 cm.

NO_2 values are plotted in Figure 26. The hypothesis for depth is significant, and values for NO_2 are low. At 10 cm very low values were recorded in all months except October.

$NO_2 + NO_3$ values are plotted in Figure 27. There is no significant difference with depth or with time. Except for one measurement at the surface in April (Figure 27, Appendix 5) all the measurements were low.

The two-way ANOVA's for environmental variables at the bare surface vs. grass surface showed most significant differences are with time (Table 2). In contrast, the analysis for grass surface vs. grass 10 cm shows most of the significant differences are with depth (Table 16). Moreover, the F-ratios for the latter are usually much higher. We have, then, a situation where, except for temperature, salinity, and $NO_2 + NO_3$, there are much larger differences than at the surface stations.

The environmental variables are highly correlated as shown in Table 17. High positive values occur between oxygen and Eh, oxygen and NO_2, pH and Eh, Eh and NO_2, NH_3 and PO_4, NH_3 and Si, and PO_4 and Si. High negative values occur between oxygen and NH_3, oxygen and PO_4, oxygen and Si, pH and NH_3, pH and Si, Eh and NH_3, Eh and PO_4, and Eh and Si. The correlations differ from those at the bare and grass surface

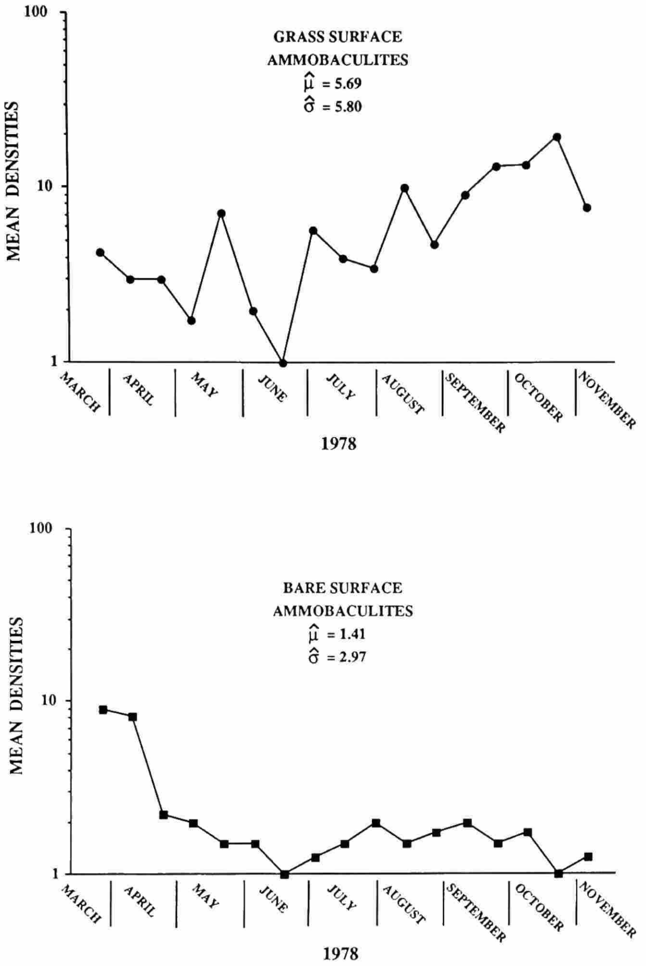

FIGURE 17.—Mean number of individuals of *Ammobaculites* per 5 ml of sediment (density).

TABLE 14.—Statistical analysis of GLM for *Ammobaculites* for bare surface and grass surface.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Stations	21.59	1	21.59	44.79	0.00
π/3 periodicity and interaction	8.56	4	2.14	4.44	0.00
π/6 periodicity and interaction	3.13	4	0.78	1.62	0.17
π/3 interaction	4.90	2	2.45	5.08	0.01
π/6 interaction	0.08	2	0.04	0.08	0.92
Environmental variables	18.26	10	1.83	3.79	0.00
Residual	55.87	116	0.48		

TABLE 15.—Regression of *Ammobaculites* and principal components for bare surface and grass surface.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.06$
Constant	1.03	0.08	12.80	0.00	
PC1	0.18	0.08	2.17	0.03	
PC2	0.17	0.08	2.07	0.04	
PC3	−0.03	0.08	−0.34	0.73	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	7.97	3	2.66	3.04	0.03
Residual	115.46	132	0.88		

(Table 3) in that PO_4, Si, and NO_2 now are highly correlated so that the matrix of correlation coefficients has many more high values. To succinctly summarize the environmental variables, and remove the covariance between them, a principal component analysis was calculated on the correlation matrix. The first three eigenvalues account for about 70% of the variability. The factor score coefficients are given in Table 18. The first vector accounting for 45% of the variability has high values for oxygen, pH, Eh, NH_3, PO_4, Si, and NO_2. The second vector accounting for 15% of the variability has the highest values for salinity and $NO_2 + NO_3$, and the third accounting for 10% of the variability has a high value for temperature. Thus, all of the water chemistry variables are accounted for by using the first three principal components, and PC1 accounts for all of them except temperature, salinity, and $NO_2 + NO_3$ which, interestingly, are the variables without significant differences with depth (Table 16).

SPECIES DENSITIES, DEPTH DIFFERENCES, PERIODICITY, AND ENVIRONMENTAL VARIABLES.—*Quinqueloculina*: *Quinqueloculina* mean densities are plotted in Figure 28, and analysis by the GLM is shown in Table 19. As noted earlier, the densities for *Quinqueloculina* at the grass surface exhibited a summer maximum in July and August (Appendix 2). At 10 cm maxima were observed in March and November. The large increase in density observed in the summer at the surface is not reflected at 10 cm.

All of the hypotheses tested by the GLM were significant (Table 19). The mean square for differences with depth is very large reflecting the two orders of difference in magnitude of the mean density between the surface and 10 cm. The set of environmental variables are significant and in the ω model $\hat{\beta}$'s for oxygen, Eh, and NH_3 were significant. Simple regressions on density vs. environmental variables indicate the F-ratios for all variables except temperature are significant (Table 20). The results of a multiple regression on the densities of *Quinqueloculina* and the first three PC's of the environmental variables are

TABLE 16.—Analysis of variance for chemical variables on grass surface and 10 cm.

Variable	Source	Sum of squares	df	mean square	F	p(F)
Temperature	depth	0.54	1	0.54	0.12	0.74
	time	273.64	16	17.10	3.72	0.01
	residual	73.63	16	4.60		
Salinity	depth	5.72	1	5.72	2.83	0.11
	time	311.96	16	19.50	9.64	0.00
	residual	32.35	16	2.02		
Oxygen	depth	87.68	1	87.68	30.77	0.00
	time	96.21	16	6.01	2.11	0.07
	residual	45.59	16	2.85		
pH	depth	2.95	1	2.95	45.09	0.00
	time	1.03	16	0.06	0.98	0.52
	residual	1.05	16	0.07		
Eh	depth	469412.50	1	469412.50	109.31	0.00
	time	107511.88	16	6719.49	1.57	0.19
	residual	68712.00	16	4294.50		
NH_3	depth	1148940.80	1	1148940.80	32.13	0.00
	time	601797.43	16	37612.34	1.05	0.46
	residual	572067.08	16	35754.19		
PO_4	depth	12189.21	1	12189.21	8.61	0.01
	time	22394.25	16	1399.64	0.99	0.51
	residual	22652.76	16	1415.80		
Si	depth	1477313.29	1	1477313.29	41.34	0.00
	time	635755.12	16	39734.70	1.11	0.42
	residual	571797.45	16	35737.34		
NO_2	depth	0.11	1	0.11	7.82	0.01
	time	0.19	16	0.01	0.85	0.62
	residual	0.23	16	0.01		
$NO_2 + NO_3$	depth	2933.23	1	2933.23	1.33	0.27
	time	35026.37	16	2189.15	0.99	0.51
	residual	35275.14	16	2204.70		

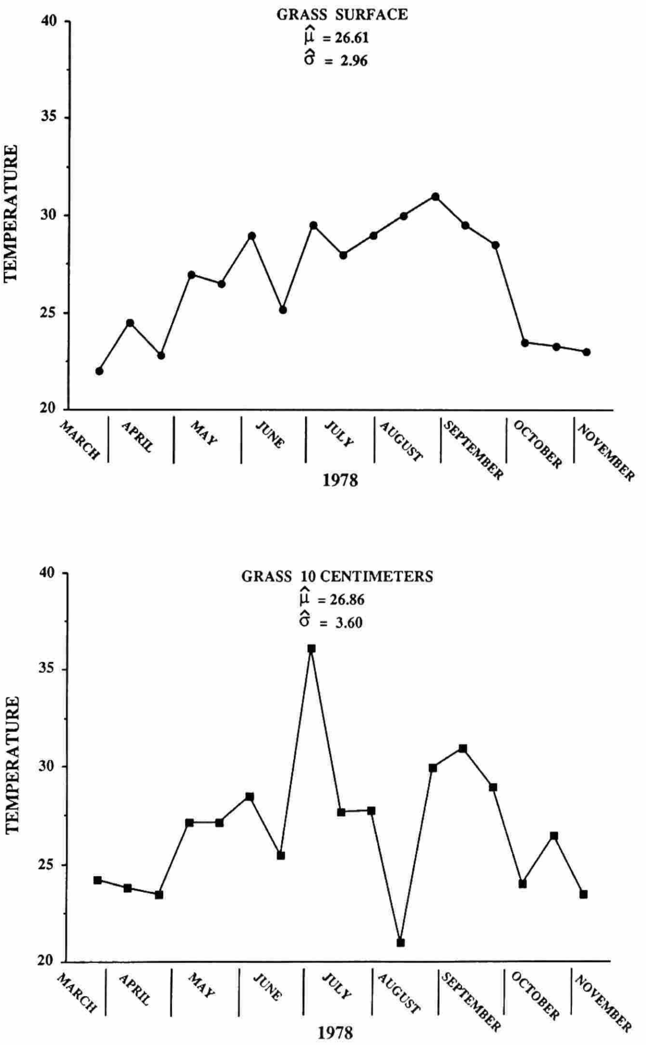

FIGURE 18.—Temperature measurements in °C.

shown in Table 21. The first and third PC's are significant indicating that only $NO_2 + NO_3$ did not contribute substantially to the significance of the analysis. The F-ratios for the simple regressions are much larger than for the bare surface and grass surface (compare Tables 6 and 20). Similarly, the F-ratio and R^2 for the multiple regression using the PC's is much larger for the grass surface and grass 10 cm than for the bare surface and grass surface (compare Tables 7 and 21). This is, of course, a reflection of the very large differences between densities and environmental variables between the surface and 10 cm. The signs of the factor score coefficients for PC1 (Table 18), the correlation matrix (Table 17), and the $\hat{\beta}$'s of the simple regressions (Table 20) show that the analysis contrasts oxygen, pH, Eh, NO_2 with NH_3, PO_4, Si.

