

INVESTIGATIONS INTO THE EXISTENCE OF ASSOCIATIONS
WITHIN BENTHIC DIATOM COMMUNITIES

By

© Gwenn M. Kruszynski

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree,
Master of Science

Department of Botany
The University of Manitoba
Winnipeg, Manitoba, Canada
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ACKNOWLEDGEMENTS

This has been a study in patience and perseverance...and now it's time to move on. I have just a few words I'd like to say. I want to thank everyone who has been there for me (and still is) maybe, one day I can return the honour. I appreciate the advice and encouragement I've received (and still am receiving...). Thank you all for sharing in this part of my life.

I am grateful of the facilities made available to me, both in the Department of Botany and at The Delta Marsh Field Station. This project was funded by a Natural Sciences and Engineering Research Council operating grant to Dr. G.G.C. Robinson.

ABSTRACT

Multivariate statistical methods were used to examine the existence of associations in haptobenthic and herpobenthic diatom communities as described in the literature. These literature sources represented data collected world-wide. Yearly and seasonal trends are described. In the yearly data, six site groups and nine species groups were recognized using cluster analysis. Correspondence analysis indicated the importance of pH, nutrient status, and general habitat (eg. lake, stream etc.) in designating species associations within benthic diatoms. In the seasonal data, seven site groups and four species groups were recognized using cluster analysis. Correspondence analysis indicated the importance of seasonality, as well as the afore-mentioned parameters in the designation of species associations. The ecological selection of environmental parameters by benthic species suggests the existence of specific associations within benthic communities. It also implies the characterization of the habitat could be useful in predicting the occurrence of specific diatom associations.

The application of similar techniques was used to predict the seasonally distinct associations within the periphytic

diatom community of the Delta Marsh, Manitoba, Canada (99° 19'W, 50° 07'N). Spring (May-June) associations included Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina. Summer associations (July) included Fragilaria capucina. Autumn associations (August-September) were represented by Rhopalodia gibba, Synedra acus, Fragilaria capucina, and Cyclotella meneghiniana. Seasonal succession of the initial colonizers was also described. Initial colonization was found to be unpredictable, as it varied weekly and yearly. Although the description of seasonal succession of initial colonizers using artificial substrata in short term studies represent one view of succession, artificial substrata were found to be ineffective as a tool for successional studies.

INTRODUCTION

While large scale relationships between benthic diatom community structure and their environment have been shown after years of investigation, the delineation of associations within aquatic habitats using multivariate techniques, has been limited. The objectives of the present study, therefore, were two-fold:

1. to examine the existence of associations amongst the benthic diatom community through the determination of the ecological selection of environmental parameters by benthic diatoms using a two-step multivariate analysis approach.
2. to determine whether there are, or are not, seasonally distinct diatom associations present in the benthic diatom community in the Delta Marsh, Manitoba.

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Chapter I

ASSOCIATIONS IN BENTHIC DIATOM COMMUNITIES

1.1 ABSTRACT

Multivariate statistical methods were used to examine data on haptobenthic and herpobenthic diatom communities as described in the literature. These literature sources represented data collected world-wide. Yearly and seasonal trends were described. In the yearly data, six site groups and nine species groups were recognized using cluster analysis. Correspondence analysis indicated that pH, nutrient status, and general habitat (eg. lake, stream etc.) were important in designating species associations within benthic algae. In the seasonal data, seven site groups and four species groups were recognized using cluster analysis. Correspondence analysis indicated that seasonality, pH, nutrient status, and general habitat were important in designating species associations within benthic algae. An apparent relationship between environmental parameters and benthic species suggested the existence of habitat-specific associations within benthic communities. It also implied that characterization of habitats could be useful in predicting the occurrence of specific diatom associations.

1.2 INTRODUCTION

Submerged and emergent substrata in aquatic ecosystems provide a large surface area for colonization by benthic organisms. Attached algae of littoral waters often dominate the algal biomass, with diatoms often being predominant. Although the description and the distribution of phytoplankton assemblages in space and time and associated environmental factors is well documented (eg. Shim & Lee 1987), there is a lack of equivalent information on benthic algae. This deficiency may, in part, be explained by the extreme heterogeneity of algal distribution across the exceptionally varied environmental, and biotic gradients of littoral communities (Wetzel 1983). Algal associations do, however, exist within benthic communities (Bohr 1973, Bohr et al. 1983, Luscinska 1979).

Much effort has been focussed on the description of algal communities, as ecological classification has been considered essential for the development of ecological concepts, such as succession (Round 1981). Studies of benthic diatoms growing on a variety of natural and artificial substrata have been conducted in a wide range of lotic and lentic environments (Lang & Austin 1984). Community structure has been the focus of many such studies (eg. Butcher 1932, Sladeckova 1962, Brown & Austin 1973a, Jones 1978, Green & Davies 1980, Hudon & Bourget 1981, Moss 1981, Eloranta 1982, O'Quinn & Sullivan 1983, Hoagland et

al. 1982). Considerable interest has also arisen over the relationship between diatom community structure and water nutrient status (Patrick 1936, Lund 1950, Schelske & Stoermer 1971, Moss 1976).

Factors thought to be influential in determining the ultimate structure of diatom communities have also been examined. A number of environmental factors are important for the occurrence of a distinct diatom association. The general habitat or physiognomy, whether it be lake, pond, river, stream, spring, is important in determining the diatom flora within it (Patrick 1948, Hutchinson 1967, Round 1981). The species detected in these various habitats depends on whether the water is eutrophic, mesotrophic, oligotrophic, or dystrophic (Patrick 1948). The nature of the substratum has received considerable, and still controversial, attention (Patrick et al. 1954, Prowse 1959, Castenholz 1960, Sladeckova 1962, Dillard 1969, Tippet 1970, Allen 1971, Allanson 1973, Harlin 1975, Gough & Woelkerling 1976, Siver 1977, Cattaneo 1978, Cattaneo & Kalff 1978, Eminson & Moss 1980, Gough & Gough 1981, O'Neill 1981, O'Neill Morin & Kimball 1983). The role of grazers (Mason & Bryant 1975, Lubchenco 1978, Fairchild 1981, Kesler 1981, Sumner & McIntire 1982, Bowker et al. 1983, Drake 1983, Hudon 1983, Lamberti & Resh 1983, McAuliffe 1984), current (McIntire 1966, Reisen & Spencer 1970, Lamb & Lowe 1981, Stevenson 1984), as well as pH (Patrick 1948), all influence

the structure and composition of the benthic diatom community. Seasonal changes in species composition in benthic communities have been studied intensively (Moore 1977a,b, Cattaneo & Kalff 1978, Obeng-Asamoah et al. 1980), and seasonal dominance of specific diatoms has also been noted (Klarer & Hickman 1975, Moss 1976, Cattaneo & Kalff 1978, Jones & Mayer 1983). Diatom community structure has been used to trace trophic succession of lakes (Patrick & Reimer 1966, Hosmani & Bharati 1982). Likewise, it has been used to categorize bodies of water as hard or soft; fresh, as opposed to brackish and saline; acid, neutral or alkaline (Patrick & Reimer 1966). Thus, many physiographic conditions exist which may furnish suitable habitats for diatoms.

After years of investigation, only general relationships between benthic diatom community structure and environment have been shown. Early studies, concerned with the description of diatom communities, generated extensive worldwide species lists. Species diversity, evenness and richness were later used as indicators of the structure and the ecological stability of such communities (Dickman 1968, Symons 1972, Brown 1973, Kingston et al. 1983, Peterfi & Momeu 1984). Colonization rates, standing crop and biomass measurements have supplemented the current knowledge of benthic diatom populations and communities. Interest in spatial distribution patterns and attachment mechanisms have made scanning electron microscopy more popular in the past

decade (Paul et al. 1977, Kingston et al. 1979, Hudon & Bourget 1981, Lowe et al. 1982).

Numerical methods of classification and ordination have rarely been used in phytosociological studies of diatom biogeography. The use of multivariate analyses has appeared recently. Sabater & Sabater (1988) studied diatom composition and distribution using principal components analysis (PCA) ordination of assemblages to classify assemblages based on water chemistry and disturbance by humans. Cluster analysis, followed by PCA, was used in a study on the typology of oligotrophic streams to classify records into a table comparable to phytosociological tables (Leclercq & Depiereux 1987). PCA has been used in some studies to show distribution patterns and classification related to various environmental gradients and seasonality (Handa & Nakano 1987, Wilderman 1987, Kingston et al. 1983). Whiting & McIntire (1985) used correspondence analysis (CA) to study distribution patterns in epiphytic and epipelagic diatoms. Kingston et al. (1983) used cluster analysis to identify and define diatom assemblages at varying depths. Diatom assemblages from Finnish lakes have been examined using the divisions of two-way indicator species analysis (TWINSpan) to further ecological interpretation of biological assemblages (Merilainen & Huttunen 1982). Even with the advent of multivariate methods of data analysis, relationships still remain obscure (Allen

et al. 1977). Questions have been raised over the effectiveness of these methods when applied to very large data sets (Van der Maarel et al. 1987). This concern has led to the use of a two-step method for the classification of very large phytosociological data sets (Van der Maarel 1982, Orloci & Stanek 1979, Jensen & Van der Maarel 1980).

The study of benthic algal communities presents a range of problems for the investigator (Bohr 1973). Terminology applied to benthic algae is extensive and many terms are unnecessarily complex and quite confusing. Floristic surveys of algal distribution among communities produced numerous and lengthy lists of species (Wetzel 1983). In the search for a method to distinguish ecological units of benthic algal communities, phytosociological methods used for the study of macrophytes have been adopted to the study of microphytes (Bohr et al. 1983), but have not gained widespread acceptance (Bohr 1973). If one wishes to use the concept of an association to characterize and compare benthic assemblages, then a system based on the annual complement of assemblages which is quick and effective is needed (Round 1981). This may explain why phytosociological methods have not been more widely used.

One of the most challenging areas for the development of appropriate methodology arises from efforts to understand interactions between complete benthic communities and their physical, chemical, and biological environment (Robinson

1983). The complexity of such communities and the nature of their environments, however, appear to have posed difficulties for the analyses of such detailed interactions (Robinson 1983). The inter-relationships between two sets of measurements (biotic and environmental) made on the same subjects can be studied using a two-step analysis. This would involve (1) demonstration of selection of environmental parameters by benthic species and (2) use of this information to determine the existence of habitat specific associations within benthic diatom communities. This has been the purpose of the present study.

1.3 MATERIALS & METHODS

A data set was compiled from a sample of publications describing periphytic diatom communities or assemblages. Selection of the data set was based upon the the use of recent taxonomy and upon the presence of site specific environmental information. The result consisted of a compilation of species lists, their classification as benthic species and corresponding parameters of pH, nutrient status, current and general habitat. Physiognomic and environmental characterizations are modifications of Hustedt (1937-1938), Smith (1966), Lowe (1974), and Foged (1974,1977). Parameters were defined as follows:

1. pH (ranges after Hustedt 1937-1938)

acidic: occurs at pH less than 7
indifferent: occurs around pH 7
alkaline: occurs at pH greater than 7

2. Nutrient (after Smith 1966)

eutrophic: occurs in water with high nutrient concentrations
mesotrophic: occurs in waters with moderate nutrient concentrations
oligotrophic: occurs in waters with low nutrient concentrations
dystrophic: occurs in waters rich in humic material

3. Current (after Hustedt 1937-1938)

limnophilous: occurs in standing water but may be found in running water
indifferent: common to both flowing and standing water
rheophilous: characteristic of running water but may be found in standing water

4. General Habitat (after Lowe 1974 and Foged 1974, 1977)

estuary: occurs in both estuaries and brackish water
lake: occurs in large inland bodies of standing water
pond: occurs in small inland bodies of standing water
river: occurs in larger streams and rivers
stream: occurs in smaller streams and rivers
springs: occurs in springs
lagoon: occurs in lagoons
pools: occurs in pools
swamp: occurs in swamps and bogs

5. Classification of Benthic Species (after Lowe 1974)

epipsammic: occurs on sand grains
epipelagic: occurs in mud
epilithic: occurs on rock
epiphytic: occurs on macrophytes
periphytic: occurs on artificial substrata

It should be emphasized that this study employed presence/absence data only. Data were analyzed based on yearly or seasonal records, the former referring to records that did not specify seasons and the latter referring to

records that specified seasons. Data sources are cited in Tables 1.1 and 1.2. Species that occurred less than two times or in less than two sites were removed from the data set as it was felt that they contained insufficient information on interspecific affinities (Kenkel 1987). Cluster analysis was used to classify physiognomic and environmental characteristics into site groups and associated species lists into species groups. In both cases the Ochiai coefficient (Orloci 1978) was used as input into an agglomerative sum of squares cluster analysis (Ward 1963).

Correspondence analysis was used to examine the relationships within and among the site groups and species groups generated by cluster analysis. The original data matrix was ordered according to the species and site groups, and then the number of occurrences for species of a given group within a given site type was recorded. This resulted in a $q \times t$ contingency table (q = # of species groups; t = # of site types), which was then examined using correspondence analysis after adjustment to equal block size (Feoli & Orloci 1979). The result was a simultaneous ordination of site groups and species groups through a partitioning of the total contingency chi-squared (Kenkel 1987).

Table 1.1. Literature citations for the yearly data .

Site	Citations
1	Bowker,D.W. & P.Denny,1980
3	Bruno,M.G. et al.,1982
4	Dor,I.,1974
5	"
7	Ennis,G.L. & L.J.Albright,1982
8	"
9	Happey-Wood,C.M. & J.Priddle,1984
10	"
11	"
12	"
13	Hickman,M.,1971
14	Lachavanne,J.B.,1980
15	Mueller-Haekkel,A. & H.Hakansson,1978
16	Moore,J.W.,1981
17	Meuller,C.,1980
18	Moore,J.W.,1974
19	"
20	"
21	"
22	"
23	"
24	"
25	"
26	Moore,J.W.,1972
27	Round,F.E.,1953
28	"
29	Sullivan,M.,1975
30	Strenski,M.R.,1979
31	Schoemen,F.R.,1982
32	Whitford,L.A.,1956
33	"
34	"
35	Ward,J.V. & R.G.Dufford,1979

Table 1.2. Literature citations for the seasonal data.

Site	Citations
1	Dickman, M. et al., 1983
2	Dickman, M., 1973a
4	"
5	Dickman, M., 1974
6	"
7	"
8	Dickman, M., 1973b
9	Economou-Amilli, A. & K. Anagnostidis, 1981
10	Eminson, D., 1978
11	"
12	"
13	"
14	"
15	"
16	Hoagland, K.D. et al., 1982
17	"
18	"
19	"
20	"
21	"
22	"
23	"
24	Hickman, M., 1982
25	"
26	"
27	Happey-Wood, C.M. & J. Priddle, 1984
28	Hansmann, E.W. & H.K. Phinney, 1972
29	"
30	"
31	"
32	"
33	Jenkerson, C.G. & M. Hickman, 1983
34	"
35	Korte, V.L. & D.W. Blinn, 1983
36	"
37	Leland, H.V. & J.L. Carter, 1984
38	"
39	"
40	"
41	"
42	Lazareck, S., 1982
43	"
44	Moore, J.W., 1981b
45	"
46	Moore, J.W., 1980
47	"
48	Moore, J.W., 1974b
49	Obeng-Asamoah, E.K. et al., 1980
50	"
51	"
52	"
53	Pip, E. & G.G.C. Robinson, 1982
54	Stevenson, R.J. & E.F. Stoermer, 1981
55	Sheath, R.G. et al., 1982
56	"

1.4 RESULTS

1.4.1 Yearly Classification of Sites

The cluster analysis dendrogram of the 33 sites included in the data set is presented in Figure 1.1. Six site groupings have been recognized. Table 1.3 summarizes environmental characteristics of the six recognized groups, based on the available site data. The results suggest that most groupings are characterized by a unique combination of environmental factors that may be expected to influence the overall species composition. Nutrient status, pH, general habitat, and to a lesser extent current all appear to be important factors.

1.4.2 Yearly Classification of Species

The cluster analysis dendrogram of the 195 species included in the data set is presented in Figure 1.2. Nine species groups have been recognized. Table 1.4 presents a list of the groupings of the 195 species encountered in the study. Environmental characteristics of the groupings are described briefly in Table 1.5. The species groups suggest the occurrence of interspecific associations in response to pH, nutrient status and general habitat.

Figure 1.1: Sum of squares agglomeration dendrogram based on Ochiai coefficient of the 33 sites included in the yearly data set. Six groupings (A-F) are indicated.

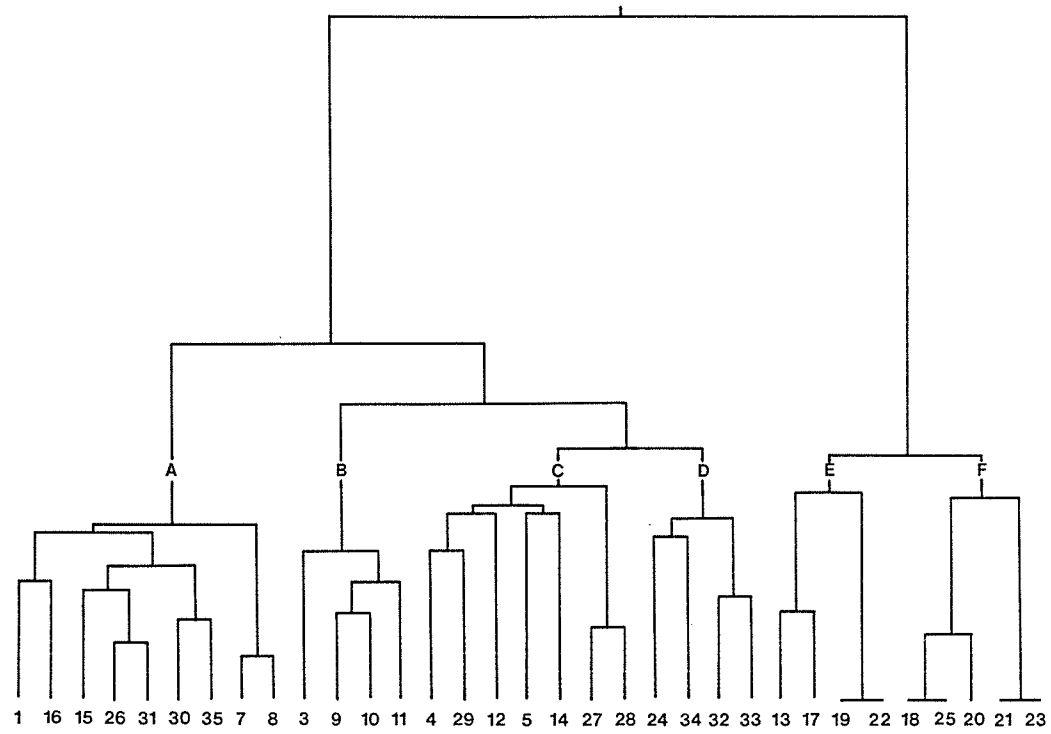


Table 1.3. Environmental characterization of the six site groupings generated by cluster analysis (Figure 1.1) for yearly data.

	A	B	C	D	E	F
Classification of Periphytic Species	Epilithon	Epipelon	Epipelon	Periphyton	Epipelon	Epipelon
General Habitat	River, Stream	Lake	Lake	Spring	River	River
Nutrient Status	Eutrophic, Mesotrophic	Eutrophic	Eutrophic	Mesotrophic, Saline, Oligotrophic	Mesotrophic, Oligotrophic	Mesotrophic
Current	Lotic	Lentic	Lentic	Lotic	Lotic	Lotic

Figure 1.2: Sum of squares agglomeration dendrogram of the 195 species encountered in the yearly study. Nine ecological groups (1-9) are indicated. Species names associated with these groups are given in Table 1.4.

