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Diatoms Associated with Bryophyte Communities Growing at Extreme Depths in Lake Michigan[1]

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Diatom assemblages on limestone cobbles collected from 42.7 m depth in the mid-lake high region of Lake Michigan are characterized by low total abundance and low diversity. The flora present contains three associations. A large allochthonous component, comprised of planktonic species and very low numbers of benthic species usually found in shallow water is present. A limited number of dominant taxa appear to be particularly associated with deep habitats in oligotrophic lakes. Other species, usually reported from terrestrial habitats, appear to be associated with the bryophyte *Fissidens fontanis* which is present in the collections.
INDEX DESCRIPTORS: Diatoms, Lake Michigan, Great Lakes, benthic communities, diversity.

The algal associations of extreme or unusual environments have long fascinated phycologists. This is indicated by the fact that the floristic associations of certain extreme habitats are perhaps better known than their more widely distributed and ecologically important counterparts. From the viewpoint of algal ecology, this interest is motivated by two primary considerations.

In the first place, scientific induction often proceeds from the inspection of extreme or limiting cases. In this sense, communities which occur under extreme conditions may provide a tool for understanding more general processes. Such communities often have relatively simple organization and are composed of a limited number of taxa. The complexities of biotic interactions are thus reduced. This, combined with the fact that a single environmental variable or a limited suite of variables is often controlling in such habitats, leads to more straightforward evaluation of cause-effect relationships.

Secondly, the highly disjunct distribution patterns often characteristic of species which inhabit extreme environments have presented a genuine challenge to phytogeographers. Understanding of the mechanisms which allow certain species to occupy widely dispersed habitats characterized by specific extreme conditions may allow evaluation of the factors which limit the distribution of less specially adapted species.

In diatoms, a number of apparent examples of specific habitat associations are known. *Achnanthes grimmei* Krasske is a major dominant in thermal springs in many parts of the world. Many authors have commented on the association of *A. hungarica* Grun. with *Lemna* spp. A limited suite of characteristic species are found in concentrated sodium carbonate lakes world-wide. Other species seem to be almost universally associated with bryophyte communities occurring in moisture limited habitats (Bock, 1963).

Very early in my association with Professor Dodd, interest in similar communities led us to investigate the diatom species associated with bryophyte communities in Iowa (Dodd and Stoermer, 1962). In the following, I report an association occurring under vastly different physical conditions which has certain floristic similarities to these terrestrial communities.

MATERIALS AND METHODS

Samples discussed come from limestone cobbles, apparently of glacial origin, collected at 42.7 m depth from the "mid-lake high" region of Lake Michigan (43°20.5′N; 87°9.0′W). Individual rocks were collected by divers, enclosed in polyethylene bags, and returned to the surface for inspection and sampling. Inspection of the samples collected at random from an approximately 3 m² area of the "boulder reef" sample revealed a very depauperate biological community. The most apparent macroscopic elements were occasional bryozoan colonies and aquatic mosses *(Fissidens fontanis)*. Two rocks were selected and the mosses growing on them and a small section of the associated substrate was scraped from them with a sharp knife. These samples, GLRD 1514 and GLRD 1515, were immediately preserved in formalin-alcohol.

After return to the laboratory each sample was split. One split of each sample was retained, without further treatment, as a voucher specimen. The other splits were cleaned according to the method of Patrick and Reimer (1966) and prepared as strewn mounts in Hyrax for diatom analysis.

The diatoms present were identified and enumerated on 10 transects of each prepared slide using a Leitz Ortholux microscope at 1200× and 1.32 numerical aperature.

RESULTS AND DISCUSSION

Results of the diatom population analyses for the two samples examined are given in Table 1. A number of points are apparent from inspection of this data. Compared to other benthic algal assemblages in the upper Great Lakes (Stoermer, 1975), both the number of species present and the calculated diversity are quite low. Further, it is apparent that the diatom species present are a composite of benthic and phytoplankton forms. All representatives of the genera *Cyclotella, Melosira, Rhizosolenia, Stephanodiscus,* and *Synedra* present in these collections undoubtedly grew in the plankton. Observation of the living material showed that the majority of planktonic cells in these particular collections contained apparently normal cell contents. Although other investigations of deep-living benthic algal communities in Lake Michigan (Stevenson and Stoermer, submitted for publication) have shown a significant fraction of living cells derived from the plankton, these cells probably did not grow at the site of collection and are not a component of the community in the usual sense.