Elphidium: Elphidium mean densities at the grass surface and grass 10 cm are plotted in Figure 29. The summer maximum observed at the surface for *Quinqueloculina* was not observed for *Elphidium* (Appendix 2). Minima at the surface were observed in June and November which is similar to the pattern of *Quinqueloculina* (Appendix 2). At 10 cm a maximum occurred in March due to high number of individuals in two of the four replicates (Appendix 3). Once again, however, the densities at 10 cm were very low, averaging less than two individuals.

Table 22 indicates the largest mean square is for the hypothesis contrasting depth. The $\pi/3$ periodicity with interaction is significant while the $\pi/6$ is not. The set of environmental variables are significant, and individual $\hat{\beta}$'s of the ω model for Eh and NH_3 were significant. F-ratios of all variables except temperature and salinity are significant for simple regressions (Table 20). The results of a multiple regression on the densities of *Elphidium* and the first three PC's of the environmental variables indicate that all three PC's, and, consequently, all the environmental variables contribute substantially (Table 23).

Ammonia: Ammonia densities for the grass surface and grass 10 cm are plotted in Figure 30. A maximum density was

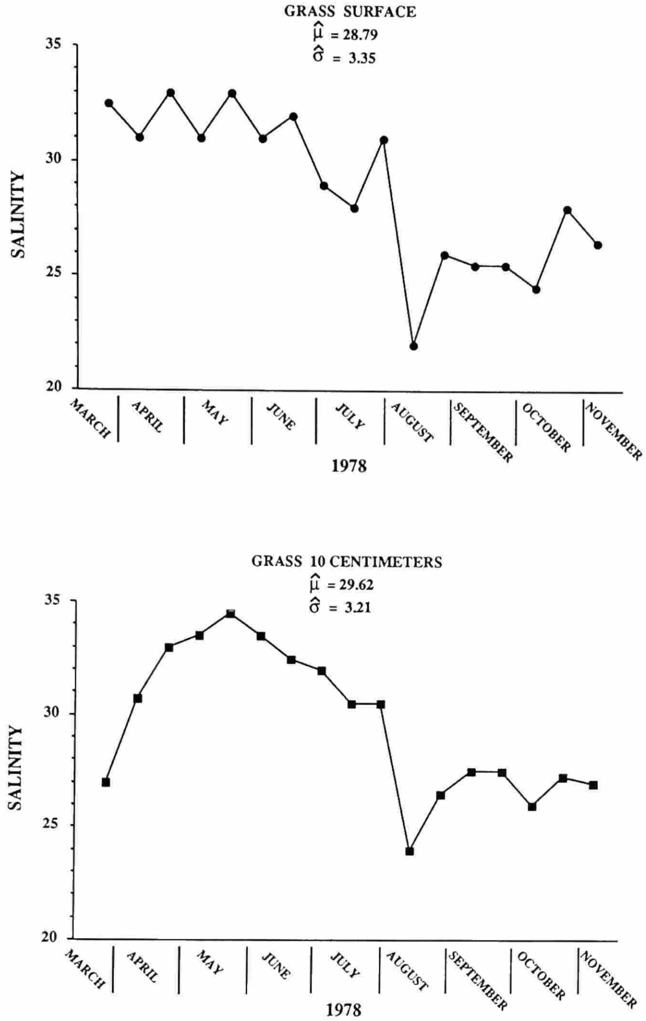

FIGURE 19.—Salinity measurements in ‰.

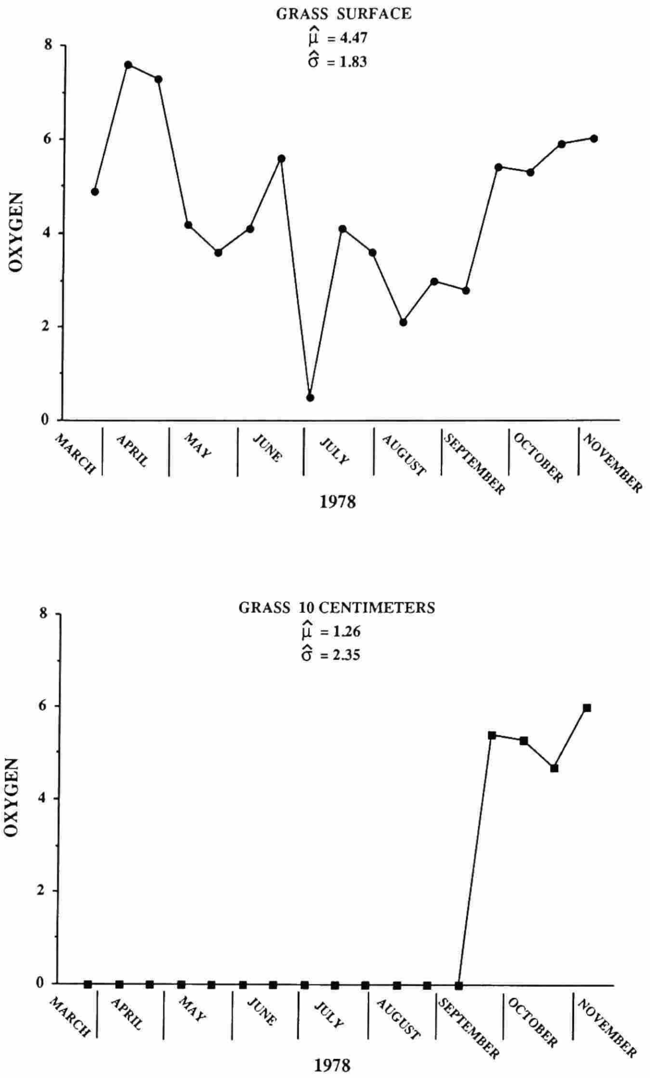

FIGURE 20.—Oxygen measurements in mg-at/l.

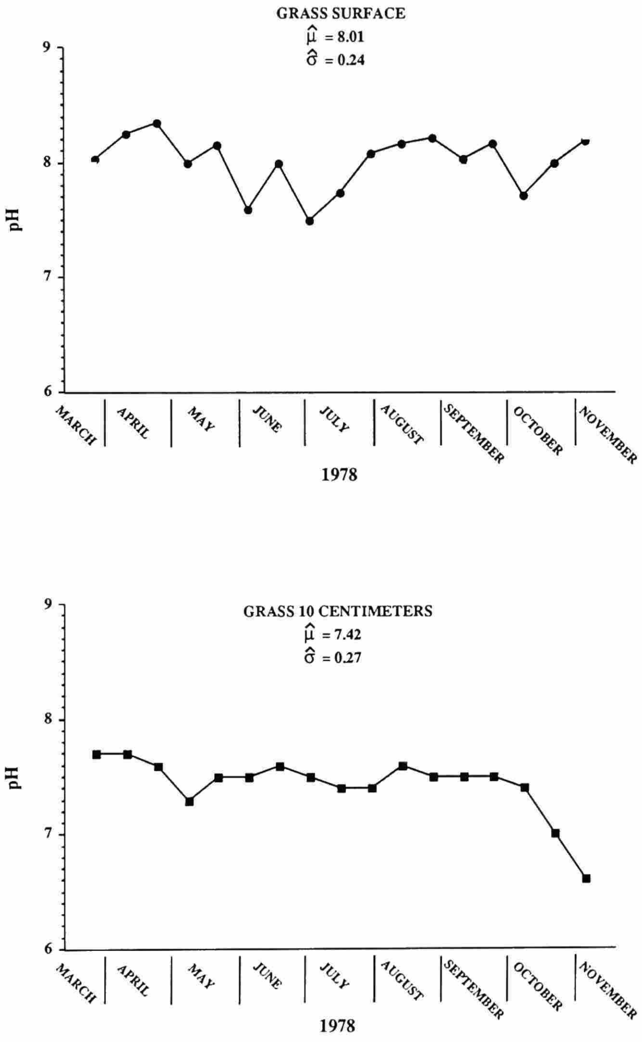

FIGURE 21.—pH measurements.

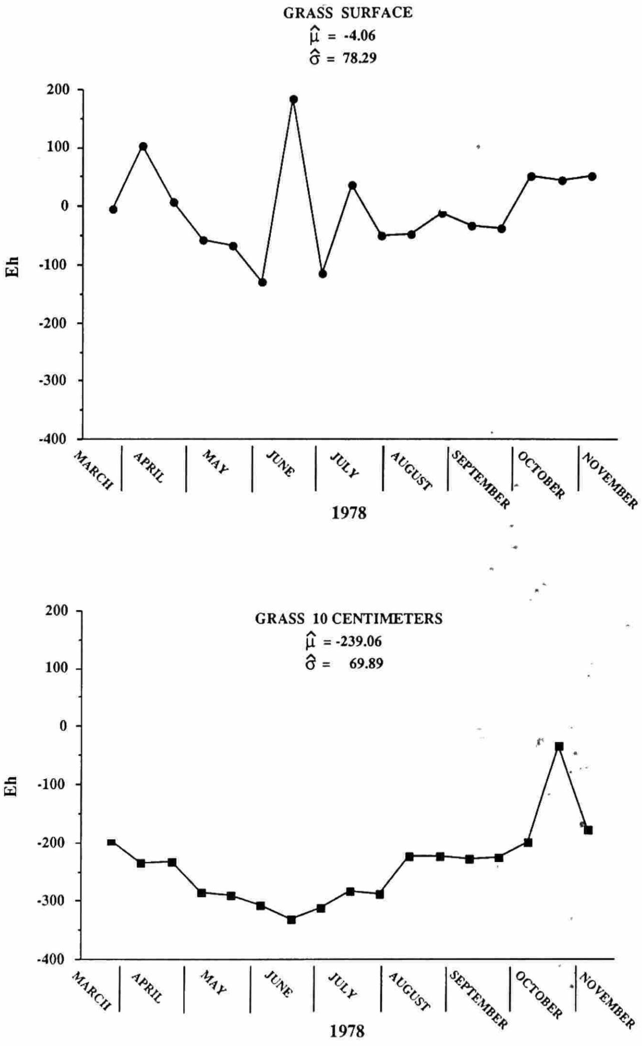

FIGURE 22.—Eh measurements in mV.