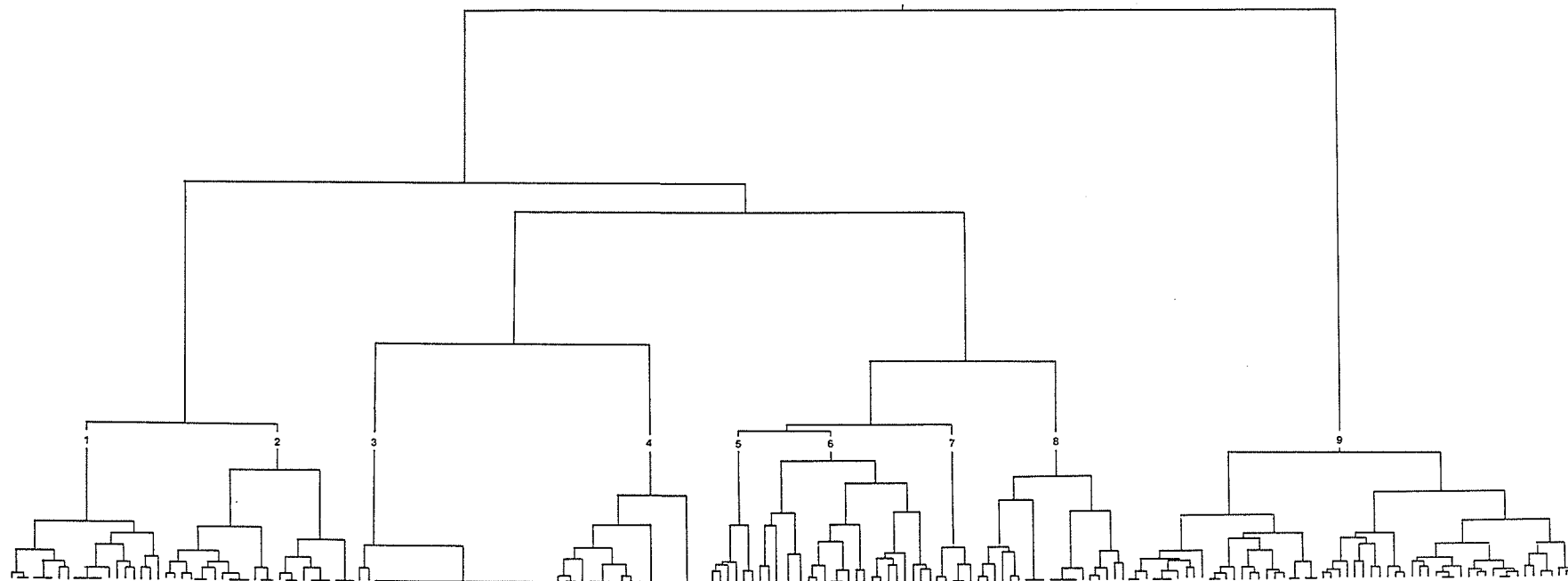


Table 1.4. List of the 195 species encountered in the yearly study. Ordering of species corresponds to the dendrogram in Figure 1.2. From left to right.

Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9
<i>Achnanthes allinis</i>	<i>Achnanthes exigua</i>	<i>Achnanthes hungarica</i>	<i>Caloneis bacillum</i>	<i>Achnanthes marginulata</i>	<i>Anomooneis senans</i>	<i>Amphipora peludosa</i>	<i>Cymatopleura allipuca</i>	<i>Achnanthes clevei</i>
<i>Eunotia curvata</i>	<i>Cocconeis podiculus</i>	<i>Navicula capitata</i>	<i>Cymbella microcephala</i>	<i>Eunotia tenella</i>	<i>Mastogloia smithii</i>	<i>Bacillaria paradoxa</i>	<i>Pinnularia maior</i>	<i>Diatoma hiemale</i>
<i>Gomphonema angustata</i>	<i>Caloneis lewisii</i>	<i>Caloneis limosa</i>	<i>Navicula vulpina</i>	<i>Tabellaria flocculosa</i>	<i>Melosira araneata</i>	<i>Epithemia adnata</i>	<i>Cymatopleura solida</i>	<i>Fragilaria leptostauron</i>
<i>Cymbella tumida</i>	<i>Cyclotella stelligera</i>	<i>Cymbella amphicephalae</i>	<i>Navicula radiosa</i>	<i>Melosira distans</i>	<i>Epithemia musculus</i>	<i>Synedra robusta</i>	<i>Cymbella lanceolata</i>	<i>Diatoma vulgare</i>
<i>Opahora maryii</i>	<i>Fragilaria pinnata</i>	<i>Diplooneis smithii</i>	<i>Cyclotella kutzingiana</i>	<i>Navicula cocconeiformis</i>	<i>Platysigma angulatum</i>	<i>Synedra fasciculata</i>	<i>Pinnularia vidua</i>	<i>Navicula inopunctata</i>
<i>Sutroella angustata</i>	<i>Navicula cuspidata</i>	<i>Fragilaria vulgaris</i>	<i>Cymbella cymbiformis</i>	<i>Nitzschia thermalis</i>	<i>Nitzschia gendershemiensis</i>		<i>Nodium dubium</i>	<i>Sutroella ovata</i>
<i>Epithemia lurgida</i>	<i>Nitzschia amphibia</i>	<i>Gyrosigma atenuatum</i>	<i>Cymbella lepicoromis</i>		<i>Cyclotella manghiniana</i>		<i>Cymbella lata</i>	<i>Nitzschia linearis</i>
<i>Navicula viridula</i>	<i>Melosira varians</i>	<i>Gyrosigma scalproides</i>	<i>Cymbella lurgida</i>		<i>Navicula cincta</i>		<i>Navicula gastrium</i>	<i>Gomphonema parvulum</i>
<i>Asterionella formosa</i>	<i>Navicula oligonensis</i>	<i>Hantzschia amphioxys</i>	<i>Diplooneis oblongifolia</i>		<i>Navicula protracta</i>		<i>Navicula graciloides</i>	<i>Nitzschia acicularis</i>
<i>Diplooneis elliptica</i>	<i>Navicula exigua</i>	<i>Navicula accomoda</i>	<i>Rhoosaxella gibba</i>		<i>Nitzschia apiculata</i>		<i>Cymbella dilatata</i>	<i>Denticula elegans</i>
<i>Navicula pelliculosa</i>	<i>Synedra rumpans</i>	<i>Navicula anglica</i>	<i>Cymbella inaequalis</i>		<i>Nitzschia hungarica</i>		<i>Pinnularia brodiaei</i>	<i>Cyclotella glomerata</i>
<i>Nodium binodo</i>	<i>Cymbella naviculiformis</i>	<i>Navicula atomus</i>	<i>Cymbella inaequalis</i>		<i>Navicula clamenis</i>		<i>Nodium bisulcatum</i>	<i>Fragilaria crotonensis</i>
<i>Navicula bacillum</i>	<i>Gyrosigma sponcorii</i>	<i>Navicula lanceolata</i>	<i>Synedra kniegeri</i>		<i>Navicula grogaria</i>		<i>Nodium allina</i>	<i>Navicula scutelloides</i>
<i>Gyrosigma acuminatum</i>	<i>Sutroella tenera</i>	<i>Navicula moniculata</i>	<i>Synedra capitata</i>		<i>Cymbella maxicana</i>		<i>Nitzschia angustata</i>	<i>Amphora collariformis</i>
<i>Nitzschia sigmoides</i>	<i>Achnanthes linearis</i>	<i>Navicula muica</i>	<i>Navicula bryophila</i>		<i>Gomphonema sphaerophora</i>		<i>Stauroneis phoenocentron</i>	<i>Navicula hantzschiana</i>
<i>Rhizosolenia curvata</i>	<i>Fragilaria brevistriata</i>	<i>Navicula pygmaea</i>	<i>Navicula somnium</i>		<i>Eunotia pectinatis</i>		<i>Synedra delicatissima</i>	<i>Nitzschia sigma</i>
<i>Caloneis ventricosa</i>	<i>Gomphonema truncatum</i>	<i>Navicula subhamulata</i>	<i>Stephanodiscus hantzschii</i>		<i>Melosira granulata</i>		<i>Stauroneis encaps</i>	<i>Navicula salinarum</i>
<i>Navicula rhynchocephala</i>	<i>Navicula minima</i>	<i>Nitzschia communis</i>	<i>Synedra nana</i>		<i>Gomphonema longicaeps</i>		<i>Synedra radians</i>	<i>Nitzschia dissipata</i>
<i>Frustulia rhomboides</i>	<i>Nitzschia lenticola</i>	<i>Nitzschia denticula</i>	<i>Synedra tenera</i>		<i>Navicula haueri</i>			<i>Nitzschia frustulum</i>
	<i>Stauroneis smithii</i>	<i>Nitzschia houlihaniana</i>			<i>Nitzschia filiformis</i>			<i>Cyclotella ocellata</i>
	<i>Synedra parastica</i>	<i>Nitzschia recta</i>			<i>Nitzschia tryblionella</i>			<i>Ditymosiphonia gominata</i>
	<i>Gomphonema clevei</i>	<i>Nitzschia sinuata</i>						<i>Gomphonema lanceolatum</i>
	<i>Gomphonema subclavatum</i>	<i>Pinnularia bicaps</i>						<i>Sutroella angusta</i>
	<i>Sutroella ovalis</i>	<i>Pinnularia subcapitata</i>						<i>Achnanthes lanceolata</i>
		<i>Rhopalodia gibbarula</i>						<i>Cocconeis placontula</i>
								<i>Synedra vlna</i>
								<i>Anomooneis vitrea</i>
								<i>Nitzschia palea</i>
								<i>Epithemia sorex</i>
								<i>Gomphonema horculeana</i>
								<i>Amphora ovalis</i>
								<i>Navicula cryptocephalae</i>
								<i>Navicula pupula</i>
								<i>Achnanthes microcephala</i>
								<i>Amphipora peludosa</i>
								<i>Cymbella prostrata</i>
								<i>Diatoma tenue</i>
								<i>Gomphonema olivaceum</i>
								<i>Hantzsoa arcus</i>
								<i>Mendon circularis</i>
								<i>Achnanthes minutissima</i>
								<i>Cymbella minuta</i>
								<i>Cymbella sinuata</i>
								<i>Cymbella sinuata</i>
								<i>Fragilaria vaucheriana</i>
								<i>Fragilaria capucina</i>
								<i>Cyclotella comia</i>
								<i>Tabellaria fenestrata</i>
								<i>Stephanodiscus asuraea</i>
								<i>Stephanodiscus tenuis</i>
								<i>Cymbella allinis</i>
								<i>Gomphonema truncatum</i>
								<i>Synedra acuta</i>

Table 1.5. Environmental characterization* of the nine species groupings generated by the cluster analysis (Figure 1.2).

	1	2	3	4	5	6	7	8	9
Dominant Genera	Navicula	Navicula, Gomphonema, Nitzschia, Surirella, Achnanthes, Synedra, Fragilaria	Navicula, Nitzschia	Cymbella, Navicula, Synedra	Achnanthes, Eunotia, Tabellaria, Melosira, Navicula, Nitzschia,	Navicula, Nitzschia, Melosira, Gomphonema	Amphiprora, Bacillaria, Epithemia, Surirella, Synedra	Neidium, Cymbella, Pinnularia	Nitzschia, Gomphonema, Achnanthes, Fragilaria, Navicula, Cymbella
pH**	Alkaline	Alkaline	Alkaline	Alkaline, Indifferent	Acidic	Alkaline, Indifferent, Acidic	Alkaline, Indifferent	Alkaline, Indifferent	Alkaline
Nutrient Status**	Eutrophic, Mesotrophic	Eutrophic, Mesotrophic	Eutrophic, Mesotrophic	Eutrophic, Mesotrophic	Mesotrophic, Oligotrophic	Eutrophic, Mesotrophic, Oligotrophic	Eutrophic	Mesotrophic, Oligotrophic	Eutrophic, Mesotrophic, Oligotrophic
Current**	Limnophilous, Indifferent, Rheophilous	Indifferent	Indifferent	Limnophilous, Indifferent	Limnophilous, Indifferent	Limnophilous, Indifferent, Rheophilous	Indifferent, Rheophilous	Limnophilous, Indifferent	Limnophilous, Indifferent, Rheophilous
General Habitat**	Lake, Pond, River, Swamp, Spring, Pool, Lagoon	Lake, Pond, River, Spring, Swamp	Lake, Pond, River	Lake, Pond	Lake, Spring, Swamp	Lake	Lake, Pond	Lake	Lake, Pond, Spring

* Physiognomic-environmental characterization of species was compiled from Beaver (1981).

** Classifications of pH, nutrient status, current and general habitat were based on respective modifications of Hustedtl (1937-1938), Smith (1966), Kolbe (1927), Hustedtl (1937-1938), Lowe (1974) and Feged (1974, 1977).

1.4.3 Yearly Ecological Relationships

A two-dimensional scattergram resulting from correspondence analysis is presented in Figure 1.3. This scattergram has a one to one correspondence (Gittins 1985). As a result, both site ordinations and species ordinations were plotted on the same graph. Partitioning of the total contingency chi-squared (Table 1.6) revealed that 81.4% of the total variation was accounted for by the first two canonical axes.

Interesting trends in the relationships between site groupings and species groupings are apparent. Four distinct clusters can be seen. (I) Sites A and B show a strong affinity with species groups 1,2,3, 4, and 9, indicating eutrophic-mesotrophic conditions, waters of high alkalinity and of varying current. Species characterizing this grouping are epilithic or epipellic. (II) Site D shows highest affinity with species groups 6 and 8, that are characteristic of mesotrophic-oligotrophic waters of an alkaline or pH indifferent, and non-flowing nature. Periphytic species characterize the group. (III) Site C shows very high association with species group 7, again reflecting eutrophic conditions, an indifference to pH or a slight tendency towards alkaline conditions and running water. Species of this group were found in the epipelon. (IV) Site groups E and F show very high association with species group 5. This grouping of epipellic species is

Figure 1.3: Two-dimensional concentration analysis ordination of the 6 site groupings (A-F, Figure 1.1) and the nine species groupings (1-9, Figure 1.2). This ordination has a one to one correspondence.

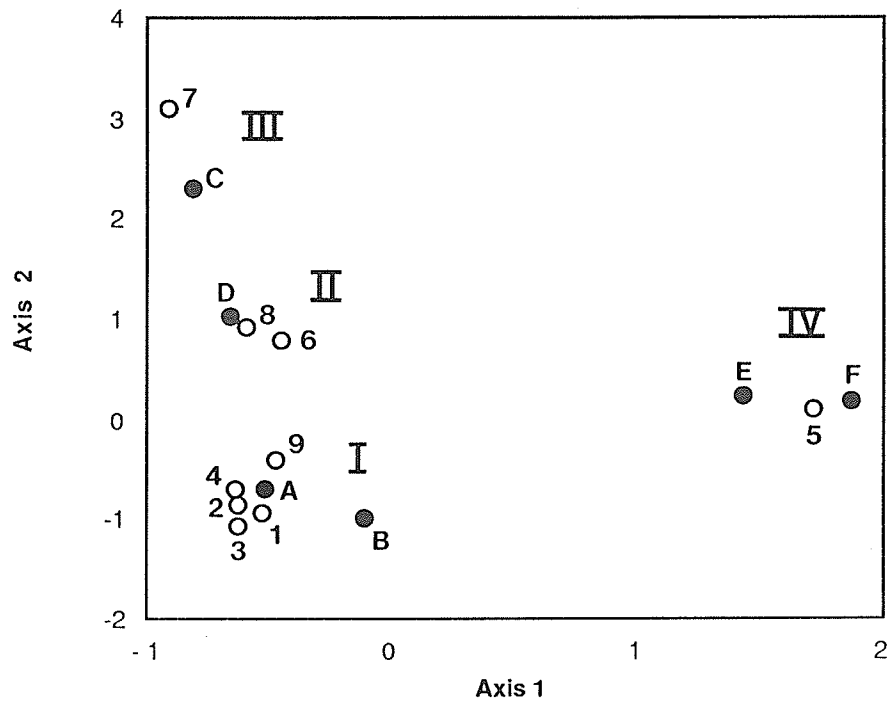


Table 1.6. Partitioned total contingency chi-squared in correspondence analysis (Figure 1.3) of yearly data.

Canonical variate	Canonical correlation	χ^2	Percent
1	0.8378	541.930	54.69
2	0.5867	265.705	26.81
3	0.3917	118.421	11.95
4	0.2898	64.846	6.55
Total		990.902	100.00

associated with acidic, oligotrophic-mesotrophic, and standing water.

1.4.4 Seasonal Classification of Sites

The cluster analysis dendrogram of the 56 sites included in this data set is presented in Figure 1.4. Seven site groupings were recognized. Table 1.7 summarizes environmental characteristics of the six groups based on available site data. Results suggest that groups are characterized by a unique combination of environmental factors that may be expected to influence overall species composition. Nutrient status, pH and general habitat appear to be important factors.

1.4.5 Seasonal Classification of Species

The cluster analysis dendrogram of the 138 species included in this data set is presented in Figure 1.5. Four species groups were recognized. Table 1.8 presents a list of the groupings of the 138 species encountered in the study. Environmental characteristics for the groups are described in Table 1.9. The species groups suggest the development of interspecific associations in response to pH, nutrient status, current and habitat.

Figure 1.4: Sum of squares agglomeration dendrogram based on the Ochiai coefficient of the 56 seasonal sites. Seven site groupings (1-7) are recognized.