There is a somewhat similar problem in determining if some of the taxa which usually grow in benthic communities are actually occupying this particular habitat. The available detailed investigations of planktonic diatom assemblages in Lake Michigan (Stoermer and Yang, 1969; Schelske et al., 1976) show that low levels of benthic species are commonly found in plankton collections, even in offshore localities. Thus, in the samples considered here many of the taxa present, although they usually grow in benthic communities, could have been

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Table 1. *Abundance of diatoms in samples 1514 and 1515. Total count is followed by relative abundance in parentheses ( ).*

	Sample			
	1514		1515	
Achnanthes				
A. affinis Grun.	1	(0.01)	9	(0.30)
A. amoena Hust.	2	(0.02)	2	(0.07)
A. clevei Grun.	1540	(13.6)	300	(9.8)
A. conspicua A. Mayer	1	(0.01)	1	(0.03)
A. deflexa Reim.	-0-	-0-	3	(0.10)
A. lanceolata var. *abbreviata* Reim.	39	(0.35)	6	(0.20)
A. marginulata Grun.	2	(0.02)	-0-	-0-
A. minutissima Kütz.	1	(0.01)	2	(0.07)
A. pinnata Hust.	1960	(17.3)	300	(9.8)
Achnanthes sp. #1	1	(0.01)	-0-	-0-
Amphipleura				
A. arctica Patr. and Freese	-0-	-0-	2	(0.7)
A. pellucida (Kütz.) Kütz	1	(0.01)	3	(0.10)
Amphora				
A. ovalis var. *pediculus* (Kütz.) V.H.	515	(4.6)	28	(0.92)
Asterionella				
A. formosa Hass.	-0-	-0-	1	(0.03)
Caloneis				
C. bacillum (Grun.) Cl.	2	(0.02)	2	(0.07)
C. bacillum var. *lancettula* (Schulz) Hust.	5	(0.04)	-0-	-0-
Cocconeis				
C. diminuta Pant.	252	(2.22)	25	(0.81)
C. pediculus Ehr.	1	(0.01)	-0-	-0-
Cyclotella				
C. comta (Ehr.) Kütz.	14	(0.12)	6	(0.20)
C. kuetzingiana Thw.	2	(0.02)	-0-	-0-
C. meneghiniana fo. *plana* Fricke	-0-	-0-	1	(0.03)
C. michiganiana Skv.	11	(0.10)	14	(0.46)
C. ocellata Pant.	45	(0.40)	24	(0.79)
C. operculata (Ag.) Kütz.	2	(0.02)	1	(0.03)
C. pseudostelligera Hust.	-0-	-0-	1	(0.03)
C. stelligera (Cl. and Grun.) V.H.	2	(0.02)	4	(0.13)
Cymatopleura				
C. solea (Bréb. and Godey) W. Sm.	5	(0.04)	5	(0.16)
Cymbella				
C. cesati (Rabh.) Grun.	-0-	-0-	1	(0.03)
C. latens Krasske	-0-	-0-	1	(0.03)
C. microcephala Grun.	-0-	-0-	1	(0.03)
Denticula				
D. tenuis var. *crassula* (Näg.) W. and G.S. West	1	(0.01)	-0-	-0-
Diatoma				
D. tenue var. *elongatum* Lyngb.	1	(0.01)	1	(0.03)
D. vulgare Bory	3	(0.03)	-0-	-0-
Eunotia				