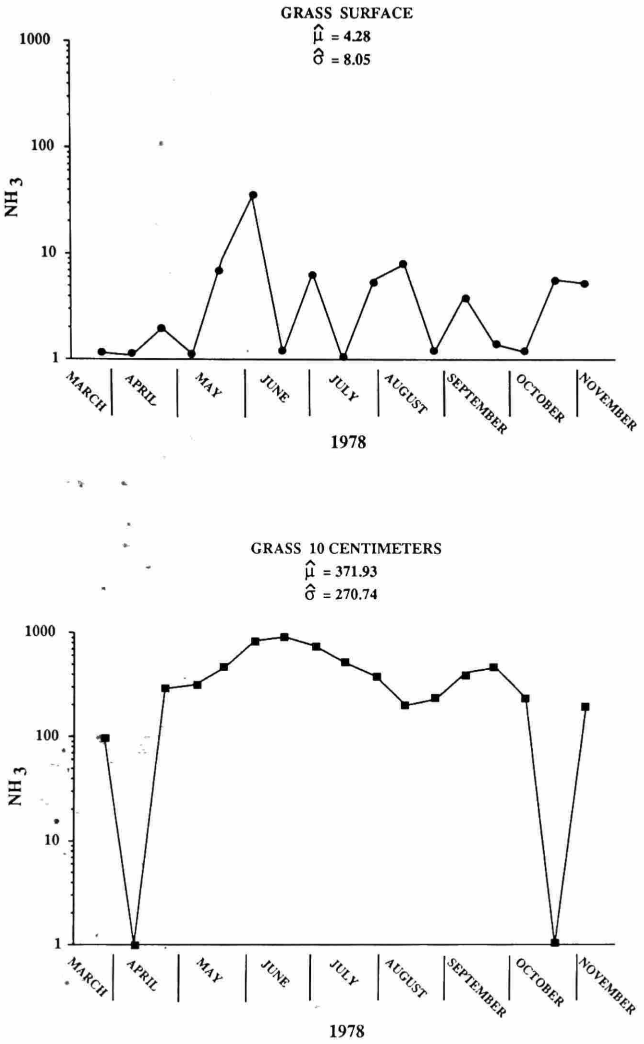

FIGURE 23.—NH_3 measurements in µg-at/l.

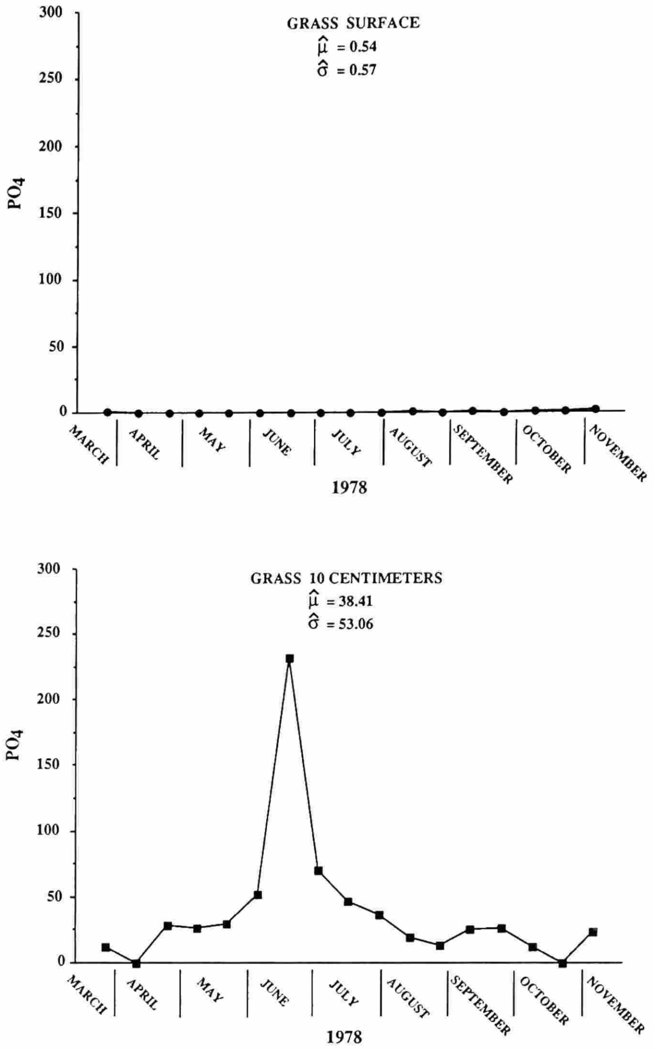

FIGURE 24.—PO_4 measurements in µg-at/l.

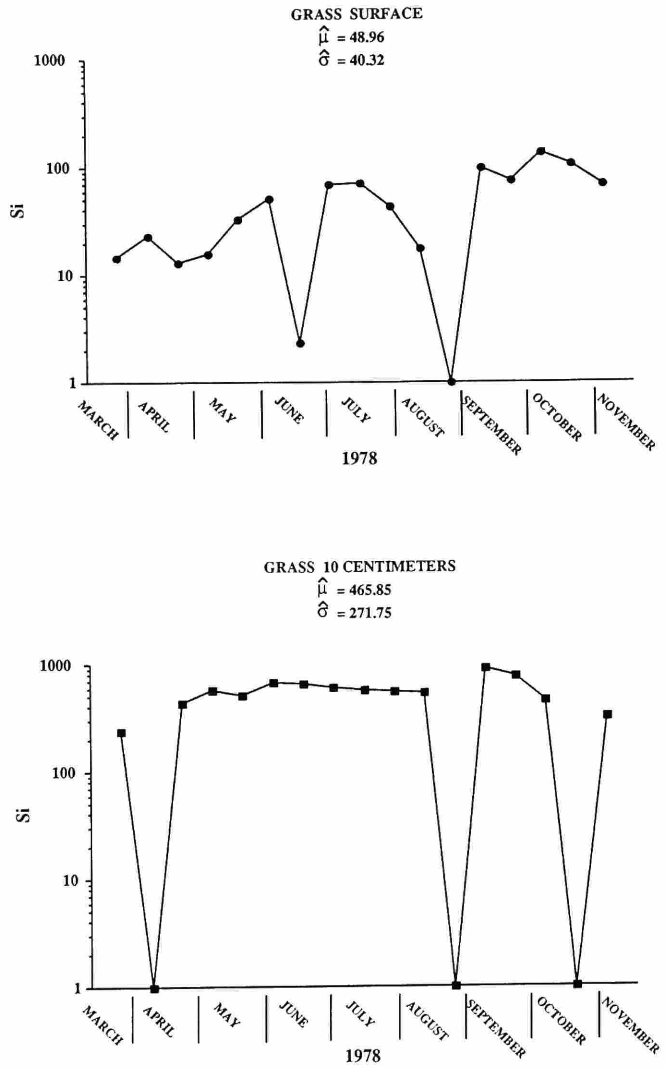

FIGURE 25.—Si measurements in µg-at/l.

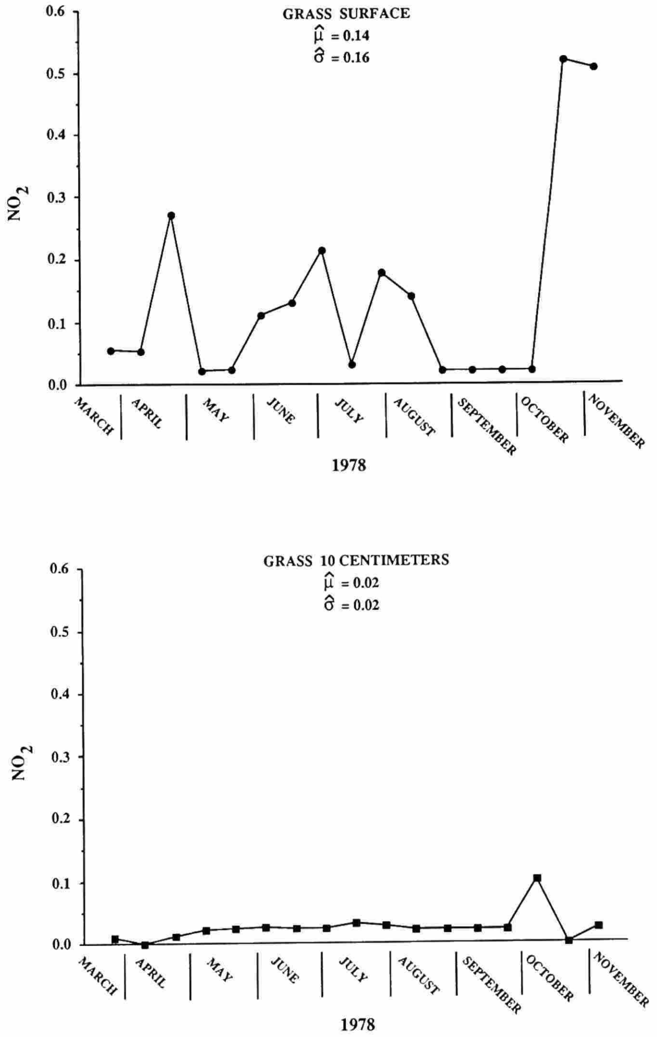

FIGURE 26.—NO_2 measurements in µg-at/l.