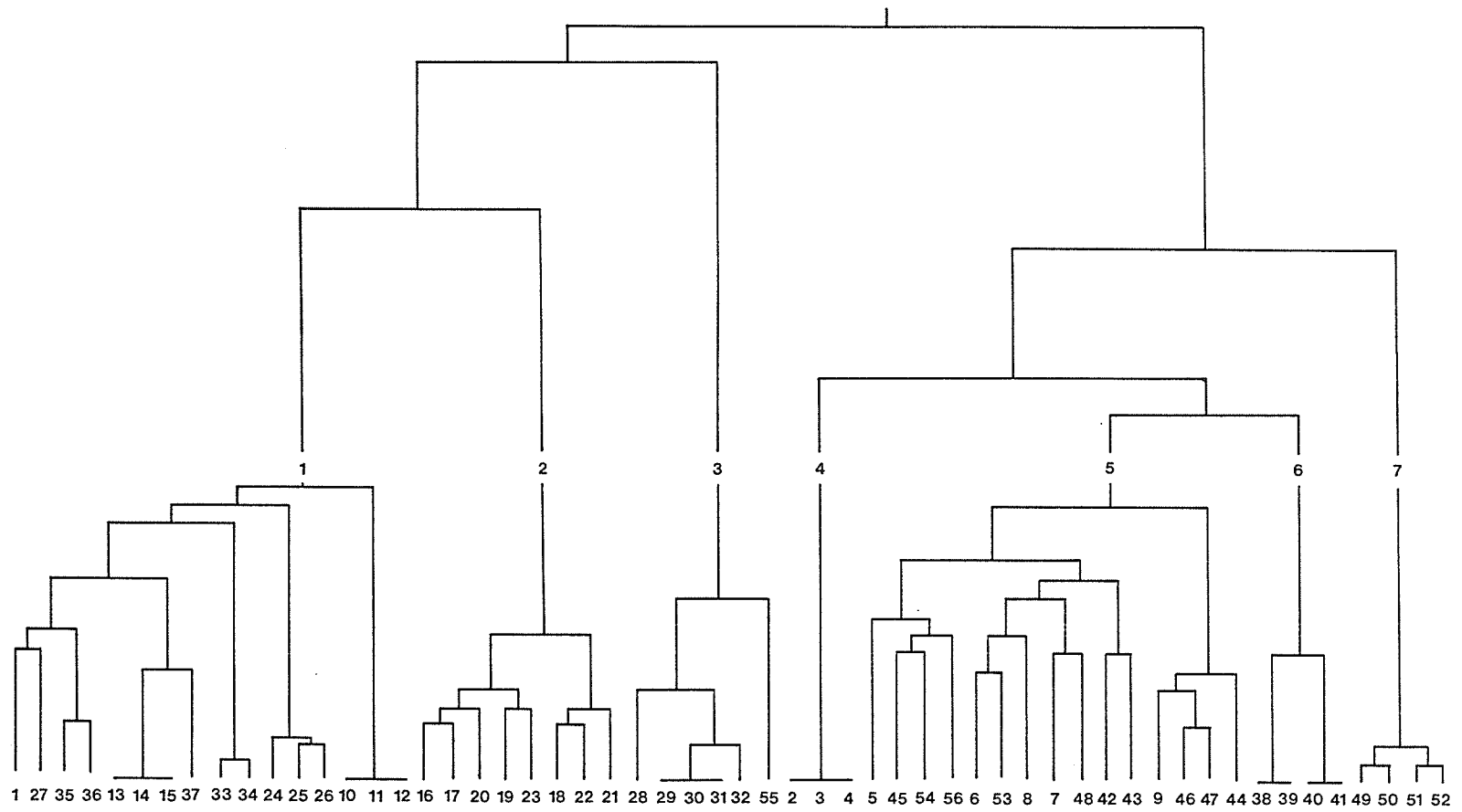


Table 1.7. Environmental characterization of the seven site groupings generated by the cluster analysis (Figure 1.4) for seasonal data.

	1	2	3	4	5	6	7
Classification of Periphyton Species	Epiphyton	Periphyton	Periphyton	Epilithon	Periphyton, Epilithon, Epiphyton	Epilithon, Periphyton	Epiphyton
General Habitat	Lake, Dyke	Reservoir	Stream	River	Lake	Stream	Lake
Current	Lotic, Lentic	Lentic	Lotic	Lotic	Lentic	Lotic	Lentic
Nutrient Status	Eutrophic, Mesotrophic, Oligotrophic	Eutrophic	Mesotrophic	Mesotrophic	Mesotrophic, Oligotrophic	Oligotrophic	Mesotrophic
Season	Spring, Summer	Spring, Summer, Fall, Winter	Spring, Fall	Spring, Summer, Fall	Summer	Summer, Fall	Spring, Summer, Fall, Winter

Figure 1.5: Sum of squares agglomeration dendrogram of the 138 species encountered in the seasonal study. The four ecological groups (A-D) are indicated. Species names associated with these groups are given in Table 1.8.



Table 1.8. List of the 138 species encountered in the seasonal study. Ordering of species corresponds to the dendrogram in Figure 1.5, from left to right.

Group A	Group B	Group C	Group D
<i>Achnanthes flexella</i>	<i>Achnanthes lanceolata</i>	<i>Amphipleura pellucida</i>	<i>Achnanthes linearis</i>
<i>Fragilaria lapponica</i>	<i>Eunotia arcus</i>	<i>Synedra pulchella</i>	<i>Gomphonema angustatum</i>
<i>Fragilaria virescens</i>	<i>Achnanthes lapponica</i>	<i>Gomphonema intricatum</i>	<i>Navicula bacillum</i>
<i>Navicula peregrina</i>	<i>Amphora perpusilla</i>	<i>Melosira granulata</i>	<i>Caloneis bacillum</i>
<i>Pinnularia intermedia</i>	<i>Melosira italica</i>	<i>Fragilaria vaucheriae</i>	<i>Diploneis occulata</i>
<i>Synedra amphicephala</i>	<i>Cymbella lanceolata</i>	<i>Gomphonema olivaceum</i>	<i>Denticula tenuis</i>
<i>Meridion circulare</i>	<i>Fragilaria capucina</i>	<i>Rhokosphenia curvatum</i>	<i>Navicula viridula</i>
<i>Asterionella formosa</i>	<i>Navicula elginensis</i>	<i>Navicula menisculus</i>	<i>Nitzschia sigmoidea</i>
<i>Fragilaria pinnata</i>	<i>Epithemia turgida</i>	<i>Navicula salinarum</i>	<i>Neidium dubium</i>
<i>Hannaea arcus</i>	<i>Gomphonema gracile</i>	<i>Nitzschia dissipata</i>	<i>Cocconeis pediculus</i>
<i>Pinnularia viridis</i>	<i>Achnanthes minutissima</i>	<i>Nitzschia amphibia</i>	<i>Cymbella sinuata</i>
<i>Navicula pupula</i>	<i>Gomphonema parvulum</i>	<i>Nitzschia palea</i>	<i>Diploneis puella</i>
	<i>Cocconeis placentula</i>	<i>Amphora veneta</i>	<i>Eunotia curvata</i>
	<i>Navicula cryptocephala</i>	<i>Nitzschia acuta</i>	<i>Cymbella prostrata</i>
	<i>Caloneis ventricosa</i>	<i>Cymbella affinis</i>	<i>Cymatopleura solea</i>
	<i>Diatoma tenue</i>	<i>Navicula capitata</i>	<i>Hantzschia amphioxys</i>
	<i>Epithemia sorex</i>	<i>Diatoma vulgare</i>	<i>Surirella angustata</i>
	<i>Mastogloia smithii</i>	<i>Melosira ambigua</i>	<i>Fragilaria brevistriata</i>
	<i>Rhopalodia gibba</i>	<i>Nitzschia linearis</i>	<i>Melosira varians</i>
	<i>Cymbella aspera</i>	<i>Gomphonema affine</i>	<i>Anomoeneis vitrea</i>
	<i>Cymbella cuspidata</i>	<i>Nitzschia tryblionella</i>	<i>Synedra radians</i>
	<i>Navicula amphibola</i>	<i>Cyclotella meneghiniana</i>	<i>Synedra tenera</i>
	<i>Gomphonema clevei</i>	<i>Stephanodiscus hantzschii</i>	<i>Eunotia incisa</i>
	<i>Navicula lanceolata</i>	<i>Navicula halophila</i>	<i>Navicula gracilloides</i>
	<i>Navicula tuscula</i>	<i>Surirella ovata</i>	<i>Cymbella cistula</i>
	<i>Cyclotella comta</i>	<i>Navicula schroeteri</i>	<i>Diploneis elliptica</i>
	<i>Navicula seminulum</i>	<i>Navicula tenera</i>	<i>Cymbella cymbiformis</i>
	<i>Gomphonema subclavatum</i>	<i>Stephanodiscus dubius</i>	<i>Gomphonema acuminatum</i>
	<i>Navicula arvensis</i>		<i>Achnanthes pinnata</i>
	<i>Cymbella microcephala</i>		<i>Gyrosigma spencerii</i>
	<i>Fragilaria crotonensis</i>		<i>Frustulia rhomboides</i>
	<i>Cymbella minuta</i>		<i>Cyclotella kutzingiana</i>
	<i>Fragilaria construens</i>		<i>Nitzschia frustulum</i>
	<i>Synedra rumpens</i>		<i>Nitzschia kutzingiana</i>
	<i>Gomphonema truncatum</i>		<i>Eunotia praerupta</i>
	<i>Synedra ulna</i>		<i>Navicula pseudoscutiformis</i>
	<i>Amphora ovalis</i>		<i>Nitzschia angustata</i>
	<i>Anomoeneis zellensis</i>		<i>Synedra parasitica</i>
	<i>Epithemia adnata</i>		<i>Stauroneis anceps</i>
	<i>Navicula radiosa</i>		<i>Tabellaria flocculosa</i>
	<i>Tabellaria fenestrata</i>		<i>Navicula vulpina</i>
	<i>Cymbella meulleri</i>		<i>Nitzschia acicularis</i>
	<i>Cymbella turgida</i>		<i>Nitzschia capitellata</i>
	<i>Gomphonema lanceolatum</i>		<i>Nitzschia filiformis</i>
	<i>Neidium iridis</i>		<i>Nitzschia fonticola</i>
	<i>Synedra fasciculata</i>		<i>Nitzschia subtilis</i>
	<i>Cymbella tumida</i>		<i>Stephanodiscus astraea</i>
	<i>Navicula rhyncocephala</i>		<i>Pinnularia nodosa</i>
	<i>Synedra acus</i>		<i>Neidium affine</i>

Table 1.9. Environmental characterization * of the four species groupings generated by the cluster analysis (Figure 1.5).

	A	B	C	D
Dominant Genera	Fragilaria, Navicula, Pinnularia	Navicula, Cymbella, Gomphonema, Synedra	Navicula, Nitzschia, Gomphonema	Nitzschia, Navicula, Cymbella, Synedra, Eunotia, Diploneis
pH**	Alkaline, Indifferent	Alkaline	Alkaline	Alkaline
Nutrient Status**	Eutrophic, Mesotrophic	Eutrophic, Mesotrophic	Eutrophic	Eutrophic
Current**	Indifferent	Indifferent	Limnophilous, Indifferent, Rheophilous	Limnophilous, Indifferent, Rheophilous
General Habitat**	Lake, Pond, Spring	Lake, Pond, Spring	Lake, Pond, River, Estuary	Lake, Pond, Spring

* Physiognomic-environmental characterization of species was compiled from Beaver (1981).

** Classifications of pH, nutrient status, current and general habitat were based on respective modifications of Hustedt (1937-1938), Smith (1966), Hustedt (1937-1938), Lowe (1974), and Foged (1974, 1977).

1.4.6 Seasonal Ecological Relationships

The two-dimensional scattergram resulting from correspondence analysis is presented in Figure 1.6. This scattergram has a one to one correspondence (Gittins 1985). Partitioning of the total contingency chi-squared (Table 1.10) revealed that 80.6% of the total variation was accounted for by the first two canonical axes. Four distinct clusters were separated by the analysis.

Trends in the relationships between site groupings and species groupings are apparent. (I) Species group B shows a very high association with site groups 1,3,6, and 7. This group is characterized by epiphytic, periphytic, and epilithic species occurring primarily in summer and fall, in a wide range of nutrient conditions and currents. (II) Species group D shows highest affinity with site group 5. This group described an association of periphytic, epipelagic, and epiphytic species occurring during the summer months under mesotrophic-oligotrophic, lentic conditions. (III) Species group C shows a strong affinity with site group 2. Periphytic species occur year round under eutrophic, lentic conditions. (IV) Species group A shows a strong affinity to site group 4 indicating that these epilithic species occur in spring, summer, and fall, under mesotrophic, lotic conditions.

Figure 1.6: Two-dimensional concentration analysis ordination of the 7 site groupings (1-7, Figure 1.4) and the 4 species groupings (A-D, Figure 1.5). This ordination has a one to one correspondence.

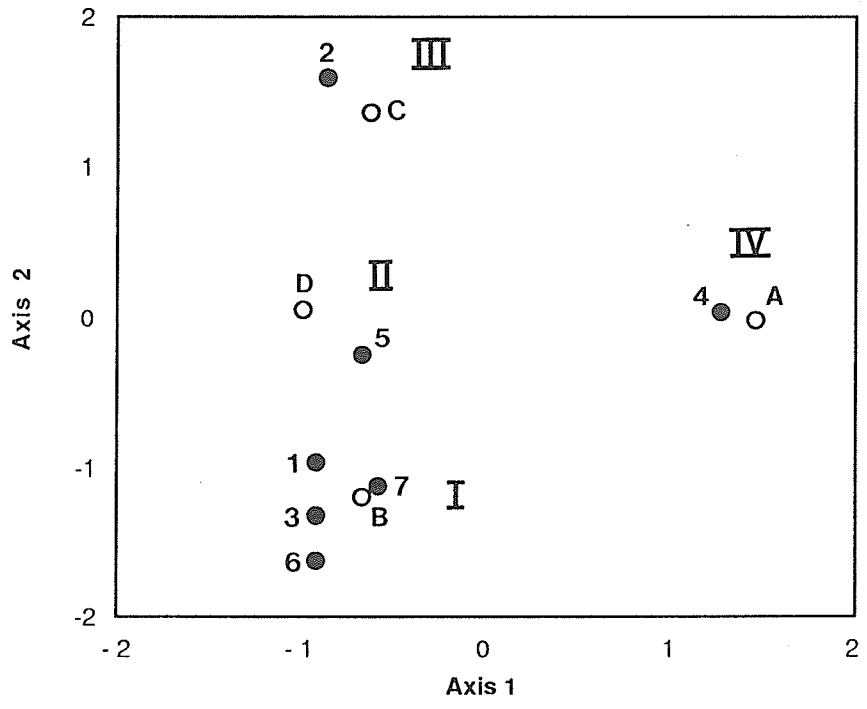


Table 1.10. Partitioned total contingency chi-squared in correspondence analysis (Figure 1.6) for seasonal data.

Canonical variate	Canonical correlation	χ^2	Percent
1	0.7286	439.007	52.90
2	0.5273	229.938	27.71
3	0.4411	160.917	19.39
Total		829.862	100.00

1.5 DISCUSSION

The use of a two-step approach to analyzing the data with multivariate techniques resulted in an interpretable analysis of the data. Cluster analysis proved to be effective in reducing the original data set into smaller, more manageable matrices and in classifying site and species groups. These clusters were checked for floristic interpretability before being used to create a reduced matrix that could easily be run in a multivariate program. Correspondence analysis is particularly useful as it is specifically designed to summarize the relationships between row groups (species) and column groups (sites) simultaneously.

Although multivariate analyses are appearing more frequently in benthic algal literature, their use has not become standard practice, and little change has occurred in data manipulation or presentation (Brown 1969). The study of single environmental parameters and their effect on the development and structure of the community does not take into account either the complexity of benthic algal communities or possible synergistic interactions between periphyton communities and their physical, chemical, and biological environments. This problem of discerning the inter-relationships between the abiotic and biotic measurements can be solved using multivariate techniques. Multivariate analysis can be viewed as a tool with which the

effect of any number of interacting parameters can be analyzed simultaneously.

Results from the yearly data indicate a strong relationship between species and site groupings. The separation of four distinct associations reflects the ecological selection of certain environmental parameters, or combinations of these parameters, by benthic species. Benthic algal communities may, thus, be represented as a series of discontinuous units with combinations of environmental parameters being associated with characteristic species associations (Goodall 1963, Kenkel 1987).

An algal association is a part of a community, that has; a relatively consistent floristic composition, a uniform physiognomy, and a distribution which is characteristic of a particular habitat (Barbour et al. 1980). Wherever a particular habitat repeats itself in a given region, similar associations of taxa are found. This does not mean that every species occurs, nor even that the majority of species occurs. Some species are extremely widespread, with broad tolerance ranges, and can be found in many habitats and in many associations. If clusters of species repeatedly associate together, then, not only does it indicate the stringent requirements of those species, but also provides indirect evidence for strong interactions between them (Barbour et al. 1980). Such evidence favors a view that

communities are indeed integrated units. The development of distinct associations within the benthic community is implied by the strong canopy-understory groupings. Although the majority of species in the data set are represented in the epipelon, this serves to exemplify the separation of these communities into distinct associations each with specific ecological requirements. However, there is some degree of intergradation in the epipelagic groups that is indicative of a wider tolerance to variation in sediment habitats.

Recent benthic diatom ecology studies have suggested that illumination and temperature are two principal environmental factors important in the development of epipelagic, epiphytic, epilithic, and periphytic communities (Round 1953, Moore 1974, Mueller-Haeckel & Hakansson 1978, Ward & Dufford 1979). Mueller (1980) and Hickman (1982), in their studies on periphytic and epiphytic communities respectively, mentioned that changes in water chemistry were responsible for changes in species composition of these communities. Sullivan (1975) and Bowker & Denny (1980) suggested that pH, salinity, differences in amounts of standing water, concentrations of dissolved substances, as well as the influence of the macrophyte also affect community composition. It has been generally accepted that diatom distribution is dependent on the environmental factors existing in a given region (Patrick 1948). This study, in

which a number of basic environmental parameters were used to classify benthic algal associations, supports this view. The separation of benthic diatom communities, in this study, on the basis of their substratum reinforces the concept of habitat specific communities. The grouping of two or more different substratum types, suggested that different species associations had similar ecological requirements. Environmental factors that appeared to be important from this study were pH, nutrient status and general habitat. Freshwater habitats are generally classified into two groups, lotic and lentic. Certain progressive, predictable changes occur in the lotic and lentic systems that result in a continuum of environmental factors. It is this continuum of environments in both systems that may lead one to expect a continuum of algal associations. If such a species continuum is absent and discrete, discontinuous units are present, this may suggest the existence of associations within the benthic community. Unfortunately, most species in this study were indifferent to current. Those classed as limnophilic or rheophilic had a wide tolerance for current.

Species characteristic of Group IV have been described as acidophilous. Important taxa in this group included Achnanthes marginulata, Eunotia tenella, Tabellaria flocculosa, Melosira distans, Navicula distans, Navicula cocconeiformis, and Nitzschia thermalis. Many of these species were also similar to those recorded in ponds near

North Somerset (Hickman 1971), or the rivers of South Baffin Island (Moore 1974). The slightly acidic or indifferent lakes in Lyn Llydaw, Cwellyn and Padarn (Happey-Wood & Priddle 1984) contained similar alkaliphilous species, with the exception of Frustulia rhomboides. These species were classified in Group I. The acidic Thompson Lake (Moore 1981a) contained many alkaliphilous, indifferent, acidophilous species that were classified together in Group II. These species included Anomeoeneis serians, Cymbella diluviana, Gomphonema gracile, Mastogloia smithii, Neidium affine, Neidium bisulcatum, Nitzschia angustatum, Pinnularia brebissonii and Stauroneis phoenicentron. A number of rivers on S.Baffin Island (Moore 1974) contained acidophilous species grouped in Group IV, these included Achnanthes marginulata, Eunotia tenella, Melosira distans and Tabellaria flocculosa. More alkaline tolerant species, Navicula clementis and Navicula gregaria, were placed into Group II. Other species more tolerant to alkaline waters were placed in Group I (Nitzschia acicularis, Nitzschia palea). The acidic species Anomeoeneis serians and Frustulia rhomboides, were grouped into Groups II and I, respectively. The placement of Frustulia into a more alkaline group might indicate a wider tolerance to pH than previously expected.

Group III is a distinct group, with the majority of species being epipelagic. Species of this group have been

found in saltsprings in Florida (Whitford 1956) and saltmarshes (Sullivan 1975). Dor (1974) found similar species in periphytic studies on Lake Kinneret. Studies of epipelton conducted in Lyn Maelog and Lyn Caron by Happey-Wood & Priddle (1984), Thompson Lake by Moore (1981a) and Malharm Tarn by Round (1953) did not record these species, but rather, species that were clumped into one of the largest groups, I, containing epipellic or epilithic species in eutrophic, mesotrophic, alkaline conditions. The majority of species in the yearly data set fall into Group I. This ubiquitous group represents a group in which the environmental conditions are tolerable by most species. The three other groups that exist are quite specific in their habitat requirements and hence, quite distinct in the analysis.

