THE ECOLOGY, AND TAXONOMY OF THE EPIPELIC DIATOMS OF BERROW, SOMERSET (U.K.)

by

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TO MUM, DAD AND MIKE

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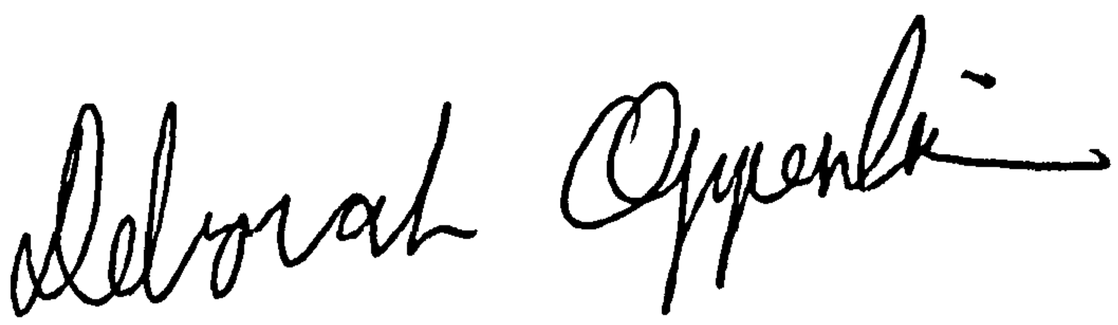
MEMORANDUM

No part of this work has been previously submitted in a degree thesis to this, or any other University. The work described, is the result of my own research, with the assistance of those mentioned in the acknowledgements.



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ABSTRACT

The epipelic diatom community associated with the intertidal sediments along a transect crossing a saltmarsh, sandflat, and mudflat at Berrow Flats has been examined. With gradient changes in pH, salinity, watercontent, levels of organic matter and light availability along the transect there are concurrent changes in diatom assemblages. These assemblages have been analysed in terms of temporal and spatial changes of the dominant taxa, together with a computer analysis niche breadth, and centroid cluster analysis. Of the 120 taxa identified 70 diatom taxa have been described, including one new species of Tropideneis. Comparative sampling strategies and frequency distribution studies of the cells on the sediment are also discussed

LIST OF GRAPHS — Graph No.

CHAPTER 1 INTRODUCTION

Benthic diatoms have long been recognised as important primary producers in estuarine, and coastal ecosystems (Pomeroy 1959, Edsbagge 1965). Since benthic diatoms can attach to a variety of substrata a more precise terminology is required. Epiphytic diatoms attach to other plant hosts. Epilithic diatoms attach to rock surfaces. Epipsammic forms attach to sand grains. Epipelic diatoms are freely motile unicells or colonies living in the sediment either on or near the sediment surface. Other benthic biota also exist: endolithon, endophyton, and epizoon are those collection of non-parasitic organisms living attached in rock cavities, in plant tissues and on animals respectively.

Some of the earliest records of benthic diatoms are of Fragilaria and Bacillaria recorded in 1773 (Müller quoted in Round 1971). Since that time, a considerable amount of literature has been published. The reviews of Round (1971) and McIntire & Moore (1977) give an account of early floristic studies on living and fossil assemblages, the more refined ecological work of the 1950s, and the experimental studies widely published in the 1960s. Admiraal (1984b) gives a more extensive account of the wider aspects of benthic diatom estuarine ecology. In this introduction I shall attempt to highlight the points which are important for a consideration of the ecology of the diatoms on the Berrow marsh. The literature of the epipelic flora of marshes and mudflats will be treated in detail, and earlier sources are only briefly considered when a relevant concept is mentioned.

Important hypotheses emerged from earlier ecological work. Different diatom assemblages are associated with specific habitats (Aleem 1950,

Round 1957a-f, 1960, 1961). Seasonal growth falls into two main categories: (a) without marked peaks in growth as shown by a small number of species, (b) distinct seasonal growth as shown by a large number of abundant species (Round 1953). The progressive change in composition of a community of organisms is known as succession. This has been described for the epipelic bacillariophyta (Round 1957e) and the blue-green algae (Round 1961a) in the English lake district. The growth pattern consists of a large spring bloom, a summer decline, followed by a smaller autumn growth. From these ecological studies the lake systems can be distinguished on the basis of either physico-chemical characteristics or floristic composition (Round 1957f). Several patterns of spatial distribution could also be recognised (Round 1957d). Diatoms can be widely distributed, or strictly confined to a single habitat.

Rigorous quantitative studies of benthic diatoms inhabiting brackish water and marine littoral habitats are scarce. A selected list of some studies is given below:

Table I Selected Benthic diatom studies from various estuarine or marine coastlines.

Geographic Region	Source	Substrata
Wadden Sea/Holland	Colijn & Nienhuis (1978)	Epipsammon/Epipelon
Öresund/Sweden	Sundbäck (1983)	Epipsammon
Yaquina Est./U.S.A.	McIntire & Overton (1971)	Epiphyton
Texas Coast /U.S.A.	Medlin (1983)	Epiphyton
Yaquina Est./U.S.A.	Martin (1970)	Epilithon
Yaquina Est./U.S.A.	Moore & McIntire (1977)	Epilithon
Clyde Est./U.K.	Gowe (1984)	Epilithon
Severn Est./U.S.A.	Wilderman (1984)	Epilithon/logs
Whistable/U.K.	Aleem (1950)	Epipelon
River Dee/U.K.	Round (1960)	Epipelon
Ouse Est./U.K.	Hopkins (1964)	Epipelon
Sapelo Island/U.S.A.	Williams (1964(a))	Epipelon
Yaquina Est./U.S.A.	Amspoker & McIntire (1978)	Epipelon
Baie de Bourgneuf/France	Rincé (1979)	Epipelon
Mersey Est./U.K.	Gargari (1980)	Epipelon
Mississippi/U.S.A.	Sullivan (1982)	Epipelon
Louisiana/U.S.A.	Cook & Whipple (1982)	Epipelon
Nord-Finistère/France	Riaux (1983)	Epipelon

Recent experimental studies have examined factors that effect growth and productivity. These will be discussed in turn.

1.1.1 Light

Light is the primary source of energy for diatom populations and a substantial number of papers examine how light affects the photosynthetic rate, biomass, and species composition of diatom assemblages in the field and in culture. Benthic algae growing in intertidal areas are exposed to considerable variation in light intensity (Joint 1981). However many studies have shown that most estuarine epipelic diatoms exhibit no photoinhibition at high light intensities. (Williams 1964a, Taylor 1964, Colijn & Van Buurt 1975, Admiraal 1977a, Rasmussen et al. 1982). The growth response of benthic diatoms to different daylength and quantum irradiance, did not differ from that of planktonic diatoms, except for the absence of photoinhibition at high levels of irradiation (Admiraal 1977a).

Although Colijn & Van Buurt (1975) did not observe photoinhibition of natural populations in the field, cultures of Amphiprora alata did show photoinhibition at light intensities greater than 200 μE $m^{-2}s^{-1}$ in March, 175 $\mu Em^{-2}s^{-1}$ in May, and 360 $\mu Em^{-2}s^{-1}$ in September (Rasmussen et al. 1982), yet the light intensity measured during incubation in the field greatly exceeded the minimum light requirement for saturation. Using ^{14}C fixation measurements the algal primary production was shown to increase in spring before the grass canopy of the saltmarsh grew at a site in North America (Estrada et al. 1974).

Admiraal (1976) examined the influence of light measured at the sediment surface on division rates of diatom cultures incubated in the field.

He found that division rates were the same as those of cultures under light saturation conditions in the laboratory, when incubated at the same temperature (Admiraal 1977a).

Castenholz (1964) cultured 4 littoral epilithic diatoms, and found that optimum growth occured at different photoperiods and irradiance levels for each species. Furthermore these observed differences were compatible with the seasonal occurrence of each species. Admiraal (1977a) considers the photoperiod to be the important factor in determining different optimum growths. Of the 4 different epipelic diatoms he investigated, Amphiprora cf. paludosa, and Nitzschia sigma had the highest division rates with an 8 hour photoperiod at 12°c, while Nitzschia dissipata and Navicula arenaria required a 16 hour photoperiod. The effect of decreasing the optimum photoperiod, caused a decrease in the division rate of A. cf. paludosa, but produced no obvious effect on N. arenaria. Admiraal (1977a) was not able to relate his experimental results to field observations.

The length of the light period is critical in determining the potential doubling rate of natural populations. The length of the photoperiod is effected by tidal immersion (especially in turbid waters), and seasonal changes (Admiraal 1980). These deductions coincide with Dijkema's (1975) observations that the position of dense diatom populations up and down the shore can be linked with daylength and levels of irradiance.

The ability of diatoms to move beneath the surface of the sediment will affect the light intensity they are exposed to, and this will influence diatom growth. Taylor (1964) measured the photosynthetic capacity of benthic diatoms and calculated that they would be above compensation

level down to a depth of 3mm. However a considerable part of the diatom population is usually found in the aphotic layer, and hence receives no light for varying periods of time (Aleem 1950, Pamatmat 1968, Steel & Baird 1968, Cadée & Hegman 1974). Fenchel & Staarup (1971) examined the depth of the photic zone and found that light penetrated to different depths according to the grain size of the sediment. The coarser the grain size, the deeper the light penetrates. Organisms are thought to compete for light along the light-depth gradient. Round (1979) suggested that this light limitation may selectively favour species with effective migratory behaviour. Admiraal (1980) concluded that the vertical light gradient could partly explain spatial and temporal differences in distribution.

In saltmarsh habitats light intensity is affected by the vascular plant vegetation. Pomeroy (1959) observed that the algal productivity did not vary with the radiation reaching the sediment surface in a saltmarsh, nor seasonally, or with cloud cover, but was influenced by the density of the Spartina cover, depth of the water at high tide, and its turbidity. Thus light becomes a limiting factor due to a shading effect. Carpenter et al. (1978) observed that shading by Spartina reduced the nitrogen-fixing capacity of the blue-green algal mats. Self shading of diatoms in cultures appears to have no affect on the division rate (Admiraal et al. 1983).

Sullivan (1976) examined the effect of shading on epipelic diatom composition. He found that differences in the structure of the assemblages inhabiting the sediments beneath 3 dominant marsh grasses, were not primarily caused by differences in light intensity reaching the sediment surface. Clipping the dominant marsh grass Spartina alterniflora

increased the light intensity and produced a shift in the assemblage structure to a community more characteristic of that found in salt pan. However Moore & McIntire (1977) considered the seasonal changes in diatom assemblages to be associated with changes in available light energy. Light intensity also appeared to be an important variable in determining the structure of diatom assemblages in laboratory stream experiments (McIntire & Wulff 1969, McIntire 1968a McIntire 1968b).

1.1.2 Temperature

It is difficult to distinguish between the effect of temperature and light conditions on diatom growth. This is due to the synchronous changes through the seasons. Conclusions vary between studies. Work on the phytoplankton shows that temperature has a pronounced effect on diatom biomass and productivity, and Ryther (1954) observed that changes in temperature coincide with changes in seasonal succession. Diatoms in culture display optimum growth at different temperatures, but a precise relationship between growth and termperature has not been found. Similarly Jitts et al. (1964) found that in the case of Dunaliella sp and Monochyrsis sp the maximum temperature ranges for optimum growth corresponded to their seasonal temperature for growth. Jørgensen (1960) measured the concentrations of different forms of chlorophyll found in Nitzschia ovalis. He found that chlorophyll content changed with different combinations of light and temperature. Federov et al. (1968) reported an increased photosynthetic rate with increased temperature of N. ovalis and Nitzschia kuetzingiana.

Unlike conditions in the open water, temperature on a mudflat system fluctuates considerably since it is influenced by 3 main variables: (1) the water temperature at high tide (2) the air temperature at low

low tide, and (3) irradiance reaching the sediment surface at low tide (Admiraal 1980). Structural changes in epiphytic diatom assemblages appears to be strongly influenced by seasonal changes in temperature (Oquinn & Sullivan 1983).

A weak correlation between light, temperature,and seasonal changes of the diatom assemblages colonizing PVC plastic sampling devices was observed (McIntire 1978). Epipelic diatom assemblages are affected by the combination of light intensity, water temperature and exposure (Amspoker & McIntire 1978). Sundbäck (1983) considers temperature to be the main controlling factor in determining the seasonal variation in the primary production of epipsammic assemblages.

Admiraal et al. (1982) believes that epipelic diatom cell division is temperature dependant, and an important factor influencing seasonal succession. Maximum growth rates occur at higher temperatures in culture than in the field (Admiraal 1977a). Short term fluctations in temperature did not alter diatom division rates (Admiraal 1980). Yet cultures maintained at similar temperatures as in the field showed the same division rates (Admiraal 1980).

High division rates of Amphiprora cf.paludosa, Nitzschia sigma, Nitzschia cf.dissipata, and Navicula arenaria are reached between 20°c and 30°c in culture, but higher temperatures were inhibitory (Admiraal & Peletier 1980a). In contrast field incubated samples of A. cf. paludosa, N.arenaria Navicula salinarum and Gyrosigma spencerii divided rapidly at a daily maximum temperature of 29°c and even higher temperatures measured at the mudflat surface (Admiraal 1980). Pomeroy (1959) observed that sediment

temperatures were often higher than air temperatures. High temperatures do not affect division rate in the short term,but if sustained they can be inhibitory (Admiraal 1980).

Dijkemas' (1975) observations of a sandflat transect in the Eems-Dollard estuary add support to Admiraals' findings. High temperature tolerant species occur in summer populations in the field, while less temperature tolerant taxa such as Navicula flantica become less abundant. In summary, temperature plays a critical role in diatom cell division. Summer minima in benthic diatom biomass however cannot be ascribed to inhibition by high temperatures (Admiraal 1980).

1.1.3 Salinity

Phytoplankton live within a watermass of defined salinity while estuarine benthic diatoms are confined to the surface sediment subjected to varying salinity. The stress in maintaining cell turgor, the passage of nutrients, and water, across the cell membrane is much greater in the benthos. This is due to greater changes in salinity chiefly caused by evaporation, and tidal submergence (Joint 1981). Salinity is the principal factor influencing spatial distribution, and estuarine diatoms are extremely tolerant of the large salinity range occuring.

Salinity tolerance is not a unique feature of estuarine diatoms. It has been observed in a wide variety of algal groups, some examples of which are shown in Table II. These studies show (a) the tolerance to both rapid salinity change or "osmotic shock" (b) adaptations over various periods of time to varying exposures to media of different salinities, or mechanisms using active pumps which keep certain cations inside the cell to the exclusion of Na^+, and (c) that sugars are accumulated in order to maintain isotonic conditions.

TABLE II SALINITY TOLERANCE OF DIFFERENT ALGAL GROUPS

ORGANISM	SOURCE	MECHANISM	COMMENTS
Sycracosphaera sp (Coccolithinaea) Cryptomonas sp (Cryptomonadinaea) Amphidinium sp (armoured) Exuviaella baltica (unarmoured) } Dinoflagellates	Braarud (1951)	-	Variation measured in terms of rate of reproduction.
Nannochloris bacillaris Chlorophyceae	Brown (1982)	-	Osmotic shock had little effect. Cell wall withstands considerable changes in pressure.
Cyclotella cryptica planktonic diatom	Liu & Hellebust (1976)	-	Shows lag in growth with increasing salinity shock.
Porphyra perforata	Eppley & Cyrus (1960)	Accumulation of K and Ca which excludes Na.	Volume control due to shrinkinge and swelling of extra cellular structural polysaccharides and not H_2O secretion.
Dunaliella sp	Ginzberg & Ginzberg (1981)	Accumulation of glycerol to maintain isotonic concentrations with external concentration of Nacl.	Exact relationship or mechanism is unclear. Salinity tolerance varies with conditions of light and temperature.
Chlamydomonas uva-maris	Vosjan & Siezen (1968)	-	NaCl and distilled water had the same effect on photosynthetic rate as natural sea water.

There have been no studies of the diatoms to determine what substances are involved in the tolerance of osmotic stress. Since diatoms possess a rigid siliceous cell wall osmotic stress might be explained by mechanisms (b) or (c). Future work on benthic diatoms should focus on models of this nature.

Salinity influences the distribution of the plankton (Ryther 1954, Kain & Fogg 1958, Uyeno 1957, Iwai 1962, Saunders et al. 1967), the epiphyton (Drum & Webber 1966, Edsbagge 1965, Main & McIntire 1974, Medlin 1983) the epilitlon (Martin 1970, Moore & McIntire 1977, McIntire & Overton 1971, McIntire 1978, Gow & Mclean 1983, Wilderman 1984) and the epipelon (Drum & Webber 1966, Williams 1964a Admiraal 1977d,Amspoker & McIntire 1978, Gargari 1980, Cook & Whipple 1982, Rasmussen et al. 1982).

Results from fieldwork, particularly studies of the epipelon, indicate that diatom assemblages have broadly overlapping distributions along the salinity gradient (Amspoker & McIntire 1978, Gargari 1980, Gow & Mclean 1983).

The distribution of epilithic diatoms in the Yaquina estuary are related to vertical desiccationand insolation gradients, as well as the salinity gradient (McIntire 1978, McIntire & Overton 1971). Moore & McIntire (1977) suggest that it is the mean salinity which governs spatial distribution.

Fisher (1964) attempted to examine salinity tolerance using cultures of planktonic, epipelic, and epiphytic diatoms. His results showed that the diatoms displayed a flexible response to salinity change. Plasmolysis was tolerated for prolonged periods. He concluded that diatoms exhibiting both quantitative and qualitative differences to osmotic stress could be observed in the same microhabitat.