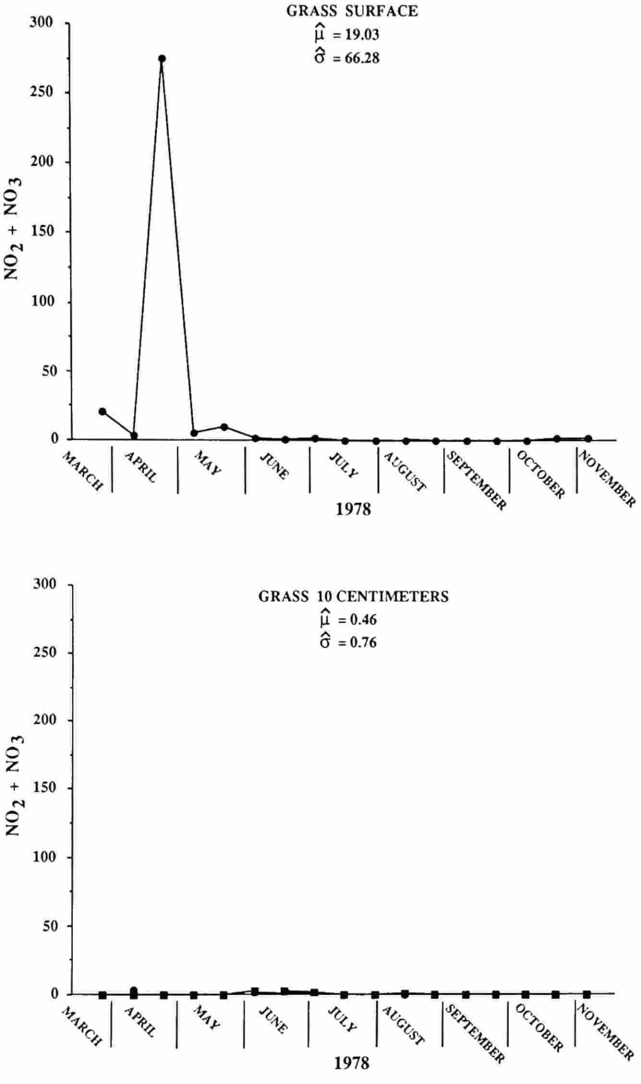

FIGURE 27.—$NO_2 + NO_3$ measurements in µg-at/l.

observed at the surface in July. Like *Quinqueloculina* and *Elphidium*, a minimum occurred in June (Appendix 2). Similar to the aforementioned taxa, at 10 cm the maximum was observed in March (Appendix 3). In general, densities were very low at 10 cm averaging slightly less than two individuals.

Table 24 shows the results of the GLM analysis. Again the hypothesis for depth has a very large mean square and is highly significant. The $\pi/3$ periodicity with interaction is significant while the $\pi/6$ is not. The set of environmental variables are significant and the $\hat{\beta}$'s of the ω model for NH_3 and $NO_2 + NO_3$ are significant. The results of a multiple regression on the densities of *Ammonia* and the first three PC's of the environmental variables indicate that the first and third PC's are significant (Table 25). Consequently, all the variables except for salinity and $NO_2 + NO_3$ are involved. The analysis for the grass surface and 10 cm stands in marked contrast to the analysis for bare surface and grass surface where the F-ratio and R^2 was relatively small (compare Tables 11 and 25).

Bolivina: *Bolivina* mean densities at the grass surface and grass 10 cm are plotted in Figure 31. At the surface the maximum occurred in May and the June minimum observed for the three previously discussed taxa is also shown by *Bolivina* (Appendix 2). From July to September the density steadily decreased at the grass surface (Figure 31). At 10 cm the maximum occurred, similar to the previous taxa, in March. The average number of individuals observed was slightly less than one, and at seven sampling times no individuals were observed at 10 cm (Appendix 3).

Table 26 shows the statistical analysis of the GLM. The mean square for depth is once again large and highly significant. The hypotheses for $\pi/6$ periodicity and interaction, and $\pi/3$ interaction are significant. This combination is not observed for any of the other taxa analyzed. The set of environmental variables are significant, and the $\hat{\beta}$'s of the ω model for temperature and salinity are significant. The F-ratios for simple regressions on densities vs. environmental variables

TABLE 17.—Correlation matrix for chemical variables on grass surface and 10 cm. 0.05 level is underlined.

	Temperature	Salinity	Oxygen	pH	Eh	NH_3	PO_4	Si	NO_2	$NO_2 + NO_3$
Temperature	1.00									
Salinity	−0.02	1.00								
Oxygen	−0.35	−0.17	1.00							
pH	−0.06	−0.02	0.37	1.00						
Eh	−0.26	−0.25	0.78	0.63	1.00					
NH_3	0.31	0.36	−0.57	−0.47	−0.79	1.00				
PO_4	0.10	0.29	−0.42	−0.27	−0.56	0.81	1.00			
Si	0.19	0.18	−0.51	−0.53	−0.77	0.85	0.57	1.00		
NO_2	−0.25	−0.09	0.41	0.38	0.44	−0.31	−0.20	−0.30	1.00	
$NO_2 + NO_3$	−0.23	0.23	0.31	0.31	0.18	−0.14	−0.09	−0.17	0.27	1.00

TABLE 18.—Factor score coefficients for chemical variables for grass surface and 10 cm.

Chemical variable	Factor		
	PC1(45%)	PC2(15%)	PC3(10%)
Temperature	0.08	−0.25	0.76
Salinity	0.07	0.44	0.28
Oxygen	−0.17	0.11	−0.20
pH	−0.14	0.16	0.51
Eh	−0.21	−0.02	0.07
NH_3	0.20	0.17	0.03
PO_4	0.16	0.24	−0.03
Si	0.19	0.08	−0.18
NO_2	−0.12	0.23	−0.10
$NO_2 + NO_3$	−0.07	0.47	0.09

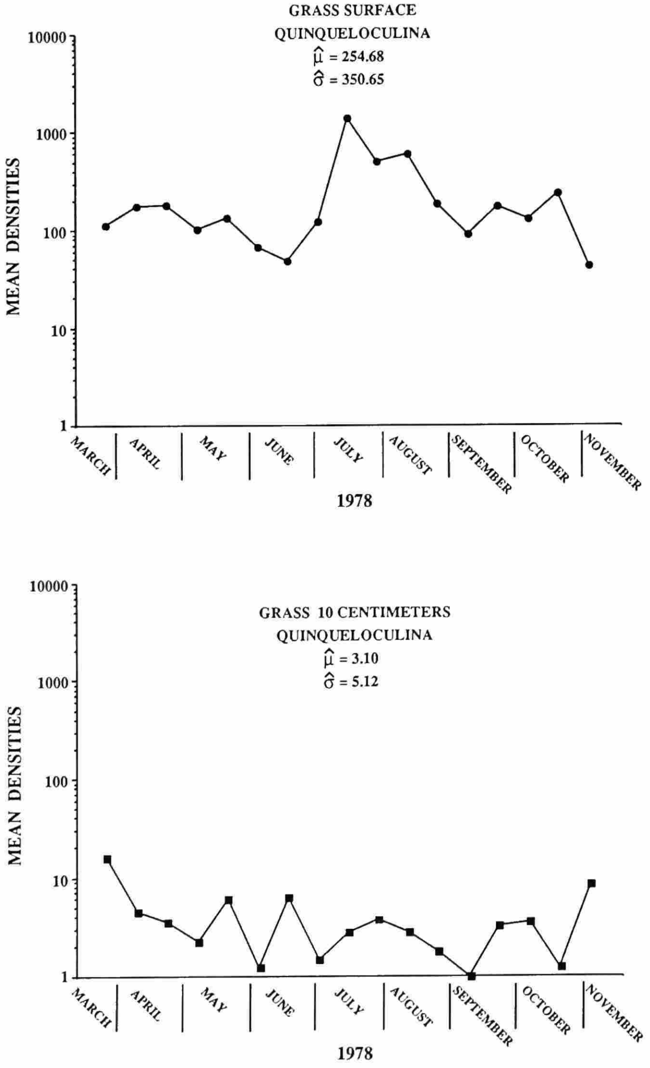

FIGURE 28.—Mean number of individuals of *Quinqueloculina* per 5 ml of sediment (density).

are all significant (Table 20). The results of a multiple regression on the densities of *Bolivina* and the first three PC's of the environmental variables (Table 27) indicate that all three PC's (all the environmental variables) are significant. Comparison of Tables 13 and 27 indicate that for the bare surface and grass surface only PC2 was significant while at the grass surface and 10 cm all three PC's were significant. Simple regressions for the bare and grass surface had four variables significant (Table 6), while at the grass surface and 10 cm all were significant (Table 20). The F-ratio for salinity at the bare surface and grass surface is significant and the $\hat{\beta}$'s for the ω model's for salinity in both analyses is significant. We recall that at the bare surface and grass surface the densities of *Bolivina* decrease during the period of our observations (Figure 16) and salinity exhibits the same trend (Figure 4). Salinity, then, may be important in regulating the density of *Bolivina,* but at 10 cm the decrease and increase in other variables probably overshadows its importance.

Ammobaculites: Ammobaculites mean densities for the grass surface and grass 10 cm are shown in Figure 32. In keeping with the low densities observed in June for the other taxa at the grass surface station, no living individuals of *Ammobaculites* were observed on 19 June (Appendix 2). At 10 cm, the maximum number of individuals (three) were observed, as with the other taxa, in March (Appendix 3). One living individual was observed in April and one in June (Appendix 3).

Table 28 displays the results of the statistical analysis of the GLM. The hypothesis for depth has the highest mean square and is significant. All of the periodicity hypotheses are significant except for π/3 interaction. The set of environmental variables are significant, and the $\hat{\beta}$'s of the ω model for salinity, oxygen, NO_2, and $NO_2 + NO_3$ are significant. The F-ratios for simple regressions on densities vs. environmental variables are significant for all variables except temperature and $NO_2 + NO_3$. Multiple regression of the densities of *Ammobaculites* and the first three PC's of the environmental variables (Table 29) indicate that the first and third PC's are significant. Therefore, all the environmental variables except for salinity and NO_2 +

TABLE 19.—Statistical analysis of GLM for *Quinqueloculina* for grass surface and 10 cm.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Depth	24.18	1	24.18	49.85	0.00
π/3 periodicity and interaction	22.99	4	5.75	11.85	0.00
π/6 periodicity and interaction	28.80	4	7.20	14.85	0.00
π/3 interaction	16.26	2	8.13	16.76	0.00
π/6 interaction	17.30	2	8.65	17.83	0.00
Environmental variables	15.37	10	1.54	3.17	0.00
Residual	56.28	116	0.48		

TABLE 20.—Values of F-ratio's for simple regressions on species densities and environmental variables at grass surface and grass 10 cm. (+ indicates signficant (.05 level) positive value of β; – significant negative value of β.)