This study shows that there is a high affinity between species groups and seasonality within site groups. As mixed assemblages of organisms, epiphytic, epilithic, epipellic, and periphytic communities exhibit seasonal patterns in species composition which reflect the biotic and abiotic factors impinging on the community. Although ecological parameters in each group are very similar, this allows for the examination of the effect of seasonality on these communities, unhindered by environmental conditions. There appears to be a separation of species that occur early and remain throughout the year, those that occur in summer, and

those that occur later in the year. Seasonality has been loosely referred to in terms of prevailing environmental conditions, ie., the physical and chemical parameters (Hoagland et al. 1982). Seasonally distinct algal associations have been said to be simple, as one may recognize a spring-summer and winter association in many lakes (Round 1981).

The idea of season specific species was supported by Castenholz (1960), Stockner & Armstrong (1971), Brown & Austin (1973a), Klarer & Hickman (1975), Moss (1976), Cattaneo & Kalff (1978), Hickman (1978), Jones & Mayer (1983), and Roos (1983). Seasonal patterns in species composition of algal communities have been followed with the intention of relating seasonal succession to a single environmental factor. Recent studies have shown that illumination as well as fluctuation in water level were responsible for seasonal changes in the species composition of benthic algal communities (Obeng-Asamoah et al. 1980, Jenkerson & Hickman 1983). Hickman (1982) and Moore (1980) mentioned changes in composition due to temperature. Stevenson & Stoermer (1981) further mention wave disturbance. In addition, pH, liming, high metal stresses and waste discharge have been cited as factors responsible for changing species composition and diversity (Moore 1981a, Sheath et al. 1982, Lazarek 1982, Dickman et al. 1983).

The species found in Group IV of the seasonal data are quite distinct. The majority of the species are similar to those found in the Rideau River near Ottawa (Dickman 1973a). Asterionella formosa has also been found in samples collected from the epiphyton (Obeng-Asamoah et al. 1980) and the periphyton (Hoagland et al. 1982). Moore (1981a) found Navicula pupula in epipelagic samples from Gordon Lake, as well as Hannaea arcus, Fragilaria pinnata, and Pinnularia viridis from Great Slave Lake (1980). Achnanthes flexella has been found in the periphyton sampled in Lago Banolas, Spain (1974). Meridion circulare has also been found in periphytic samples (Economou-Amilli & Anagnostidis 1981).

However, there are other epilithic species found in Group I, that are present mainly during the summer and the fall. The majority of species from a stream near the Sierra Nevada, California are similar to the species found in this group (Leland & Carter 1984). In addition, Dickman (1973a) also found Cocconeis placentula, Fragilaria construens, Synedra rumpens, Cymbella minuta, Diatoma tenue, Navicula radiosa, Synedra ulna, and Tabellaria fenestrata occurring in the summer and fall. Similar species were found in the periphyton (Hansmann & Phinney 1972, Dickman 1973b, 1974, Economou-Amilli & Anagnostidis 1981, Hoagland et al. 1982, Korte & Blinn 1983, Leland & Carter 1984). In addition to these, Economou-Amilli & Anagnostidis (1981), Hoagland et al. (1982), Dickman (1974), Hansmann & Phinney (1972),

Korte & Blinn (1983) listed Achnanthes lanceolata, Amphora ovalis, Cymbella lanceolata, Eunotia arcus, Fragilaria capucina, Gomphonema subclavatum, G. gracile, G. clevei, G. parvulum, Navicula lanceolata, N. cryptocephala, Melosira italica, Rhopalodia gibba, and Synedra fasciculata. Eminson (1978), Obeng-Asamoah et al. (1980), Moore (1980), Hickman (1982), Lazarek (1982), Pip & Robinson (1982), Dickman et al. (1983), and Jenkerson & Hickman (1983) found similar species in the epiphyton to those listed in the periphyton and epilithon. They also described Cymbella muellerii, C. tumida, C. turgida, Diatoma tenue, Epithemia adnata, E. sorex, E. turgida, Gomphonema lanceolatum, G. truncatum, Navicula amphibola, N. arvensis, N. elginensis, Mastogloia smithii, Neidium iridis, and Tabellaria fenestrata.

An epiphytic association is found in Group II that has characteristically summer species. Moore (1980) described a number of similar species. Pip & Robinson (1982) found similar species, as well as, Nitzschia fonticola and Diploneis elliptica. Obeng-Asamoah et al. (1980) found Melosira granulata occurring in the summer. Gomphonema intricatum, found in the spring, is also included in this group. Melosira varians, present in a lake near Edmonton (Hickman 1982) was listed as a summer species. Lazarek (1982) found Eunotia incisa, sampled in the spring, to be listed in this group. A number of similar periphytic species are also found in this group. Dickman (1974) included

Cocconeis pediculus and Cymbella cistula. Dickman (1973a) included Gomphonema acuminatum, Neidium affine, Nitzschia subtilis, Pinnularia nodosa, and Stephanodiscus astraea. Korte & Blinn (1983) included Nitzschia frustulum and Nitzschia kutzingiana. Cymatopleura solea, Denticula tenue, Fragilaria brevistriata, Hantzschia amphioxys, Melosira varians, Surirella angustatum, Nitzschia sigmoidea, N. fonticola, and Neidium dubium were found by Economou-Amilli & Anagnostidis (1981). Hoagland et al. (1982) found Caloneis bacillum, Cymbella prostrata, Fragilaria brevistriata, Navicula gracilliodes, N. capitata, N. vulpina, Nitzschia fonticola, N. acicularis, N. filiformis, and Stephanodiscus astraea. Epipellic species found to occur in the summer have been reported by Happey-Wood & Priddle (1984) and Moore (1980,1981a,b).

Periphytic species found in Group III have been reported by Dickman (1974), Economou-Amilli & Anagnostidis (1981) and Korte & Blinn (1983). Happey-Wood & Priddle (1984), Sheath et al. (1982) and Moore (1980,1981a,b) have found Navicula capitata, Amphipleura pellucida, Gomphonema olivaceum, G. intricatum, Fragilaria vaucheriae, Navicula pupula, and N. menisculus, in the epilithon to be similar to those in Group III. Leland & Carter (1984) and Dickman (1973b) listed Amphipleura pellucida, Fragilaria vaucheriae, Gomphonema intricatum, Melosira granulata, Nitzschia palea and Synedra pulchella in the epilithon. Dickman et al. (1983) found

Fragilaria vaucheriae, Nitzschia dissipata, and N. palea in the epiphyton. In addition, Hickman (1982) described Amphipleura pellucida and Diatoma vulgare. Jenkerson & Hickman (1983) added Cyclotella meneghiniana. Moore (1980) listed Cymbella affine, Fragilaria vaucheriae, Gomphonema olivaceum and Nitzschia palea as epiphytes, as well. Obeng-Asamoah et al. (1980) also found Gomphonema intricatum and Melosira granulata in the epiphyton.

The idea that numerous environmental factors are responsible for the seasonal changes in species composition within communities was based on studies that were conducted in single locations. No comparisons have been attempted to correlate environmental factors in seasonality over a wide range of geographic locations. Although this study is preliminary in nature, an attempt has been made to relate species composition, environmental variation and seasonality on a world-wide scale. The separation of characteristic species by season leads one to consider the idea that associations within the haptobenthic and herpobenthic communities are determined by season.

1.6 CONCLUSIONS

The principles underlying associations have been examined for benthic diatom communities. Several associations have been shown to exist in the epiphytic, epipelagic, epilithic, epipsammic, and periphytic diatom communities. These

associations show fixed environmental variables and constant floristic compositions. These benthic algal associations are closely related to limnological status, nutrient status, pH, general habitat, and season.

The use of cluster analysis to establish groupings, followed by correspondence analysis to examine the relationship between environmental and floristic composition simultaneously, effectively delineated associations within the benthic community. This two-step analysis was also very effective in dealing with the large data sets used in this study.

Further work is required to adequately delineate and describe associations within aquatic habitats and to relate their species composition to environmental parameters. The delineation of benthic associations as basic units will eventually permit the generation of wider syntheses and generalizations regarding the ecology, productivity and practical importance of the benthic algae in aquatic systems.

Chapter II

A DESCRIPTION OF SEASONALLY DISTINCT ASSOCIATIONS WITHIN THE PERIPHYTIC DIATOM COMMUNITY IN DELTA MARSH, MANITOBA

2.1 ABSTRACT

Seasonal succession of initial colonizers in the periphytic diatom community of the Delta Marsh, Manitoba (99° 19'W, 50° 07'N) is described. Distinct associations, based on season, were found to exist within the periphytic algal community in the Delta Marsh. Spring (May-June) associations included Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina. The summer (July) association was dominated by Fragilaria capucina. The autumn (August-September) associations were represented by Rhopalodia gibba, Synedra acus, Fragilaria capucina, and Cyclotella meneghiniana.

2.2 INTRODUCTION

The seasonality of haptobenthic algal communities in freshwaters is often described by following periphyton accumulation throughout an entire growing season. Such communities may, however, become established at any time during the season when substrata become available. Since ultimate community structure and function may depend upon initial substrate colonization, it is important to have some knowledge of that initial stage throughout the growing season.

Early studies of the distribution and ecology of periphytic diatom communities were largely descriptive (Hoagland 1983). Seasonal patterns in the composition of periphytic algal communities have been examined by numerous workers (Jones & Mayer 1983). Many such studies utilized periphytic diatoms as indicators of water quality (eg. Patrick et al. 1954, Patrick 1973, Klarer & Hickman 1975, Moss 1976, Eloranta 1988), while others examined primary productivity with respect to overall lake productivity (Newcombe 1949, Gruendling 1971, Cattaneo & Kalff 1979). Still others have documented seasonal succession on both natural and artificial substrata (Stockner & Armstrong 1971, Evans & Stockner 1972, Brown & Austin 1973a, Cattaneo & Kalff 1978, Jones & Mayer 1983).

Due to the variability of natural substrata, artificial substrata have been adopted (Brown 1976, Eloranta 1982, Wetzel 1983). The use of artificial substrata allows some control of experimental conditions (Brown 1976) as the development of attached communities tends to be more uniform than that on natural substrata (Hoagland 1983). Temporal phases of development are also more readily defined, as substratum exposure periods and surface area are directly quantifiable. Despite some controversy over the validity of periphyton studies which have used artificial substrata (Cooke 1956, Sladeckova 1962, Dillard 1969, Dumont 1969, Hynes 1970, Tippet 1970, Patrick 1973, Herder-Brouwer 1975, Cattaneo & Kalff 1979, Loeb 1981), many studies are being conducted with artificial substrata as they are considered a standard for quantifying periphyton biomass and production (Hoagland et al. 1982, Eloranta 1982, Wetzel 1983).

To obtain representative periphyton samples, substratum exposure periods of between two weeks (Patrick et al. 1954, Castenholz 1960, Weber & Raschke 1970) and one month (Brown & Austin 1971, Lowe & Gale 1980) have been used. However, colonizing diatoms can be detected on previously bare substrata within 7-14 days (Tuchman & Blinn 1979), followed by a period of rapid succession (14-35 days) when community structure changes and competition for space occurs (Hoagland et al. 1982). Studies of substratum colonization and periphyton community development have revealed a predictable

seasonal sequence of dominant diatom growth forms (Hudon & Bourget 1981, Hoagland et al. 1982, Korte & Blinn 1983). In the initial stage, mucopolysaccharides accumulate on bare substrata (Zobell 1943, Baier 1973). This may or may not be followed by active attachment of bacteria (Jones et al. 1969, Hirsch & Pankratz 1970, Geesey et al. 1978). Gordon et al. (1969) and Hirsch & Pankratz (1970) suggested that the bacterial layer may promote secondary colonization by providing suitable nutrients and attachment sites. Allanson (1973) has suggested that the bacterial layer facilitates uptake of dissolved organic carbon or other dissolved organic materials by the enzyme-mediated transport at the surface of bacterial cells. However, some scanning electron microscopy studies have revealed that bacterial colonization is not a pre-requisite for diatom colonization (Sieburth & Thomas 1973, Paul et al. 1977). Secondary colonization is invariably by benthic diatoms. However, adnate forms (those attached by most of one valve) are also among the initial diatom colonizers, forming a compact two-dimensional community (Hoagland et al. 1982). Further incorporation of elongate, upright diatoms, attached by means of mucilaginous pads or stalks, create a three-dimensional community (Hudon & Bourget 1981, Hoagland et al. 1982, Korte & Blinn 1983).

The change from a prostrate, two-dimensional community to an erect, three-dimensional community is considered to be characteristic of periphyton colonization of artificial

substrata, and to be representative of the temporal succession of diatom communities. However, a recent study by Miller et al. (1987) of succession in epipsammic communities showed that although both prostrate and stalked forms were present, colonization did not appear to progress from a flat, two-dimensional community to an erect, three-dimensional one. Other studies on periphyton diatom colonization in the oligotrophic Matamek River (Hamilton & Duthie 1984, Hudon et al. 1987) indicated that the primary colonizer was Tabellaria flocculosa, a diatom which forms upright zig-zag colonies. Typical primary colonizers, small motile forms able to adhere flat to the surface, were not abundant. Although occurring in oligotrophic conditions, it was suggested that the periphytic community may be regarded as a nutrient recycling system at a micro-environmental level. Steinman & McIntire (1986), in a study on the effects of current velocity and light on the structure of periphyton assemblages, also found a physiognomic sequence that differed from the pattern observed by Hoagland et al. (1982) in a lentic habitat. Steinman & McIntire (1986) observed early colonization by large rosette and chain-forming species of Synedra, followed by the development of an Achnanthes spp. understory. Such studies also indicated that algal biomass can accumulate rapidly on surfaces lacking a well-developed bacterial flora.

Diatom species succession appears to be strongly influenced by seasonal changes, although it is unlikely that any single factor is responsible for seasonal periodicity (Roberts & Boylen 1988). Seasonal changes in water velocity, temperature, and light can dramatically affect the species composition of periphytic diatom communities (Round 1981, Seaburg & Parker 1983, Oemke & Burton 1986). Sub-optimal light levels, changes in day length, and seasonal fluctuations in nutrient availability may also play a role in determining species composition (Roberts & Boylen 1988). Conditions on the surface of substrata affect the successional sequence of diatom colonization (Hudon et al. 1987). Alteration of substrata by colonizers may, in turn, affect current flow, nutrient status, or removal of metabolites (Sand-Jensen 1983, Hudon et al. 1987). Taxonomic structure of periphytic communities is also influenced by the available inoculum of species, dispersal and colonization rates, competition, herbivory, the chemical and physical environments, as well as spatial and temporal patterns of disturbance (Steinman & McIntire 1986).

In this study, data are presented on initial diatom colonization of artificial substrata positioned in the shallow waters of the Delta Marsh, Manitoba, Canada, throughout the ice-free periods of 1984 and 1985. The objectives of study were: (1) to describe seasonal changes in the composition of initial colonizers over weekly

periods; (2) to re-evaluate the importance of initial colonizers in 'traditional' models of periphyton succession; and (3) to determine if the initial colonizers are representative of seasonally distinct periphytic communities.

2.3 MATERIALS & METHODS

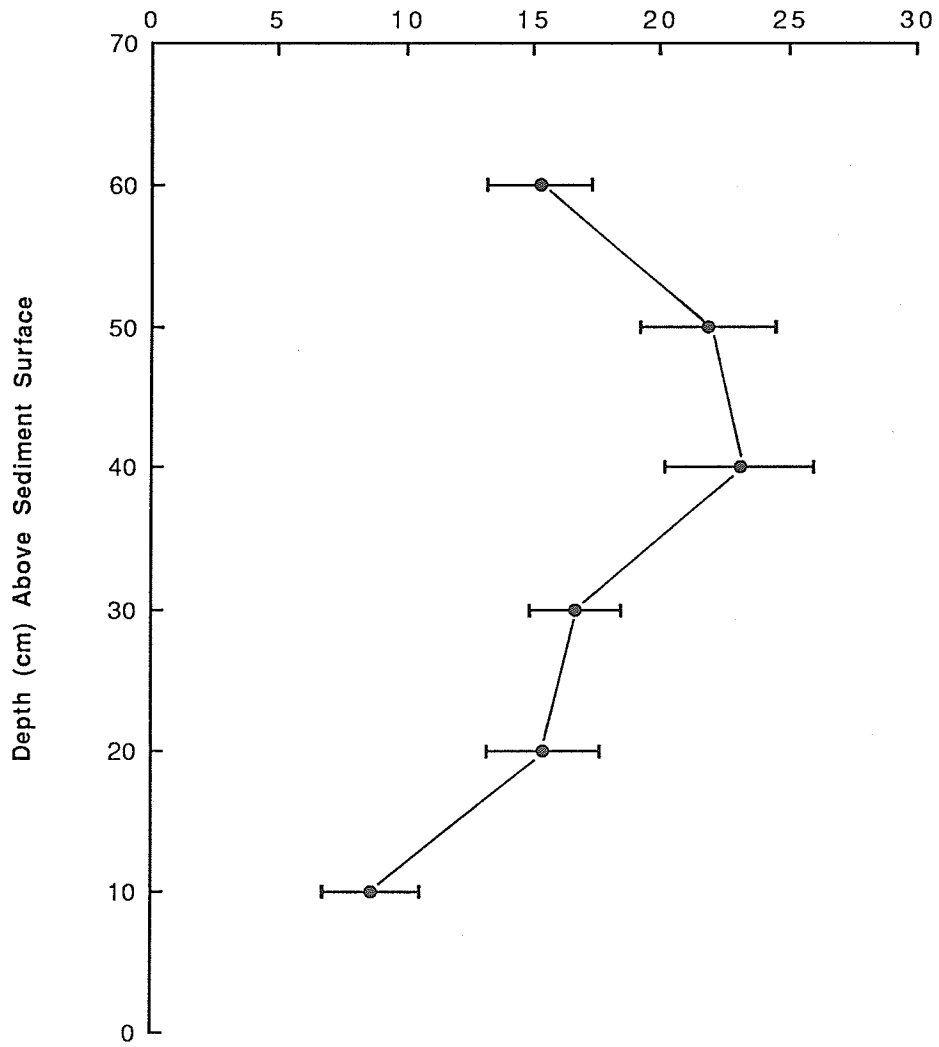
Experiments were conducted in the Blind Channel, Delta Marsh (99° 19'W, 50° 07'N) Manitoba, Canada. Periphytic diatoms were sampled between 8 May and 31 August 1984, and 3 May and 18 August 1985.

Substrata for periphytic algal colonization consisted of extruded acrylic rods (1m length, 0.63cm diameter) that were embedded 30cm into the sediment and extended into the overlying water column. The depth of the marsh averaged 60cm. Rods were scored with a hacksaw blade at 10cm intervals to facilitate sampling at various depths. In Delta Marsh, maximum periphyton production occurred between 10-20cm below the water surface (Figure 2.1). All samples were, therefore, taken from this depth.

In 1984, following initial placement of rods on 8 May, sampling and subsequent replacement of rods was conducted after allowing 7 days exposure. Every second week, single rods were randomly sampled after 1,2,3,4, and 7 days of exposure.

Figure 2.1: Seasonal mean proportion of the total cell density of periphytic diatoms at each depth. Error bars are the standard error of the weekly samples (n=15).

Seasonal Mean Proportion of Total Cell Density at Each Depth (n=15)



In 1985, following initial rod placement on 3 May, sampling and subsequent replacement of rods was conducted bi-weekly, with three rods being randomly sampled after 1,2,3,4,5,6, and 7 days exposure.