Williams (1964b) grew 14 species of pennate diatoms in media ranging from 1 to 68‰ salinity. In media of 10-30‰ all species grew well. Several species divided rapidly over the entire salinity range. At 20‰ , maximum division rates were observed. Preconditioning had no affect on photosynthetic rate, except in the case of Rhopalodia musculus (now called Rh. operculata (CA. Agardh.) Hakansson, see Chapter 4). This showed higher division rates when preconditioned at 68‰. Diatom division rate was also related to cell size. Small cells had faster division rates than large cells.

Martin (1970) cultured 6 strains of Amphora, and measured the effect of light, and salinity on photosynthesis in terms of O_2 production/hr dry weight. Amphora spp (all strains), were very tolerant to salinity change. No correlation between experimental results and field observations was made.

The two most abundant epilithic species in the Clyde estuary, Navicula mutica var. cohnii and Opephora martyi var. exhibited complementary though not mutually exclusive distribution patterns (Gow & Mclean 1983). Field assemblages brought into the laboratory demonstrated a euryhaline response to varying salinity, but showed maximum photosynthetic rates at salinities approximating mean field values.

Admiraal (1977d) measured the net photosynthetic rates of unialgal and mixed cultures. Like the previous work, photosynthesis was largely unaffected by a wide salinity range (4-60‰). This was also true for fluctuations in salinity. Navicula salinarum thrived in low salinities but still possessed a high photosynthetic rate at high salinities.

However in the field,this species did not occupy all the range of salinities that it was potentially capable of exploiting (Admiraal & Peletier 1980b).

Rasmussen et al.(1982) measured the interstitial salinity of the surface sediments. Salinity increased from 30‰ to 50‰ during exposure at low tide in spring, and 30‰ to 48‰ in September. Optimum salinity for growth was 15-30‰ measured in the laboratory incubations of mixed populations. Unlike the results of Admiraal (1977) growth decreased by more than 60% at a salinity of 50‰ . A rapid increase in salinity coincided with a strong decrease in primary production.

Many studies have no experimental evidence provided with field investigations. Therefore it is not possible to evaluate the direct effect of salinity on diatom growth or productivity. Often salinity gradients run in parallel with chemical gradients. Therefore it is difficult to interpret their exact roles (Admiraal 1980).

A considerable discrepancy between the physiological and ecological optima of benthic diatom species can be found (Martin 1970, Admiraal 1980). Only combined information of experimental studies and fieldwork will provide enough information to achieve the greatest understanding of the mechanisms by which salinity or any other factor governs diatom distribution (Admiraal 1980).

Estuarine mudflats and brine pools are occupied by the same species (Admiraal 1984b). Diatoms species growing in intercontinental saline lakes, and estuarine mudflats are also extremely similar (Rushforth personal communication). Can different genetic strains have evolved

as Admiraal (1984b) suggests? Would it not also be of great use to analyse the ionic composition of the interstial water rather than taking only one general measure of salinity? Closer examination of salt-tolerance of fresh water and marine benthic diatoms is not only required (as recommended by Admiraal 1984 b.). A thorough examination of the water chemistry of the interstial water will also reveal more information concerning the relationship between salinity and diatom ecology. This is extremely useful information used in understanding the ecology of diatoms growing in saline lakes (Rushforth personnal communication).

Salinity may also influence other physical conditions of a micohabitat. Flocculation of suspended mud particles increases to a limit, at greater salinities and at higher suspended concentrations (Owen 1973).

1.1.4 Ph & Inorganic carbon availability

Little work has examined the effect of pH on microalgae communities. Pomeroy (1959) measured high pH values in daylight and suggests that CO_2 may become limiting at times. Sundbäck (1983) found a positive correlation between pH and daily primary production. Work in the Eems-Dollard estuary has shown that photosynthetically active diatom populations occasionally deplete inorganic carbon concentrations in intertidal pools. (Admiraal 1980). A combination of low concentrations of inorganic carbons, high concentrations of O_2, high pH, temperature, and levels of irradiance, lead to a reduced photosynthetic carbon fixation rate which in turn stimulates photorespiration, and the excretion of organic substances (Admiraal 1980).

While an increase in pH coincides with an increased rate of photosynthesis (up to pH 9.3). High pH of interstitial water causes a low CO_2

availability. Laboratory studies have demonstrated that diatoms use HCO_3 as well as CO_2 Rasmussen et al. (1982).

1.1.5 Chemical Factors

Chemical factors cover a wide range of topics: e.g. nutrient availability toxins, and diffusion gradients of gases through the sediments.

Important results emerge from phytoplankton studies. Donaghay et al. (1978) have suggested that carbon/nitrogen ratios might be useful in estimating growth rates in nitrogen limiting conditions. Frey and Small (1980) observed that major and micronutrients have fundamental effects on growth and composition.

1.1.6 Nitrogen and Phosphorus availability

Results from studies on the microphytobenthos are limited, and inconclusive. The addition of urea, or sewage had no effect on the amount of chlorophylla on the mudsurface of a salt marsh. Fertilization caused an increase in standing crop of grass in the marsh which in turn decreased the amount of light reaching the mud surface. Therefore the vertical distribution of chlorophylla in the sediment was dependant on the light availability which varied according to the species and biomass of marsh grass present (Estrada et al. 1974).

Admiraal (1976) added inorganic phosphorus and nitrogen compounds into micro-ecosystems containing natural sediments and diatom populations. The nutrient additions had no effect on the density or species composition. However, placing plastic screens beneath the sediment surface, interfered with growth, therefore replenishment of nutrients from sub-surface layers seems to be essential.

Ten different diatom cultures were tested in varying concentrations of NH_4^+ and NH_3, NO_2, NO_3 and orthophosphate against varying light and pH. (Admiraal 1977 c.). Nitrate and orthophosphate have no affect on chlorophylla production. NO_2 showed only a limited inhibition of O_2 and Chlorophylla production. NH_3 had a pronounced inhibitory affect which was enhanced by increased irradiance, temperature, and particularly pH.

Admiraal (1977c, 1977b, Admiraal et al.1982) concluded that the supply of major nutrients (P and N) are not critical factors in the growth rate of mudflat diatoms. These nutrients are found in large quantities and therefore are not thought to be limiting. However Williams (1964a) observed that NH_3 had a stimulatory affect on N starved algae. NO_3 and NH_3 caused an increase of photosynthesis. While the standing crops of saltmarsh benthic algae are limited by both N and P (Sullivan & Daiber 1975) the type of nutrient limitation varies from season to season. Adding nitrogen and phosphorus fertilizers (NH_3 NO_3 and $CaH_2(PO_4)_2$) increased chlorophylla production relative to control plots.

Sullivan (1976) investigated the effect of manipulating light and nutrient enrichment on the diatoms growing in a Spartina alterniflora marsh over 1 year. Phosphorus enrichment caused a decrease in species diversity with either clipping or shading in the cord grass. Nitrogen enrichment reduced the number of diatom species in a sample.

A decrease in diversity of benthic diatoms with the addition of either sewage or urea has also been observed (Van Raalte et al. 1976a). Navicula salinarum composed 5-9% of the population in the control plots. This increased to 20-25% in the fertilized plots. Admiraal & Peletier (1979b) also found N. salinarum to be very tolerant of high levels of

NH_3 resulting in its flourishing in brackish and highly polluted mudflats.

Further examination of the influence of nutrient enrichment on algal production was undertaken (Van Raalte 1976b). Carbon fixation rates increased with nutrient enrichment. Regardless of the type of nutrient treatment algal production followed the normal seasonal pattern.

Darley et al. (1981) transplanted small cores from a nutrient rich marsh (Creek bank) to a nutrient poor marsh (Spartina marsh). After the depletion of the initial nitrogen supply the Creek bank cores in Spartina marsh were unable to sustain algal biomass at the same level. Daily enrichment of cores in a Spartina marsh placed inside fiddler crab enclosures showed significant increases in chlorophylla production.

Sundbäck (1983) examined the effect of nitrogen and phosphorus enrichment in the field and in the laboratory using natural populations. Samples taken from a nutrient rich site (Lomma) showed no increase in biomass after the addition of nutrients. While samples from a nutrient poor site (Falsterbo) showed an increase in biomass after the addition of nitrogen. No phosphorus limitation was observed.

Admiraal & Werner (1983) examined the affect of limiting concentrations of orthophosphate on phosphorus starved cultures of Cyclotella cryptica and Nitzschia closterium. Threshold concentrations of $PO_4^=$ were found to exist for both species. When phosphorus starved diatoms were grown in media containing $PO_4^=$ concentrations below their threshold level phosphorus - compounds leak out from the diatoms. Leakage begins with

phospholipids and continues with the excretion of nucleotides under more extreme starvation conditions.

1.1.7 Silica availability

There is even less work on other major nutrients. Admiraal (1976) added Si solutions to microecosytems and an increased population density was observed under laboratory conditions, but no effect was observed in the field. Si is thought to have had no affect in the field because the water within the microecosystem was saturated with silica. Silica is not considered to occur in limiting concentrations in certain mudflats of the Eems-Dollard estuary (Admiraal et al. 1982). Nevertheless benthic diatom populations occur along steep gradients of soluble silica both vertically in the sediment and horizontally along the shore. (Admiraal 1980).

1.1.8 Sulphur

Admiraal & Peletier (1979a) examined the effect of different concentrations of free suphides on unialgal and mixed cultures. Certain species e.g. Navicula salinarum had a greater tolerance to high concentrations of sulphide than other species. Diatoms cultured from sulphide free areas in the field were extremely sensitive to sulphide in culture conditions. Admiraal & Peletier (1980 b) examined the effects of NH_3 and sulphide in relation to diatom distribution on estuarine mudflats. While NH_3 proved a critical selective factor in diatom distribution; sulphurous mud provided a habitat for those species tolerant of high sulphide concentrations in the sediment. The influence of a sulphide system on a microbial community is also depth dependent. Fenchel & Riedl (1970) consider the boundary of the sulphide biome to be the point where the reducing processes change to oxidizing processes known as the RPD zone. Lange-Bertalot (1979) distinguished groups of diatom species living in

rivers according to their tolerance of waste waters and saprobity.

1.1.9 Diffusion gradients

While major nutrient supply does not appear to inhibit diatom productivity in the Eems-Dollard, diffusion of CO_2 and O_2 have a greater limiting influence. The slow diffusion of CO_2 and O_2 restricts diatom growth to a greater degree, than nitrogen or phosphorus starvation. (Admiraal et al. 1982). This is due to the fact that N/P uptake is possible at high or low tide, and during the day or night. The ability of the diatoms to migrate to subsurface layers increases their potential N/P resources. The conditions which limit photosynthesis (described in pH and inorganicarbon section), induce "self-inhibition" through the limited diffusion of gases in dense benthic diatom populations. This may account for increased stress with increasing population density.

Far more work on nutrients is required. There is also a need to re-examine the measurment of microphytobenthos biomass and productivity. No work has been done on the influence of micronutrients, or the effect of heavy metal pollution. The role of nutrient cycling needs a great deal of consideration since nutrient replenishment appears to play an important role (Admiraal 1976).

1.1.10 Physical quality of the sediment

In considering physical factors which might influence diatom assemblage structure, one must also include the physical nature of the sediment itself. The sediment quality in an estuary is dependant on the topography of the habitat, the rate of erosion or deposition, as well as plant cover. Teverson (1983) summarizes the external factors operating on a saltmarsh

as follows:

(1) Tidal range - length of innundation

(2) Exposure - strength and direction of prevailing winds, degree of wave attack

(3) Channel migration - and tidal currents

(4) Water quality - salinity, turbidity etc..

(5) Sediment supply

(6) General estuarine productivity & nutrient supply

Most of the factors listed above are very difficult to quantify. Imberger et al. (1983) carefully examined the effect of water motion on the distribution and transport of materials in a saltmarsh. They found a variety of carbon souces were either rapidly recycled, or exported by longitudinal mixing caused by the tide. Internal water cycling of carbons was considered to be more important than their export.

Also associated with sediment type is organic content. This increases from sandy to silty sediment types (De Jonge 1980). Studies have shown that the percentage of organic matter in samples is indicative of groups of algae dominating the community (Amspoker & McIntire 1978). Van Es & Van Arkel (1980) found a clear correlation between levels or organic matter and the distribution of aerobic bacteria. Clay content and sub-strate type play a critical role in the distribution of sulphate reducing bacteria (Schröder 1977). Therefore these factors might also prove to be important in controlling epipelic diatom distribution.

The presence, distribution, and mineralization of organic matter and its impact on diatom assemblages in the Eems-Dollard estuary is reviewed by Admiraal (1980c). Two major points are made : (1) Decomposition of organic matter in estuarine sediments will potentially increase the

availability of certain organic compounds, (2) uptake of the organic compounds may be of quantitative importance in determining the heterotrophic capability of certain diatom species.

1.1.11 Community interactions and adaptations

Only abiotic factors of the environment have thus far been considered. However some diatoms have been able to adapt to particular stresses. These adaptations together with the biotic interactions between different organisms inhabiting the epipelon, will affect the population dynamics of the diatoms.

In the previous section the subject of heterotrophy was mentioned briefly. Admiraal and Peletier (1979b) found that certain diatom species have the capability of converting from autotrophy to heterotrophy. Ten species of benthic diatoms found to be dominant in natural communities were grown in axenic culture under varying combinations of irradiance and supply of organic substrates. Approximately half the different diatom taxa cultured showed either heterotrophic or photoheterotrophic capabilities.

Do such capabilities reduce the stress of interspecific competition? Competitive effects have hardly been studied yet. The affects of interspecific are not easily observed. When mixed populations of epipelic diatoms in culture were exposed to extremes of salinity over varying periods, they only displayed a broad tolerance to any changes (Admiraal 1977d). However interspecific competition becomes increasingly important with increasing population density.

One possible strategy of insuring success against severe interspecific competition is to secrete a chemical inhibitor. Hoc (1980) has suggested

that Oscillatoria rubescens and Anabaena circinalis in the plankton exhibit allelopathic inhibition. However no chemical inhibitor was isolated or identified. Only recently has such a phenomenon been observed in the benthos. Severe allelopathic interactions between 3 species of benthic and semi-planktonic species: Cylindrotheca closterium, Amphiprora cf. paludosa, Navicula salinarum. (Jonge & Admiraal in Press from Admiraal 1984b).

As well as competative ability, the microphytobenthos must adapt to different forms of stress. Toxins such as NH_3 have already been discussed. Desiccation is another important stress factor (Admiraal et al. 1984). Once possible defense against desiccation is to produce a thick mucilage coat covered in silt particles. Such protective layering may serve to withhold moisture. Krammer (1981) has demonstrated using the electronmicroscope, that the valves of many benthic diatoms have self-supporting structures enabling the valve to carry additional loads e.g. a mucilage coat. No experimental work examining the role of mucilage production has been undertaken. It s function still remains unclear. Coles (1979) has suggested that mucilage secretion by epipelic diatoms and blue-green algae help the accretion of fine sediment in more sheltered mudflat areas. Benthic algae are the pioneering organisms of saltmarsh zones.

One last aspect to consider is the affect of predation on a diatom population. This topic is discussed more extensively by Admiraal (1984b). Admiraal et al. (1984a) have suggested that the seasonal occurence of Navicula pygmaea, and Navicula salinarum corresponds to their response by grazing of herbivorous meiofauna. Natural amphipod densities (Bathyporeia pilosa) were found to be limited by the chlorophylla content of the epipsammic diatoms (Sundbäck 1983). However little selective

grazing was observed. Selective grazing appears to be determined more by how accessable the food is to the grazer (Medlin 1981, Sundbäck 1983). Medlin (1981) found that stalked forms such as Rhoicosphenia adolfi or Opephora marina were more efficiently grazed by limpets than low lying forms such as Nitzschia frustulum or Cocconeis scutellum var. stauroneiformis. Admiraal et al. (1984a) suggested that rather than accessability, the cells of N. pygmaea were more resistant to puncturing by the mouth parts of the nematode Eudiplogaster paramatis. This might account for N. pygmaea's abundance in summer in the Eems-Dollard estuary.

Grazers appear to affect benthic diatom assemblages in 3 ways: (1) by removal of cell material, (2) by the nutrients, and (3) by disturbance of the sediment surface thereby disrupting mat formation. Admiraal (1984b).

1.1.12 Cell motility and cell burial

Vertical migration plays a critical role in light and nutrient availability. An understanding of the mechanisms of locomotion and the behavior of the cells which make use of this ability, may allow a better understanding of their ecology.

The mechanism of diatom locomotion has intruiged many workers (reviewed in Edgar 1984). A current model suggests that the cell secretes mucilage strands which attach to the substrate. Using the locomotive force generated by microfilaments, these mucilage strands slide backwards along the raphe, and propel the cell forward (Edgar 1983a, 1983b). Thus movement is dependent on two main events, the efficient secretion of mucilage, and its attachment to the substrate. The environment may influence mucilage secretion. The locomotive abilities of diatom taxa, respond differently to varying temperature and oxygen supply (Harper 1977).

Perhaps the different types of movement can also be related to the diatoms varying ability to attach to different types of substrata.

Such vtariability may explain how different patterns of vertical migrations can be observed (Round 1979), which in turn may trigger different patterns in other biological rhythms eg. photosynthetic capacity (Brown et al. 1972). Therefore an understanding of the mechanism of diatom locomotion may help the ecologist to understand the variable behaviour of these organisms in the field.

However not all diatoms remain at the surface. Studies have shown that diatoms with viable cell contents, become buried in the sediment to depths of 6 cm (Moul & Mason 1957), and even up to 20 cm (Steele & Baird 1968). So viable cells are present below the photic zone, and they are capable of retaining viability for long periods in the dark (Smayda & Mitchel Innes 1974 from Joint 1981). Wave action is responsible for covering and uncovering diatom populations lying deep below the sediment surface (Steele & Baird 1968).

1.1.13 Cell size

A large range in cell size of epipelic diatoms has often been observed. Williams (1964a) found a large number of small sized diatom species, and a small number of large sized taxa. He concluded that both the cell number, and the division rate were important factors to consider when calculating the productivity of a diatom population. Division rate was considered to be a function of cell size.