Environmental variables	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*
Temperature	0.47	1.57	1.29	4.39^{-}	0.28
Salinity	4.07^{-}	0.22	0.64	6.10^{+}	20.94^{-}
Oxygen	55.17^{+}	39.62^{+}	29.75^{+}	18.93^{+}	26.27^{+}
pH	130.66^{+}	155.71^{+}	110.81^{+}	38.94^{+}	71.08^{+}
Eh	182.37^{+}	136.34^{+}	108.64^{+}	38.74^{+}	73.90^{+}
NH_3	112.61^{-}	89.91^{-}	74.87^{-}	23.52^{-}	50.86^{-}
PO_4	26.66^{-}	19.75^{-}	15.44^{-}	4.88^{-}	15.60^{-}
Si	132.61^{-}	113.69^{-}	84.40^{-}	34.70^{-}	48.41^{-}
NO_2	20.84^{+}	23.28^{+}	25.01^{+}	8.70^{+}	34.35^{+}
$NO_2 + NO_3$	4.76^{+}	7.98^{+}	2.38	9.00^{+}	0.24

NO_3 are contributors according to the multiple regression analysis. As with most of the other taxa the F-ratio and R^2 for the multiple regression at the bare surface and grass surface are much smaller than at the grass surface and 10 cm (Tables 15 and 29).

Comparison of Analyses

For the three most abundant taxa, *Quinqueloculina, Elphidium,* and *Ammonia,* the difference in overall densities at the bare surface and grass surface stations is not significant. In contrast, at the grass surface and 10 cm the differences in overall density for all taxa are significant. This is not at all surprising. The "living zone" for foraminifera in this area was previously determined to be about 6 or 7 cm (Buzas, 1977). Clearly, a depth of 10 cm in this area is an inhospitable environment for foraminifera, and the observed living individuals may be due to haphazard excursions or to bioturbation by other organisms (Severin et al., 1982; Severin, 1987; Wetmore, 1988). The statistical analyses of the GLM for the grass surface and 10 cm confirm what is abundantly clear by glancing at the plots of densities at the grass surface and at 10 cm (Figures 28-32).

TABLE 21.—Regression of *Quinqueloculina* and principal components for grass surface and 10 cm.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.66$
Constant	3.00	0.11	26.61	0.00	
PC1	−1.70	0.11	−14.91	0.00	
PC2	−0.02	0.11	−0.13	0.90	
PC3	0.69	0.11	6.04	0.00	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	446.03	3	148.68	86.26	0.00
Residual	227.50	132	1.72		

In both comparisons hypotheses for periodicity are significant for all taxa except *Bolivina* at the bare surface and grass surface. Except for the aforementioned case, the periodicites differ (interaction hypotheses) for all taxa between the areas being compared. At the surface stations there was a spring maximum at the bare station which was not observed at the grass station where maximum densities occurred in summer. Densities were very low at 10 cm, but nevertheless, the significance of the interaction hypotheses indicates no synchronization between the surface and 10 cm.

Two-way ANOVA's on 10 environmental variables indicate that at the bare surface and grass surface most of these differ significantly with time while at the grass surface and 10 cm with depth. The analyses of both GLMs indicate that the environmental variables are significant for all taxa. The environmental variables are highly correlated so that the significance of any one is difficult to determine. In general, oxygen, pH, and Eh are positively correlated with one another, and negatively with NH_3. Principal component analyses on both data sets indicate that the first three PC's account for all of the variables. Multiple regression of the first three PC's and densities of taxa indicate higher F-ratios and R^2 for the grass surface and 10 cm analysis. In this analysis, PC1 and PC3 are always significant, and all three are for *Bolivina.* On the other hand, for the bare surface and grass surface PC1 and PC2 are significant for *Elphidium* and *Ammobaculites,* and PC1 and PC3 for *Quinqueloculina.* Although these PC's also account for most of the variables and are significant, the strength of the regression relationship as judged by R^2 and F-ratios are much smaller. For *Bolivina* only the F-ratio for PC2 is significant and salinity contributes heavily to this PC. This species also has a very high F-ratio for salinity on simple regression and is further identified as a significant $\hat{\beta}$ in the ω model. At the bare surface and grass surface only PC3 (accounting for 14% of the variability) is significant for *Ammonia.* NO_2 is the largest contributor to this PC, and like salinity for *Bolivina,* is also identified by simple regression and in the ω model.

Thus, no simple relationship between one or two environmental variables and density emerges. In both analyses oxygen, pH, and Eh are contrasted with NH_3, and in the grass surface and 10 cm NO_2 is added to the former and PO_4 and Si to the latter. Except for *Bolivina,* the most commonly considered variables, temperature and salinity, have little involvement, and any attempt to predict faunal densities from them is futile. The very large change in density between the surface and 10 cm, perhaps, equivalent to a faunal change, is much more strongly related to the environmental variables than the smaller significant change with time at the surface sites.

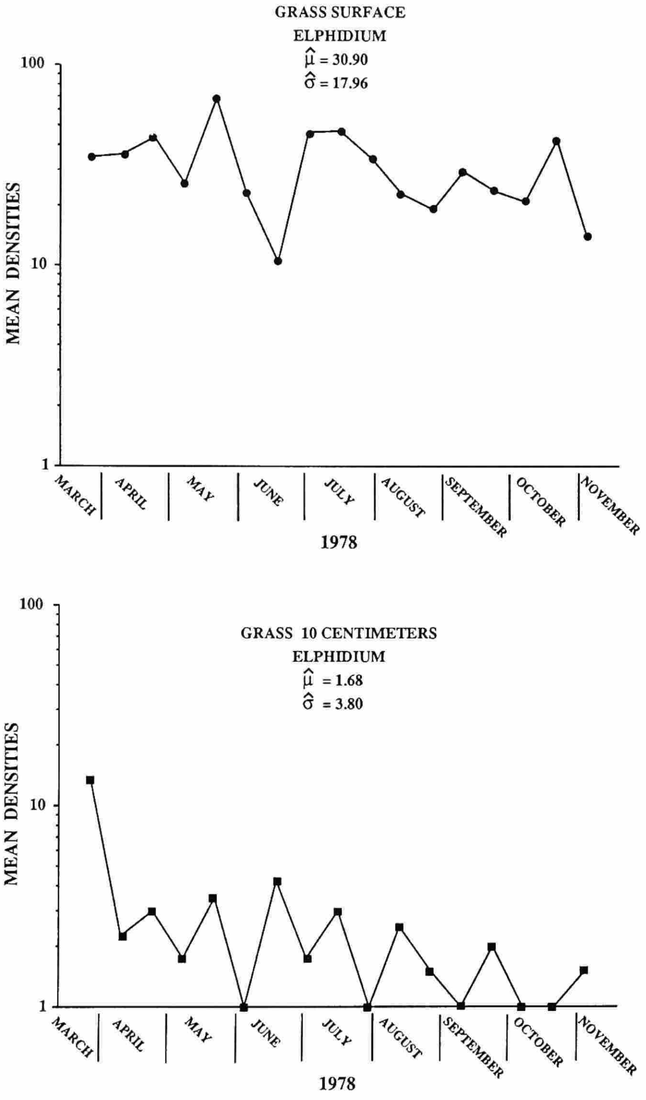

FIGURE 29.—Mean number of individuals of *Elphidium* per 5 ml of sediment (density).

TABLE 22.—Statistical analysis of GLM for *Elphidium* for grass surface and 10 cm.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Depth	20.79	1	20.79	54.29	0.00
$\pi/3$ periodicity and interaction	6.49	4	1.62	4.23	0.00
$\pi/6$ periodicity and interaction	1.57	4	0.39	1.02	0.40
$\pi/3$ interaction	5.63	2	2.82	7.35	0.00
$\pi/6$ interaction	1.07	2	0.53	1.39	0.25
Environmental variables	15.05	10	1.50	3.93	0.00
Residual	44.39	116	0.38		

TABLE 23.—Regression of *Elphidium* and principal components for grass surface and 10 cm.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.64$
Constant	1.94	0.08	24.20	0.00	
PC1	−1.11	0.08	−13.65	0.00	
PC2	0.17	0.08	2.13	0.04	
PC3	0.51	0.08	6.25	0.00	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	200.81	3	66.94	76.62	0.00
Residual	115.32	132	0.87		

Comparison with Other Studies

Quinqueloculina is the most abundant taxon making up about 75% of the total living foraminifera at the surface stations. The fortnightly observations of mean densities from March until November, 1978, exhibit a pronounced periodicity. The differences between maxima and minima densities are two orders of magnitude at both stations. At the grass station the maximum was recorded in summer and at the bare station in spring. In Aransas Bay, Texas, Phleger and Lankford (1957) also observed a summer maximum for *Quinqueloculina*. Jones and Ross (1979) found *Quinqueloculina* only during the summer months in Samish Bay, Washington. The temperature regimes in Aransas Bay (19°–30°C) and in the Indian River (22°–32°C) are similar. However, the waters of Samish Bay are much colder (5°–20°C), and the maximum at Samish Bay is the equivalent to the minimum at the other two areas.