In both years, rods were removed from the Channel and the 10cm segments were separated using two pairs of needle-nosed pliers, placed in distilled de-ionized water and preserved with a 5% Lugol's iodine solution. In the laboratory periphyton was removed with a rubber 'policeman'. The iodine solution was removed with repeated centrifugations and resuspensions in distilled de-ionized water. The final suspensions were made to 10mL and again preserved.

One mL of each 10mL sample was washed free of iodine and three 0.1mL aliquots were pipetted onto coverslips and air-dried. Coverslips were then ashed at 600°C for 7 minutes to remove organic material. Permanent diatom mounts were made with Naphrax mountant to facilitate counting.

Diatom frustules were identified and counted in microscope fields of known area along transects until 100-1500 valves were recorded. A minimum of one hundred valves was used to ensure adequate estimates of diversity and frequency. Counting was done with a 400X objective, 12.5X eyepieces a 1.25X nosepiece, and phase contrast microscopy. Nomenclature followed Patrick & Reimer (1966,1975), Germain (1981), and Hustedt (1985). Estimates

of diatom densities were made from samples using the following equation:

$$\text{cells mm}^{-2} = \frac{(\text{cell count})(\text{coverslip area mm}^2)(10\text{mL})}{(\#\text{fields})(\text{field area mm}^2)(\text{rod SA mm}^2)(0.1\text{mL})}$$

where SA represents the surface area of the sampled rod segment. Mean densities and colonization rates were determined using triplicate subsamples from each of the three substratum segments.

This study employed species density data for given sampling periods throughout the year. In 1984, five days were sampled within each sampling period (1,2,3,4,7). In 1985, all seven days were sampled within the weekly sampling period. The data collected for each sampling day in each year was arranged tabularly. After a logarithmic transformation of the data ($X' = \ln(x+1)$), the time periods by species matrices were analyzed using correspondence analysis (Hill 1974). The result was an ordination summarizing the changes in the community structure over time through in additive partitioning of the total contingency chi-squared. The relationship between the overall species density and time period was graphically represented as two-dimensional scattergrams (axis 1 vs. 2). The weeks were joined by a line to indicate temporal change.

The daily samples for each week sampled throughout 1984 and 1985 were graphed using the relative density of the species occurring with >10% frequency. Rare species (<10% frequency) were grouped into the category 'others'.

2.4 RESULTS

One hundred and six diatom taxa representing 31 genera were encountered in 1984 and 1985 (Table 2.1). Fragilaria sp., Diatoma sp., Synedra spp., Nitzschia spp., and Cyclotella sp. occurred commonly throughout the sampling periods.

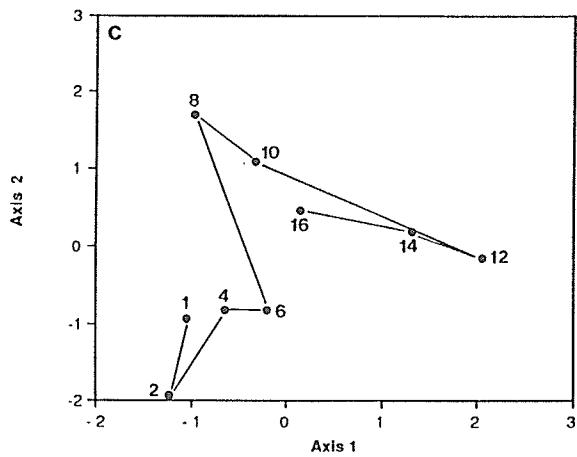
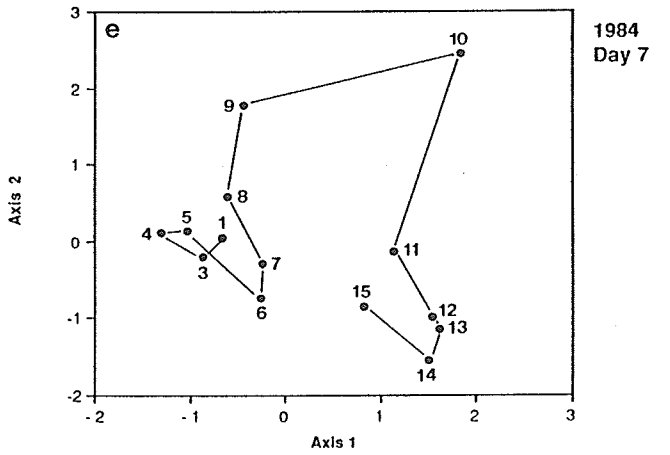
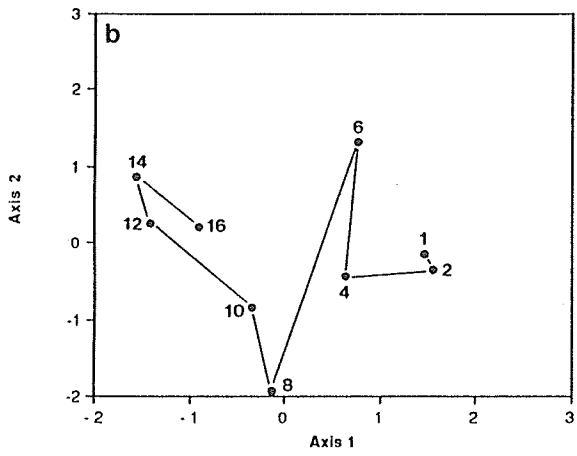
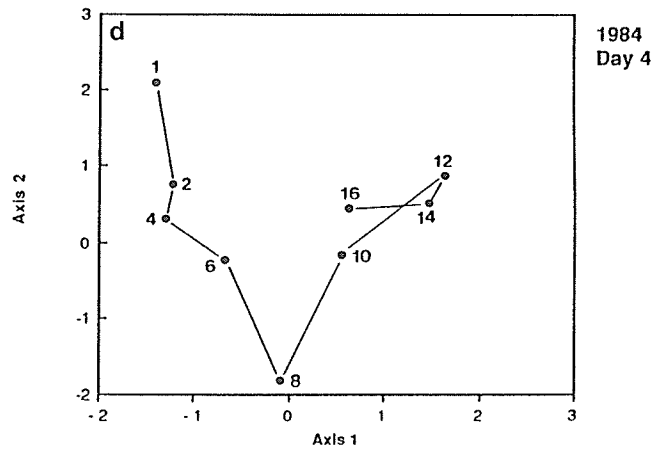
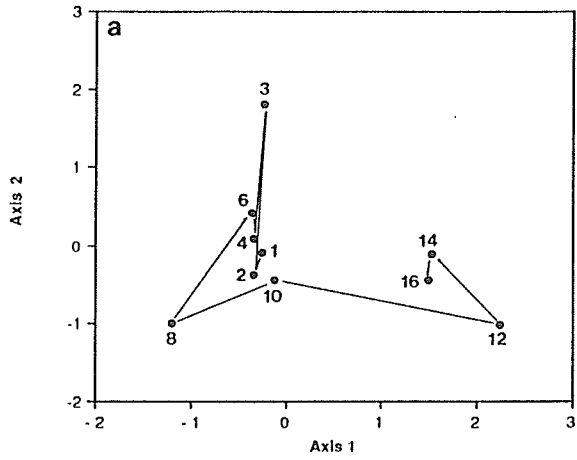
2.4.1 Ordination

The scattergram for the ordination of 1984 Day 1 data is presented in Figure 2.2a. The first two axes accounted for 50% of the canonical structure in the data. Weeks 1 (8 May), 2 (22 May), 4 (5 June), 6 (19 June), and 10 (17 July) were similar in species composition and abundance and had grouped closely together on the scattergram. Week 3 (29 May) was dissimilar to the first grouping, separating apart due to the large numbers of Fragilaria capucina and low numbers of Diatoma elongatum. Week 8 (3 July) differentiated from earlier weeks as Fragilaria capucina dominated. Week 10 (17 July) still had very high Fragilaria capucina densities, but a number of new species were present, making this week similar to weeks 1,2,4, and 6. Weeks 12 (31 July), 14 (14

Table 2.1. List of the diatom species recorded over the study period on the artificial substrata positioned in the Delta Marsh, Manitoba, Canada. 1984 - 1985.

<i>Achnanthes lanceolata</i> Breb. ex Kutz.	<i>Navicula gastrum</i> (Ehr.) Kutz.
<i>Amphiprora</i> sp.	<i>N. halophila</i> (Grun.) Cl.
<i>Amphora coeformis</i> (Ag.) Kutz.	<i>N. lacustris</i> Greg.
<i>A. ovalis</i> (Kutz) Kutz.	<i>N. miniscula</i> Grun.
<i>Anomoeoneis costata</i> (Kutz.) Hust.	<i>N. oblonga</i> (Kutz.) Kutz.
<i>Bacillaria paxillifer</i> (Muller) Hendey	<i>N. peregrina</i> (Ehr.) Kutz.
<i>Caloneis amphisbaena</i> (Bory) Cl.	<i>N. pseudoscutiformis</i> Hust.
<i>C. bacillum</i> (Grun.) Cl.	<i>N. pupula</i> Kutz.
<i>C. lewisii</i> Patr.	<i>N. rheinhardii</i> (Grun.) Grun.
<i>C. limosa</i> (Kutz.) Patr.	<i>N. rhyncocephala</i> Kutz.
<i>Cocconeis placentula</i> Ehr.	<i>N. salinarum</i> Grun.
<i>Cyclotella meneghiniana</i> Kutz.	<i>N. viridula</i> (Kutz.)
<i>Cylindrotheca gracilis</i> (Breb.) Grun.	<i>Neidium affine</i> (Ehr.) Pfitz.
<i>Cymatopleura elliptica</i> (Breb.) W.Sm.	<i>N. bisulcatum</i> (Lagerst.) Cl.
<i>C. solea</i> (Breb.) W.Sm.	<i>N. iridis</i> (Ehr.) Cl.
<i>Cymbella citula</i> (Ehr.) Kirchn.	<i>N. temperei</i> Reim.
<i>C. cymbiformis</i> var. <i>nonpunctata</i> Font.	<i>Nitzschia acicularis</i> W.Sm.
<i>C. lanceolata</i> (Ag.) Ag.	<i>N. apiculata</i> (Greg.) Grun.
<i>C. meullerii</i> Hust.	<i>N. hungarica</i> Grun.
<i>C. minuta</i> Hilse ex Rabh.	<i>N. linearis</i> W. Sm.
<i>C. prostrata</i> (Berk.) Cl.	<i>N. longissima</i> (Breb.) Ralfs.
<i>C. ventricosa</i> Kutz.	<i>N. palea</i> (Kutz.) W.Sm.
<i>Denticula elegans</i> Kutz.	<i>N. sigmoidea</i> (Ehr.) W.Sm.
<i>Diatoma elongatum</i> (Lyngb.) Ag.	<i>N. stagnorum</i> Rabh.
<i>Diploneis elliptica</i> (Kutz.) Cl.	<i>N. tryblionella</i> Hantz.
<i>D. occulata</i> (Breb.) Cl.	<i>N. tryblionella</i> var. <i>levidensis</i> (W.Sm.) Grun.
<i>D. ovalis</i> (Hilse) Cl.	<i>N. vermiculus</i> (Kutz.) Grun.
<i>Epithemia sorex</i> Kutz.	<i>Opephora martyii</i> Herib.
<i>E. turgida</i> (Ehr.) Kutz.	<i>Pinnularia brebissonii</i> (Kutz.) Rabh.
<i>E. zebra</i> (Ehr.) Kutz.	<i>P. gentilis</i> (Donk.) Cl.
<i>Eunotia parallela</i> Ehr.	<i>P. microstauron</i> (Ehr.) Cl.
<i>Fragilaria capucina</i> Demazieres	<i>Pleurosigma australe</i> Grun.
<i>F. construens</i> (Ehr.) Grun.	<i>P. delicatissima</i> W.Sm.
<i>F. construens</i> var. <i>binodis</i> (Ehr.) Grun.	<i>P. elongatum</i> W.Sm.
<i>F. crotonensis</i> Kitton	<i>Rhoicosphenia curvatum</i> (Kutz.) Grun. ex Rabh.
<i>Gomphonema acuminatum</i> Ehr.	<i>Rhopalodia gibba</i> (Ehr.) O.Mull.
<i>G. brebissonii</i> Kutz.	<i>Stephanodiscus</i> sp.
<i>G. constrictum</i> Ehr.	<i>Surirella linearis</i> W.Sm.
<i>G. lanceolatum</i> Ehr.	<i>S. ovalis</i> Breb.
<i>G. parvulum</i> Kutz.	<i>S. utahensis</i> Grun.
<i>G. subclavatum</i> (Grun.) Grun.	<i>Synedra acus</i> Kutz.
<i>G. ventricosa</i> Greg.	<i>S. capitata</i> Ehr.
<i>Gyrosigma acuminatum</i> (Kutz.) Roth.	<i>S. delicatissima</i> W.Sm.
<i>G. macrum</i> (W.Sm.) Griff. & Henfr.	<i>S. filiformis</i> Cl.-Eul.
<i>G. spencerii</i> (Quek.) Griff. & Henfr.	<i>S. rumpens</i> Kutz.
<i>Melosira granulata</i> (Ehr.) Ralfs.	<i>S. ulna</i> (Nitzsch.) Ehr.
<i>M. italica</i> (Ehr.) Ralfs.	Unknown A
<i>Navicula capitata</i> Ehr.	Unknown B
<i>N. cryptocephala</i> Kutz.	Unknown C
<i>N. cuspidata</i> (Kutz.) Kutz.	Unknown D
<i>N. elginensis</i> (Greg.) Ralfs.	Unknown E
<i>N. exigua</i> Greg. ex Grun.	Unknown F
<i>N. explanata</i> Hust.	Unknown G

Figure 2.2: Correspondence analysis ordination for Day 1,2,3,4 and 7 samples, 1984. Numbers 1-16 correspond to sample weeks, May (8,22,29), June (5,12,19,26), July (3,10,17,24,31) and August (7,14,21,28).



August), and 16 (28 August) differed from weeks 1,2,4,6,8, and 10 due to the appearance and high densities of Rhopalodia gibba and Synedra acus. Interestingly, early weeks (May-June) were similar to each other and separated from the two weeks that occurred in July. Another group in August was differentiated. This group appeared to be similar to the first group.

The ordination of the Day 2 samples in 1984 is shown in Figure 2.2b. The first two axes accounted for 47% of the canonical structure in the data set. Weeks 1 (8 May), 2 (22 May), and 4 (5 June) group together. Week 6 (19 June) separated as Fragilaria capucina increased in density. Weeks 8 (3 July) and 10 (17 July) separated from week 6 as Fragilaria capucina continued to increase. Weeks 12 (31 July), 14 (14 August), and 16 (28 August) grouped together with the appearance of Rhopalodia gibba. Week 12 had lower Fragilaria densities and higher Rhopalodia densities than the others. Week 14 had maximum numbers of Rhopalodia. Week 16 had decreasing amounts of Fragilaria, increasing amounts of Rhopalodia, and Synedra acus, making this week more similar to weeks 1,2, and 4. May-June samples were different from July samples that were different from August samples. August samples again circle back toward spring (May-June) samples due to the re-appearance of Synedra acus.

Figure 2.2c shows results of the ordination of Day 3 samples. The first two axes accounted for 49% of the

canonical structure in the data. Similar trends to those described earlier were apparent in the data. Weeks 1 (8 May), 2 (22 May), 4 (5 June), and 6 (19 June) were very similar. This grouping was different from weeks 8 (3 July) and 10 (17 July). Week 12 (31 July) was different from weeks 8 and 10. Weeks 14 (14 August) and 16 (28 August) were progressively different from week 12 and became more similar to weeks 8 and 10.

The scattergram (Figure 2.2d) for Day 4 samples, revealed another interesting trend. The first two axes accounted for 44% of the canonical structure in the data. There was a progression from week 1 (8 May) through week 10 (17 July) with increasing dissimilarity. Weeks 12, 14, and 16 were very similar, and week 16 regressed towards week 1.

Figure 2.2e shows ordination results for Day 7 samples. Thirty-eight percent of the canonical structure of the data is accounted for by the first two axes. Weeks 1 (8 May), 3 (29 May), 4 (5 June) and 5 (12 June) were very similar. Weeks 6 (19 June), 7 (26 June), 8 (3 July), 9 (10 July) and 10 (17 July) were increasingly different from the early group. Weeks 11 (24 July), 12 (31 July), 13 (7 August), 14 (14 August), and 15 (21 August) clustered tightly, and showed some affinity for the early group and weeks 6 and 7.

The first two axes in the ordination for Day 1, 1985, accounted for 69% of the canonical structure of the data