Riaux (1983) defines sub-groups of the diatom population, which he

divides into two size groups: the "microphytobenthos"(>20-30 um), and the "nannophytobenthos"(<20-30 um). In the summer months the microphytobenthos and the nannophytobenthos co-exist as 2 distinct groups, while in the winter, the range in cell size becomes more of a continuous gradation from large cells to small cells. The exact significance of these observations are unclear. However Riaux (1983) suggests that the nannophytobenthos are opportunists which grow in between the sediment grains in the interstitial water. Their growth patterns are influenced by the physical parameters of the environment. While the microphytobenthos colonize on the sediment surface on a more permanent basis, showing little or no seasonal change. It is unfortunate that Riaux (1983) provides no experimental evidence for these hypotheses.

The population dynamics of the benthos is influenced by a wide range of factors. The ecology of the epipelic diatoms covers many different aspects. All the environmental factors discussed show a high degree of variability, giving rise to a multitude of growth responses by the algal population. There is an interplay between all these factors, and these will influence diatom succession and distribution. Therefore no single model can explain the mechanisms operating in a habitat, so the greater the number of studies of different ecosystems; the greater an overall understanding of diatom ecology.

1.1.14 Sampling the sediment

The difficulties of sampling diatoms associated with the sediment are many. The separation of diatoms from the sediment for slide preparation, the determination of contaminant species, and the problems of recognizing the dead and live material are some of the many tasks the benthic diatom ecologist must tackle (McIntire & Moore 1977). The results obtained are a reflection of the method used, and a close examination of

methods available will help to place the aims of this study into perspective.

Reinke (1858) was the first to suggest the use of cloth or muslin in which to trap the diatoms moving up onto the sediment surface. Williams (1963) substituted netting for cloth, but discovered that only a fraction of the motile diatoms migrated into the netting, but the diatoms could not be completely removed from the material. Eaton and Moss (1966) compared two different sampling techniques: a coverglass technique and a second method using Green's grade 105 lens tissue. Only 75% of the microalgae were removed from the sediment surface using the coverglass method, while the lens tissue retrieved a higher percentage. Direct sediment counts and coverglass counts were 94.43% similar using the similarity formula:

$$S(A,B) = \sum_{1}^{n} \min (a,b)$$

a,b = the percentages of each of the members of the series of n taxa.

A,B = two counts (Eaton 1967)

The number of diatoms retrieved was considerably lower when cyanobacteria were abundant at the sediment surface, (Eaton 1967).

Bowen et al. (1972) were the first to use a quantitative density gradient centrifugation technique to separate planktonic organisms. Ludox (an osmotically inactive inorganic silica colloid), was the most successful gradient material for centrifugation. Price et al.(1974) improved the use of Ludox as a gradient material by partially substituting Al for Si, this was done by dialyzing the gradient medium. Different algae gave different recovery rates from density centrifugation (Price et al. 1974). Other studies refined the technique by varying the basic centrifugation method. Jonge and Price (1975 from De Jonge 1979)

added organic and inorganic compounds to the silica gradients which influenced banding densities of Zooplankton organisms. Price et al. (1977) could achieve more complete separation of fish eggs and larvae from invertebrate plankton using an isopycnic sedimentation in silica gradients.

De Jonge & Bouwman (1977) were the first to apply a gradient technique as a method of separation of organisms inhabiting the sediment. The method of separation was based on differences in specific weight of the meiobenthos, and sediment organisms in the Ludox-TM medium. They found that the sediment sank into the bottom layers in the medium while the organisms remained above the less dense layers,and could then be removed into vacuum flasks. The solution containing the benthic organisms was then rinsed, and the Ludox removed. De Jong (1979) using similar techniques, then separated benthic diatoms from the sediment. He discovered that the diatoms have a relatively high density, and the density range of the diatoms was restricted. With such a confined density range, the diatoms could be separated using a multi-step density gradient. A sub-sample of sediment could be loaded into a gradient of 5 different densities. Upon centrifugation the diatoms would band out into one band. On the basis of chlorophyll determinations De Jonge (1979) concludes that centrifugation shows less variation and greater reliability than the lens tissue or coverglass techniques.

More recently the compound Percol has been used as a better medium for separation (Whitelam et al. 1983). Throndsen (1978) comments that reliability of the centrifugation method is varied. Reliability is dependant on the settling efficiency of the cells, and the general accuracy of the particular method used.

Bearing this background information in mind, two methods were attempted, coverglass technique and a centrifugation method (see section 2.3).

1.2 Aims

Few long term quantitative ecological study of marine littoral studies of epipelic diatoms has been previously undertaken in Britain. Following the guidelines from other major estuarine studies in the Wadden Sea and Oregon Coast, the present study investigates the differing diatom assemblages growing along a single transect across the intertidal zone of a saltmarsh, sandflat, mudflat at Berrow in the Severn estuary.

Spatial and temporal changes of the diatoms and several important physical factors were measured each month over a 30 month study period.

As an initial study the following questions were addressed: What species are present? How do the species vary seasonally and spatially?

Can these variations in time and space be correlated with the physical gradients observed? Are the diatoms associated in discrete assemblages along the transect?

1.3 DESCRIPTION OF SITE

Berrow Flats Somerset, U.K. (O.S. ST2852/2952)

Berrow Flats is located in the south western area of the Severn estuary, along the Somerset coast where it is bordered by recent rock such as alluvium,with an underlying carboniferous limestone basin (Plate 1). Sand dunes on this part of the Severn coast are limited to a five and a half mile stretch facing west between Burnham-on-Sea and Brean Down. The Berrow dunes are located at the southern end of this dune coast line and here they are most extensively developed, forming parallel ridges of up to half a mile in width (Hope-Simpson & Willis 1955, Kendall 1936).

The westerly aspect results in exposure to strong off shore winds which due to the flow into the Bristol channel, leads to more saline currents along the Berrow shore (Teverson 1983). Hence a more marine influence prevails in this area. Tidal scour is caused by wind induced wave action dissipating energy over the extensive mudflats. At low tide these mudflats extend out 4½ miles at their widest point. The extent of these mudflats offers some protection to the saltmarsh vegetation along the upper fringe of the shore. Further protection to saltmarsh vegetation is given by the sand dunes on the landward side.

The main damaging erosional factors affecting this site are the strong storm winds combined with high spring tides. Their damaging effect is determined by the strength and duration of the storm at the time of high

Plate 1 (overleaf)

Map of the U.K. showing the location of Severn estuary and the Bristol Channel (boxed). Details of Severn estuary are illustrated below. Map taken from Bassindale 1943. Site of transect is marked with an "X".

Fig. 1. MAP OF THE SEVERN ESTUARY AND BRISTOL CHANNEL

(Map prepared by H. Freke)

tide (Teverson 1983). It is believed that storm waves carry greater erosive power than normal tidal scour, because their energy is not lost over the shallow water crossing the mudflats (Trott 1970).

Berrow Flats are part of an estuary possessing a tidal range that is second largest in the world. With a tidal range of 14 meters, ten million tons of mud is maintained in suspension in the estuary by the turbulent mixing of river and sea water (Ferns et al. 1976). Thus the area studied is covered by the most turbid waters in the U.K. (Kirby & Parker 1977).

Another important water source is the fresh water draining diagonally across the study area from drainage pipes leading from the golf course. This freshwater output is dependent on the mean monthly rainfall. Hence a strong freshwater influence is present at the study area as well as marine.

The study area consists of a transect crossing a saltmarsh, sandflat, and mudflat, with six stations and 3 sampling sites at each station, except at Station VI where only one site was sampled. Station I is located in the upper marsh, Station II in the middle marsh, Station III in the lower marsh, Station IV on the upper sandflat, Station V on the lower sandflat, and Station VI on the mudflat. A profile of the transect is illustrated in Figure 1.

1.3.1 History of the Saltmarsh vegetation at Berrow

According to Moss' observations in 1907, Berrow Flats was devoid of vascular plant vegetation:

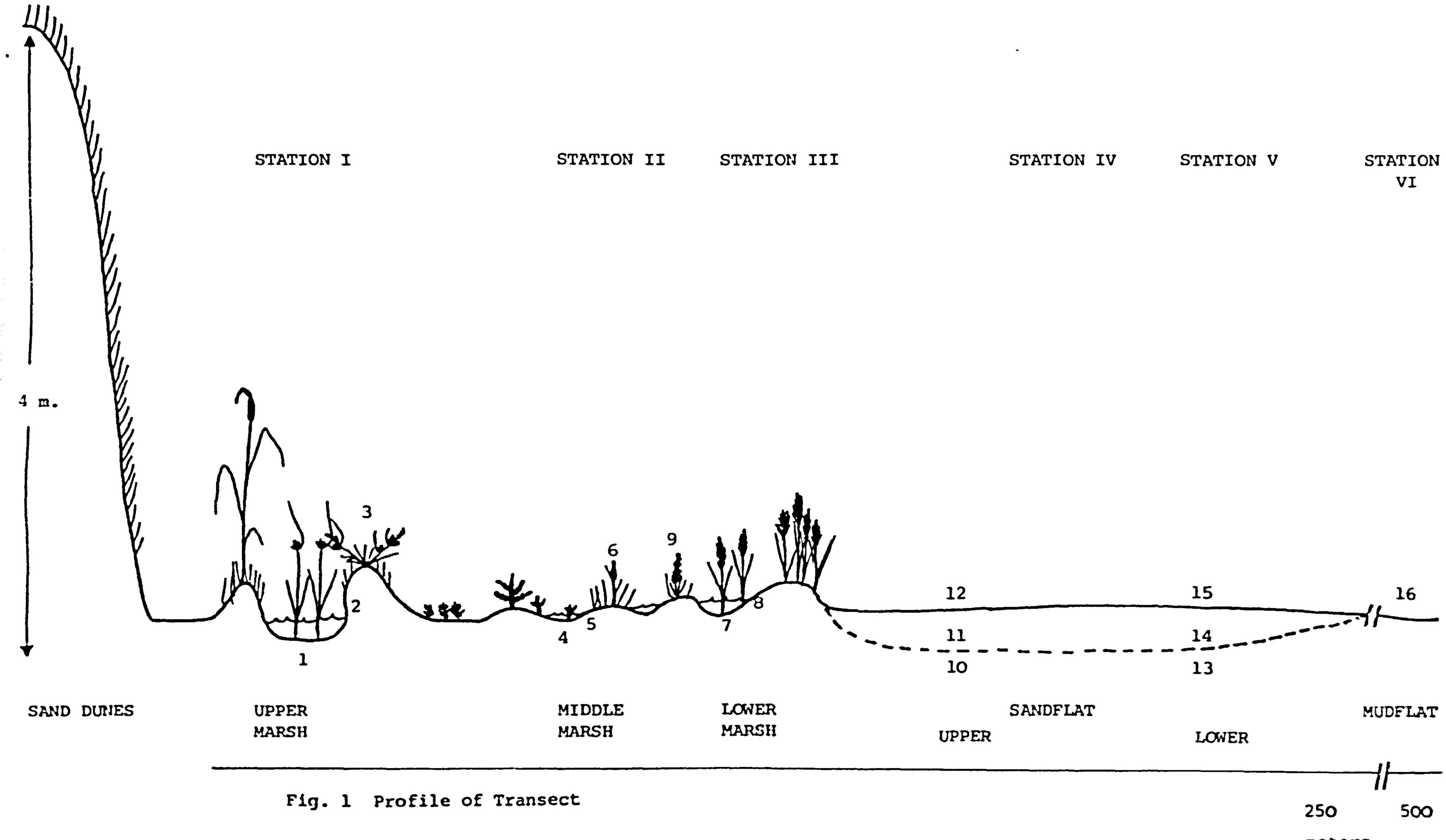


Fig. 1 Profile of Transect

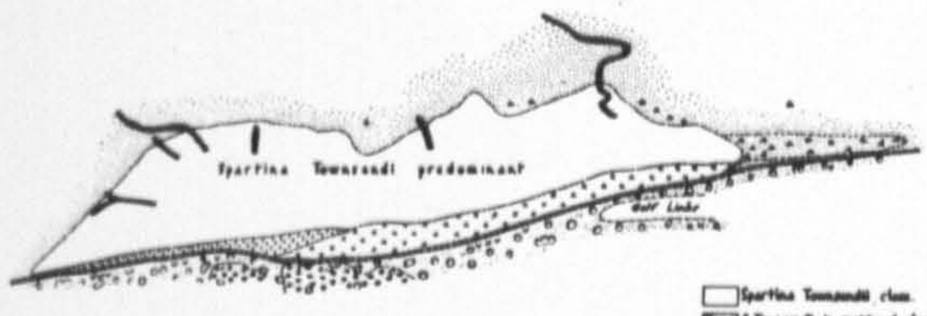
> "Owing to constant movements of the surface caused by the ebb and flow of the tides, the flats possess no vegetation. The prevailing westerly and south-westerly winds blowing over the flats drive tiny particles of sand onwards; and in times of high winds sand blizzards are frequent"
>
> (Moss 1907 from Thompson 1922)

Saltmarsh plants were believed to have initially colonized the mudflats sometime between 1910 and 1912 (Thompson 1922). Thompson was the first ecologist to investigate the vegetation growing at Berrow, which had developed into a saltmarsh covering an area of 41.67 ha. This saltmarsh developed because of the formation of a new channel branching off the river Parret which diminished the scour of the sea over the mudflat (Platæla Thompson 1922).

The initial dominant mud coloniser was Puccinellia maritima (formerly Glyceria maritima). Salicornia could also be found in great abundance e.g. S. ramosissima and S. europea (S. europea was S. herbaceae). Other typically halophytic plants were found in local abundance such as Aster tripolium in association with P. maritima, Suaeda maritima and Triglochin maritima. One of the initial colonizers which was to have the greatest impact on Berrow marsh was Spartina anglica. Two parent swards were observed in July 1921 (Thompson 1922). The introduction of Spartina at Berrow is believed to be from natural spread from other sites along the Severn estuary, but its exact source is not known. (Hope-Simpson & Willis 1955). Thompson (1922) believed that S. anglica had spread naturally from the first Spartina planting in Clevedon. However Kendall (1938) suggests the parent plants came from Yatton plantings.

Thompson returned to Berrow many times in later years monitoring changes in the vegetation up to 1930. He observed 3 stages in saltmarsh succession

MARSH NORTH OF BURNHAM LOW LIGHTHOUSE.

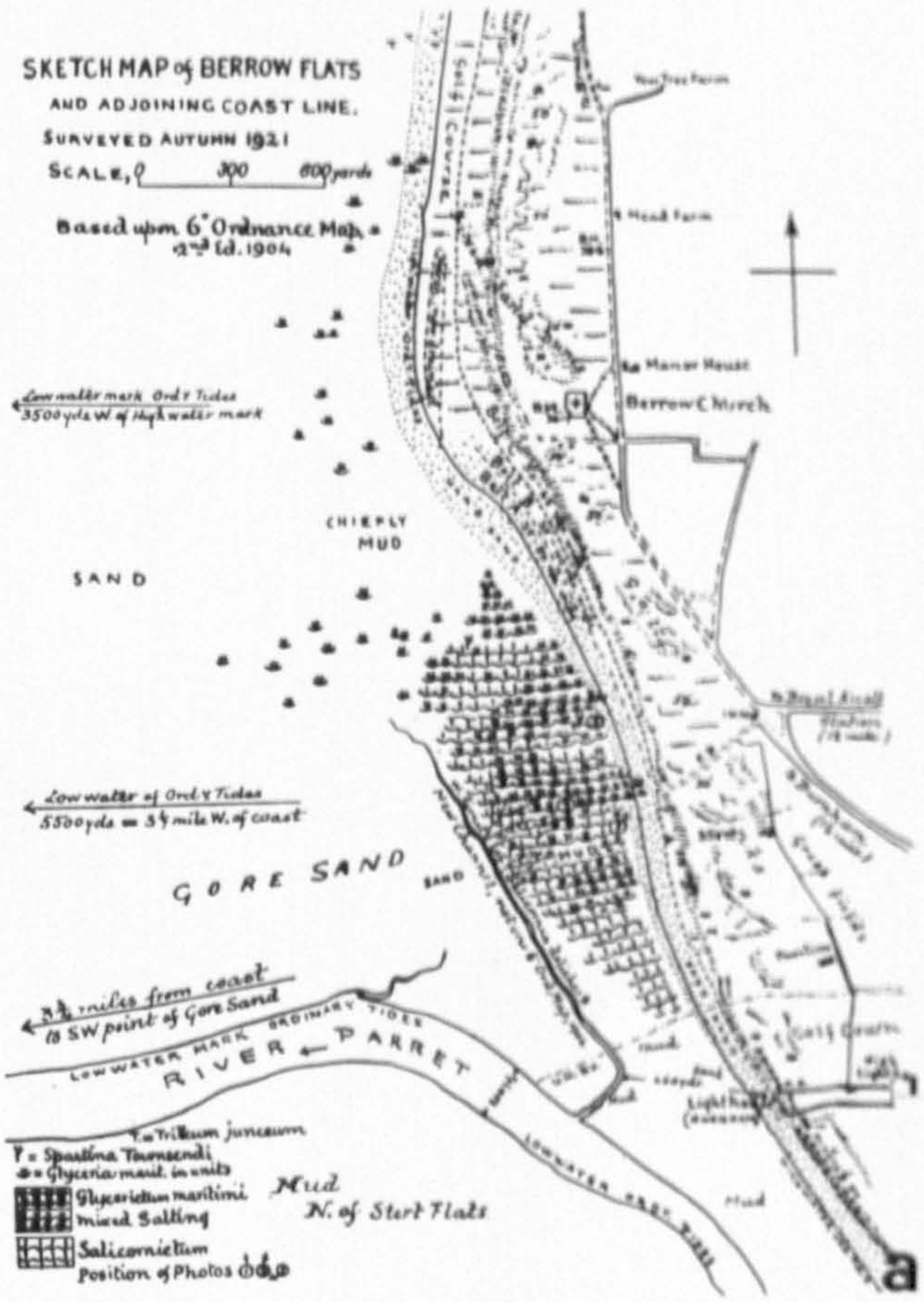


SKETCH MAP of BERROW FLATS AND ADJOINING COAST LINE.

