

Gulf Research Reports

Volume 7 | Issue 3

January 1983

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DOI: 10.18785/grr.0703.07

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Recommended Citation

Maples, R. S. 1983. Community Structure of Diatoms Epiphytic on Pneumatophores of the Black Mangrove, *Avicennia germinans*, in a Louisiana Salt Marsh. *Gulf Research Reports* 7 (3): 255-259.

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COMMUNITY STRUCTURE OF DIATOMS EPIPHYTIC ON PNEUMATOPHORES OF THE BLACK MANGROVE, *AVICENNIA GERMINANS*, IN A LOUISIANA SALT MARSH

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ABSTRACT The taxonomy, diversity, and similarity of diatom assemblages epiphytic on pneumatophores of black mangrove, *Avicennia germinans* (L.) L., in southeastern Louisiana were investigated. A total of 109 taxa representing 27 genera were identified in samples from five sites. The most abundant taxa were *Nitzschia brittonii* Hagelstein, *Nitz. frustulum* (Kütz.) Grun., *Navicula diserta* Hust., *Denticula subtilis* Grun., and *Amphora tenuissima* Hust. Comparisons with previous studies indicate that the diatom flora epiphytic on *A. germinans* in this study is much more characteristic of temperate salt marshes than of subtropical mangrove communities.

INTRODUCTION

Studies of edaphic and epiphytic diatom assemblages of coastal Louisiana have been few. Maples and Watson (1979) reported several genera of edaphic diatoms associated with salt pannes and surrounding angiosperm zones. Stowe (1980, 1982) investigated the vertical distribution of epiphytic diatoms on the culms of *Spartina alterniflora* Loisel. Cook and Whipple (1982) described the spatial and temporal distribution of edaphic diatom communities along a complex gradient from brackish to saline marshland. However, mangroves have not been previously sampled for epiphytic diatoms in Louisiana or from the Gulf coast of any other state.

The study of Navarro (1982) (Indian River, Florida) is the only report of diatoms epiphytic on mangroves in the continental United States. Outside the continental United States mangrove diatoms have been collected by Hagelstein (1938) in Puerto Rico, Reyes-Vásquez (1975) in Venezuela, Foged (1979) in New Zealand, and Sullivan (1981) from Bimini Harbor, Bahamas. The purpose of this investigation was to study the taxonomy, diversity and similarity of benthic diatom assemblages associated with the pneumatophores of the black mangrove, *Avicennia germinans* (L.) L., in Louisiana.

Description of study area

A. germinans has been observed in coastal Louisiana since the 1800's (Moldenke 1960). Present distribution is along canals and roadside ditches in the salt marshes of southeastern Louisiana.

Collections were made from five sites in two coastal salt marshes. Sites A, B, and C were near Fourchon City, Louisiana (Table 1). These sites were intertidal on a canal system connecting Bay Champagne to Bayou LaFourche. The ambient salinity was 25 ppt. Major angiosperm species associated with these sites were *Iva frutescens* L., *Distichlis spicata* (L.) Greene, and *Spartina alterniflora*. Sites D and E were along roadside ditches located on Grand Isle (Table 1) and

not subject to tidal fluctuations. Salinity at site D was 15 ppt; and at site E, 22 ppt. The major associated angiosperm species were *S. alterniflora*, *D. spicata*, *Salicornia bigelovii* Torr., and *Suaeda linearis* (Eli.) Moq.

TABLE 1.
Location of study sites in two salt marshes of southeastern Louisiana.

Site	Longitude	Latitude
A	90° 11.3'	29° 06.9'
B	90° 10.5'	29° 07.2'
C	90° 10.2'	29° 07.4'
D	89° 59.4'	29° 13.8'
E	89° 59.6'	29° 14.2'

MATERIALS AND METHODS

Epiphytic diatoms were collected from *A. germinans* on February 20, 1982. A representative composite sample was collected at each site by scraping several exposed pneumatophores with a knife. Water column salinities were measured in the field with an A&O refractometer.