Elphidium is the second most abundant taxon comprising about 14% of the total number of living individuals at the two surface stations. The genus is composed mainly of *E. mexicanum* and *E. gunteri*. This taxon did not have significant differences between stations, but did exhibit a $\pi/3$ periodicity and interaction. Maxima occurred at the bare surface in early spring and at the grass surface in early summer. The spring maximum at the bare surface was much larger than at the grass surface. A number of researchers have demonstrated through observation of juveniles and density changes that *E. excavatum* reproduces all year round, often at different rates with maxima

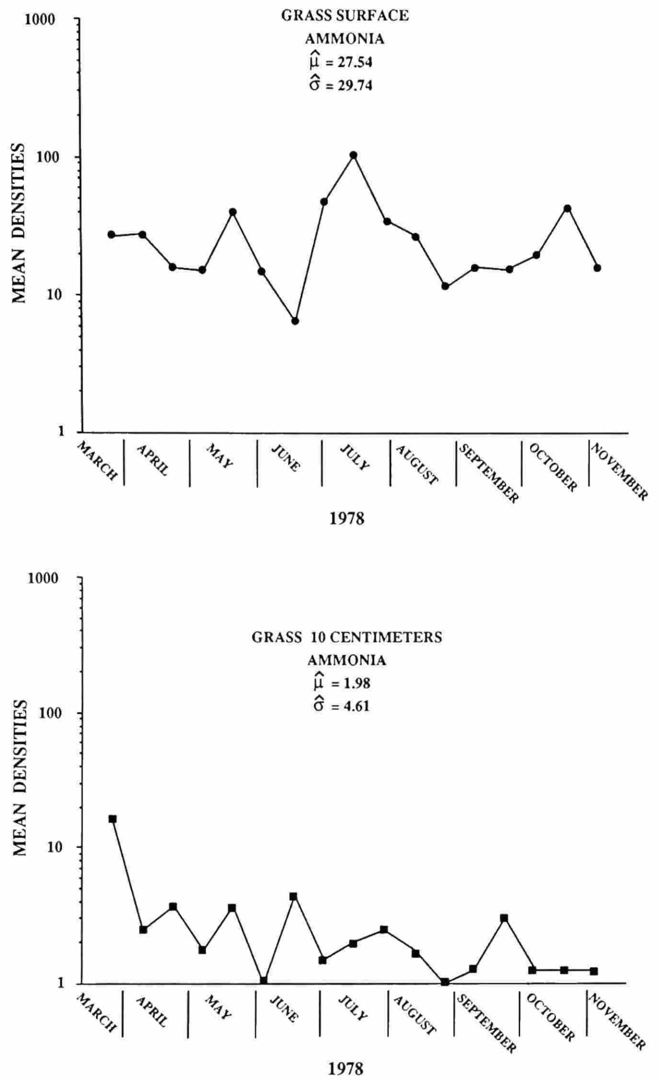

FIGURE 30.—Mean number of individuals of *Ammonia* per 5 ml of sediment (density).

TABLE 24.—Statistical analysis of GLM for *Ammonia* for grass surface and 10 cm.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Depth	11.13	1	11.13	23.89	0.00
π/3 periodicity and interaction	11.75	4	2.94	6.31	0.00
π/6 periodicity and interaction	4.35	4	1.09	2.33	0.06
π/3 interaction	7.58	2	3.79	8.14	0.00
π/6 interaction	2.34	2	1.17	2.50	0.09
Environmental variables	15.07	10	1.51	3.24	0.00
Residual	54.05	116	0.47		

TABLE 25.—Regression of *Ammonia* and principal components for grass surface and 10 cm.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.52$
Constant	1.85	0.08	21.65	0.00	
PC1	−0.96	0.09	−11.04	0.00	
PC2	0.08	0.09	0.93	0.36	
PC3	0.41	0.09	4.73	0.00	

Analysis of variance

Source	Sum of squares	df	Mean square	F-ratio	P
Regression	143.94	3	47.98	48.40	0.00
Residual	130.85	132	0.99		

varying from year to year (Buzas, 1965, 1969; Haake, 1967; Haman, 1969; Wefer, 1976). Other species of this genus follow a similar pattern (Boltovskoy and Lena, 1969). The different timing between stations (interaction) observed here was also observed by Buzas (1969) in the Choptank River, Maryland. Thus, the results of the present study are in accord with earlier observations.

The environmental variables for *Elphidium* were significant as a group. Simple regressions on individual variables were highest for salinity and pH, however, the first two PC's proved significant and they account for all the variables except NO_2. Buzas (1969) using a similar analysis concluded the environmental variables were significant as a group as did Wefer (1976).

Ammonia, consisting of *A. beccarii* (most of the individuals belong to the form called *tepida*), constitutes about 8% of the total living population at the bare and grass surface stations. More information is available for this species than any other, much of which is summarized by Walton and Sloan (1990). In this study, *A. beccarii* showed a π/3 periodicity with interaction. The bare surface had maxima in spring, summer, and fall while the grass surface had maximum densities in summer. This species also exhibited periodicity in the Choptank River, Maryland (Buzas, 1969), Texas Bays (Phleger and Lankford, 1957), Samish Bay, Washington (Jones and Ross, 1979), and Puerto Deseado (Boltovskoy and Lena, 1969). As in this study, Phleger and Lankford (1957) and Buzas (1969) reported different densities with time between stations, while Boltovskoy and Lena (1969) between years. On the other hand, in Narragansett Bay, Rhode Island, Brooks (1967) found

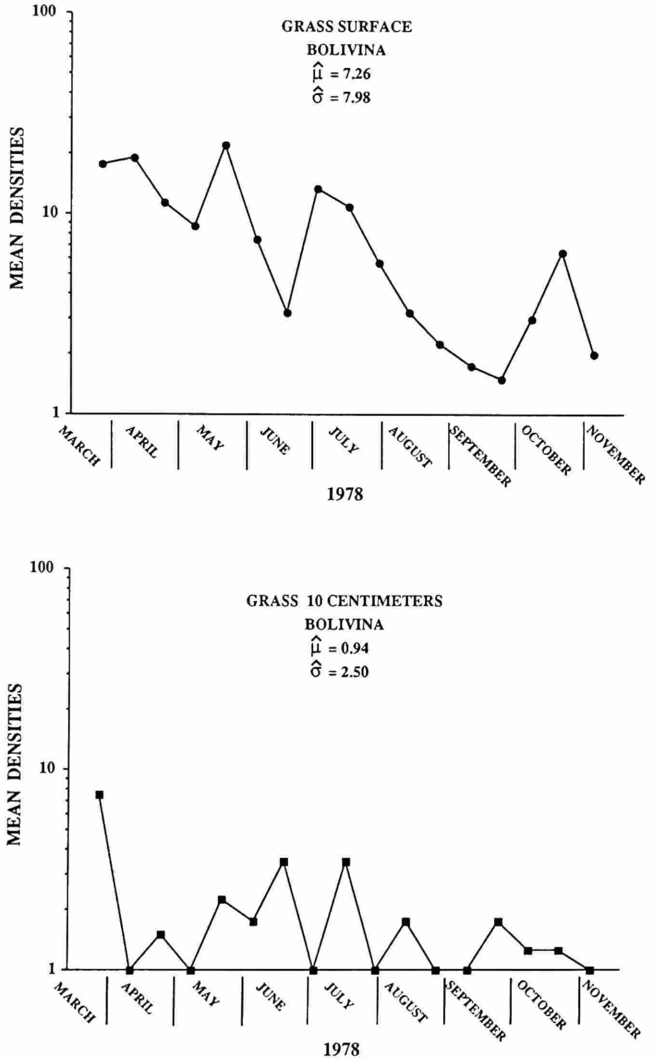

FIGURE 31.—Mean number of individuals of *Bolivina* per 5 ml of sediment (density).

TABLE 26.—Statistical analysis of GLM for *Bolivina* for grass surface and 10 cm.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Depth	6.70	1	6.70	11.05	0.00
π/3 periodicity and interaction	4.84	4	1.21	2.00	0.10
π/6 periodicity and interaction	6.27	4	1.57	2.59	0.04
π/3 interaction	4.63	2	2.31	3.82	0.02
π/6 interaction	0.04	2	0.02	0.03	0.97
Environmental variables	24.25	10	2.42	4.00	0.00
Residual	70.25	116	0.61		

TABLE 27.—Regression of *Bolivina* and principal components for grass surface and 10 cm.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.33$
Constant	0.99	0.08	12.75	0.00	
PC1	−0.51	0.08	−6.52	0.00	
PC2	0.29	0.08	3.72	0.00	
PC3	0.22	0.08	2.81	0.01	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	52.24	3	17.41	21.40	0.00
Residual	107.38	132	0.81		

no difference in densities between monthly sampling during 1963, and, likewise, Buzas et al. (1977) found no difference in densities between monthly sampling during 1969–1970 in Jamaica. Most authors agree that reproduction takes place throughout the year. Given enough data, it seems likely that a particular station could show periodicity in some years, and not in others, while a nearby station might behave in an altogether different manner.

In the present study of *Ammonia*, analysis by the GLM showed that the environmental variables were significant as a group. Simple regressions on density vs. individual environmental variables indicated that only salinity and NO_2 were significant. Regression analysis on the PC's indicated that only the third PC accounting for 14% of the variability in the environmental variables was significant. The largest factor score coefficients for PC3 are NO_2, Si, and temperature. Interestingly, the sign of the simple regression coefficient for temperature, although not significant, was negative. In the Choptank River, Maryland, Buzas (1969) found the group of measured environmental variables were significant for *Ammonia*; however, in Jamaica, they were not (Buzas et al., 1977). The laboratory work of Bradshaw (1961) and Schnitker (1974) indicate a temperature of at least 17°–22°C is required for reproduction (Walton and Sloan, 1990, give an extensive discussion). The temperatures in Jamaica and in the present study are always above these limits. In the Choptank River, however, the temperature is below 15°C for 7 months of the year (Buzas, 1969), and *Ammonia* exhibits significant increases in density during this period. In Narragansett Bay where temperatures vary from 0°–20°C, Brooks (1967) found no

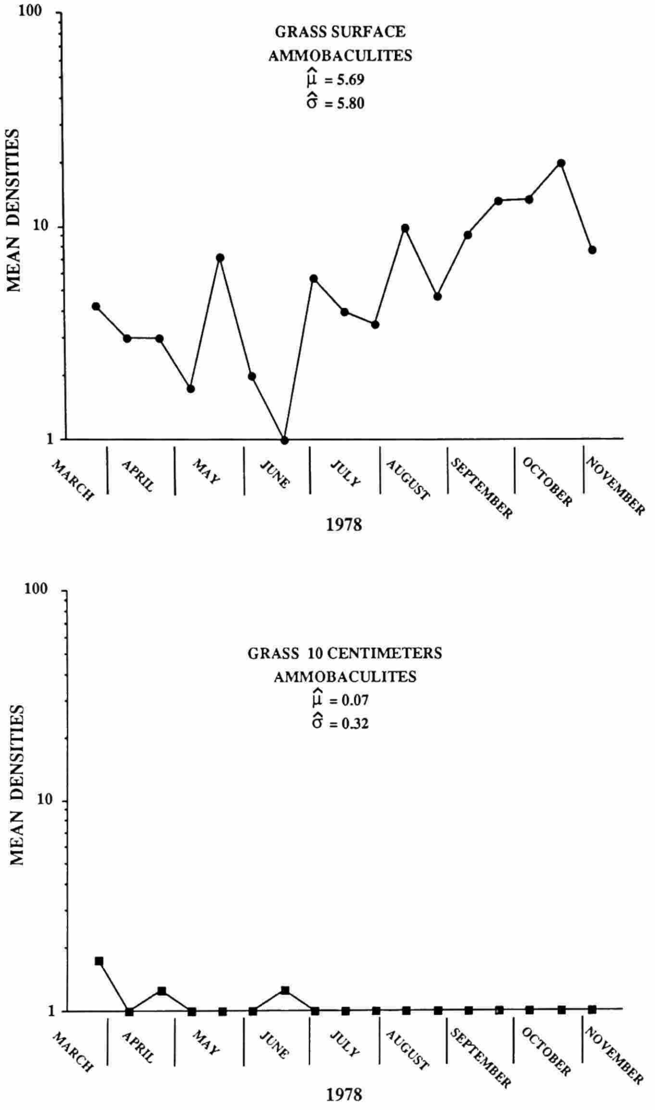

FIGURE 32.—Mean number of individuals of *Ammobaculites* per 5 ml of sediment (density).