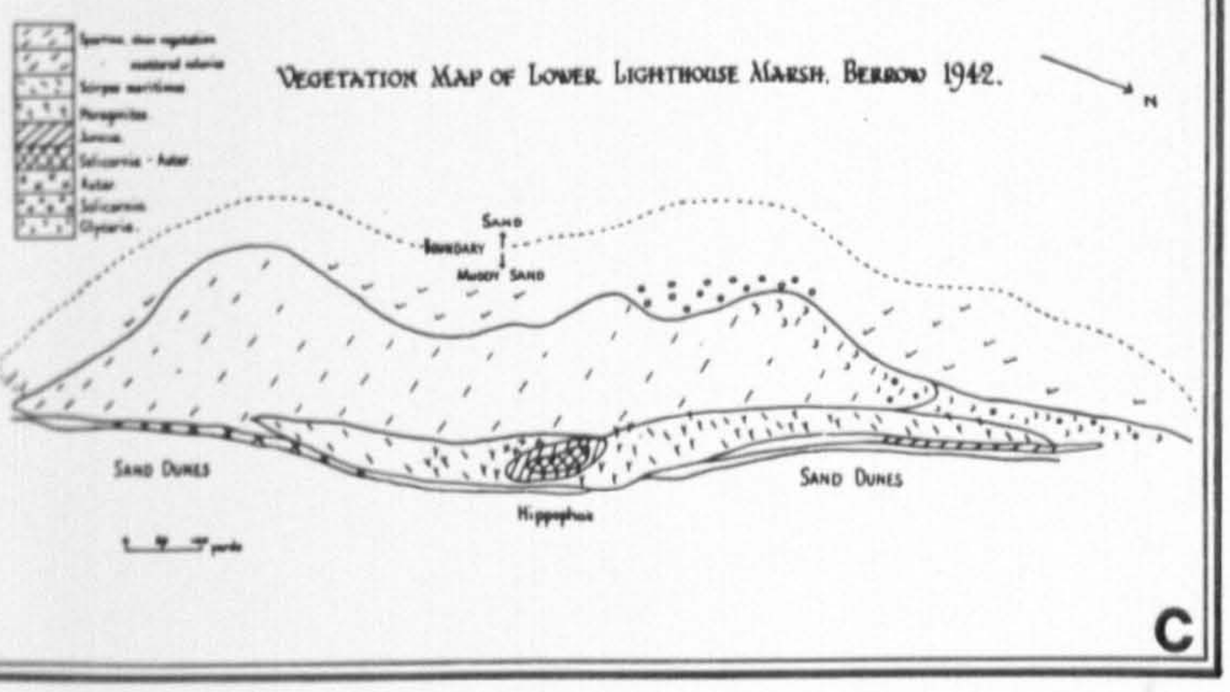
SURVEYED AUTUMN 1921

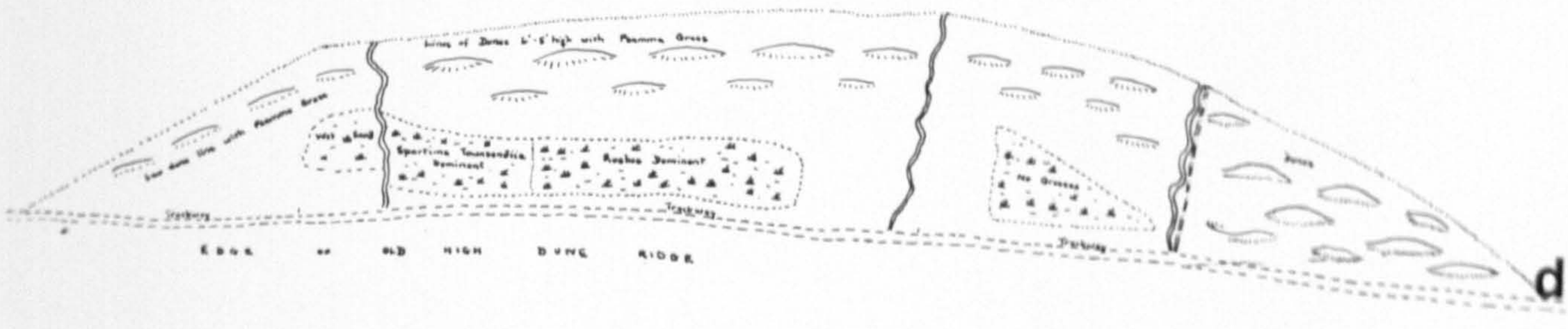
SCALE, 0 300 600 yards

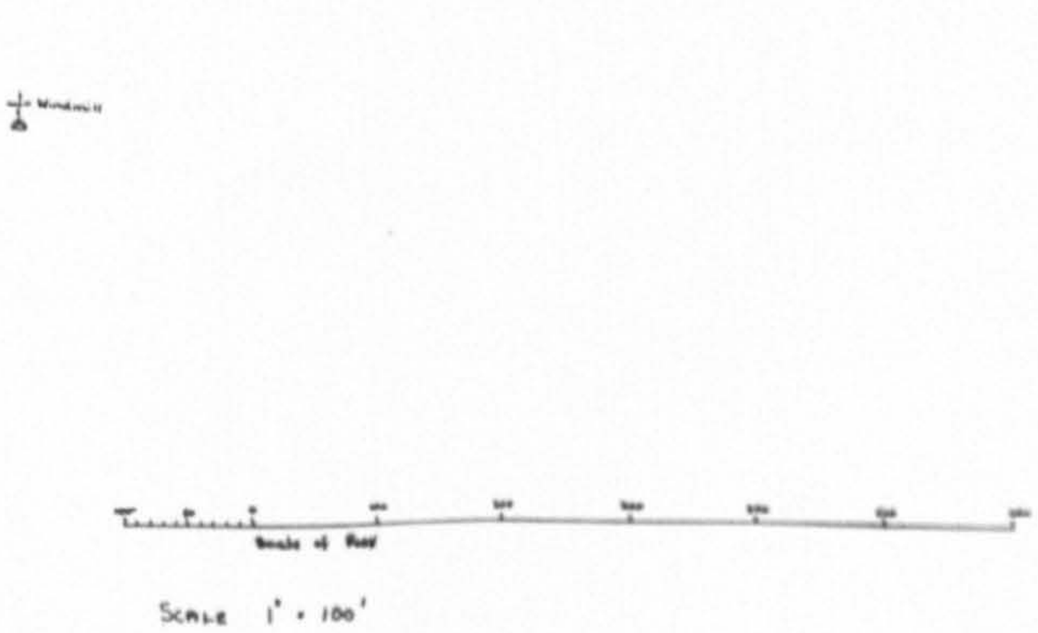
Based upon 6" Ordnance Map 2nd Ed. 1904



VEGETATION MAP OF LOWER LIGHTHOUSE MARSH, BERROW 1942.







(a) the rapid colonization of Spartina outcompeting P. maritima and Salicornia, (b) the colonization and spread of Aster tripolium and the formation of a Scirpus maritimus zone on the landward border of the marsh and (c) the appearance of non-halophytic species e.g. Typha latifolia. The change in vegetation occured with a concurrent change in the shape of the marsh. By 1923 the northern border of the marsh extended 100 yards north west of Berrow church, while 2 years earlier this border was 600 yards south west of it. Simultaneously with this change, the marsh retreated at the southern end, which Thompson attributed to the silting up of the seaward channel branching off the river Parret. In later years Spartina formed a seaward belt, with Scirpus maritimus colonizing the landward edge (Whereat 1934), as the marsh grew seawards (James 1934).

Kendall continued the survey of the saltmarsh in 1936. She observed that the northern borders had become drier than the south. The marsh was reduced to an area of 18.33 ha. (Kendall 1938, see Plate 2b). The bulk of this area was covered by a closed Spartina sward. Other species occupied a marginal area on the landward side of the marsh. Small creeks had formed on the seaward side of the S. anglica zone (Kendall 1938).

By 1943 the vegetation and dimensions of the marsh had changed significantly (Boley 1943). The marsh had continued to extend northwards, with further development of creeks (see Plate 1c). Three vegetation zones were observed: (1) a seaward Salicornia-Puccinellia zone (2) a central Spartina zone and (3) a Scirpus maritimus zone on the landward side. Forty nine different species were identified in the marsh including many freshwater aquatic forms. A few years earlier another smaller saltmarsh

was observed 400 yards northwest of Berrow church, which was being rapidly surrounded by sand dunes (see Plate 1d, Pope & Turner 1938). The Spartina zone of the larger marsh was spreading rapidly seawards leaving few open spaces in between the swards (Cowder 1942).

These historical records establish that the saltmarsh has undergone all but the last stage of succession, and reached maturity within a very short space of time. The last stage in saltmarsh succession is a phenomenon known as "die-back" where Spartina swards die for no apparent reason, leaving a salt pan to form afterwards. Salt pan formation has not been recorded anywhere in the Severn estuary at present (Teverson 1983). Why this last event has not taken place, remains unexplained. A more recent report describes further dune development which dissected the Berrow marsh at the southern end. This southern area became surrounded by sand dunes and transformed into a Phragmites communis reed bed (Smith 1979). Only a small northern section of Berrow marsh remains today.

1.3.2 Present Vegetation at Berrow

The area of Berrow marsh remaining is approximately 4.3 ha. (measured in July 1983), 1/10 of the 1922 extent. The northern border extends just over 100 yards northwest of Berrow Church. The transect for the present study is directly west of the Church. The width of the marsh is more or less uniform (85 meters), widening slightly at the northern end.

The Spartina forms a closed sward at the seaward edge of the marsh extending landward and gradually forming a less dense canopy. In the middle marsh the vegetation is more open and the ground surface becomes more even allowing different marsh plants to colonise. In the third zone

at the landward side of the marsh, the greatest variety of plants may be observed, while Spartina is scarce. Here a large variety of halophytic plants and freshwater aquatics are present. A very dominant benthic Oscillatoria sp also grows in the upper marsh zone either on the sediment, floating on the pool surface or attached to the base of the marsh plants (Malin personal communication).

With the help of a group of workers a species list of the saltmarsh vegetation was compiled (Table III). The relative abundance of dominant species in the three zones in the marsh are listed in Table IV. No previous work has been done on the algal microflora of this site. Smith (1979) mentions the presence of Vaucheria. However a very diverse microflora exists, some of the major genera are listed in Table IVa. This list is deceptively small since a large number of species were observed, most notably in the genera Oscillatoria and Anabaena.

The flora indicates that in the region sampled, a mature marsh exists, and the records from the literature show that development to maturity took no more than 40 years. Therefore it is important to emphasize that the diatom assemblages now growing here form a community which has established on a site which has undergone considerable changes in a very short period of time.

Table III A list of Plants Recorded from the saltmarsh of Berrow Church 18th August 1983.

Alisma plantago-aquatica
Alnus glutinosa
Anthoxanthum odoratum
Apium graveolens
Aster tripolium
Atriplex hastata
Berula erecta
Carex extensa
Carex flacca
Carex otrubae
Centaurium erythraea
Centaurium pulchellum
Cochlearia anglica
Euphorbia paralias
Festuca rubra
Glaux maritima
Juncus aritculatus
Juncus bufonius
Juncus gerardii
Juncus inflexus
Limonium binervosum
Melilotus altissima
Oenanthe crocata
Oenanthe lachenalii
Parapholis strigosa
Phragmites communis
Plantago coronopus
Plantago maritima
Puccinellia distans
Puccinellia maritima
Ranunculus sceleratus
Salicornia europea (or stricta)
Scirpus maritimus
Sparganium emersum
Spartina anglica
Spergularia media
Triglochin maritima
Triglochin palustris
Typha latifolia
Veronica anagalis-aquatalis

Table IV Zonation of Saltmarsh plants

Zonation

UPPER MARSH

Dominants: Scirpus maritimus
Phragmites communis

Common: Typha latifolia
Carex extensa
Glaux maritima
Festuca rubra
Triglochin maritima

Scattered: Aster tripolium
Centaurium pulchellum
Juncus bufonius
Juncus inflexus
Plantago coronopus
Parapholis strigosa
Plantago maritima

Rare: Alisma plantago-aquatica
Apium graveolens
Oenanthe lachenalii

MIDDLE MARSH

Dominants: Salicornia europeas
Glaux maritima

Common: Cochleria anglica
Festuca rubra
Plantago maritima
Spartina anglica
Triglochin maritima

Scattered: Aster tripolium
Centaurium pulchellum
Juncus bufonius
Spergularia media

Rare: Apium gravaeolans
Limonium binervosum

LOWER MARSH

Dominants: Spartina anglica
(forming closed sward
at seaward edge).

Scattered: Festuca rubra
(on tufts)
Plantago maritima
(on tufts)
Cochleria anglica
Aster tripolium

EDGE OF MARSH

Carex otrubae (Northern corner
of marsh)
Euphorbia paralias (Southern end)
Sparganium emersum (middle marsh)
Veronica anagalis-oquatis
(Southern end)
Puccinella distans (near sand dunes)
Oenanthe crocata

Table IVa List of the major algal genera

Anabaena
Calothrix
Chroococcus
Hydrocoleus
Lyngbya
Merismopedia
Nodularia
Nostoc
Oscillatoria
Phormidum
Pseudanabaena
Spirulina

Euglena
Phacus
Green monads

CHAPTER 2 MATERIALS AND METHODS

2.1 Measurement of physical factors

Light Intensity

Light intensity was measured using a portable Luna six 3 lux light meter. The light intensity above and below the vegetation canopy was measured where present.

Temperature

Temperature was measured using a mercury thermometer calibrated at 0.5^{o}C intervals. Temperature was recorded at each site by placing the thermometer bulb in the sediment. Air temperature was also recorded.

Salinity

The interstitial water was extracted from the sediment directly using a pasteur pipette, or by centrifugation for 2-5 minutes at maximum speed in a MSE centrifuge. A sub-sample of the interstitial water was placed in an American Optical hand refractometer, and the salinity recorded.

pH

pH was measured in the field using an EIL portable pH meter (model 50B), and later a WPA C6/T portable pH meter. pH deviation due to temperature was corrected. A special spear-head soil electrode was used.

Watercontent

Watercontent was measured in terms of waterloss per gram on a wet weight/dry weight basis. Wet sediment was collected in pre-weighed watertight containers in the field. Their weights were recorded as soon as the samples were brought back to the laboratory, and then dried in an oven at 30-40^{o}C for a minimum of 1 week, and then re-weighed. Due to supersaturation caused by the hydration of ions in the sediment percentage watercontent was not calculated.

Tidal heights

The height of each site was measured by timing tidal innundation. Tidal

heights were then calculated using ordinance datum.

Organic matter

Levels of organic matter were measured using a loss on ignition procedure described in Avery & Bascombe (1974).

2.2. Methods for valve identification

Acid treatment

Six coverslips were placed over a single layer of Whatman 105 lens cleaning tissue on the sediment. After 2-4 hours the coverslips were removed and placed in a beaker containing equal volumes of concentrated nitric acid and sulphuric acid. The acid solution was heated gently for twenty to forty minutes on a hotplate. Once cooled the acid solution was transferred to a 10 ml centrifuge tube and centrifuged at speed 4-5 in a MSE minor 'S' centrifuge for 5 minutes. The diatom pellet was resuspended and rinsed by repeated centrifugation seven times with distilled water.

Hydrogen Peroxide treatment

Six coverslips were placed over a single layer of Whatman 105 lens cleaning tissue on the sediment, as above. Once removed, they were placed in a beaker containing 20 ml 30% w/v H_2O_2 (100 volumes). The solution was mixed and left to settle overnight. The supernatant was decanted, and resuspension and settling of the remaining diatom solution was repeated seven times using distilled water. When frustules were particularly delicate 15% w/v H_2O_2 was used.

Preparation of permanent slides

One or two drops of acid or peroxide cleaned material was placed on a 19 mm diamter coverslip. A further 1 ml of distilled water was added to disperse the material. The diatom valves were dried onto the coverslip by evaporating the water using a 200-240V Cryselco heat lamp. The coverslip was mounted in Naphrax mountant (refractive index 1.74), and left to dry overnight. After drying the slides were ringed with a shellac sealant.

Preparation of sealant

50% meths (v/v) was mixed with a few drops of analine blue and then filtered to remove solid particles. 45% shellac (v/v) and 5% castor oil (v/v) were then mixed into the solution. The sealant was stored in a stock bottle at room temperature.

2.3 Comparative sampling strategies

Sampling the Sediment

All samples were taken at low tide using a petri dish. A uniform surface area at each sampling site was scraped off and flattened out into a petri dish.

Sampling for diatoms using the coverglass method

Once in the laboratory the mud surface was flattened to produce an even surface in the petri dish. Distilled water was added using a dropper which was applied at the petri dish margin. This was to ensure that the watercontent in the mud was sufficiently high to sustain the diatom population over the time of sampling. A coverslip was placed on the mud surface and left for a minimum of 2 hours before being removed and mounted on the slide with diluted glycerol jelly and ringed with Depex.

The mud from each sampling site was sampled in this fashion twice at two different times in the day (12:00 hrs and 15:00 hrs). Each coverslip was placed on a different area of mud in the petridish.

One traverse across each coverslip, 70 microscope fields on a Vickers Instruments Compound microscope, was counted at 400x magnification. An Olympus COl compound microscope was used later, but a grid was placed in the eyepiece to ensure that the same surface area was examined. The mean of the two counts was taken for each site.