Each of the five composite samples was boiled first in HCl then boiled in HNO₃ with K₂Cr₂O₇ to oxidize all organic matter. A portion of each sample was mounted in Hyrax for identification and counting of diatoms with a Leitz Dialux 20EB light microscope. A sample consisted of exactly 500 valves from five counts of 100 valves where each count was made from a separate slide prepared from the composite sample. After each sample had been analyzed taxonomically, community diversity statistics were calculated. The Shannon-Weiner Information Index (Pielou 1975) was used as one measure of community diversity:

$$H' = - \sum_{i=1}^S \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

where H' (species diversity) is expressed as bits/individual, n_i is the number of valves of the i -th taxon, N is the total number of valves, and S is the total number of taxa in the sample. The second measure of community diversity calculated was redundancy (Main and McIntire 1974):

$$R' = \frac{H'_{\max} - H'}{H'_{\max} - H'_{\min}}$$

where

$$H'_{\max} = \log_2 S$$

and

$$H'_{\min} = \log_2 N - \frac{(N - S + 1)}{N} \log_2 (N + S + 1).$$

R' is a useful measure of the relative degree of dominance in the sample and has no units. Values of R' range from 0, when all taxa are equally common, to 1, when all taxa except one are represented by a single valve. Selected pairs of samples were compared using Stander's (1970) Similarity Index:

$$\text{SIMI} = \frac{\sum_{i=1}^S P_{ij} P_{in}}{\sqrt{\sum_{i=1}^S P_{ij}^2} \sqrt{\sum_{i=1}^S P_{in}^2}},$$

where P_{ij} and P_{in} are the proportion of the i -th taxon in the j -th and n -th samples respectively. SIMI has limits of 0 and 1. The larger the SIMI value, the greater the similarity between two samples. The niche breadth (B_i) of individual taxa was measured by the expression:

$$B_i = \exp \left[-\sum_{r=1}^Q \frac{n_{ir}}{N_i} \log_e \frac{n_{ir}}{N_i} \right],$$

where n_{ir} is the number of individuals of the i -th taxon found in the sample from the r -th site, and N_i the summation of individuals of the i -th taxon found at all Q sites (Levins 1968). B_i values can range from 1 to Q ($=5$ in present study) and is a measure of how evenly distributed a given taxon is in the samples under consideration. B_i is not necessarily related to a taxon's total relative abundance in all samples.

RESULTS

A total of 109 taxa representing 27 genera were identified in the samples. The identity and relative abundance of each diatom taxon is listed in Table 2. The dominant four genera, in terms of numbers of taxa encountered, were *Navicula* (28), *Nitzschia* (26), *Amphora* (12), and *Achnanthes* (5). The dominant four genera, in terms of relative abundance, were *Nitzschia* (37%), *Navicula* (22%), *Amphora* (18%), and *Denticula* (10%). The five most abundant taxa epiphytic on *A. germinans*, in order of decreasing abundance, were as fol-

lows: *Nitzschia brittonii*, *Navicula diserta*, *Nitz. frustulum*, *Denticula subtilis*, and *Amphora tenuissima*. These five accounted for 58% of the 2500 valves counted. *Nitz. brittonii*, the most abundant diatom, was found only at sites A, B, and C and its limited distribution is reflected in its low B_i value of 2.73. Species of *Synedra* were abundant at sites D and E but not at sites A–C.

Each of the community diversity statistics listed in Table 3 was calculated from the data of Table 2. The highest species diversity value was found at site A (4.522) and the lowest, at site E (3.206). Redundancy was lowest at site D (0.300) and highest at site B (0.464). The largest number of species was found at site A (67) with the lowest at site E (36). No obvious differences in community diversity between sites A–C or sites D and E were apparent.

The highest degree of structural similarity (SIMI) existed between sites B and C (Table 4). These two sites shared 85.0% of the maximum similarity possible. The lowest SIMI value was between sites B and E. These sites shared only 15.5% of the maximum similarity possible. A somewhat surprising result was the relatively low SIMI value (0.478) for a comparison of the two Grand Isle sites. Sites A and B possessed the most taxa in common (34) and sites C and E the least (15) (Table 4).

Navicula tripunctata var. *schizonemoides* possessed the highest niche breadth (B_i) value but was represented by only nine valves in the samples (Table 2). With respect to the five most abundant taxa, only three were evenly distributed (i.e., $B_i > 4.00$). These were *Nitzschia frustulum* (4.58), *Denticula subtilis* (4.56), and *Navicula diserta* (4.20). B_i values for *Nitz. brittonii* and *Amphora tenuissima* were both < 3.00 . A total of 56 taxa exhibited the minimum value of 1.00, since they were present in only one sample.