E. praerupta Ehr.	1	(0.01)	-0-	-0-
Fragilaria				
F. capucina Desm.	1	(0.01)	4	(0.13)
F. construens (Ehr.) Grun.	2	(0.02)	1	(0.03)
F. crotonensis Kitton	18	(0.16)	5	(0.16)
F. intermedia var. *fallax* (Grun.) A. Cl.	45	(0.40)	7	(0.30)
F. pinnata Ehr.	1400	(12.39)	251	(8.22)
F. vaucheriae (Kütz.) Peters.	-0-	-0-	2	(0.07)
Gomphonema				
G. intricatum Kütz.	1	(0.01)	-0-	-0-
Melosira				
M. granulata (Ehr.) Ralfs	64	(0.57)	6	(0.20)
M. granulata var. *angustissima* O. Müll.	9	(0.80)	9	(0.30)
M. islandica O. Müll.	1960	(17.34)	368	(12.06)
M. italica subsp. *subarctica* O. Müll.	400	(3.54)	140	(4.59)
Navicula				
N. contenta fo. *biceps* (Arn.) Grun.	2170	(19.20)	1190	(38.99)
N. lanceolata (Ag.) Kütz.	1	(0.01)	-0-	-0-
N. minima Grun.	6	(0.05)	5	(0.16)
N. monoculata Hust.	-0-	-0-	1	(0.03)
N. mutica var. *cohnii* (Hilse) Grun.	1	(0.01)	-0-	-0-
N. paludosa Hust.	8	(0.07)	3	(0.10)
N. recondita Torka	1	(0.01)	-0-	-0-
N. seminuloides Hust.	8	(0.07)	5	(0.16)
N. subocculata Hust.	3	(0.03)	18	(0.59)
Navicula sp. #5	-0-	-0-	1	(0.03)
Nitzschia				
N. dissipata (Kütz.) Grun.	52	(0.46)	28	(0.92)
N. frustulum var. *perminuta* Grun.	1	(0.01)	-0-	-0-
N. palea (Kütz.) W. Sm.	-0-	-0-	1	(0.03)
N. recta Hantz.	2	(0.02)	3	(0.10)
Nitzschia sp. #1	53	(0.47)	8	(0.26)
Nitzschia sp. #2	8	(0.07)	5	(0.16)
Pinnularia				
P. borealis Ehr.	1	(0.01)	-0-	-0-
Rhizosolenia				
R. eriensis H.L. Sm.	2	(0.02)	-0-	-0-
R. gracilis H.L. Sm.	-0-	-0-	1	(0.03)
Stephanodiscus				
S. alpinus Hust.	168	(1.47)	55	(1.80)
S. binderanus (Kütz.) Krieg.	3	(0.03)	1	(0.03)
S. minutus Grun.	109	(0.96)	46	(1.51)
S. niagarae Ehr.	7	(0.06)	8	(0.26)
S. tenuis Hust.	1	(0.01)	-0-	-0-
S. transilvanicus Pant.	105	(0.93)	56	(1.84)
Stephanodiscus sp. #5	2	(0.20)	-0-	-0-
Surirella				
S. angusta Kütz.	18	(0.16)	4	(0.13)
S. ovata Kütz.	2	(0.20)	1	(0.03)
Synedra				
S. delicatissima var. *angustissima* Grun.	-0-	-0-	2	(0.06)
S. demerarae Grun.	1	(0.01)	-0-	-0-
S. filiformis Grun.	-0-	-0-	5	(0.16)
S. minuscula Grun.	-0-	-0-	1	(0.03)
S. ostenfeldii (Krieg.) A. Cl.	-0-	-0-	1	(0.03)
S. ulna var. *chaseana* Thomas	-0-	-0-	2	(0.06)
S. ulna var. *danica* (Kütz.) V.H.	2	(0.02)	1	(0.03)
Tabellaria				
T. fenestrata (Lyngb.) Kütz.	209	(1.8)	34	(1.11)
T. flocculosa (Roth) Kütz.	50	(0.44)	28	(0.92)
Total specimens	11304		3052	
Total species	64		64	
Diversity	2.3		2.3	
Evenness	0.55		0.54	