Sampling for diatoms using a centrifugation technique

This method is a modification of the multi-step gradient of de Jonge (1979). Twenty-five milliliters of surface sediment was placed in a beaker and diluted 50% (v/v) by a Ca, Mg free artificial seawater medium (as in de Jonge 1979), which is isotonic with 8.75‰ sea water. A sub-sample of 2 cm^3 of diluted sediment was taken with a plastic syringe from which the conical top had been cut off.

The sub-sample was transferred into a large plastic bottle with a water-tight screw top lid, and rinsed with Ca/Mg free artificial seawater to a final volume of 25 ml. The bottle was shaken for 60 seconds and the sandgrains allowed to settle for 15 seconds before the supernatant was drawn off using a 60 ml plastic syringe. The bottle was rinsed 3 times using 7 ml of artificial seawater each time allowing 15 seconds for the sand grains to settle.

Ten milliliters of the supernatant was sub-sampled (after thorough mixing), and poured into a 4" x 1" centrifuge tube. Six milliliters of concentrated LUDOX - TM was loaded as a cushion into the centrifuge tube using a pasteur pipette, forming a single step gradient.

The sample was centrifuged at 1,800 rpm for 15 minutes. When centri-fugation was complete 4 bands of solution were produced. Each band was drawn off and placed in a separate graduated test tube and the volume noted. Two drops of lugols iodine was added to each test tube. The iodine added to the concentrated ludox was diluted 10 times in order to avoid flocculation. The solution in each test tube was made up to a total of 15 ml shaken and left to settle for a minimum of 24 hours.

After 24 hours the solution above the settled sediment was drawn off so that a known volume was left in the test tube (1-2 ml). This final solution in the graduated test tube was shaken and a sub-sample taken and counted on a haemocytometer slide. With all the volumes of the sub-samples known, the total cell number per cubic centimeter could then be calculated.

Comparing results of the two methods

The two methods were compared to see how the population inhabiting the sediment was reflected by the method used. Since the coverglass method examined a surface area, and the centrifugation technique measured a volume, the results were compared in terms of the percentage abundance.

Table V Percentage abundance of the dominant taxa

Species	Centrifugation %	Coverglass %
Amphora ovalis var. libyca	3.05	3.86
Navicula trivialis	0.87	5.5
Navicula pygmaea	0	1.71
Navicula cari/N. cincta	11.97	67.86
Navicula spp.	4.14	7.35
Nitzschia sigma var.	1.91	1.16
Nitzschia acuminata	0.29	1.71
Total % accounted for	22.23	89.15

A greater number of taxa were counted in the centrifugation technique. These included the less motile araphid forms from the epipsammic assemblage. Species with high percentage abundance were the same in both methods e.g. Navicula cari and N. cincta, Navicula spp, and Amphora ovalis var. libyca. The percentage abundance of Navicula trivialis showed the greatest difference between the two methods.

The number of empty frustules sampled in the centrifugation technique was

many orders of magnitude greater than the coverglass method: with totals calculated as: 8.10 x 10^6 Frustules/cm^3 (centrifugation), and 9.59 x 10^2/ cm^2 (coverglass).

Problems with the Centrifugation Technique

One of the worst problems encountered was cell breakage. Centrifugation was not a delicate treatment. Spines or more delicate valve appendages, were always damaged, and dinoflagellates were destroyed. All associations of diatoms attaching to blue-green algae, and silt clustering around the diatom cells disintegrated.

de Jong (1979) claims that diatoms have a restricted density range. Most of the diatoms did separate into one density band after centrifugation, but some cells were found in all layers including the silt pellet below the Ludox cushion. It was impossible to establish if the diatoms entered into the different layers randomly; or because of differing densities. Certain genera such as Amphora adhere to the sediment with greater force than others (Harper & Harper 1967). This may be another cause for an unbalanced separation. A more critical examination of how the various diatom taxa separate into different density bands is required. This would mean that a considerable amount of work would need to be done before this technique could be used for regular field sampling.

Large amounts of silt were still present in the main diatom band after centrifugation, making counting difficult. Preserving the cells in lugols iodine caused retraction of the chloroplasts which also caused difficulty in cell identification.

Aside from being a complicated and time consuming method there are further problems. The most serious of which is that diatoms growing in different

diatom assemblages within the microlayers of the sediment cannot be distinguished. Thus the ecology of the epipelon and the epipsammon become confused. The dormant cells buried in the aphotic zone still containing viable cell contents are also sampled with the actively growing populations causing further confusion. This would explain why a high species diversity was recorded in the centrifugation technique. Although the centrifugation technique is considered to be a better method for measuring the amount of chlorophyll within the sediment (de Jonge 1979), the problems to overcome for a rigorous quantitative ecological study are enormous.

Problems with the coverslip technique

The main limitation with this method is that the surface is the only substratum sampled. This excludes the possibility of studying the epipsammon. Some epipelic diatoms may be more capable of adhering to the undersurface of the coverglass than others. This means that some species may be over-represented and others under-represented (Eaton 1967). In order to reduce variation from non-random distribution, and from different patterns of vertical migration rhythms within the sediment, more than one coverglass must be removed from the mud and these must be taken at different times of the day.

The Advantages of the coverslip method and the Justification of its use.

The coverslip method is both quick and simple. In using such a technique many types of organisms may be sampled without damage. Slides may be mounted and kept for re-examination for up to 2 years. Even though abundance per unit volume cannot be measured, the proportional representation of actively growing members of the epipelic population can be measured (Eaton 1967). For the purposes of an ecological study this method fulfills the aims required. The more dormant cells lying beneath the surface are not sampled; only a small fraction of empty frustules remaining

at the surface adhere to the undersurface of the coverglass and these can be ignored whilst counting. The really important advantage is that the actively growing cells can be counted.

Sampling Strategy for the fieldwork

Due to the high degree of variability encountered in the field a rigorous quantitative study of the epipelon was confined to a single transect. Coring the sediment was not possible. Fluid uncorable sediment was present at a few sites. Scraping a uniform surface area ($\sim$120 cm^2), provided a consistent method for all sites making results comparable. Adding distilled water to the petridishes in the lab instead of water from the pools in the field was done to avoid contamination by semi-planktonic forms, which might settle onto the sediment. Adding distilled water to samples of all salinities did not affect diatom migration, as epipelic diatoms are known to be extremely tolerant to salinity change (Admiraal 1977d). It is disturbance of the sediment by a rainfall which disrupts migration (Rasmussen et al. 1982). For this reason distilled water was applied to the petridish margin, and the sediment was allowed to settle overnight before being sampled.

Various fixation techniques using, lugols iodine, glutaraldehyde and formalin were attempted. All fixatives used, caused retraction of the chloroplasts. Since the number of cells counted across one traverse of a coverglass mounted in diluted glycerol jelly did not change in a week, no fixation method was used. The less the cells were tampered with, the easier their identification. Duplicate counts at each site were taken each month. Counting all 32 slides took no longer than 1 week. To ensure against bubble formation caused by photosynthesis, all slides were kept in the dark.

In addition to the live cell counts, additional coverglasses were placed on the sediment surface and cleaned (as described in section 2.2). Identification of the live cells was achieved by matching the live cells to the acid cleaned material.

There is no sampling technique that is free of variability. This is due to the uneven distribution of the diatoms on the sediment. Therefore understanding the information derived from sub-sampling is dependant upon a knowledge of the frequency distribution of the population (Venrick 1978). This can be achieved by the direct analysis of replicate sub-samples from whatever method is chosen.

Future work needs to examine vertical distribution of the diatoms in situ. A box corer sampling device which freezes the sediment in place could be adapted for this purpose (Hüttunen & Meriläinen 1978). This would also involve a critical investigation of the organisms inhabiting different microlayers in the sediment. This might also be achieved by adapting a "Neuston-sampling device" which is a stainless steel or plastic mesh mounted in a frame which can be drawn horizontally in the water column at a specific depth (Parker 1978).

2.4 Assemblage Composition Measures

Similarity measure

Of the different similarity measures available, a city block similarity matrix was calculated to compare the similarity between different taxa. First each mean count y(i),y(j) was scaled within a range of zero to one:

1)

$$x(i) = \frac{Y(i)}{\max Y(i)} \qquad x(j) = \frac{Y(j)}{\max Y(j)}$$

In order to scale abundance from zero to one each mean count of any two

taxa (y(i) and y(j)) was divided by the maximum mean count observed for that taxon (max y(i) and max y(j)). Therefore if the abundance of a given taxon is 1 (i.e. y(i)/max y(i) = 1), then this is the true maximum count of this taxon. The similarity between 2 species can be calculated for one site on one occasion using the formula:

2)

$$S_X(i,j) = 1 - \left| \frac{x(i) \; 1 \; x \; (j)}{R_X} \right|$$

$S_X(i,j)$ is the similarity measure between x(i) and x(j) at one site on one occasion. R_X is the difference between the maximum and minimum counts of all species recorded at the particular site and occasion under consideration. Thus the counts have been scaled in two ways: in terms of the range counted for each species and also in terms of the range of counts for a given site and occasion.

The final calculation of similarity for all sites and occasions is defined by the equation:

3)

$$S(i,j) = \frac{\sum_X W_X(i,j) S_X(i,j)}{\sum_X W_X(i,j)}$$

Where W_X can have 2 possible values: if at one site and occasion x(i) and x(j) were zero then W_X was zero. If x(i) and/or x(j) were present then W_X was one. Therefore $\sum_X W_X(i,j)$ was the sum of sites and occasions where x(i) and x(j) could be compared. Where both x(i) and x(j) were absent then the zero made no contribution to the similarity measure. Also any count that was less than 5% of its true maximum was ignored. So the higher the S(i,j) the more closely associated the pair.

Different methods of measuring similarity have been attempted, such as comparing species on the basis of presence or absence in counts. However

the city block similarity measure described, used the greatest amount of information available and offered a more detailed measure of similarity. S(i,j) is calculated for 82 taxa and the results are represented by a similarity matrix for each year.

Niche Breadth

Niche breadth is an expression of the ability of a taxon to grow well at all sites along the transect, and is measured by the equation:

$$Bj = \exp\left[- \sum_{r=1}^{Q} \left(\frac{nir}{Ni}\right) \log_e \left(\frac{nir}{Ni}\right)\right]$$

(McIntire & Overton 1971)

nir is the number of individuals of the ith taxon observed at site r, and Ni is the sum of counts of i at all sites Q. The values of Bj (niche breadth), can range from one, meaning a taxon is only successful at one site, to Q, meaning that a taxon is equally successful at all sites. However Bj is not necessarily associated with a taxons relative abundance.

2.5. Multivariate Statistical Analysis

A hierarchical cluster analysis assigns units (species) to clusters. Initially all units are in separate clusters. First the clusters with the highest similarity merge, forming a new cluster (or clusters). Then the clusters are redefined and the calculations are repeated, until all units belong to a single cluster. The grouping together of two or more units occurs at different "merging levels" which decreases as the algorithm proceeds. The merging levels are shown graphically by a dendrogram, showing the order in which clusters join together.

Five different methods of cluster analysis are available in the GENSTAT package used. Using the similarity measure described, 3 different methods of clustering were attempted: single linkage, average linkage, and

centroid clustering. If there are no isolated clusters in single linkage clustering, then the results group all units together in one large cluster, leaving a few ungrouped units. This occured when a single linkage cluster analysis was attempted on the present data, therefore this method was not followed up. Both average linkage and centroid clustering produced extremely similar results for each years data. Centroid clustering was finally selected as a method to display the results.

The recalcuated similarites in centroid cluster analysis are the weighted means of similarities between each of the two merged clusters and any third cluster (for the formula see section 9.6.1 of the GENSTAT reference manual Part II 1983). Centroid cluster analysis, like all other methods other than single linkage, maintains compact clusters without regard to the possibility that two similar units may be assigned to different major clusters. This means that a small change in the data could produce a large change in the cluster solution. For this reason it is sensible to try out different cluster methods and not rely too heavily on one single cluster solution. However all cluster solutions (with the exception of single linkage), produced consistent results in this study.

A principal coordinate analysis produces a graphical inspection of the data. This is recommended when a large cluster is produced by the single linkage method. This analysis was also attempted for all 2½ years data. This analysis finds coordinates in n-dimensional space for the different objects (species), so as to reproduce the dissimilarities between them, (similarities may easily be transformed to dissimilarities). Each axis accounts for a proportion of the total dissimilarity or "variance" within the groups of objects.

CHAPTER 3 RESULTS

3.1 PHYSICAL DATA

3.1.1 Light

All light intensity measurements were taken above and below the vegetation canopy where saltmarsh vegetation was present. The aim of these measurements was to compare the shading effect of the different vegetation canopies in the different zones of the saltmarsh.

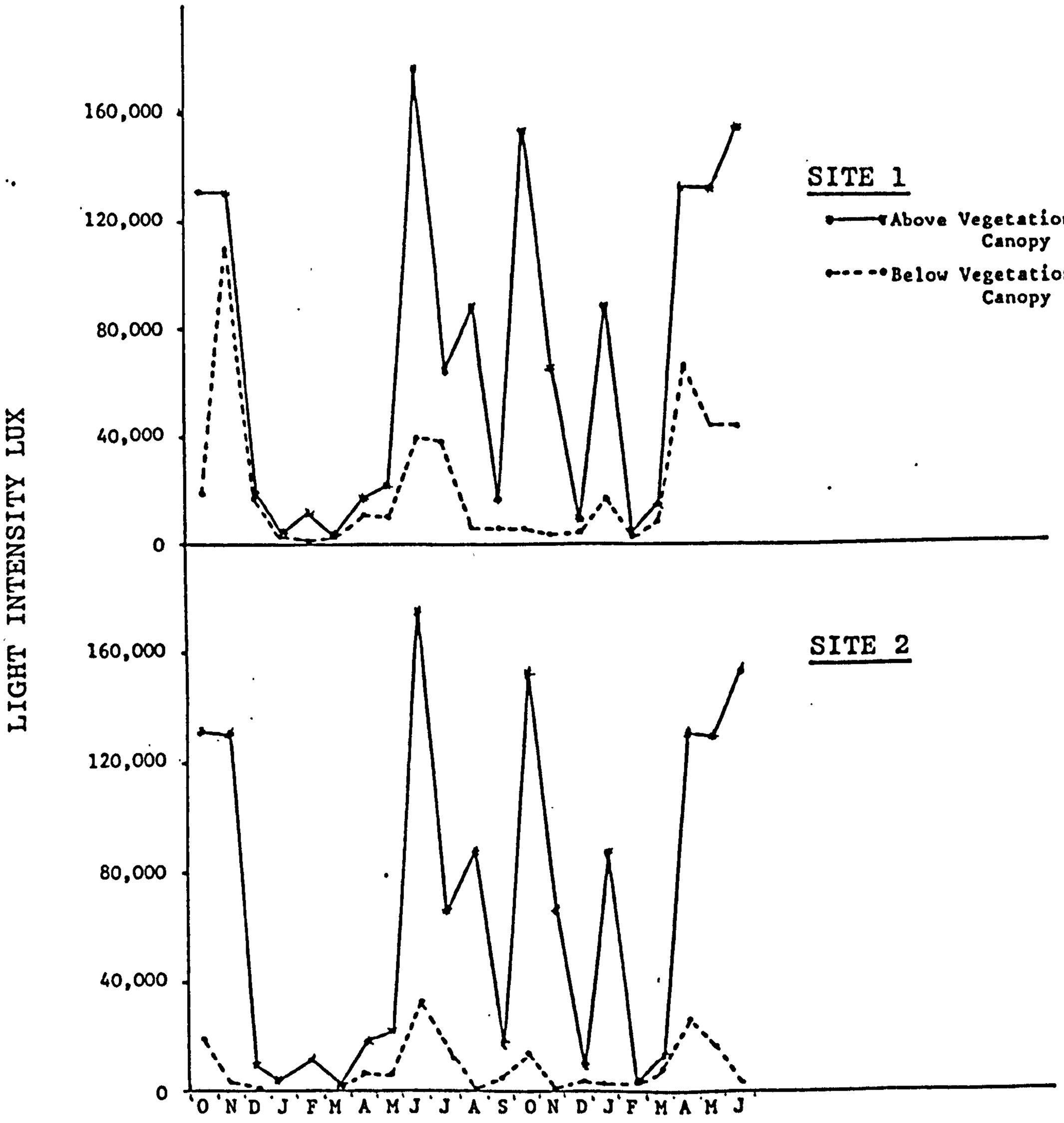
Station I (Sites 1-3) Upper marsh

In the upper marsh region the pools were shaded by abundant growth of Scirpus maritimus which formed its most dense canopy in the summer months. This can be seen in graph 1 by the decline in light intensity under the vegetation canopy in the months: August-November 1983. As the Scirpus maritimus died in winter, the understorey light intensity increased until spring, prior to renewed growth.

The vegetation canopy covering sites 2 and 3 were predominantly Puccinellia maritima, Festuca rubra and Carex extensa. Together with the other marsh plants in this zone a dense vegetation canopy covered the mud surface. Consequently much lower light intesity readings were recorded over most months (graphs 2 and 3) of these sites.