DISCUSSION

Of the 109 diatom taxa identified, 50 are new records for Louisiana. The dominant genera found on the pneumatophores of *A. germinans* in this study are the same ones reported by Stowe (1982) as epiphytes on *Spartina alterniflora* in a salt marsh north of my study area. With the exception of *Denticula*, the dominant genera from my study are the same found in edaphic salt marsh diatom assemblages in Mississippi by Sullivan (1978) and in Louisiana by Cook and Whipple (1982). A comparison of taxa in common with other studies revealed that 52% of the taxa reported by Stowe (1982), 59% of those reported by Cook and Whipple (1982) and 45% encountered by Sullivan (1978) were found in this study. It should be noted that Stowe (1982) reported only the dominant taxa. Fifty-three percent of the taxa found in the present study were also found in the *S. alterniflora* or *D. spicata* zones in a Mississippi salt marsh (Sullivan 1978). These two angiosperms were the most prominent ones associated with *A. germinans* in the study area. A comparison of the epiphytic diatom flora associated with *A.*

TABLE 2.

Relative abundance (expressed as number of valves in a sample of 500) and niche breadth values (B_i) of epiphytic diatom taxa on *A. germinans* in southeastern Louisiana. $\Sigma n_i = 5$ samples pooled as one.

Diatom taxon	Site					Σn_i	B_i	Diatom taxon	Site					Σn_i	B_i
	A	B	C	D	E				A	B	C	D	E		
<i>Achnanthes brevipes</i>								<i>N. capitata</i> var. <i>hungarica</i>							
var. <i>intermedia</i> (Kütz.) Cl.	11	10	15	23		57	3.77	(Grun.) Ross					1		1 1.00
<i>A. curvirostrum</i> Brun					1	1	1.00	<i>N. circumtexta</i> Meister	1						1 1.00
<i>A. hauckiana</i> Grun.	2		3	3		8	2.95	<i>N. contenta</i> Grun.	35	2	1				38 1.55
<i>A. lemmermanni</i> Hust.				7		7	1.00	<i>N. creuzburgensis</i>							
<i>A. tempereri</i> M. Perag.		8	8	1		17	2.40	Krasske	1				1		2 2.00
<i>Amphiprora paludosa</i> W. Sm.	1					1	1.00	<i>N. cryptocephala</i> Kütz	1	3	1				5 2.59
<i>Amphora angusta</i> Greg.								<i>N. cryptolyra</i> Brockmann		1					1 1.00
var. <i>angusta</i>		4		8		12	1.89	<i>N. diserta</i> Hust.	23	88	44	125	36	316	4.20
<i>A. angusta</i> var.								<i>N. hudsonis</i> Grun.	2	1			2	3	8 3.75
<i>ventricosa</i> (Greg.) Cl.	1					1	1.00	<i>N. incomposita</i> var.							
<i>A. caroliniana</i> Giffen	4			3	2	9	2.83	<i>minor</i> Hagelstein	3	1	29				33 1.39
<i>A. coffeiformis</i> Ag.	14	4	5	28	68	119	3.19	<i>N. marina</i> Ralfs					1		1 1.00
<i>A. exigua</i> Greg.	12		3	15	12	42	3.57	<i>N. menisculus</i> Schum.	8	7	6	6	1	28	4.41
<i>A. laevis</i> var. <i>perminuta</i>								<i>N. obsoleta</i> Hust.	2	1				1	4 2.83
Grun.	4					4	1.00	<i>N. pavillardii</i> Hust.		1	1				2 2.00
<i>A. libyca</i> Ehr.		2				2	1.00	<i>N. platyventris</i> Meister	1	1	3				5 2.59
<i>A. proteus</i> Greg.				1		1	1.00	<i>N. salinarium</i> Grun.	2	1	1	3			7 3.59
<i>A. sabyii</i> Salah	11		4			15	1.79	<i>N. salinicola</i> Hust.	2	2			18	1	23 2.12
<i>A. tennerrima</i> Hust.	2	2		5		9	2.70	<i>N. schroeteri</i> Meister	1						1 1.00