TABLE 28.—Statistical analysis of GLM for *Ammobaculites* for grass surface and 10 cm.

Variability on account of	Sum of squares	df	Mean square	F	p(F)
Depth	5.77	1	5.77	21.62	0.00
$\pi/3$ periodicity and interaction	2.83	4	0.71	2.65	0.04
$\pi/6$ periodicity and interaction	9.98	4	2.49	9.34	0.00
$\pi/3$ interaction	0.63	2	0.32	1.19	0.31
$\pi/6$ interaction	2.51	2	1.25	4.69	0.01
Environmental variables	20.44	10	2.04	7.65	0.00
Residual	30.91	116	0.27		

TABLE 29.—Regression of *Ammobaculites* and principal components for grass surface and 10 cm.

Variable	Coefficient	Standard error	t	P(2 tail)	$R^2 = 0.42$
Constant	0.78	0.07	11.78	0.00	
PC1	−0.62	0.07	−9.22	0.00	
PC2	−0.11	0.07	−1.66	0.10	
PC3	0.17	0.07	2.50	0.01	

	Analysis of variance				
Source	Sum of squares	df	Mean square	F-ratio	P
Regression	55.59	3	18.53	31.34	0.00
Residual	78.05	132	0.59		

significant difference in density with time over the period of a year. Both of these authors sampled with replicates to offset the variation inherent because of spatial distribution. In Puerto Deseado, Argentina, Boltovskoy (1964) and Boltovskoy and Lena (1969) report, through observations of juveniles, continuous reproduction of this species where the maximum temperature is only 15°C. These observations suggest to us that populations of *A. beccarii* can adjust to lower temperatures for reproduction than were observed in the laboratory. The alternative suggested by Walton and Sloan (1990) is that seasonal trends may be an artifact due to the sampling of patchy distributions. We believe the replication and use of independent hypotheses through the analysis of variance technique (Brooks, 1967; Buzas, 1969) and observations of juveniles (Boltovskoy, 1964) make this conclusion unlikely.

Bolivina, consisting mainly of *B. striatula*, makes up about 1% of the total living population. The mean number of individuals at the grass station was about 7 and at the bare station 3, which was statistically significantly different. At both stations there appears an overall decrease in density during the sampling period. However, none of the hypotheses for periodicity in the GLM were significant. In Jamaica (Buzas et al., 1977), *B. striatula* was the most abundant species and it did exhibit an overall periodicity, even though most of the species analyzed in that study did not. No other data are available. Perhaps, as more data becomes available, this species will exhibit the same unpredictable behavior cited above for *Ammonia*.

In the GLM for *Bolivina* the environmental variables are significant as a group. Simple regressions indicate salinity, PO_4, Si, and $NO_2 + NO_3$ are significant. Multiple regression of densities and PC's found only PC2 significant and the factor score coefficients indicate these same variables are the main components of PC2. Buzas et al. (1977) found no statistical relationship between environmental variables and densities for this species in Jamaica.

Ammobaculites, consisting mainly of *A. exiguus,* makes up about 1% of the total living population. At the grass surface the mean density is about 6 and at the bare surface 1, which is statistically significantly different. The $\pi/3$ overall periodicity and interaction hypotheses are also significant. At the grass surface there is an increasing trend in density during the sampling period while at the bare surface a spring maximum is followed by very low densities during the sampling period. In the Choptank River, Maryland, Buzas (1969) also found a $\pi/3$ overall periodicity and interaction hypotheses significant for this species. Maximum densities occurred in all seasons. Based on size distribution histograms which showed mixed age groups throughout the year, Phleger and Lankford (1957) also concluded that *A. salsus* (probably the same or a closely related species) reproduced during all seasons of the year.

The null hypothesis for the environmental variables in the GLM for *Ammobaculites* was rejected. Simple regressions on density and individual environmental variables indicated temperature, salinity, oxygen, and NH_3 were significant. Regression analyses of density and the PC's indicated PC1 and PC2 were significant. These two components account for all the variables except NO_2. Buzas (1969) also found the environmental variables were significant for this species in the Choptank River, Maryland.

The life cycle of some foraminifera such as *Elphidium crispum* and *Glabratella ornatissima* produces a marked yearly (often spring and summer) increase in density (Myers, 1942; Erskian and Lipps, 1987). The majority of species such as those studied here apparently reproduce continuously, although they need not do so at the same rate. The interplay of life cycle behavioral characteristics and environmental variables may be more favorable at some particular times than at others. Furthermore, predation severely depletes foraminiferal densities (Buzas, 1978), and differential predation may decrease density at a particular location. Indeed, the density of potential predators often varies from season to season and year to year (Young et al., 1976). On the other hand, these causes of density regulation may offset each other and the same species may sometimes not exhibit periodicity. The observations of various researchers cited above for *Ammonia* which sometimes shows periodicity and sometimes not is best explained in this fashion.

Appendix 1

Bare Surface

Number of individuals per 5 ml of sediment.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
27 Mar	712	140	30	2	4	890
	1154	395	95	9	3	1661
	598	194	71	1	6	873
	2232	900	123	10	19	3304
10 Apr	1815	229	53	12	3	2112
	2683	606	111	18	8	3434
	2537	411	75	7	7	3038
	2021	328	55	13	11	2434
24 Apr	412	118	26	5	2	566
	404	118	25	7	1	558
	514	86	32	1	1	634
	482	94	36	1	1	615
8 May	499	78	20	3	1	604
	275	38	24	4	1	342
	280	101	22	6	2	419
	221	36	18	5	0	283
22 May	81	50	11	1	0	148
	94	45	31	8	2	185
	91	38	9	2	0	140
	29	9	26	2	0	68
5 Jun	150	24	22	9	1	220
	307	35	39	9	1	398
	78	48	20	3	0	151
	82	50	25	2	0	162
19 Jun	44	45	28	3	0	125
	47	45	44	7	0	156
	30	38	26	8	0	106
	155	51	51	9	0	279
3 Jul	97	35	70	3	0	208
	108	50	84	6	0	251
	92	30	30	5	1	167
	138	33	82	7	0	265
17 Jul	38	78	41	3	1	167
	41	12	31	1	0	91
	56	20	25	2	0	106
	90	28	29	8	1	163
31 Jul	290	32	13	6	1	351
	231	15	26	2	0	279
	175	23	11	3	2	215
	187	14	23	3	1	235
14 Aug	109	18	22	0	0	155
	261	27	18	1	2	312
	98	34	21	1	0	155
	164	24	26	1	0	220

Appendix 1.—Continued.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
28 Aug	44	11	6	1	0	64
	53	12	16	0	0	86
	93	14	8	1	1	118
	65	14	3	0	2	85
11 Sep	102	6	11	0	0	121
	137	24	11	1	0	174
	51	20	26	0	0	101
	73	24	29	1	4	131
25 Sep	59	37	16	0	1	118
	86	19	11	0	0	119
	41	22	15	2	0	82
	82	10	11	0	1	104
9 Oct	27	15	8	0	2	53
	55	14	3	0	0	72
	27	7	1	1	0	38
	46	6	14	2	1	79
23 Oct	253	77	120	0	0	451
	70	9	14	0	0	93
	233	44	28	1	0	306
	104	24	18	0	0	146
6 Nov	77	29	22	0	0	129
	69	27	41	0	1	138
	82	44	55	0	0	182
	213	165	129	1	0	508

Appendix 2

Grass Surface

Number of individuals per 5 ml of sediment.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
27 Mar	70	20	24	19	1	151
	95	28	24	13	1	166
	140	29	38	24	9	269
	136	58	17	11	2	233
10 Apr	301	49	35	8	5	411
	189	27	22	20	1	273
	137	38	29	28	0	251
	85	25	21	16	2	154
24 Apr	213	41	16	22	2	305
	98	43	9	8	0	163
	260	46	15	5	2	335
	145	40	19	7	4	224
8 May	77	14	15	7	2	122
	97	26	7	11	0	147
	103	29	18	6	1	164
	129	30	17	7	0	190
22 May	156	72	54	33	11	365
	132	68	39	21	6	283
	126	77	47	31	6	297
	115	55	15	0	2	187
5 Jun	80	26	10	9	1	137
	30	7	9	1	0	47
	113	34	24	13	3	197
	40	21	9	3	0	91
19 Jun	52	7	3	2	0	69
	63	8	7	4	0	87
	55	11	4	0	0	73
	18	12	8	3	0	42
3 Jul	91	59	40	14	3	216
	202	39	55	11	2	315
	79	40	33	7	10	176
	111	44	60	18	4	246
17 Jul	1063	30	55	10	2	1164
	1018	33	73	5	2	1151
	2163	83	222	14	7	2507
	1412	38	58	11	1	1534
31 Jul	427	26	20	5	3	502
	467	28	24	9	2	540
	524	30	17	3	4	605
	624	49	79	2	1	767
14 Aug	715	23	46	3	18	828
	526	25	15	1	5	592
	399	21	19	2	6	448
	783	19	26	3	7	849