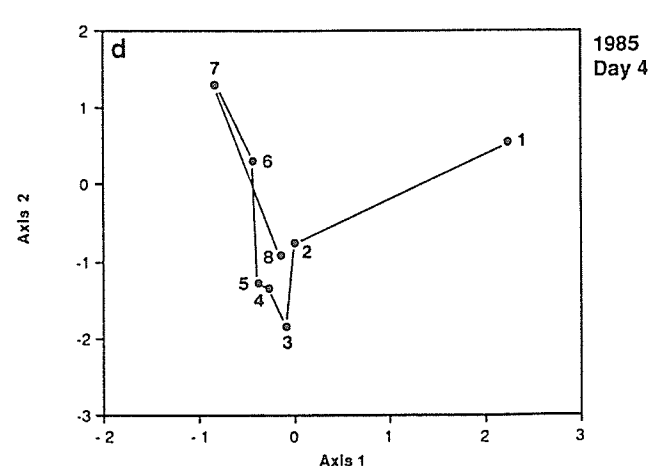
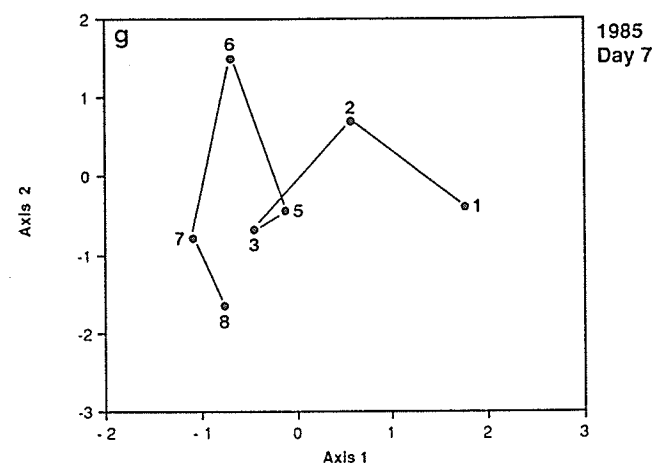
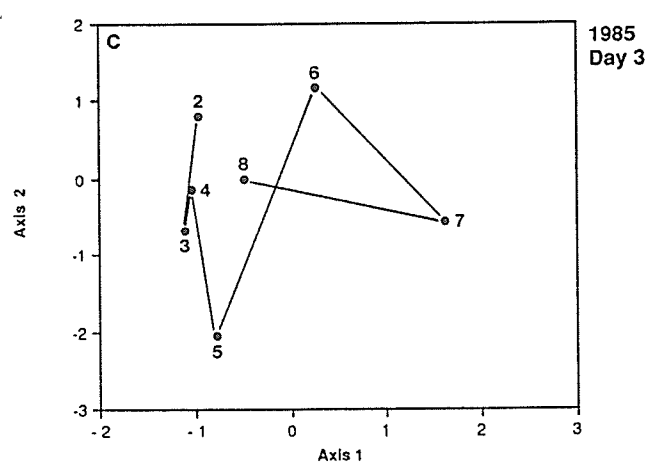
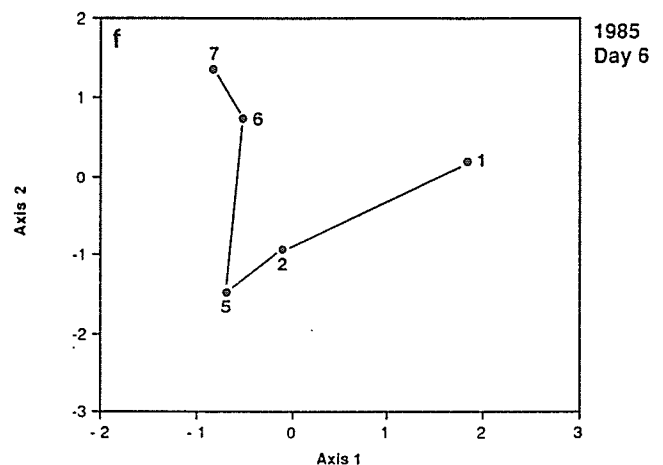
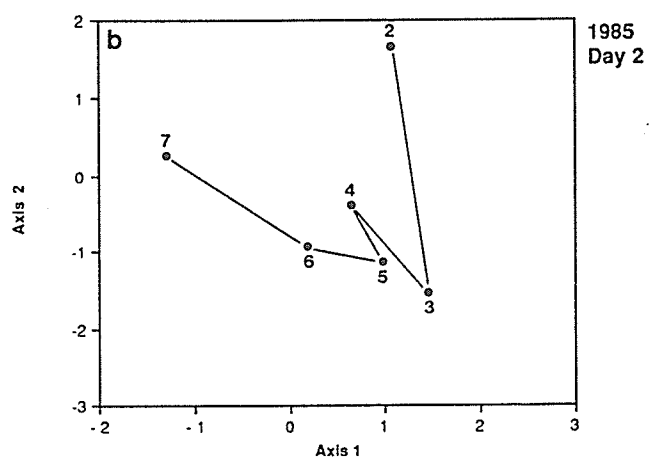
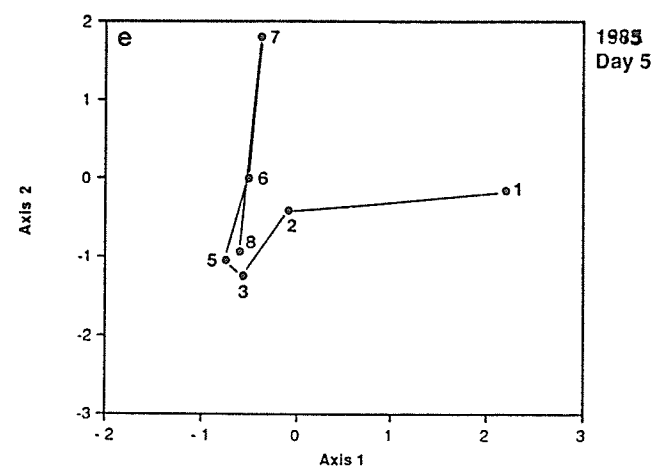
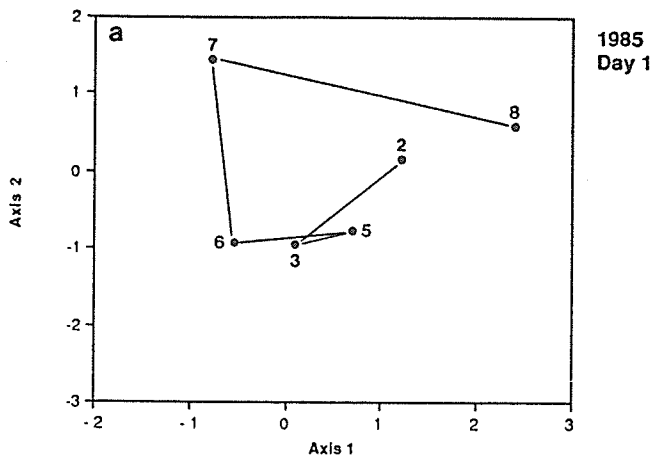
(Figure 2.3a). There was a circular progression of weeks starting at week 2 (20 May) and progressing through weeks 3 (3 June) and 5 (3 July), 6 (16 July), 7 (30 July), and 8 (12 August), with each week being similar to week 2.

Figure 2.3b revealed the separation of Day 2 samples, in which 72% of the canonical structure of the data is accounted for. Week 2 (20 May) through 7 (30 July) showed a progressive dissimilarity. Weeks 3 (3 June) and 6 (16 July) show some similarity. There was little similarity between late and early samples.

Figure 2.3c represents ordination scores for Day 3 samples. Fifty-six percent of the canonical structure of the data set was accounted for by the first two axes. Weeks 3 (3 June) and 4 (17 June) were similar to each other but different from week 2 (20 May). Week 5 (3 July) was quite different from weeks 3 and 4 due to increasing Fragilaria and Synedra ulna densities. Week 6 (16 July) was separated from week 5 due to very high densities of Fragilaria and the introduction of new species. Week 7 (30 July) was increasingly differentiated due to the appearance of Cyclotella meneghiniana. Week 8 showed an affinity with early weeks.

In the Day 4 ordination (Figure 2.3d), 66% of the canonical structure of the data set was accounted for by the first two axes. Week 1 (3 May) was very different from

Figure 2.3: Correspondence analysis ordination for the Day 1-7 samples, 1985. Numbers 1-8 correspond to sample weeks, May (3,20), June (3,17), July (3,16,20) and August (12).



weeks 2 (20 May), 3 (3 June), 4 (17 June) and 5 (3 July). Week 1 had very high densities for most species. Weeks 6 (16 July) and 7 (30 July) were different from weeks 2,3,4, and 5. Week 8 (12 August) was again similar to weeks 2 to 5.

In the ordination of Day 5 samples (Figure 2.3e), 69% of the canonical data structure was accounted for. There was a progression from week 1 (3 May) to week 2 (20 May) to weeks 3 (3 June) and 4 (17 June) to week 6 (16 July) to week 7 (30 July) to week 8 (12 August), which was very similar to weeks 3 and 5.

Figure 2.3f shows increasing dissimilarity in Day 6 samples from week 1 (3 May) to weeks 2 (20 May) and 5 (3 July) to weeks 6 (16 July) and 7 (30 July). The first two axes accounted for 65% of the canonical structure of the data set.

Figure 2.3g shows the ordination scores for Day 7 samples. Sixty percent of the canonical structure was accounted for. Week 1 (3 May) was different from week 2 (20 May). This was different from weeks 3 (3 June) and 5 (3 July), which was different from week 6 (16 July). Weeks 7 (30 July) and 8 (12 August) were progressively different from week 6. Some degree of similarity of this latter group to the first group is apparent.

In general, early sampling weeks tended to be similar. Species composition shifted in summer, becoming

progressively more different from spring samples. In late summer, species composition often began to shift back towards that seen in spring. No two days in 1984 followed the same pattern. Samples taken in 1985 showed little similarity in weekly patterns. When 1984 and 1985 are compared day for day, similar patterns were not evident.

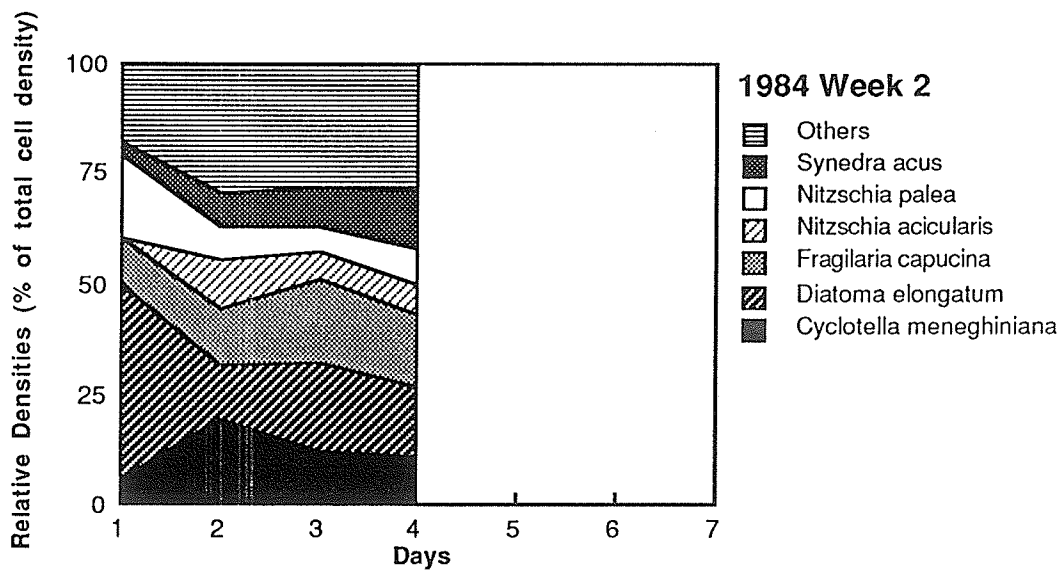
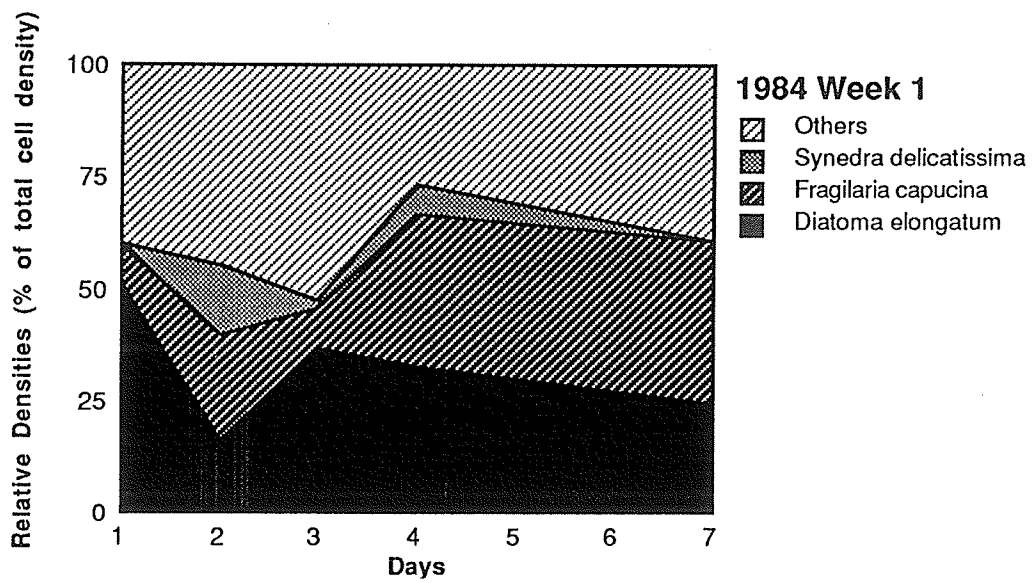
2.4.2 Species Abundance

In the Delta Marsh there was a large number of rare algal species present throughout the year. Eighty percent of the species encountered contributed very little to the total density.

1984 contained a number of missing samples. As a result, there were a number of interpolations in the graphs. Fragilaria capucina and Diatoma elongatum were abundant species in the first week (8-14 May) of sampling in 1984 (Figure 2.4). Days 5 and 6 were not sampled in this first week. At any time during the week the other species accounted for 25-50% of the total species density. Diatoma elongatum had the highest proportion (50%) at the beginning of the week but declined by day 7. Fragilaria capucina was quite low in numbers at the beginning of the week and increased to 25% of the total proportion. Synedra delicatissima was present in small numbers throughout the entire week.

Figure 2.4: Changes in the composition of the haptobenthic algal community over a 7 day period for week 1, 8-14 May, 1984. Days 5 and 6 are missing.

Figure 2.5: Changes in the composition of the haptobenthic algal community over a 7 day period for week 2, 22-28 May, 1984. Days 5, 6 and 7 are missing.



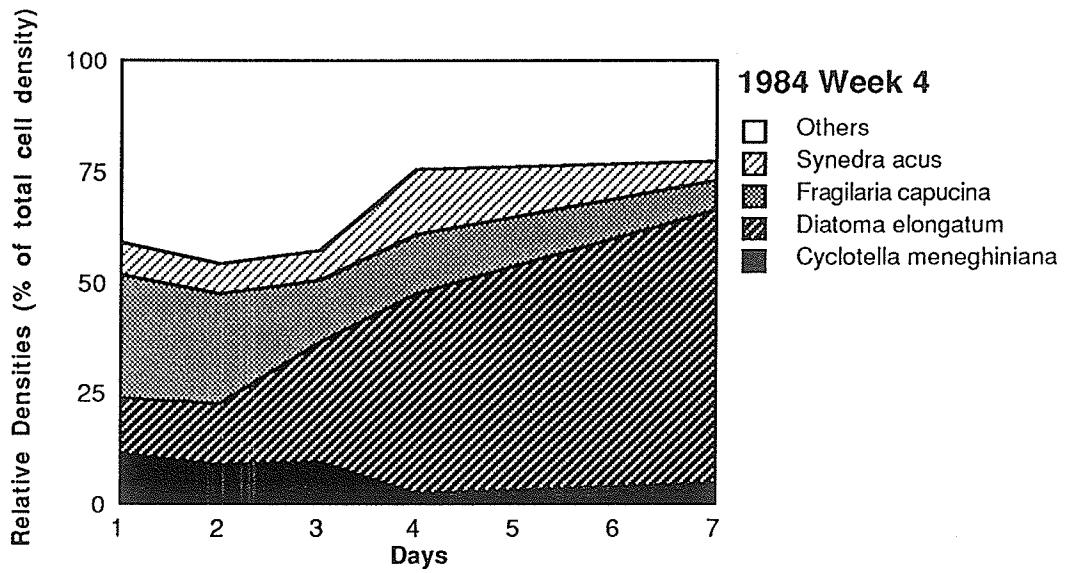
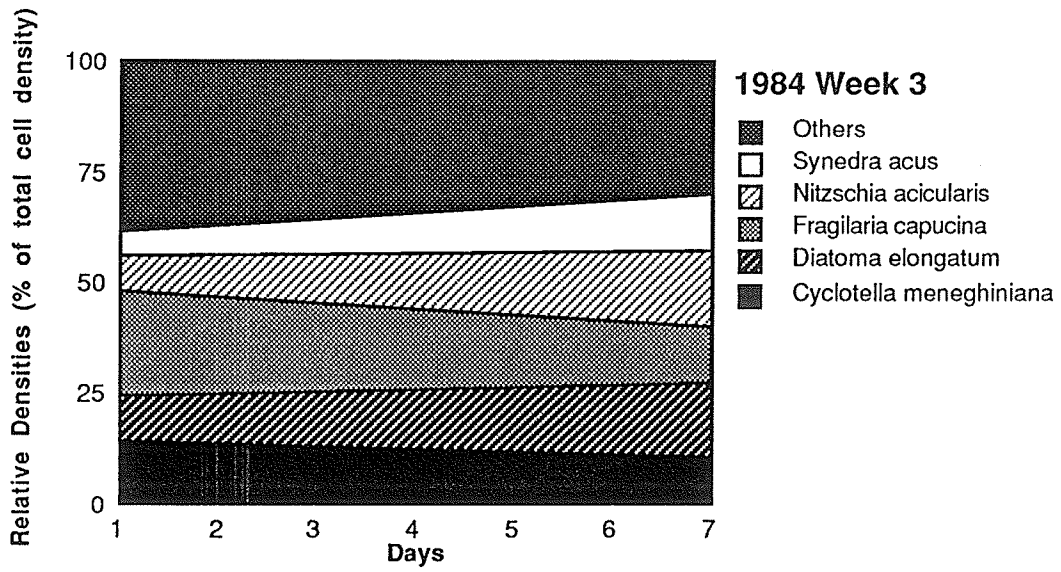
In week 2 (22-28 May), 1984 (Figure 2.5) days 1-4 were sampled. This second week had a number of co-dominant species. Other species accounted for 25 % of the total cell density at any time during the week. Synedra acus, Nitzschia palea, and Nitzschia acicularis were present in low numbers throughout the 4 days. Fragilaria capucina was uncommon during the first two days and increased to 15% by days 3 and 4. Diatoma elongatum had close to 50% total density on the first day and decreased to 15% by day 2. Cyclotella meneghiniana was uncommon at the onset, peaked at 25 % on day 2, then decreased.

Figure 2.6 shows relatively stable proportions of the abundant species in week 3 (29 May-4 June). Days 1 and 7 were the only days sampled and the rest were interpolated. The highest proportion (25-40%) of the total cell density occurred in the 'other' category. Fragilaria capucina had close to 25% of the total density, while Nitzschia acicularis, Synedra acus, Diatoma elongatum, and Cyclotella meneghiniana were consistently low.

In week 4, 5-11 June, (Figure 2.7) Diatoma elongatum started with a low proportion and progressively increased to high values. Others were high in the first 3 days and decreased to lower proportions for the remaining time. Fragilaria capucina was at it's greatest proportion the first two days and then declined. Cyclotella meneghiniana and Synedra acus were present in low amounts the whole week.

Figure 2.6: Changes in the composition of the haptobenthic algal community over a 7 day period for week 3, 29 May - 4 June, 1984. Day 2,3,4,5 and 6 are missing.

Figure 2.7: Changes in the composition of the haptobenthic algal community over a 7 day period for week 4, 5-11 June, 1984.



Week 6, 19-25 June, (Figure 2.8) showed a high proportion of other species at the beginning of the week which decreased to lower amounts for the rest of the week. Nitzschia palea occurred in low amounts the first three days then increased to higher amounts by day 7. Nitzschia acicularis and Diatoma elongatum remained low throughout the whole week. Fragilaria capucina had a higher proportion at the start of the week then decreased towards end of the week.

Week 8, 3-9 July, (Figure 2.9) was dominated by Fragilaria capucina, which occurred at 95% of the total density at any time.

Week 10 (Figure 2.10) was dominated by Fragilaria capucina. Fragilaria capucina had between 75-90% of the total density, although the proportion steadily decreased throughout the week.

Figure 2.11 (week 12, 31 July-6 August) showed two dominant species. Fragilaria capucina was at high amounts early in the week and decreased to 10 % by the end. Rhopalodia gibba, on the other hand, gradually increased from the beginning to the end of the week. Other species accounted for 25% of the total density.

Fragilaria capucina and Rhopalodia gibba were again abundant in week 14, 14-20 August (Figure 2.12). Rhopalodia gibba was predominant with its greatest proportion at day 7.

Figure 2.8: Changes in the composition of the haptobenthic algal community over a 7 day period for week 6, 19-25 June, 1984.

Figure 2.9: Changes in the composition of the haptobenthic algal community over a 7 day period for week 8, 3-9 July, 1984.