<i>A. tenuissima</i> Hust.	29	2	4	26	174	235	2.30	<i>N. subforcipata</i> Hust.		1					1 1.00
<i>Amphora</i> sp. No. 1			2			2	1.00	<i>N. tenera</i> Hust.				1	14	1	16 1.59
<i>Bacillaria paxillifer</i>								<i>N. teneroides</i> Hust.						1	1 1.00
(Müll.) Hendey	6	4		7	3	20	3.80	<i>N. tripunctata</i> var. <i>schizone-</i>							
<i>Berkelya rutilans</i> (Trent.)								<i>moides</i> (V.H.) Patr.	2	2	2	2	1	9	4.86
Grun.	2	1				3	1.89	<i>N. yarrensis</i> Grun.						1	1 1.00
<i>Caloneis westii</i> (W. Sm.)								<i>N. zostereti</i> Grun.		1	1	2			4 2.83
Hendey			1			1	1.00	<i>Navicula</i> sp. No. 1		1	1		2		4 2.83
<i>Cyclotella atomus</i> Hust.	1	2		2	1	6	3.78	<i>Nitzschia apiculata</i> W. Sm.	1	2			1		4 2.83
<i>C. striata</i> (Kütz.) Grun.	1	2	2	3	1	9	4.59	<i>N. bilobata</i> var. <i>ambigua</i>							
<i>Cylindrotheca gracilis</i>								Manguin	2	4	10	2			18 3.16
(Brëb.) Grun.	6					6	1.00	<i>N. brittonii</i> Hagelstein	56	180	128				364 2.73
<i>Cymatosira belgica</i> Grun.		1				1	1.00	<i>N. closterium</i> (Ehr.) W. Sm.	1						1 1.00
<i>Cymbella pusilla</i> Grun.	2					2	1.00	<i>N. communis</i> var. <i>hyalina</i>							
<i>Denticula subtilis</i> Grun.	71	26	55	23	66	241	4.56	Lund	3					1	4 1.75
<i>Diploneis weissflogi</i> (A.S.) Cl.					1	1	1.00	<i>N. dissipata</i> (Kütz.) Grun.	4		2			2	8 2.83
<i>D. interrupta</i> var. <i>caffra</i>								<i>N. epithemoides</i> Grun.	2					2	4 2.00
Giffen	1	8	30		1	40	2.06	<i>N. fasciculata</i> (Grun.) Grun.	5	9	17	1			32 2.98
<i>D. pseudovalis</i> Hust.	1					1	1.00	<i>N. filiformis</i> (W. Sm.) Schütt	6	3	4				13 2.88
<i>Fragilaria construens</i>								<i>N. frustulum</i> (Kütz.) Grun.	77	20	88	67	52	304	4.58
var. <i>venter</i> (Ehr.) Grun.	1	1		2	1	5	3.79	<i>N. ganderscheimiensis</i>							
<i>Gomphonema parvulum</i>								Krasske	32	19	17	17	5	90	4.42
Kütz.	1	2			1	4	2.83	<i>N. grana</i> Hohn & Hellerm.	1		1				2 2.00
<i>G. littorale</i> Hendey			1			1	1.00	<i>N. granulata</i> Grun.			1				1 1.00
<i>Gyrosigma beaufortianum</i>								<i>N. hungarica</i> Grun.	1	1			1	8	11 2.42
Hust.	1					1	1.00	<i>N. lorenziana</i> var. <i>subtilis</i>							
<i>G. fascicola</i> (Ehr.) Cl.	1					1	1.00	Grun.	1						1 1.00
<i>G. hummii</i> Hust.	1					1	1.00	<i>N. microcephala</i> Grun.			2				2 1.00
<i>G. peisonis</i> (Grun.) Hust.	1					1	1.00	<i>N. obtusa</i> W. Sm. var.							
<i>Mastogloia exigua</i> Lewis					26	26	1.00	<i>obtusaria</i>	1						1 1.00
<i>M. pumila</i> (Grun.) Cl.				1	10	12	1.76	<i>N. obtusa</i> var. <i>nana</i> Grun.	14	12	11				37 2.98
<i>Melosira nummuloides</i> Ag.		4	4			8	2.00	<i>N. palea</i> (Kütz.) W. Sm.		1					1 1.00
<i>Navicula abunda</i> Hust.		6				6	1.00	<i>N. panduriformis</i> var.							
<i>N. accomoda</i> Hust.	1					1	1.00	<i>continua</i> Grun.	1						1 1.00
<i>N. aequorea</i> Hust.	1					1	1.00	<i>N. romana</i> Grun.			2	1			3 1.89
<i>N. ammophila</i> Grun.	7	5	3	2	2	19	4.41								

TABLE 2 (Continued)

Relative abundance (expressed as number of valves in a sample of 500) and niche breadth values (B_i) of epiphytic diatom taxa on *A. germinans* in southeastern Louisiana.
 $\Sigma n_i = 5$ samples pooled as one.