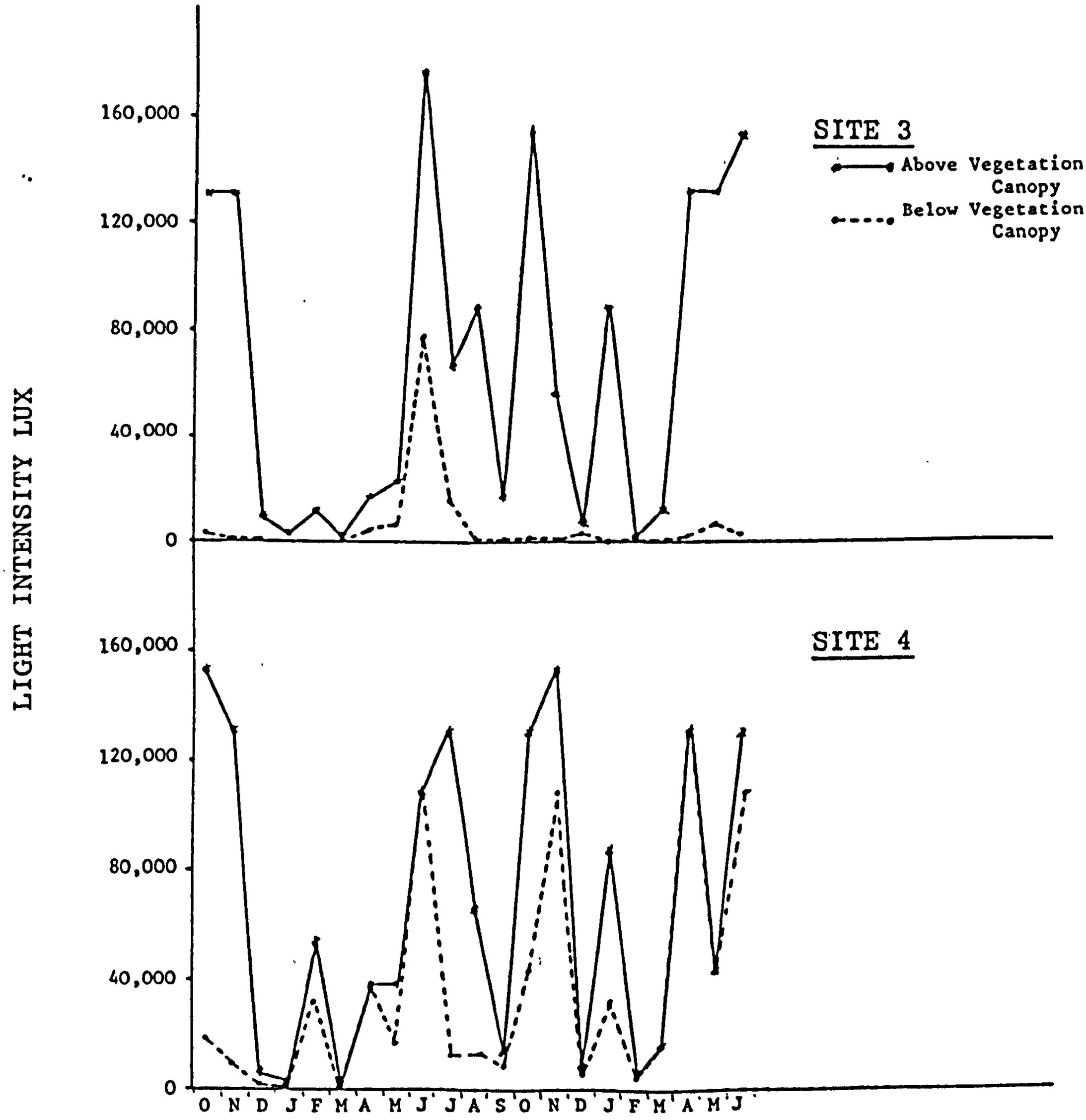
Station II (Sites 4-6)Middle marsh

Salicornia sp and Glaux maritima formed a scattered cover over the mud-flat of the middle marsh. The vegetation canopy was more open than at station I, particularly where Salicornia sp grew abundantly. Hence the comparatively high understorey light intensities observed at sites 4 and 5 (graph 2). The mound site (6) was covered with a thicker growth of Festuca rubra,Plantago maritima,Parapholis strigosa and Triglochin maritima. Therefore lower light intensities were recorded underneath the vegetation canopy than at sites 4 and 5.



GRAPH 1

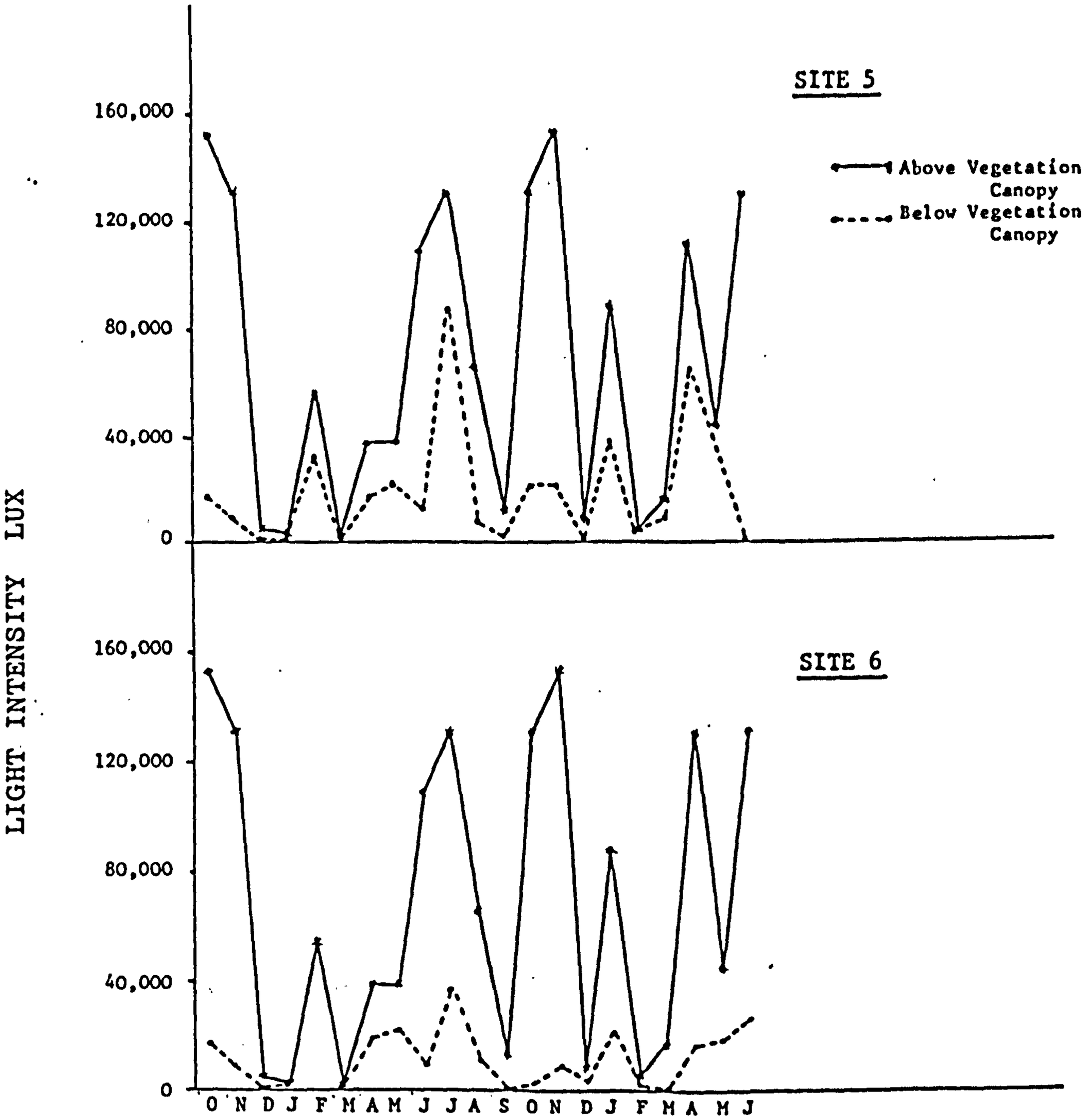
Temporal changes in the light intensity at sites 1 and 2 (*——*). Light intensity recorded above the vegetation canopy, and (*- - -*) below the vegetation canopy.



GRAPH 2

Temporal changes in the light intensity at sites 3 and 4 (*——*). Light intensity recorded above the vegetation canopy, and (*---*) below the vegetation canopy.

LIGHT INTENSITY



GRAPH 3

Temporal changes in the light intensity at sites 5 and 6 (*——*). Light intensity recorded above the vegetation canopy, and (*---*) below the vegetation canopy.

Station III (Sites 7-9) Lower marsh

Again the saltmarsh vegetation changed from pool (site 7) to the mound (sites 8 and 9). The pool was sparsely covered by the growth of the dominant plant in this zone Spartina anglica . The vegetation cover became denser in the summer and autumn months. This can be observed by the decrease in light intensity penetrating the vegetation canopy. At site 7 (graph 4) the understorey light intensity declined from June 1983 until February 1984. Peak understorey light intensities occured in the spring months: March-June 1983, and 1984; prior to vigorous growth of the Spartina canopy. Sites 8 and 9 (graphs 4 and 5) were predominantly covered by tufts of Festuca rubra and Plantago maritima. Like Station I this vegetation canopy was denser than that found over the pool site. Therefore light intensity readings under the vegetation canopy were lower than at site 7. Both sites 8 and 9 showed a sharp increase in the understorey light intensity from March-June 1984. This was due to innundation by sand at these sites.

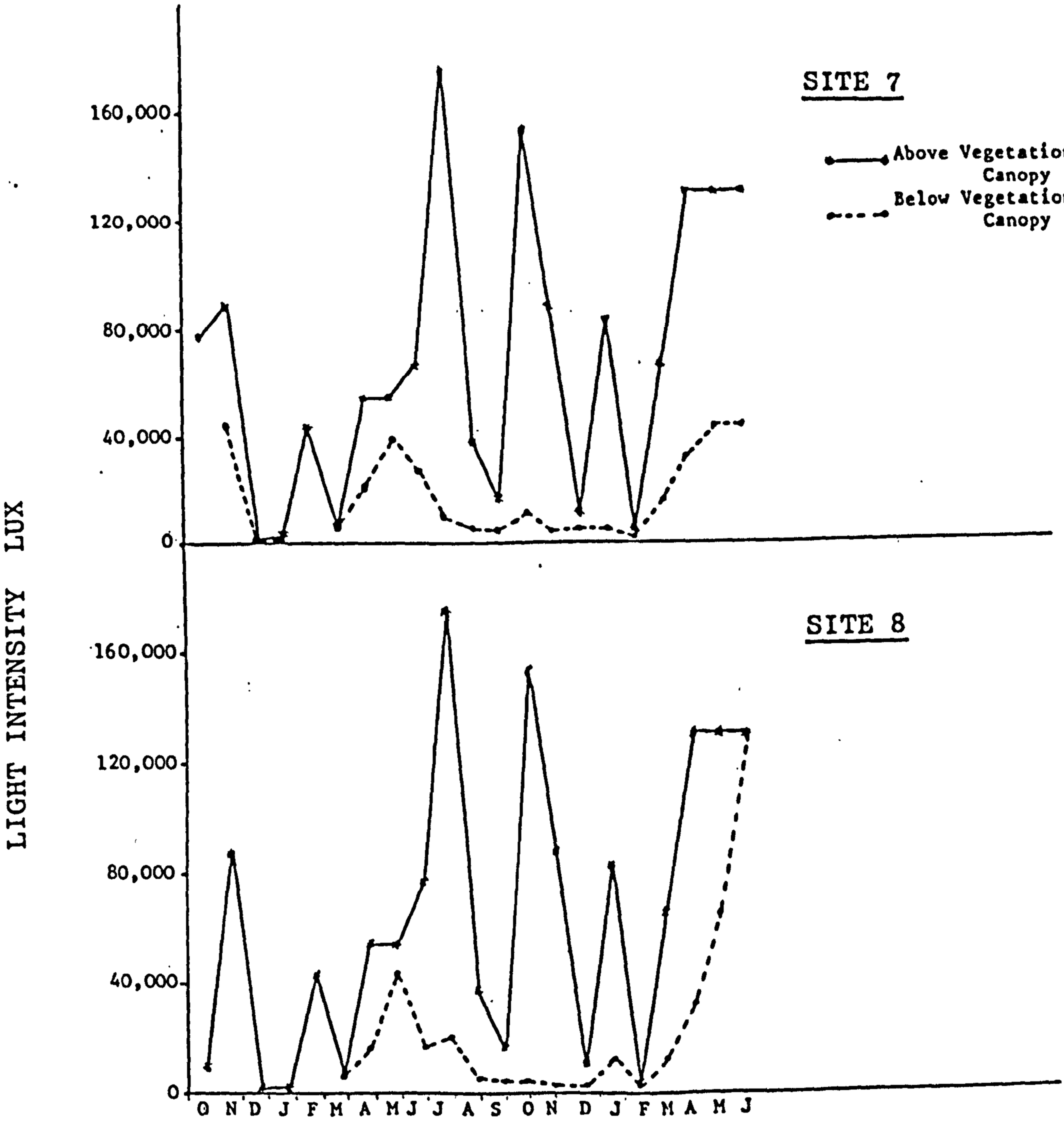
Station V and VI (Sites 10-16) Sandflat and Mudflat

There was no vegetation cover at these sites therefore the light intensity was the same. The microtopography of the sand caused little shading for most of the year. However following storm tides small cliffs were cut into the banks of the stream channel. These small cliffs had a more substantial shading effect, but they were soon flattened by wind and rain.

Summary:

All sites on the saltmarsh had reduced light intensities caused by the canopy of the saltmarsh plants. Shading was greatest at the slopes and mounds on the saltmarsh. The pools, and more open muds of the middle marsh had a greater proportion of sunlight penetrating through the vegetation canopy. There was no vegetation cover on the sandflat or mud-flat.

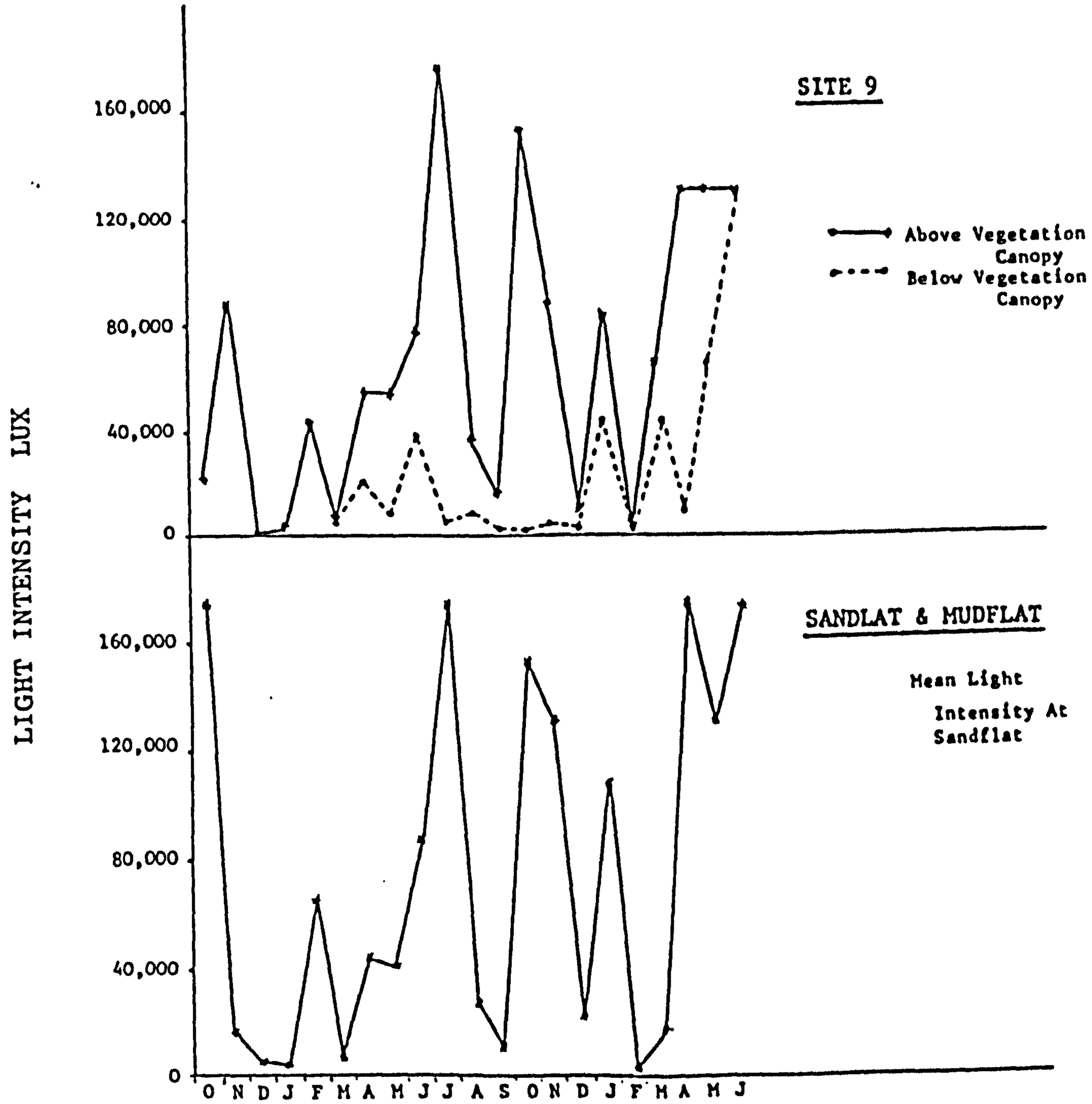
LIGHT INTENSITY



GRAPH 4

Temporal changes in the light intensity at sites 7 and 8 (*——*). Light intensity recorded above the vegetation canopy, and (*---*) below the vegetation canopy.

LIGHT INTENSITY



GRAPH 5

Temporal changes in the light intensity at site 9, and on the sandflat and mudflat (*——*). Light intensity recorded above the vegetation canopy, and (*---*) below the vegetation canopy, where present.