Appendix 2.—Continued.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
28 Aug	163	19	14	0	5	208
	196	17	10	2	2	248
	196	3	14	1	2	221
	185	33	4	2	6	247
11 Sep	117	31	11	1	12	178
	77	24	11	1	11	128
	76	18	20	0	4	127
	95	41	19	1	6	164
25 Sep	208	24	18	0	16	270
	162	29	3	0	17	217
	131	18	22	0	9	187
	199	20	15	2	7	255
9 Oct	152	33	27	3	16	239
	159	19	25	5	16	227
	145	17	19	0	10	207
	67	10	4	0	8	108
23 Oct	224	25	30	7	22	329
	304	81	56	5	18	480
	197	34	54	3	19	321
	238	25	37	7	16	336
6 Nov	115	20	33	2	14	208
	19	17	19	0	1	57
	17	6	6	0	3	39
	17	9	5	2	9	55

Appendix 3

Grass 10 cm

Number of individuals per 5 ml of sediment.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
27 Mar	2	1	2	0	0	5
	27	7	14	4	0	53
	9	18	15	5	2	54
	22	24	32	17	1	100
10 Apr	5	0	1	0	0	6
	2	0	2	0	0	4
	1	3	1	0	0	5
	6	2	2	0	0	11
24 Apr	5	4	7	2	0	20
	0	0	2	0	1	4
	5	4	0	0	0	10
	0	0	2	0	0	3
8 May	0	1	2	0	0	3
	1	1	0	0	0	2
	3	1	0	0	0	4
	1	0	1	0	0	2
22 May	3	2	1	0	0	8
	1	1	5	4	0	11
	11	3	0	1	0	16
	5	4	5	0	0	16
5 Jun	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	3	0	4
	1	0	0	0	0	1
19 Jun	14	6	5	4	0	29
	3	3	4	5	0	15
	0	0	1	0	0	1
	4	4	4	1	1	15
3 Jul	0	0	0	0	0	0
	1	0	0	0	0	1
	1	0	1	0	0	2
	0	3	1	0	0	4
17 Jul	0	1	0	0	0	2
	1	0	2	3	0	7
	2	2	0	0	0	5
	4	5	2	7	0	19
31 Jul	1	0	3	0	0	4
	4	0	1	0	0	5
	4	0	1	0	0	5
	2	0	1	0	0	3
14 Aug	1	1	1	0	0	4
	1	1	0	0	0	2
	2	1	0	0	0	3
	3	3	2	3	0	11

Appendix 3.—Continued.

Date (1978)	*Quinqueloculina*	*Elphidium*	*Ammonia*	*Bolivina*	*Ammobaculites*	Total
28 Aug	1	0	0	0	0	1
	1	0	0	0	0	1
	1	1	0	0	0	2
	0	1	0	0	0	1
11 Sep	0	0	0	0	0	0
	0	0	1	0	0	1
	0	0	0	0	0	0
	0	0	0	0	0	0
25 Sep	2	1	1	0	0	4
	5	3	2	3	0	13
	2	0	5	0	0	7
	0	0	0	0	0	0
9 Oct	2	0	0	0	0	2
	0	0	0	0	0	0
	7	0	1	1	0	9
	1	0	0	0	0	1
23 Oct	0	0	0	0	0	0
	0	0	0	0	0	1
	1	0	0	0	0	1
	0	0	1	1	0	3
6 Nov	2	0	1	0	0	3
	2	0	0	0	0	2
	6	0	0	0	0	6
	20	2	0	0	0	22

Appendix 4

Bare Surface

Pore water chemistry.

Date (1978)	Temperature	Salinity	Oxygen	pH	Eh	NH_3	PO_4	Si	NO_2	$NO_2 + NO_3$
27 Mar	24.5	32.0	7.4	8.63	31	0.1425	0.7354	13.3037	0.0721	4.3109
10 Apr	26.5	32.5	9.1	8.70	85	0.0920	0.2202	26.7167	0.0609	3.0221
24 Apr	23.5	32.5	10.2	8.75	30	0.1149	0.0320	7.1574	0.0113	4.9155
8 May	27.0	31.5	0.4	7.50	−208	0.1204	0.5373	11.5527	0.0218	27.1770
22 May	28.3	39.0	1.8	8.30	−70	21.2810	0.0412	49.3007	0.0229	3.8981
5 Jun	32.0	35.0	0.6	7.50	−151	95.9300	0.8373	70.7123	0.3944	4.5691
19 Jun	27.0	33.0	5.1	8.10	184	2.1058	0.0560	29.4110	0.3152	3.3008
3 Jul	30.0	32.0	0.4	7.55	−187	65.8357	1.1206	32.1760	0.3722	47.3260
17 Jul	31.0	30.5	3.3	7.50	47	1.4197	0.0524	68.8000	0.3134	0.1385
31 Jul	30.0	28.0	4.4	8.30	−90	0.1717	0.1915	55.7310	0.2811	1.3133
14 Aug	31.0	20.0	2.3	8.08	−28	21.3100	1.6034	51.5230	0.2359	0.5315
28 Aug	30.5	26.0	2.4	8.21	−34	0.1721	0.5327	0.0000	0.0224	0.0622
11 Sep	30.5	28.0	3.4	8.06	−46	1.8610	2.2904	104.0400	0.0215	0.0668
25 Sep	29.5	26.0	5.4	8.12	−30	0.1638	16.4580	66.4087	0.0225	0.1841
9 Oct	24.0	25.5	6.0	7.97	50	0.1790	0.0742	133.5466	0.0218	0.0844
23 Oct	24.0	26.0	5.3	8.00	44	1.2926	0.4990	105.5033	0.3724	0.6684
6 Nov	23.0	27.0	4.9	8.35	55	3.1530	1.8657	69.4803	0.6236	1.8702

Appendix 5

Grass Surface

Pore water chemistry.

Date (1978)	Temperature	Salinity	Oxygen	pH	Eh	NH_3	PO_4	Si	NO_2	$NO_2 + NO_3$
27 Mar	22.0	32.5	4.9	8.03	−4	0.1425	0.8665	13.7943	0.0549	20.8870
10 Apr	24.5	31.0	7.6	8.25	105	0.0920	0.1329	22.6467	0.0535	3.2316
24 Apr	22.8	33.0	7.3	8.35	7	0.9383	0.1563	12.0900	0.2704	275.4266
8 May	27.0	31.0	4.2	8.00	−56	0.1204	0.0391	14.7607	0.0218	5.3229
22 May	26.5	33.0	3.6	8.15	−67	7.8668	0.0412	32.5660	0.0229	10.0146
5 Jun	29.0	31.0	4.1	7.60	−128	33.7027	0.3404	50.9217	0.1105	2.2312
19 Jun	25.2	32.0	5.6	8.00	185	0.1486	0.0560	1.3497	0.1303	1.2319
3 Jul	29.5	29.0	0.5	7.50	−115	5.5559	0.4846	69.2380	0.2146	1.5599
17 Jul	28.0	28.0	4.1	7.74	38	0.0000	0.0000	70.8490	0.0313	0.0000
31 Jul	29.0	31.0	3.6	8.08	−50	4.6810	0.4182	43.1990	0.1782	0.0000
14 Aug	30.0	22.0	2.1	8.17	−47	6.9164	0.9911	16.9515	0.1416	0.0639
28 Aug	31.0	26.0	3.0	8.21	−12	0.1721	0.3936	0.0000	0.0224	0.1458
11 Sep	29.5	25.5	2.8	8.03	−33	2.9416	1.1962	98.0553	0.0215	0.0668
25 Sep	28.5	25.5	5.4	8.16	−37	0.3979	0.4561	72.2520	0.0225	0.0676
9 Oct	23.5	24.5	5.3	7.72	52	0.1790	0.5758	138.5800	0.0218	0.0844
23 Oct	23.3	28.0	5.9	8.00	43	4.6589	0.7639	106.3733	0.5176	1.4438
6 Nov	23.0	26.5	6.0	8.19	50	4.2475	2.2476	68.6020	0.5030	1.7514

Appendix 6

Grass 10 cm

Pore water chemistry.

Date (1978)	Temperature	Salinity	Oxygen	pH	Eh	NH_3	PO_4	Si	NO_2	$NO_2 + NO_3$
27 Mar	24.2	27.0	0.0	7.71	−196	96.2270	12.2930	241.4466	0.0095	0.0475
10 Apr	23.8	30.7	0.0	7.67	−235	0.0000	0.0000	0.0000	0.0000	0.0000
24 Apr	23.5	33.0	0.0	7.60	−232	285.6600	28.0770	440.2833	0.0113	0.0382
8 May	27.2	33.5	0.0	7.30	−286	312.6400	26.0440	583.6932	0.0218	0.0589
22 May	27.2	34.5	0.0	7.45	−289	463.4599	29.3460	515.6699	0.0229	0.0540
5 Jun	28.5	33.5	0.0	7.50	−307	836.8533	51.8203	688.2266	0.0254	2.2813
19 Jun	25.5	32.5	0.0	7.60	−331	929.6766	32.1800	659.5033	0.0230	2.2518
3 Jul	36.2	32.0	0.0	7.52	−312	745.4833	70.4513	616.1066	0.0235	1.4169
17 Jul	27.7	30.5	0.0	7.35	−282	518.7266	46.8573	572.8933	0.0313	0.1127
31 Jul	27.8	30.5	0.0	7.44	−288	387.2833	36.5710	559.7299	0.0282	0.0800
14 Aug	21.0	24.0	0.0	7.62	−223	198.0666	19.7187	553.3200	0.0209	0.5521
28 Aug	30.0	26.5	0.0	7.46	−223	233.1100	13.1470	0.0000	0.0224	0.3995
11 Sep	31.0	27.5	0.0	7.49	−227	417.0299	25.0397	917.0634	0.0215	0.0668
25 Sep	29.0	27.5	5.4	7.49	−225	470.0866	26.2023	785.4966	0.0225	0.2034
9 Oct	24.0	26.0	5.3	7.35	−199	240.5966	12.2607	461.1333	0.1000	0.0844
23 Oct	26.5	27.3	4.7	7.04	−33	0.0000	0.0000	0.0000	0.0000	0.0000
6 Nov	23.5	27.0	6.0	6.57	−176	187.9799	22.9157	324.8800	0.0232	0.0817

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