derived from the plankton. In the primarily benthic genus *Achnanthes* only three species, *A. clevei, A. lanceolata* var. *abbreviata,* and *A. pinnata* are present in much greater abundance than might be expected from planktonic "fallout" based on Stoermer and Yang's data (1969).

Viewed from this perspective, there are a very low number of species which are unambiguously associated with the communities investigated. These include *Amphora ovalis* var. *pediculus*, *Cocconeis diminuta*, *Fragilaria pinnata*, and *Navicula contenta* fo. *biceps*. Several other species are somewhat more abundant in the collections studied than would be expected if they were derived from the plankton assemblage. These include *Achnanthes amoena*, *Cymatopleura solea*, *Navicula minima*, *N. paludosa*, *N. seminuloides*, *N. subocculata*, and *Surirella angusta*. The abundance levels of other species present are such that they could have been derived from fallout from the plankton. This does not necessarily mean that they were not actively growing in the communities at the time of collection, but it is, as a practical matter, impossible to determine their true growth habitat. As pointed out earlier, determination of whether the cells were alive or dead at the time of collection does not necessarily resolve this problem since many diatom species can survive long periods of transport without active growth.

It is notable that most of the taxa which are conspicuous elements of benthic diatom communities at shallow and moderate depths in Lake Michigan are absent from these collections. The genus *Amphora* is represented by a single entity whereas a number of species are present in most collections from lesser depths. Most benthic collections from Lake Michigan contain an exceptional diversity of species in the genera *Cymbella* and *Gomphonema*. In the collections examined here only one species of the latter genus and one of the former were found in trace quantities. The larger vagile species of naviculoid genera are also conspicuous by their absence. No representatives of the genera *Diploneis*, *Mastogloia*, or *Stauroneis* were noted. Only two species of *Caloneis* and one species of *Pinnularia* were present. Most of the species of the genus *Navicula* present are very small forms and members of the subgenus *Navicula* (Lineolatae), which are abundant in most benthic collections from Lake Michigan, are represented by a single specimen of *N. lanceolata*. Members of the Epithemiaceae, which are often abundant in epiphytic and epiplithic habitats at moderate depth in Lake Michigan are not present and the genus *Nitzschia* is represented by only two unidentified species which occur in numbers greater than would be expected from possible plankton contamination.

Comparison of the flora present in these samples with 20 others collected from similar substrates at somewhat lesser depths (27-33 m) at the same time indicates that some of the minor taxa are particularly well represented. The only occurrences of *Achnanthes lanceolata* var. *abbreviata*, *A. marginulata*, *Eunotia praerupta*, *Navicula monocculata*, *N. recondita*, and *Pinnularia borealis* were noted in the two collections discussed here. Among this particular suite of taxa *Achnanthes marginulata*, *Eunotia praerupta*, and *Pinnularia borealis* occur in abundance in collections from shallower depths in Lake Superior and occasionally in northern Lake Michigan. The others are generally rare in collections we have examined from the Laurentian Great Lakes. Although also occurring in at least some of the other collections examined, *Achnanthes amoena*, *A. clevei*, *Navicula contenta* fo. *biceps*, *N. seminuloides*, and *N. subocculata* were most abundant in these samples. Within this suite of species *Achnanthes clevei* and *Navicula seminuloides* are generally distributed in benthic communities in Lake Michigan and the other upper Great Lakes. The others are generally rare.

The known distribution and habitat preference of the taxa particularly abundant in these collections is rather surprisingly variable.

Achnanthes amoena was originally described from a saltwater locality (Hustedt, 1952) but the author indicates that it was probably derived from freshwater. It has only recently been reported from the Great Lakes (Kreis and Stoermer, 1979) and has been found in Lake Michigan and Lake Superior.

Achnanthes clevei has been noted as a deep-living form in European lakes, particularly in the Baltic area but also in many alpine lakes (Hustedt, 1933). It is widely distributed in the upper Great Lakes, but most abundant at depths below 10 m.

Achnanthes lanceolata var. *abbreviata* was described from the Savannah River and small streams in South Carolina (Reimer, 1966). It is quite similar to other varieties described from springs and small streams in tropical areas by Hustedt (1937). Its known distribution in the Great Lakes is extremely limited and other reports from Lake Michigan come from samples taken in the vicinity of streams entering the lake.

Achnanthes pinnata was originally described from Tibet (Hustedt, 1922) and has been widely reported from Asia (Zabelina et al., 1951). Most reports from the United States come from small streams and rivers (Patrick and Reimer, 1966). It has been reported from a number of localities in Lake Michigan (Stoermer and Yang, 1969) but is usually a minor element of the diatom flora.

Amphora ovalis var. *pediculus* is a very widely distributed taxon and occurs in a variety of habitats. There are numerous records from Lake Michigan (Stoermer and Yang, 1969) but its primary habitat appears to be in epipelic communities (Stevenson and Stoermer, submitted for publication).

Cocconeis diminuta is also a very widely distributed species and is most abundant in epipelic communities in Lake Michigan.

Fragilaria pinnata is another widely distributed and apparently eurytopic species. Its most common growth habit appears to be attached to sand grains or other solid substrates. In Lake Michigan it is common in epipelic communities (Stevenson and Stoermer, submitted) and fairly sizable populations are often noted in nearshore phytoplankton samples, particularly along the western coast of the lake (Stoermer and Yang, 1970).

Navicula contenta fo. *biceps* is reported to have more specific habitat requirements. Hustedt (1962) reports that it is common in aerophytic communities in Europe. Patrick and Reimer (1966) indicate the same type of distribution in the United States and note that it is often associated with moss communities. In my experience it is nearly universally present in terrestrial moss communities and Bock (1963) remarks that it is one of the most characteristic forms found in moss communities growing in extremely dry environments. Its distribution in the Great Lakes is extremely limited and the only abundant occurrences noted come from moss communities.