3.1.2 Temperature

The difference in temperature varied between ± 0.5°C at the different sites. Therefore all temperatures from all sites were compiled; the mean monthly temperature was calculated and plotted (graph 6). Both the air and soil/water temperature was measured at each site. Over the 30 months a repetitive seasonal pattern was observed. As temperatures increased in March; the soil/water temperatures increased at a faster rate than the air temperatures. Soil/water temperatures continued to be higher than the air temperature over the summer months (July-September). As temperatures decreased by October-December the soil/water temperatures decreased to the same temperatures as the air. Although this pattern was repeated each year, the difference between soil/water temperature and air temperature varied.

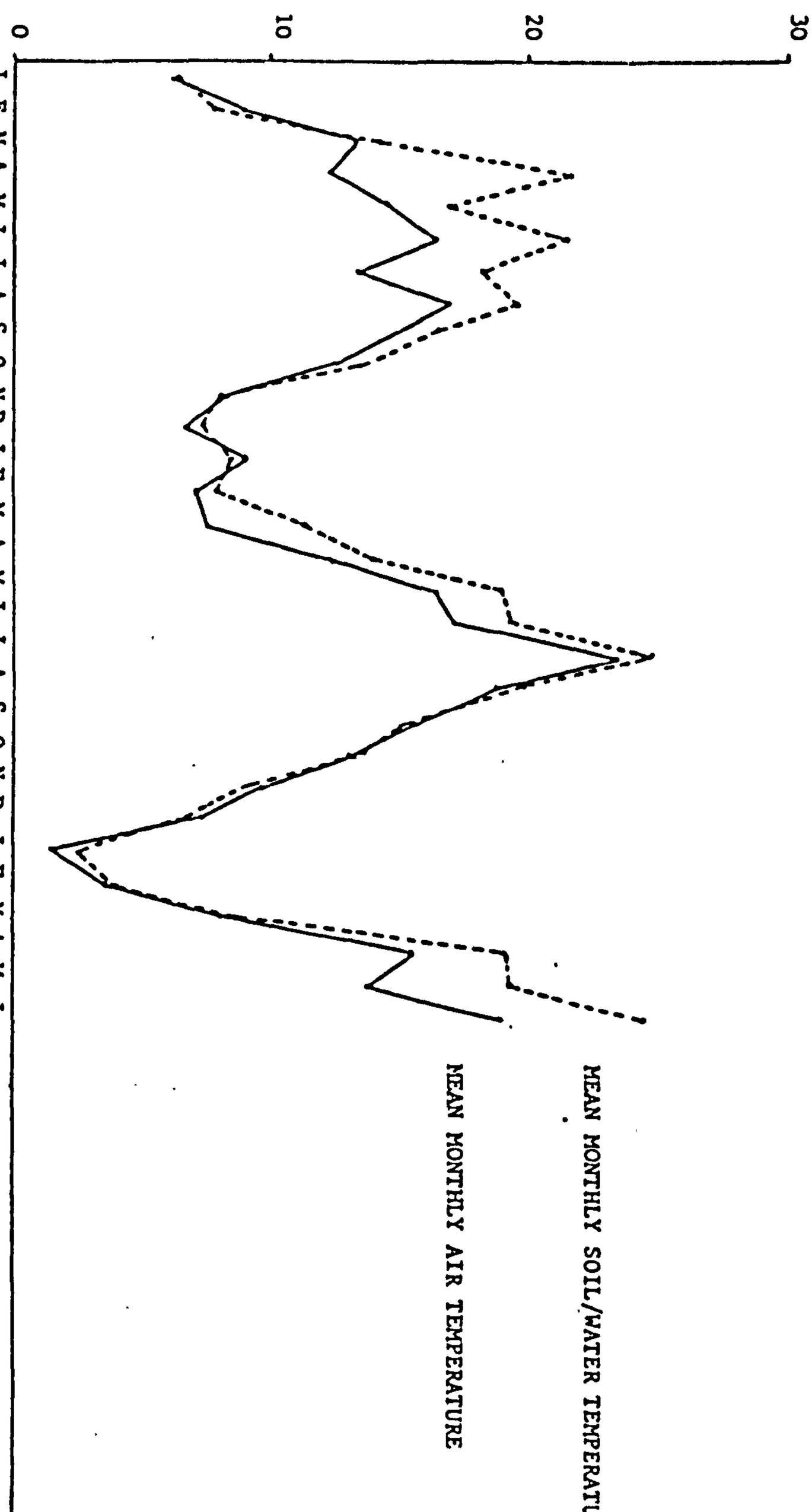
Summary:

The surface sediments maintained higher temperatures than air temperature, providing optimum temperature conditions for growth. During the cooler months of the year surface sediments maintained the same temperatures as in the air.

3.1.3 Salinity

Two aspects of salinity were examined: how the salinity range changed over distance (graph 7) and how the range altered with temperature (graph 8). The "mean range" are the mean salinity values observed at each site over the 3 years studied, and 2) the "maximum range" is the difference between the maximum and minimum salinity readings observed.

A salinity gradient along the transect was observed. The mean range on the upper marsh (Sites 1-3) was between 0-2‰. However in the driest



GRAPH 6

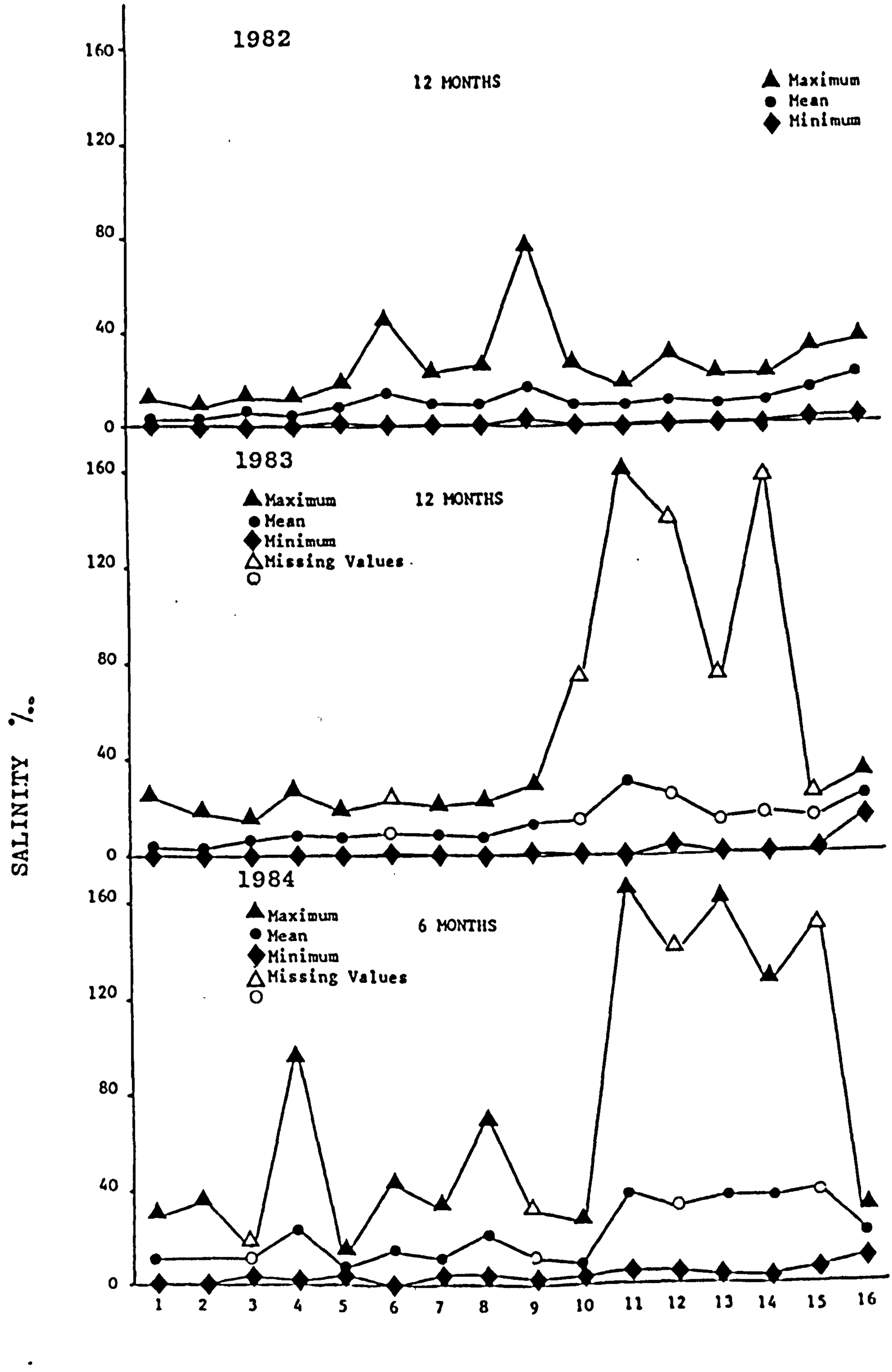
Temporal fluctuations in air temperature, and soil/water temperature.

summer months when the pool dried, tne interstitial salinity became considerably higher, hence the maximum values of 12‰, 25‰, and 31‰ for 1982-1984 respectively.

(Site 1) In the middlemarsh (sites 4-6) the mean salinity range increased more than 3 fold with a range of 2-11‰ in all 3 years. In the lower marsh (sites 7-9) the mean salinity range increased 2 fold again, ranging between 9-20‰. The further towards the sea, the higher is the mean range. A mean range of 9-33‰ was recorded at the uppersandflat (sites 10-12), 8-40‰ in the lower sandflat (sites 13-15) and 21-25‰ in the mudflat (site 16). This salinity gradient was maintained from year to year. What changed most dramatically was the maximum salinity range. In 1982 the maximum ranges at most sites were relatively small, compared to 1983 and 1984. The exceptions were the mound sites 6 and 9. The maximum salinity ranges of the sandflat were very large in 1983 and 1984, ranging between 0-160‰ . Hypersaline conditions i.e. those salinity measurements which are greater than 40‰ (Erlich 1978), were commonly recorded at most sandflat sites. Some points on graph 7 for 1983 and 1984 have missing values. This is because so much interstitial water had evaporated that a refractometer reading was unobtainable, so these points were deceptively low.

Graph 8 shows how salinity varied seasonally. In the winter months when temperatures were low, the salinity range was small. By the spring and summer when temperatures increased, the salinity range became larger with most hypersaline readings occuring during the summer. As temperatures declined in autumn, the salinity range decreased. Graph 8 shows the salinity values for 1983. The data from 1982 and 1984 had also been plotted in this manner, and showed the same results.

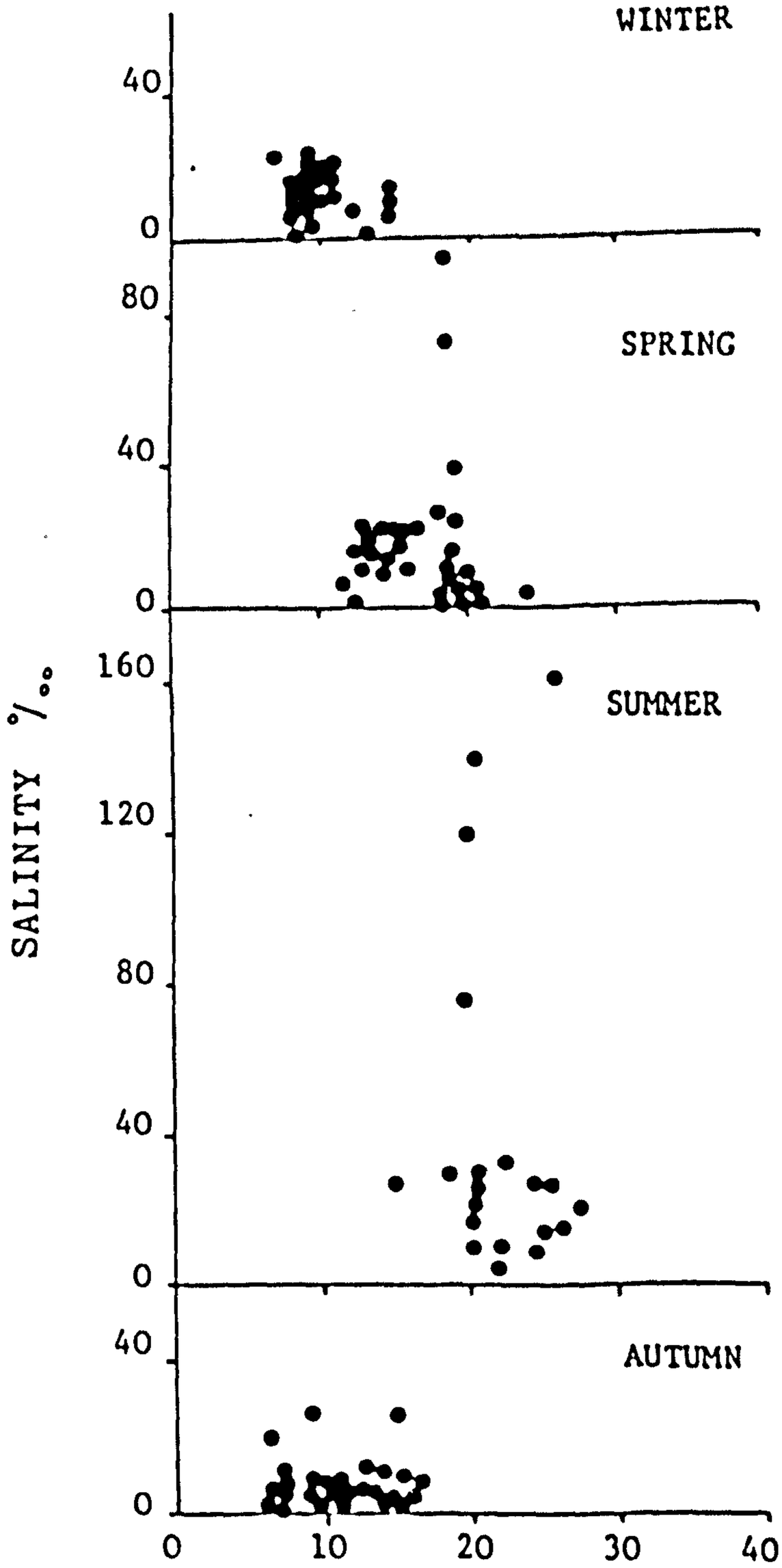
SALINITY



GRAPH 7

Spatial changes in the interstitial salinity along the transect.

SALINITY 1983



SOIL/WATER TEMPERATURE °C

GRAPH 8

Seasonal changes in the interstitial salinity in 1983.

Summary:

A salinity gradient was observed, with near freshwater conditions at the upper-marsh, brackish conditions at the middle and lower marsh, to saline/hyper-persaline conditions at the sandflat and mudflat. While this gradient was maintained each year, the maximum range varied dramatically, particularly at sandflat sites. The seasonal salinity range showed a cyclic pattern.

3.1.4 pH

pH was also examined in terms of spatial and seasonal changes. ph readings were only recorded at pool sites in 1982, but readings from all sites were recorded in 1983-84. Graph 9 illustrates the gradient change in pH along the transect. The mean range at the upper marsh varied from 7.2-8.0, 7.5-7.6 in the middle marsh, 7.3-8.2 in the lower marsh, 7.7-8.9 at the uppersandflat, 7.9-8.7 at the lower sandflat and 7.9-8.1 at the mudflat. Both the mean and maximum ranges were similar in 1983 and 1984. A gradient change along the transect was not easily detected from the limited information provided in 1982.

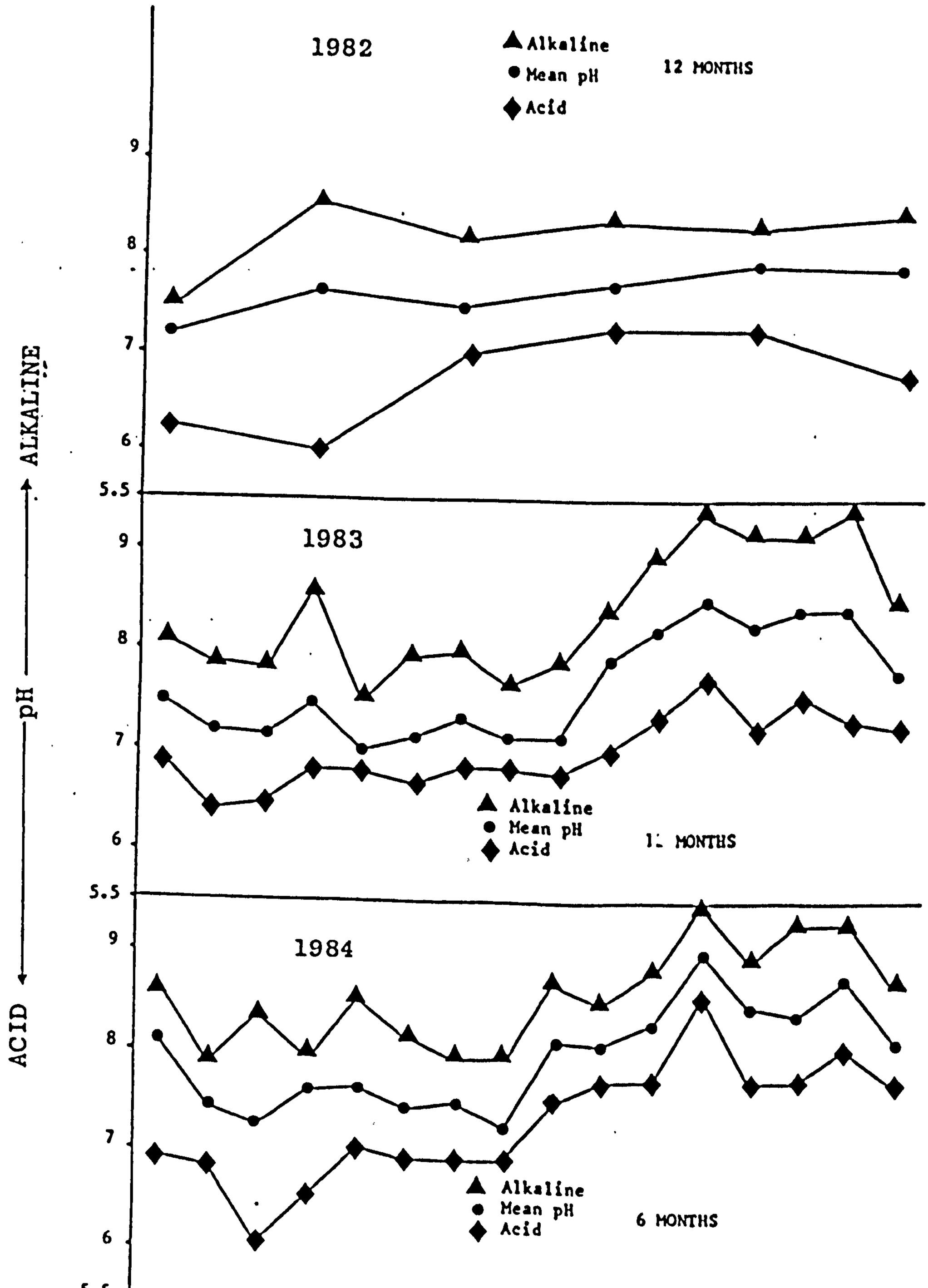
Graph 10 shows how the pH range changes seasonally in 1983. Although at first, pH range does not appear to differ from season to season, the mean pH readings were slightly higher in spring and summer. The same was true for 1982 and 1984.