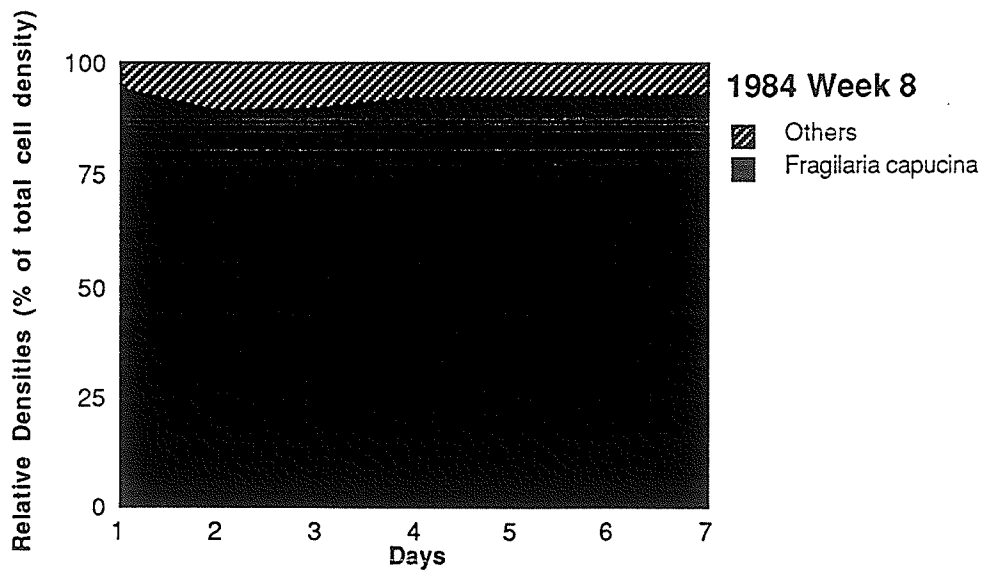
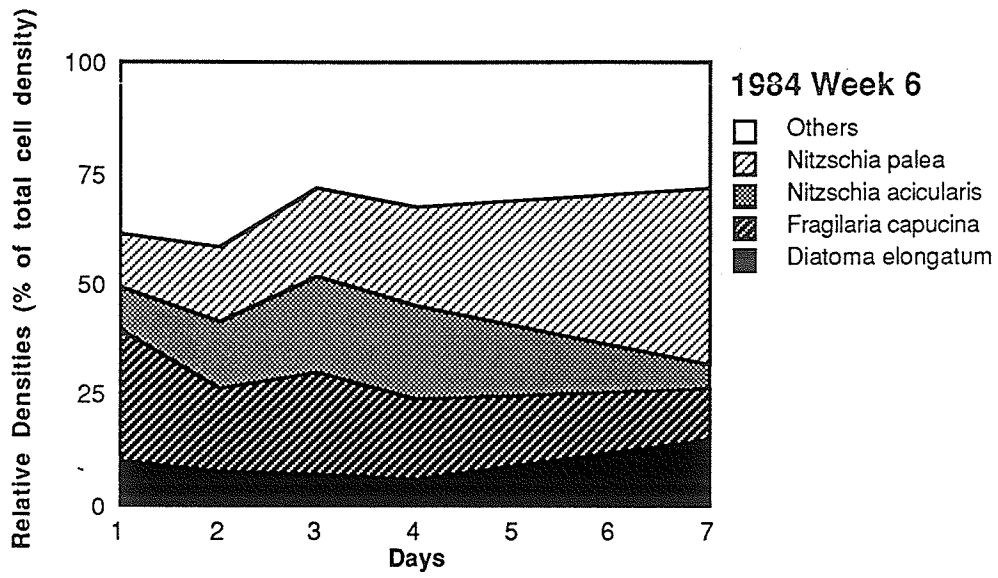


Figure 2.10: Changes in the composition of the haptobenthic algal community over a 7 day period for week 10, 17-23 July, 1984.

Figure 2.11: Changes in the composition of the haptobenthic algal community over a 7 day period for week 12, 31 July - 6 August, 1984.

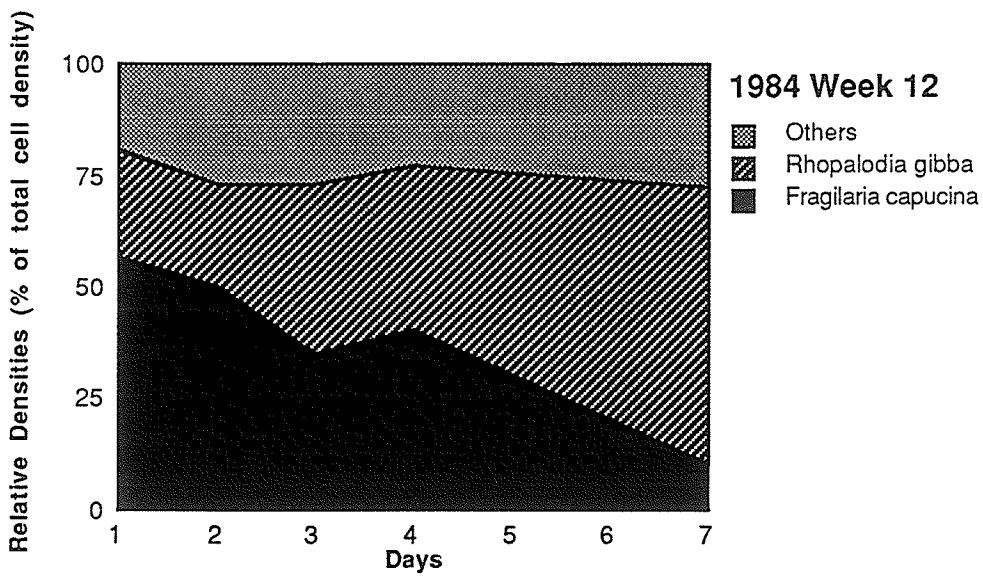
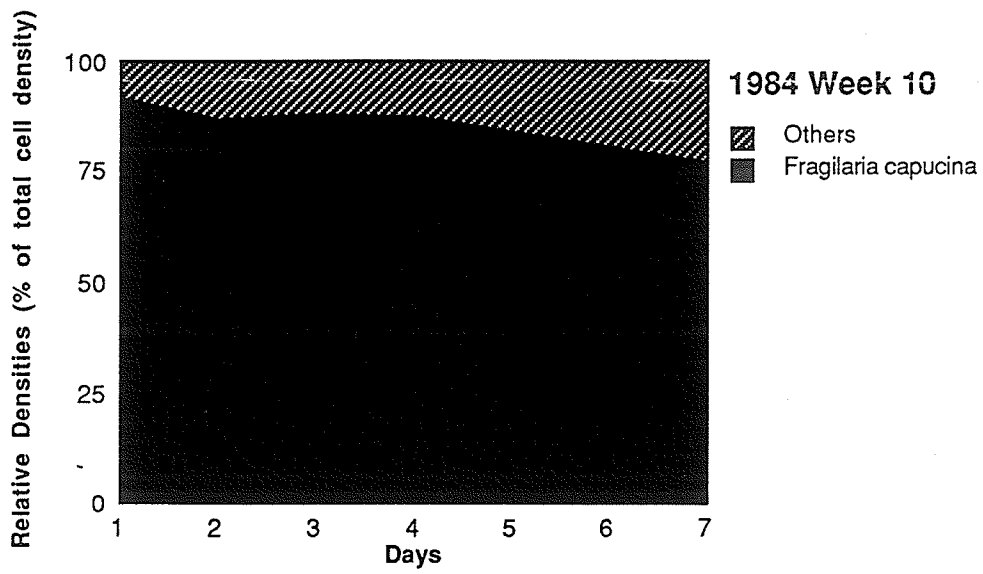
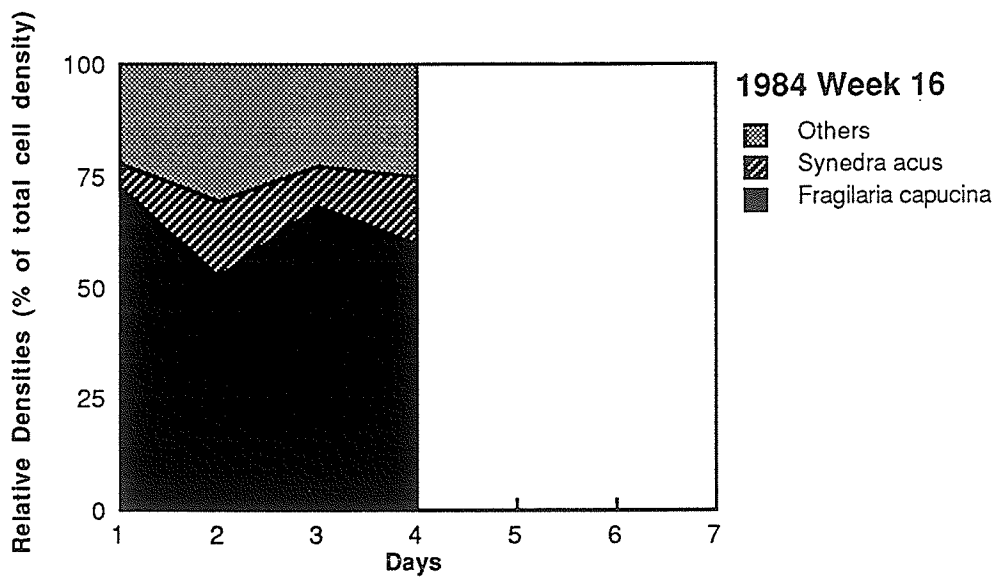
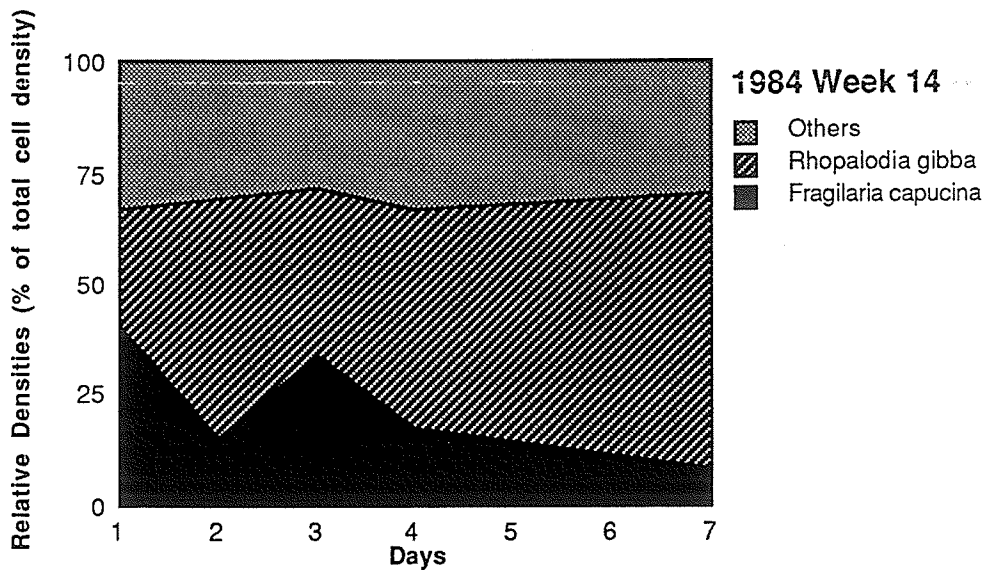


Figure 2.12: Changes in the composition of the haptobenthic algal community over a 7 day period for week 14, 14-20 August, 1984.

Figure 2.13: Changes in the composition of the haptobenthic algal community over a 7 day period for week 16, 28-31 August, 1984.



Fragilaria capucina was higher in proportions on day 1 then declined throughout the week.

Week 16, 28-31 August (Figure 2.13) was sampled only for the first four days. The sample was dominated by Fragilaria capucina at >50% proportions. Synedra acus reappeared in low proportions.

1985 contained a number of missing samples. As a result, there were a number of interpolations in the graphs. In week 1, 3-9 May, (Figure 2.14) days 4-7 were sampled. Nitzschia palea, Fragilaria capucina, Diatoma elongatum, and Cyclotella meneghiniana were present in this week. Nitzschia palea, Fragilaria capucina and other species occurred in equal proportions of the total density. Synedra rumpens, Diatoma elongatum, and Cyclotella meneghiniana occurred in low proportions all week.

Week 2, 20-26 May, (Figure 2.15) shows a good proportion of the graph dominated by Fragilaria capucina. Other species occurred at 25 % throughout. Synedra ulna, Nitzschia palea, Diatoma elongatum, and Cyclotella meneghiniana occurred in small amounts all week.

Figure 2.16 shows the data for week 3, 3-9 June. Day 6 data is missing. Fragilaria capucina and Diatoma elongatum appeared in high proportions throughout the week, although when Diatoma elongatum increased, Fragilaria capucina decreased. Synedra ulna was present in low numbers during the week. Other species accounted for the remaining 25%.

Figure 2.14: Changes in the composition of the haptobenthic algal community over a 7 day period for week 1, 3-9 May, 1985.

Figure 2.15: Changes in the composition of the haptobenthic algal community over a 7 day period for week 2, 20-26 May, 1985.

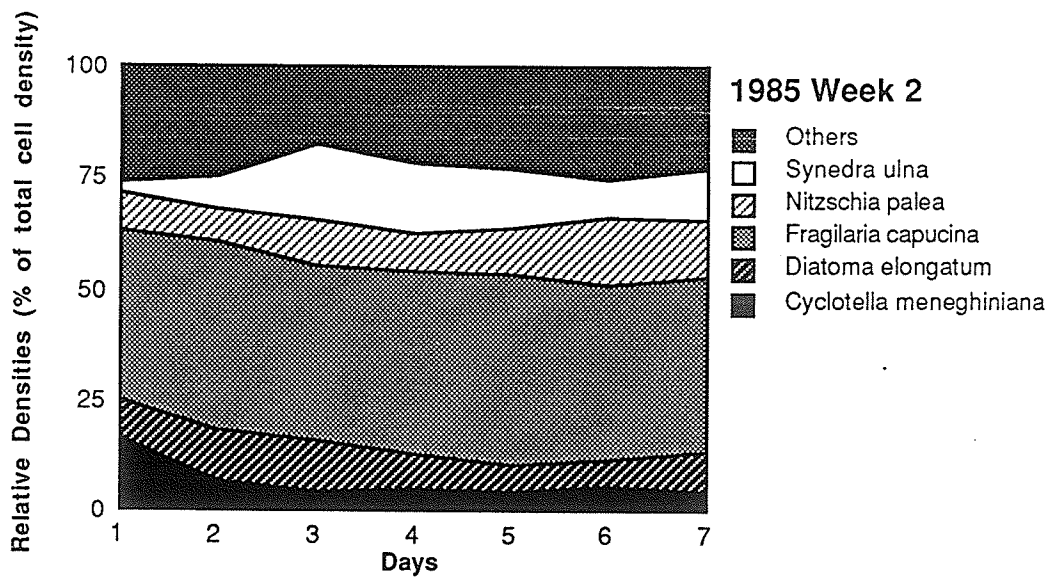
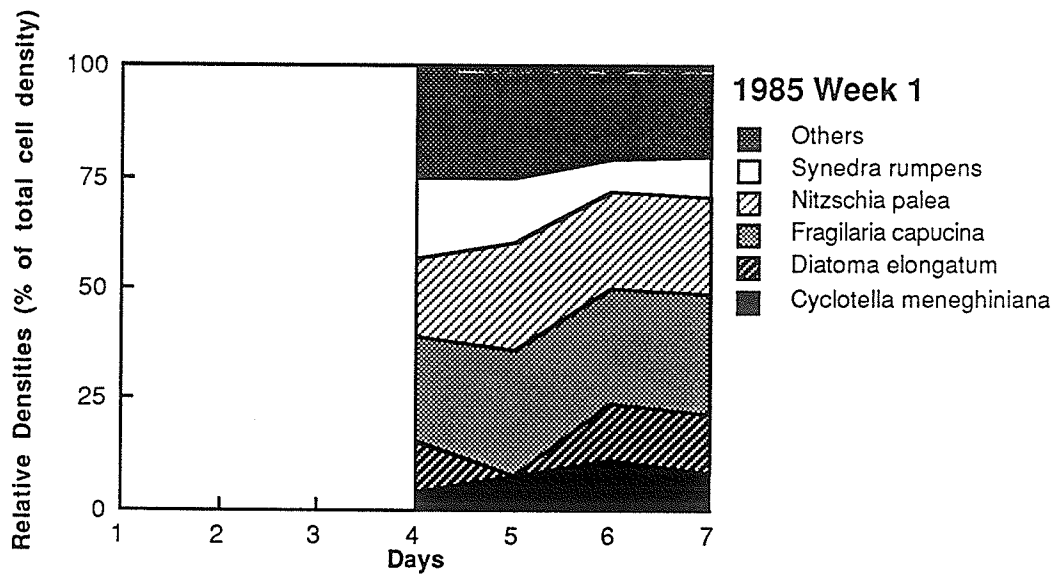
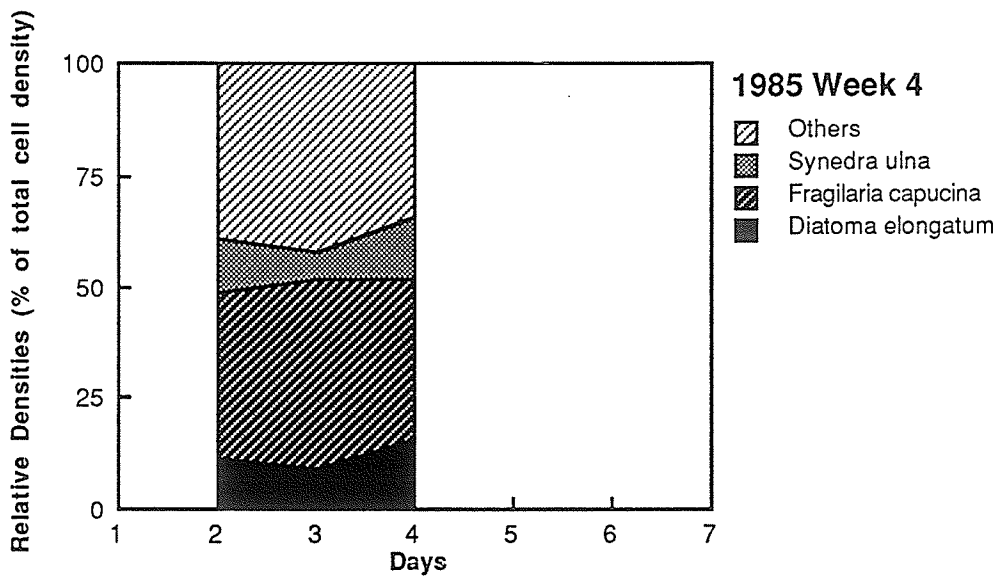
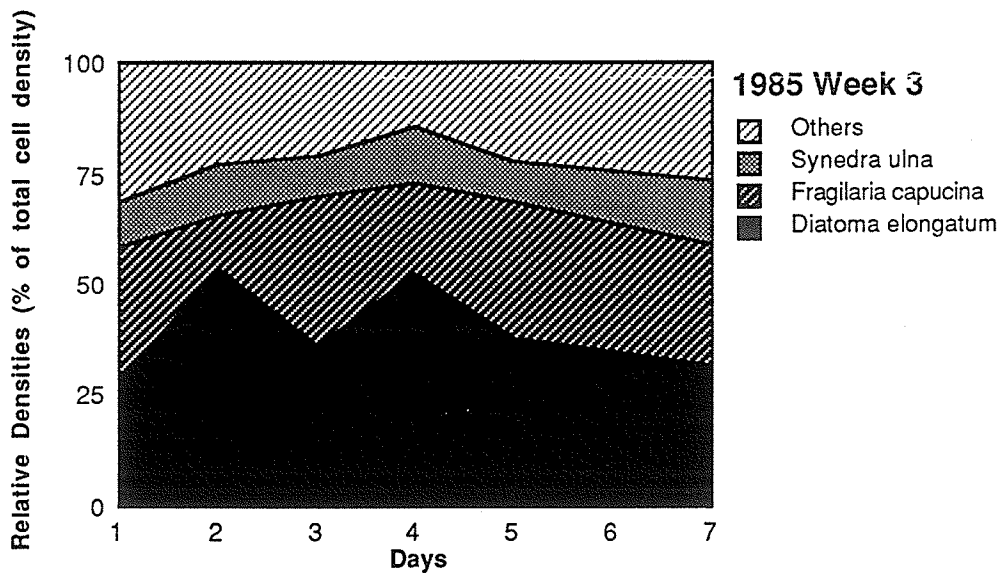


Figure 2.16: Changes in the composition of the haptobenthic algal community over a 7 day period for week 3, 3-9 June, 1985.