Diatom taxon	Site					Σn_i	B_i
	A	B	C	D	E		
<i>N. romanooides</i> Manguin	1	1	4			6	2.38
<i>N. sigma</i> (Kütz.) W. Sm.		1				1	1.00
<i>N. tryblionella</i> Hantz.				1		1	1.00
<i>N. vitrea</i> var. <i>salinarum</i> Grun.	4		8			12	1.89
<i>Nitzschia</i> sp. No. 1		1				1	1.00
<i>Opephora parva</i> (Grun.) Krasske	1					1	1.00
<i>Paralia sulcata</i> (Ehr.) Cl.		1				1	1.00
<i>Pleurosigma angulatum</i> (Quek.) W. Sm.	1					1	1.00
<i>P. salinarum</i> (Grun.) Grun.		1				1	1.00
<i>Psammodiscus nitidus</i> (Greg.) Round & Mann		4	3			7	1.98
<i>Rhopalodia gibberula</i> (Ehr.) Müll.					1	1	1.00
<i>R. musculus</i> cf. var. <i>producta</i> Grun.					9	9	1.00
<i>Stauroneis amphioxys</i> Greg. var. <i>amphioxys</i>	1					1	1.00
<i>S. amphioxys</i> var. <i>obtusata</i> Hendey	1					1	1.00
<i>S. legleri</i> Hust.	1					1	1.00
<i>Surirella atomus</i> Hust.				1		1	1.00
<i>Synedra affinis</i> Kütz.		2		10	1	13	1.99
<i>S. fasciculata</i> (Ag.) Kütz.				40		40	1.00
<i>S. demerarae</i> Grun.	2					2	1.00
<i>S. tabulata</i> var. <i>parva</i> (Kütz.) Hust.				23		23	1.00

TABLE 3.

Species diversity (H'), redundancy (R') and number of taxa (S) characterizing epiphytic diatom samples from *A. germinans* in southeastern Louisiana.

Statistic	Site				
	A	B	C	D	E
H'	4.522	3.617	3.902	4.027	3.206
R'	0.328	0.464	0.332	0.300	0.435
S	67	54	42	42	36

germinans from both Louisiana and Bimini Harbor (Sullivan 1981) showed only 18% of taxa in common, and the same value was found for a comparison with the epiphytic flora on red mangrove (*Rhizophora mangle* L.) prop roots in Indian River, Florida (Navarro 1982). The lack of similarity between this study and those of Sullivan (1981) and Navarro (1982) is not unexpected when one considers the lower lati-

TABLE 4.

Matrix of similarity values (upper right) and number of taxa in common (lower left) for comparisons for epiphytic diatom samples from *A. germinans* in southeastern Louisiana.

Sites	A	B	C	D	E
A		0.594	0.827	0.539	0.549
B	34		0.850	0.417	0.155
C	28	28		0.471	0.291
D	25	27	20		0.478
E	26	23	15	21	

tudes of their study areas.

Species diversity (H') and the number of taxa in a sample (S) are both high and similar to those reported by Sullivan (1978) and Cook and Whipple (1982) for Gulf coast salt marshes, but larger than those reported by Stowe (1982). H' and S for site A are among the highest reported in the literature and exceed those found for mangroves in Bimini Harbor by Sullivan (1981). Sites A, B, and C possessed the most similar epiphytic diatom assemblages (Table 4). With the exception of *Nitzschia brittonii*, the more abundant taxa were widely distributed across the five sites (Table 2). Discontinuous diatom distributions were due to the rare occurrences of many taxa (56 taxa were found at only one station), to unknown physicochemical differences among the habitats investigated and to stochastic processes. The first case supports the conclusion of Cook and Whipple (1982) that saline areas of southeastern Louisiana coastal marshes possess a large proportion of rare species. Comparisons with previous studies indicate that the diatom flora epiphytic on *A. germinans* in this study is much more characteristic of temperate salt marshes than of subtropical mangroves. The genus *Mastogloia* was poorly represented (only 2 species) in stark contrast to the subtropical studies of Sullivan (1981) and Navarro (1982). Most of the 109 taxa encountered are typical edaphic salt marsh diatoms. This finding lends some support to Sullivan's (1978) hypothesis that a uniform diatom flora may exist in salt marshes along the Atlantic and Gulf coasts of the United States. More importantly, this study represents the first report on epiphytic mangrove diatoms for the entire Gulf coast of the United States and Mexico, and is therefore valuable for distributional records and future, more comprehensive, work with this complex and diverse flora.

ACKNOWLEDGMENTS

I thank Dr. George Fister, Department of Biological and Environmental Sciences, McNeese State University, for his assistance with the computer programs for the community diversity statistics used in this study. I also thank Dr. Michael J. Sullivan, Biology Department, Mississippi State University, for his encouragement, valuable suggestions, and critical review of the manuscript.

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