Navicula paludosa has been reported from streams and subaerial habitats in Europe (Hustedt, 1957) and is often found in fossil deposits (Simonsen, 1958). It is widely distributed in the Great Lakes, but rarely occurs in abundance.

Navicula subocculata has previously been reported from circumneutral to alkaline lakes in northern Europe (Hustedt, 1961). It is very rare in the Laurentian Great Lakes. The only additional record we have is from another collection at 35 m depth in northern Lake Michigan.

The diatom flora present at this deep station thus has a curious association of taxa with rather strikingly different previously reported patterns of occurrence.

It is tempting to dismiss the taxa with normally planktonic growth habit as allochthonous elements. This may not be an entirely correct assumption. It should be noted that, among the planktonic taxa present, there is a great over-representation of species which reach their greatest abundance (Stoermer and Ladewski, 1976) during periods when the lake is near or below 4°C and unstratified. Due to the intensive mixing which occurs during the winter unstratified period, phytoplankton populations are uniformly dispersed throughout the water column (Stoermer and Kopczynska, 1967; Brooks and Torke, 1977). As a consequence, populations which reach maximum abundance in Lake Michigan during the winter and early spring must be able to survive extended periods of entrainment near or below light compensation. It is thus not surprising to find these populations in deep-living communities. Our current observations (unpublished) suggest that some of them are able to survive summer stratification and are reentrained into the plankton during fall circulation. Lund (1954, 1955) has shown the importance of this mechanism in certain species of *Melosira* which can survive very long periods under aphotic conditions (Nipkow, 1950; Stockner and Lund, 1970). Among the planktonic forms, the only species which has a summer growth optimum that is over-represented in these collections is *Cyclotella ocellata*. In the upper Great Lakes this species is usually associated with the summer sub-thermocline phytoplankton optimum (Schelske et al., 1976; Stoermer and Kreis, 1980) and thus appears to be particularly adapted to low temperature, low light conditions. It is interesting to note that trace quantities of planktonic species (*Cyclotella meneghiniana* fo. *plana*, *C. pseudostelligera*, *Fragilaria capucina*, *Melosira granulata*, *Stephanodiscus binderanus*, *S. tenuis*) particularly associated with eutrophied conditions in the Great Lakes (Stoermer, 1978) are present, although the most obvious shoreline sources (Milwaukee and Sheboygan, Wisconsin) are more than 60 km from the site of collection.

The only relatively large-celled species in these associations, *Cymatopleura solea* and *Surirella angusta*, are typical tychoplanktonic forms in the Great Lakes. Although their primary habitat is in epipelic communities they are commonly noted in plankton collections and *S. angusta* may be a dominant element of phytoplankton communities in eutrophied parts of the system during the winter circulation period (Stoermer et al., 1974).

The other dominant members of the community are all small species, but seem to represent adaptations which converge in the conditions found in this particular habitat. The very strong association of *Navicula contenta* fo. *biceps* with mosses strongly suggests that some symbiotic or commensal relationship exists. This also may be a factor in the case of entities such as *Achnanthes lanceolata* var. *abbreviata* which are most usually found in small stream, spring, or terrestrial habitats. In an extremely light limited habitat like the one investigated here, it is tempting to postulate that the species present are capable of heterotrophic nutrition. This has not been demonstrated for the species discussed above, but has been in *Navicula minima* (Hellebust and Lewin, 1977), a species with very wide distribution which is present in higher than "background" levels in these collections.

The remainder of the dominant abundant taxa. *Achnanthes clevei*, *A. pinnata*, *Amphora ovalis* var. *pediculus*, *Cocconeis diminuta*, *Fragilaria pinnata*, *Navicula paludosa*, *N. subocculata*, and the two unidentified *Nitzschia* species, appear to be the component of the associations which are most directly and specifically adapted to this extreme environment.

The problem of allochthonous, "guest," or "misplaced" species has seldom been formally addressed in diatom association analysis (Guillard and Kilham, 1977). The late Friedrich Hustedt, in his many papers (Behre, 1970), consistently commented on taxa which he considered to be misplaced (verschleppte!) in a particular association. Hustedt's remarks were apparently based on an intuitive understanding developed through many years of intensive observation. While few investigators can match Hustedt's level of experience, consideration of this problem would serve to sharpen the focus of many ecological investigations.

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