Figure 2.17: Changes in the composition of the haptobenthic algal community over a 7 day period for week 4, 17-23 June, 1985.



Week 4, 17-23 June, (Figure 2.17) had samples for days 2,3, and 4. Fragilaria capucina as well as other species, occurred in high proportions throughout the week. Synedra ulna and Diatoma elongatum occurred in low proportions during the week.

At the beginning of week 5, 3-9 July, (Figure 2.18) Fragilaria capucina occurred in high amounts and decreased through the week. On the other hand, Diatoma elongatum showed the reverse trend. Nitzschia palea, although very low on days 1-4, increased to 25% by day 7. Synedra rumpens occurred in very low amounts throughout the week. Synedra ulna showed high proportions on day 2 and 3, then decreased to low amounts by day 7. Other species showed a relatively high proportion at the start of the week and decreased to 25 % for the rest of the week.

Figure 2.19 showed a predominance of Fragilaria capucina and Diatoma elongatum in week 6, 16-22 July. Fragilaria capucina occurred in high proportions throughout the week, although gradually decreased. Diatoma elongatum occurred in lower proportions but gradually increased throughout the week. Other species remained constant.

In week 7, 30 July-5 August, (Figure 2.20) there was an introduction of Rhopalodia gibba, which occurred in small amounts for the first two days but increased to 25% by day 7. Fragilaria capucina occurred in high proportions day 1

Figure 2.18: Changes in the composition of the haptobenthic algal community over a 7 day period for week 5, 3-9 July, 1985.

Figure 2.19: Changes in the composition of the haptobenthic algal community over a 7 day period for week 6, 16-22 July, 1985.

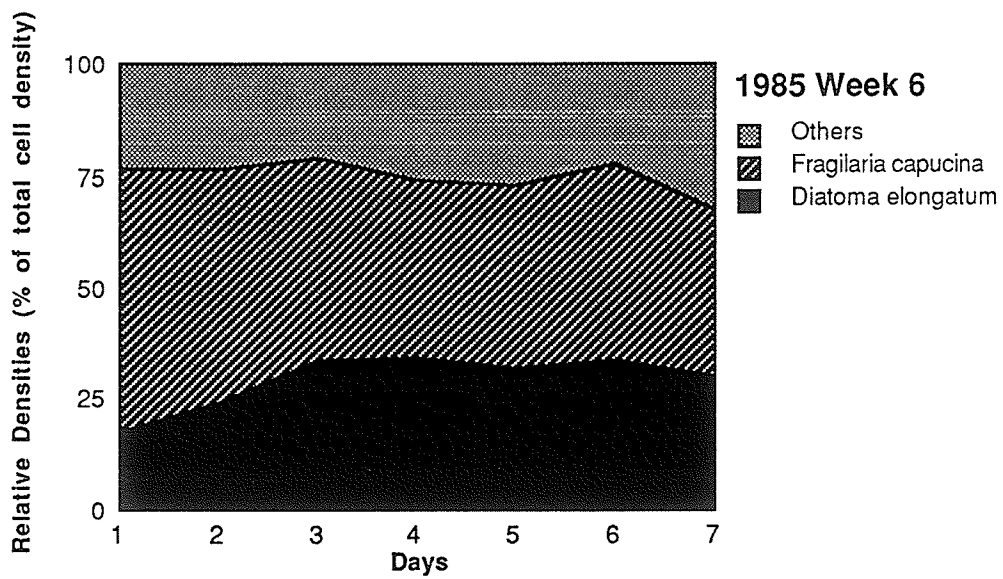
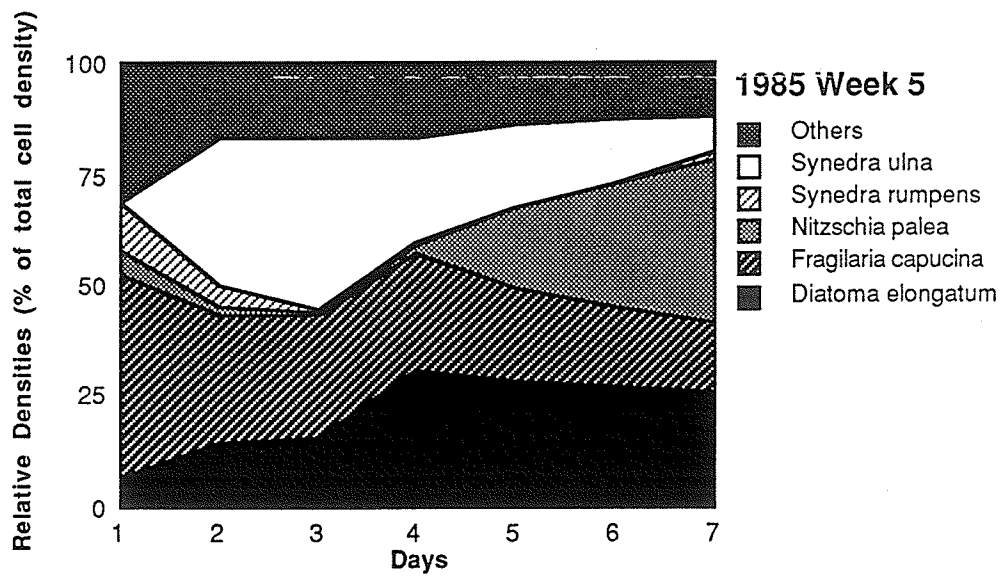
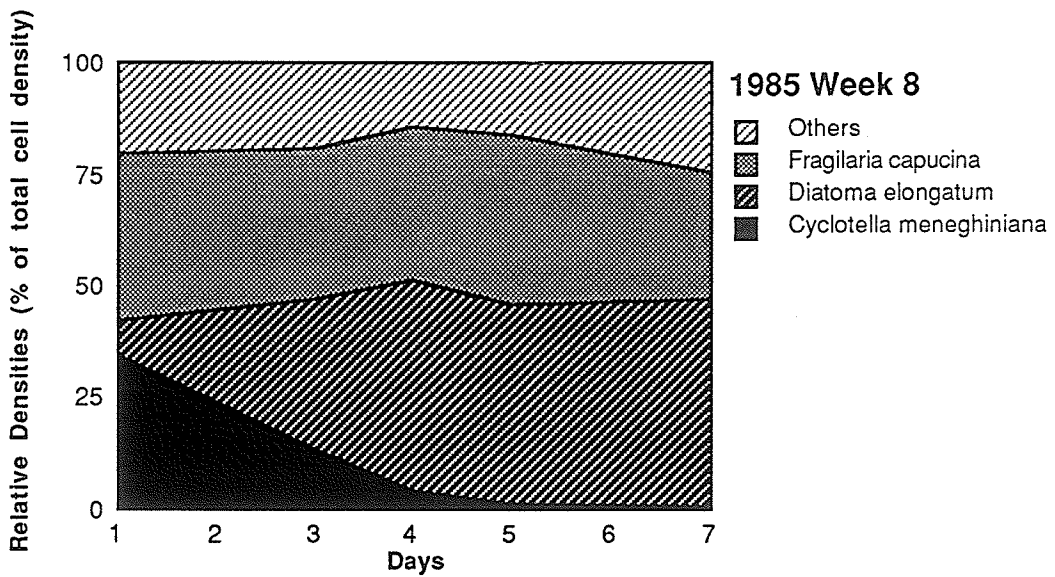
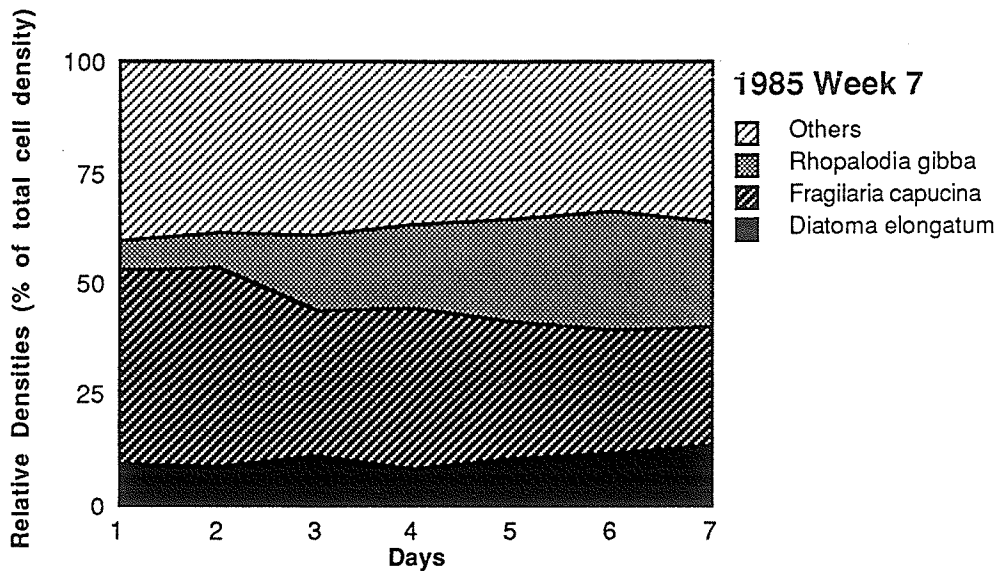


Figure 2.20: Changes in the composition of the haptobenthic algal community over a 7 day period for week 7, 30 July - 5 August, 1985.

Figure 2.21: Changes in the composition of the haptobenthic algal community over a 7 day period for week 8, 12-18 August, 1985. Days 2 and 6 are missing.



and 2, decreased slightly day 3, and remained at a constant proportion to the end of the week. Other species occurred in high proportions through the week. Diatoma elongatum was present in very low numbers during the week.

Week 8, 12-18 August, (Figure 2.21) showed constant proportions of Fragilaria capucina throughout the sampling period, although days 2 and 6 were missing. Diatoma elongatum, although low at the onset, increased dramatically throughout the rest of the week. Cyclotella meneghiniana was present in high amounts on day 1 but dropped off to 0% by day 4. Other species accounted for 25% of the total.

Similar species occurred in both years in given seasons. In spring, (May-June) Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina were common. In early summer (July) Fragilaria capucina predominated. In autumn (August-September) Rhopalodia gibba, Synedra acus, Fragilaria capucina, and Cyclotella meneghiniana were common. Although Fragilaria capucina did decline in density at the end of summer, it did not disappear at the end of the year. In both years, species observed early in the year re-appeared in samples later in the year.

2.5 DISCUSSION

This study indicates that there is no standard by which diatom colonization can be patterned. The results indicate that initial colonization varies from week to week, as well as from year to year. Hoagland et al. (1982) described an orderly predictable progression of succession for the establishment of haptobenthic diatom communities. The change from a prostrate, two-dimensional community to an erect, three-dimensional community is considered to be a general phenomenon of periphyton colonization of artificial substrata. However, the ordinations show that succession of initial colonizers follows different species pattern for each day of colonization within the year. A comparison of corresponding sample days between 1984 and 1985 suggest that patterns of one year differ from those of the other. Both of these dissimilarities are easily apparent although they can not be readily quantified.

This study illustrates the variable nature of colonization. One is led to the conclusion that the appearance of a given species within this periphytic community is largely due to chance. There is an equal opportunity for each species present in the water column to become attached to available substratum at any one time, but it is due to the intrinsic capabilities of the species itself that will determine which species will become more abundant than another. A qualifying factor to this is the

external environment at the time of attachment. Given the variable parameters of nutrient status, light, temperature, and physical disturbances, it would appear that the opportunistic species will be more capable of dominating at any time due to the prevailing conditions.

A progression from adnate to upright to stalked species was not observed in Delta Marsh in initial colonization of substrata by periphyton. Initial colonizers in spring or summer were species which formed short, upright rosettes (eg. Nitzschia palea), long zig-zag chains attached by means of a mucilaginous pad (eg. Diatoma elongatum), and long filamentous chains (eg. Fragilaria capucina). Initial colonizers that occurred in late-summer or autumn were tall, upright rosettes (eg. Synedra ulna), were adnate to the surface (eg. Rhopalodia gibba) or planktonic (eg. Cyclotella meneghiniana). In the traditional model these would normally be considered as secondary diatom colonizers responsible for the three-dimensional development of the community.

This study describes a seasonal succession of initial colonizers that is not influenced by the development of a mature community. Seasonal succession is a progressive change of an association or community over time. This seasonal succession is influenced by the physical parameters of light, temperature, nutrient availability, and wave action, as well as biological parameters (eg. effects of

grazers, macrophytes, and algal/algal interactions). Initial colonization is critical in the development of a periphytic community, although initial colonizers are not reflective of the final community. The initial colonizers are influenced by the same parameters as algae in the mature community. By studying colonization within weekly periods, one is essentially describing succession during initial colonization and changes in initial colonizers over the year. By describing a succession of organisms in the short term, the effects of many biotic and abiotic factors that might influence the community in the long term have been reduced or eliminated.

Patterns of succession seen on artificial substrata studied in the long term are different from those studied in the short term. Where substrata are constantly available throughout a growing season periphyton seasonal succession will likely show very different trends from those described here, in which substrata had become available at weekly periods throughout the season. In many situations the emergence and subsequent growth and phenology of macrophytes represents a situation in which colonizeable substrata become available and change throughout the year. It is quite possible that artificial substrata are a poor means for the examination of successional processes.

Distinct seasonal changes in initial colonizers were observed in this study. Seasonal fluctuations in densities

of initial colonizers were characterized by a late spring-early summer maximum and an autumn maximum. It has been suggested that seasonality is important in driving the process of succession (Herder-Brouwer 1975, Emerson & Zedler 1978, Oemke & Burton 1986), although the importance of seasonality in determining the pattern of periphyton community development is poorly understood (Hoagland et al. 1982). Seasonal trends in other benthic communities have been found. As mixed assemblages of organisms, epiphytic and epipelagic algal communities exhibit seasonal patterns in species abundance which reflect biotic (grazing, macrophytes, algal interactions) and abiotic (including nutrients, light, temperature, and physical disturbance) factors impinging upon the community (Hickman 1978, Jones & Mayer 1983, Steinman & McIntire 1986). Seasonal changes in epipelagic show similar patterns with low winter density, a spring maximum, variable summer growth and a late summer-autumn maximum (Round 1960, Hickman 1978). This general pattern of succession is also found in the epiphytic algal community (Klarer & Hickman 1975). Previous studies (Hooper-Reid 1978) of epiphytic algae in Crescent Pond, Delta Marsh, followed a seasonal trend of low summer and high autumn standing crops on artificial substrates after initial colonization in June. In benthic communities, spring maxima were generally higher than late summer-autumn maxima.

The repeated occurrence of Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina in spring, Fragilaria capucina in summer and Rhopalodia gibba, Fragilaria capucina, Synedra acus, and Cyclotella meneghiniana in autumn, reinforces the idea that seasonality is the driving force behind succession. It seems prudent to group these species then as 'spring' species, 'summer' species, and 'autumn' species. This classification is supported by earlier work showing spring maxima to be dominated by both Fragilaria capucina and Diatoma elongatum (Castenholz 1960, Klarer & Hickman 1975), while common summer species included Achnanthes minutissima, Gomphonema gracile, and Epithemia turgida. The re-appearance of Fragilaria capucina, Diatoma elongatum, and Synedra acus (spring dominants) in fall could have been due to low water temperatures similar to those of spring (Castenholz 1960, Klarer & Hickman 1975). Cymbella affinis, Cymbella cistula, Cymbella mexicana, Diatoma elongatum, Fragilaria vaucheriae, Gomphonema eriense, Nitzschia spp., Synedra acus and Synedra ulna are also considered spring dominants in freshwater lakes (Castenholz 1960). Summer species included Epithemia sorex, Epithemia turgida and Rhopalodia gibba. Cymbella affinis, Cymbella cistula, and Cymbella mexicana were abundant during all three seasons (fall, winter, and spring). Cymbella affinis has been reported as a summer form in a Michigan stream (Blum 1957).

The presence of the planktonic species Cyclotella meneghiniana in samples is important. Although Cyclotella meneghiniana is not considered a benthic diatom, it consistently appears in specific seasons year after year. Little is known of the interaction between littoral phytoplankton and periphyton communities. Few studies have included concurrent sampling of both these components of littoral waters (Knudson 1957, Wetzel 1964, Sladeckova 1966, Moss 1969a,b). The extent to which the two communities share common species and the effect this has on seasonal succession in the periphyton is unknown. The presence of atypical diatom species in the periphyton suggests some overlap. Brown & Austin (1973b) indicated that there was an exchange of individuals between the two communities. They suggested that temporal fluctuations in littoral periphyton populations may be dependent, in part, on fluctuations in plankton populations.

Although many factors are responsible for driving succession, the appearance of different associations towards the end of the year could be due to substratum availability. As substrata are not always available at the beginning of the year, the succession of events that occur will depend on when substrata become available. The different association occurring at the end of the year might be in response to new macrophyte growth (eg. emerging Typha sp. shoots provide more surface area as they grow and move through the water

column, or vegetative propagules produced by Myriophyllum sp. at the end of the year may provide new areas for colonization).

2.6 CONCLUSIONS

There is no standard sequence in which colonization takes place. Initial colonization patterns vary, not only from one year to another, but from one week to the next. As a result, it is necessary to develop an alternative model for describing the seasonal succession of initial colonizers. Seasonal succession of initial colonizers can be described by studying discrete time periods of initial colonization throughout the season. This represents one view of the seasonal succession of initial colonizers unaffected, or affected little, by the cumulative effects of the preceding community development, or by the effects of algal/algal interactions.

Seasonally distinct associations exist within the periphyton community in Delta Marsh. Spring (May-June) dominants include Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina. Summer (July) associations were predominated by Fragilaria capucina. Autumn (August-September) associations were represented by Rhopalodia gibba, Synedra acus, Fragilaria capucina, and Cyclotella meneghiniana.

In further study of initial colonization or seasonally distinct associations within the periphyton, studies conducted in both long and short term, as well as at the species and community level, should be emphasized. Efforts should be made to develop an alternate model of periphyton succession which involves the effects of seasonality.

Chapter III

CONCLUDING REMARKS

The use of a two-step approach with multivariate statistical methods using cluster analysis along with correspondence analysis, was effective in delineating associations within benthic diatom communities. These associations showed fixed environmental variables and constant floristic compositions. The associations described in this study were closely related to limnological status, nutrient status, pH, general habitat, and season.

The application of similar techniques on the periphytic diatom community of the Delta Marsh established three seasonally distinct associations within the periphytic community in Delta Marsh. The spring (May-June) association included Diatoma elongatum, Nitzschia acicularis, Nitzschia palea, and Fragilaria capucina. Summer (July) associations were dominated by Fragilaria capucina. Autumn (August-September) associations were represented by Rhopalodia gibba, Synedra acus, Fragilaria capucina, and Cyclotella meneghiniana.

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