Summary:

The pH exhibited a gradient change along the transect from neutral in the upper-marsh with higher values towards the sandflat and mudflat. The maximum pH range along the transect was very similar each year. Higher readings were recorded in the late spring and summer months.

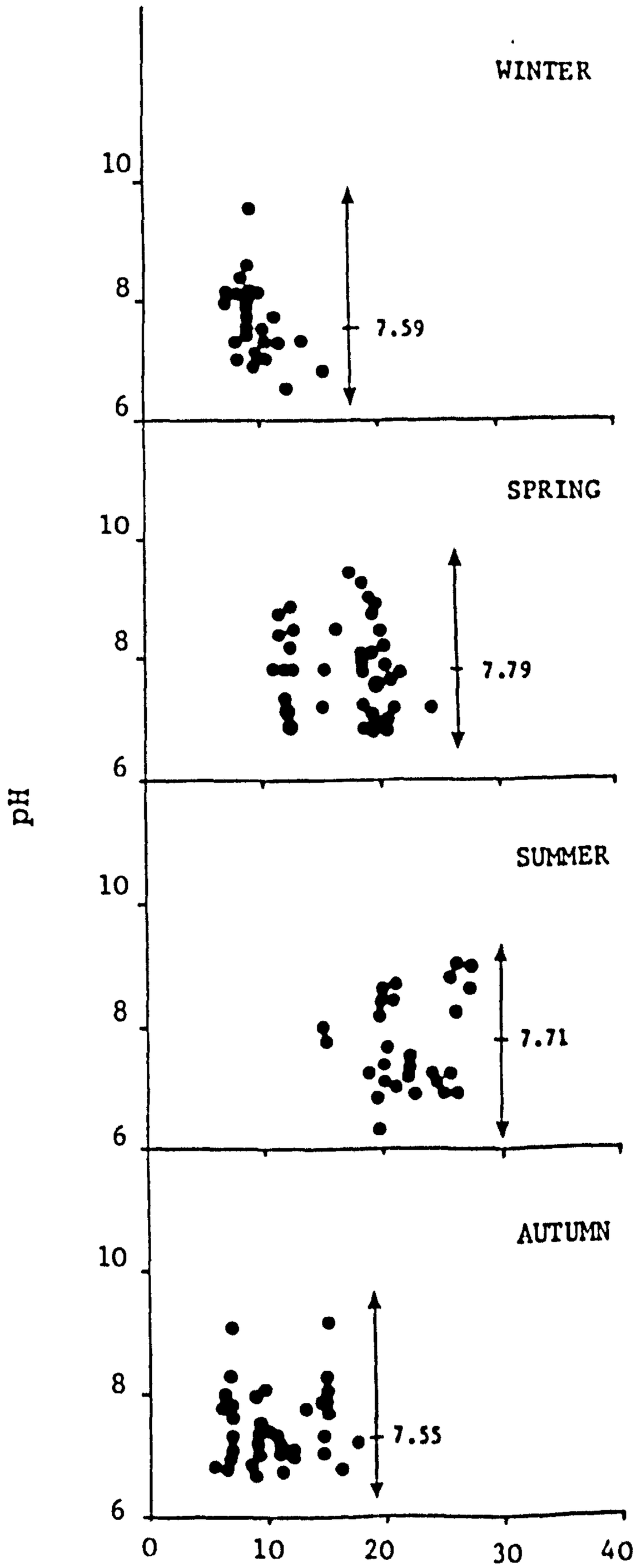
3.1.5 Watercontent

Like the previous physical factors, watercontent was examined with respect to changes in space and time, and another gradient along the transect was observed. The highest mean range in sediment moisture was recorded



GRAPH 9

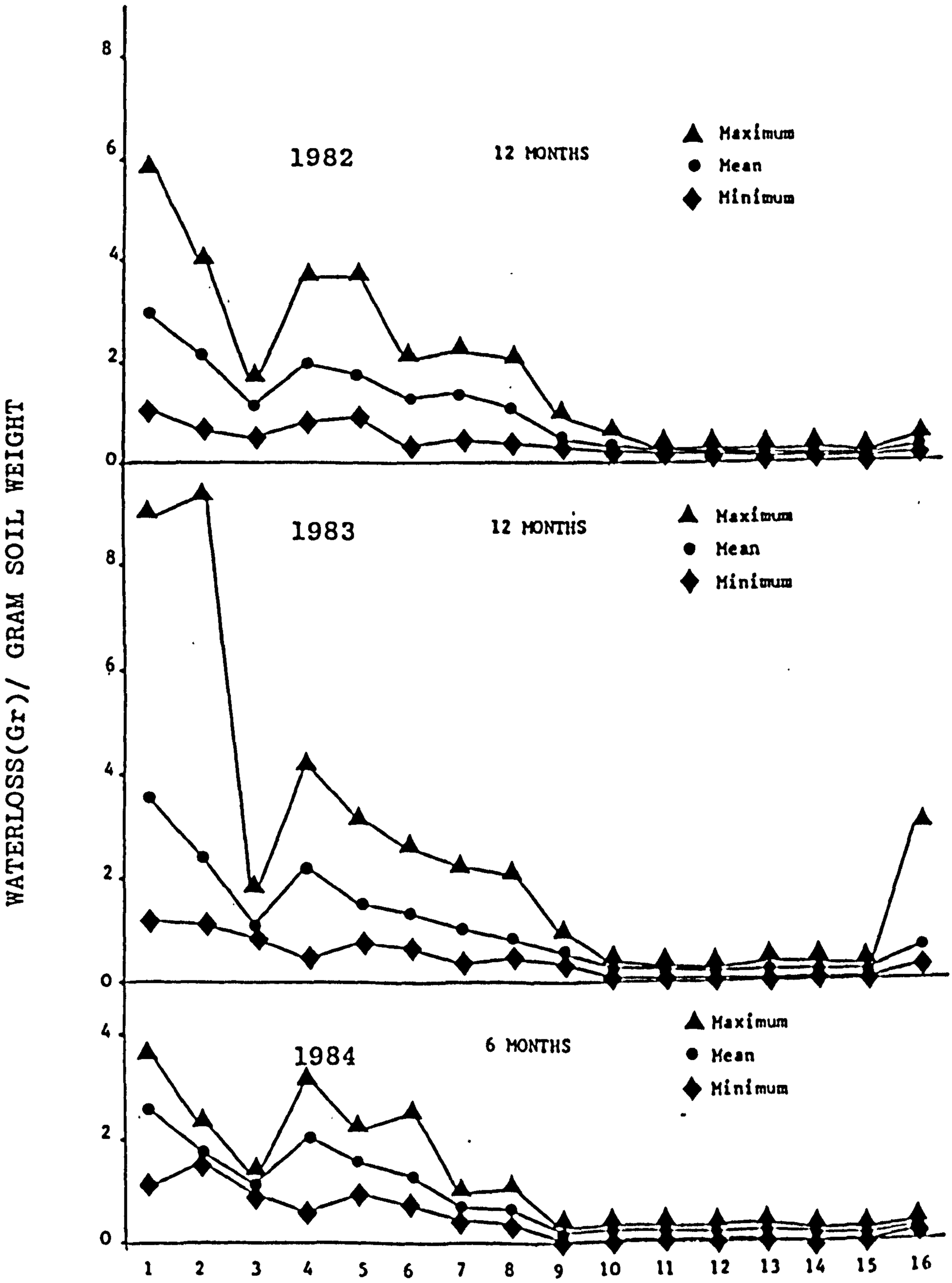
Spatial changes in pH along the transect.



GRAPH 10

Seasonal changes in pH in 1983.

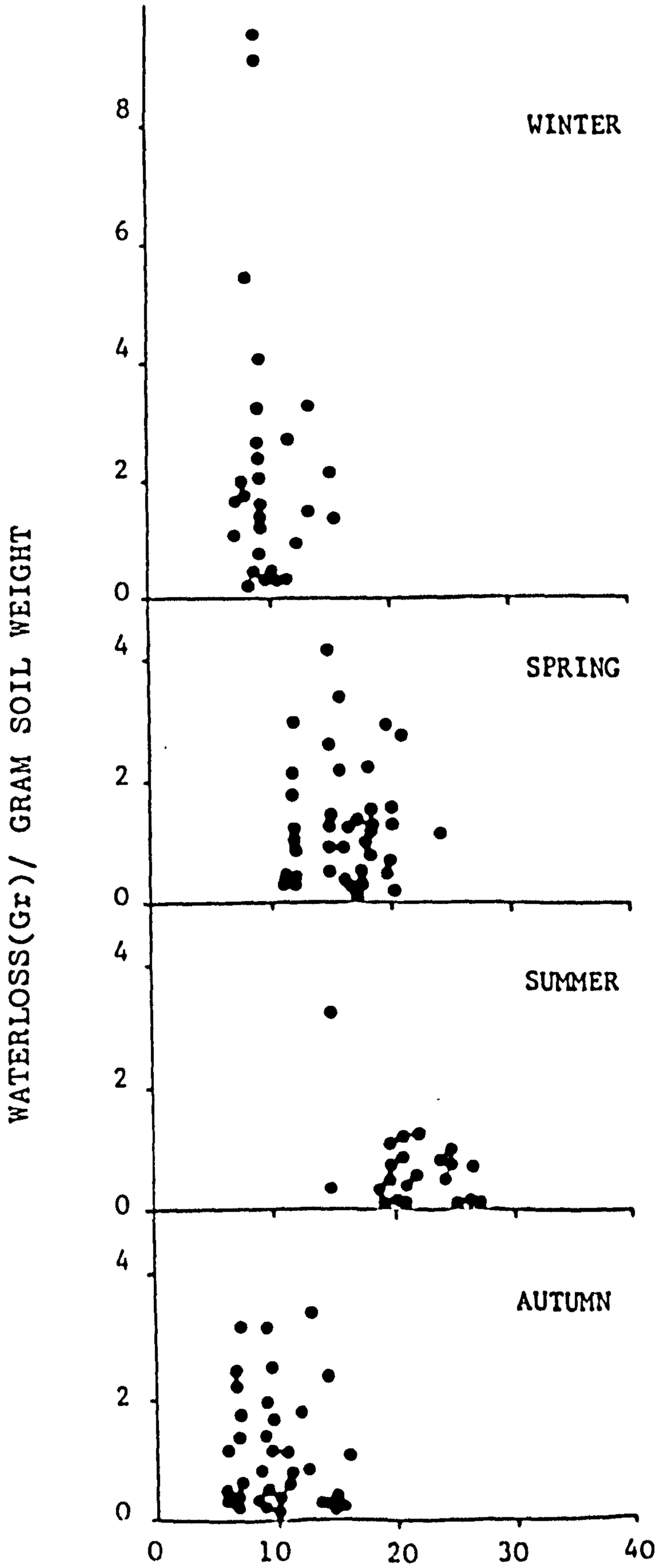
WATERCONTENT



GRAPH 11

Spatial changes in watercontent along the transect.

<u>WATERCONTENT VS. TEMPERATURE</u> 1983



GRAPH 12

Seasonal changes in watercontent in 1983.

in the uppermarsh ranging from 1.1-3.6 gr H_2O/gr mud. In the middle marsh the mean range decreased to 1.3-2.3 gr H_2O/ gr mud, and further out in the lower marsh to 0.5-1.0 gr H_2O/ gr mud. All sandflat sites had the same mean range between 0.21-0.33 gr H_2O/ gr sand (see graph 11). The maximum range in watercontent varied from year to year, with the largest maximum range observed in 1983. The maximum ranges narrowed along the transect, with the smallest variation observed at the sandflat. Site 16 had a higher maximum range than at sandflat sites.

Graph 12 shows a seasonal pattern. The largest ranges in water content were found at low temperatures in winter, and autumn. The range decreased as seasonal temperatures increased in spring and summer.

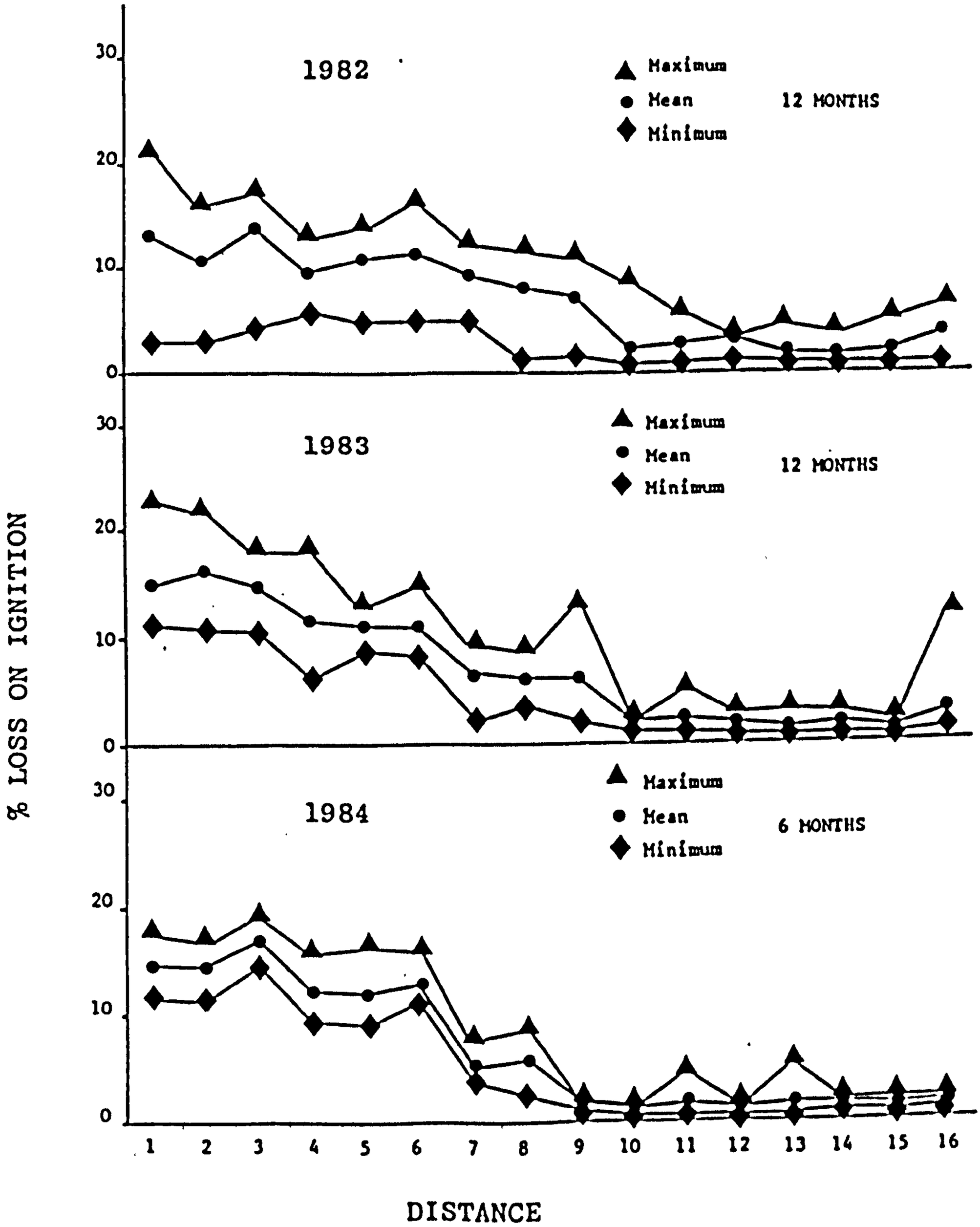
Summary:

A gradient change in watercontent was observed along the transect, with high water moisture in the upper marsh decreasing sharply in the middle and lower marshes. As the interstitial water evaporated at higher temperatures, watercontent in the sediment decreased. Watercontent measured at all sandflat sites were all uniform. Mudflat sediments were moister than, sandflat sediments, seasonal changes in watercontent showed a cyclic pattern.

3.1.6 Levels of organic matter

A gradient change in levels of organic matter was also observed along the transect. Mean loss on ignition values were highest in the upper marsh ranging from 10.7 - 17.3%, decreasing in the middle marsh, with a mean range between 9.6-12.9%, and lower still in the lower marsh, with a mean range between 1.7-9.0%. Mean levels of organic matter were uniform in the sandflat ranging between 1.4-2.8%. Loss on ignition values

LEVELS OF ORGANIC MATTER

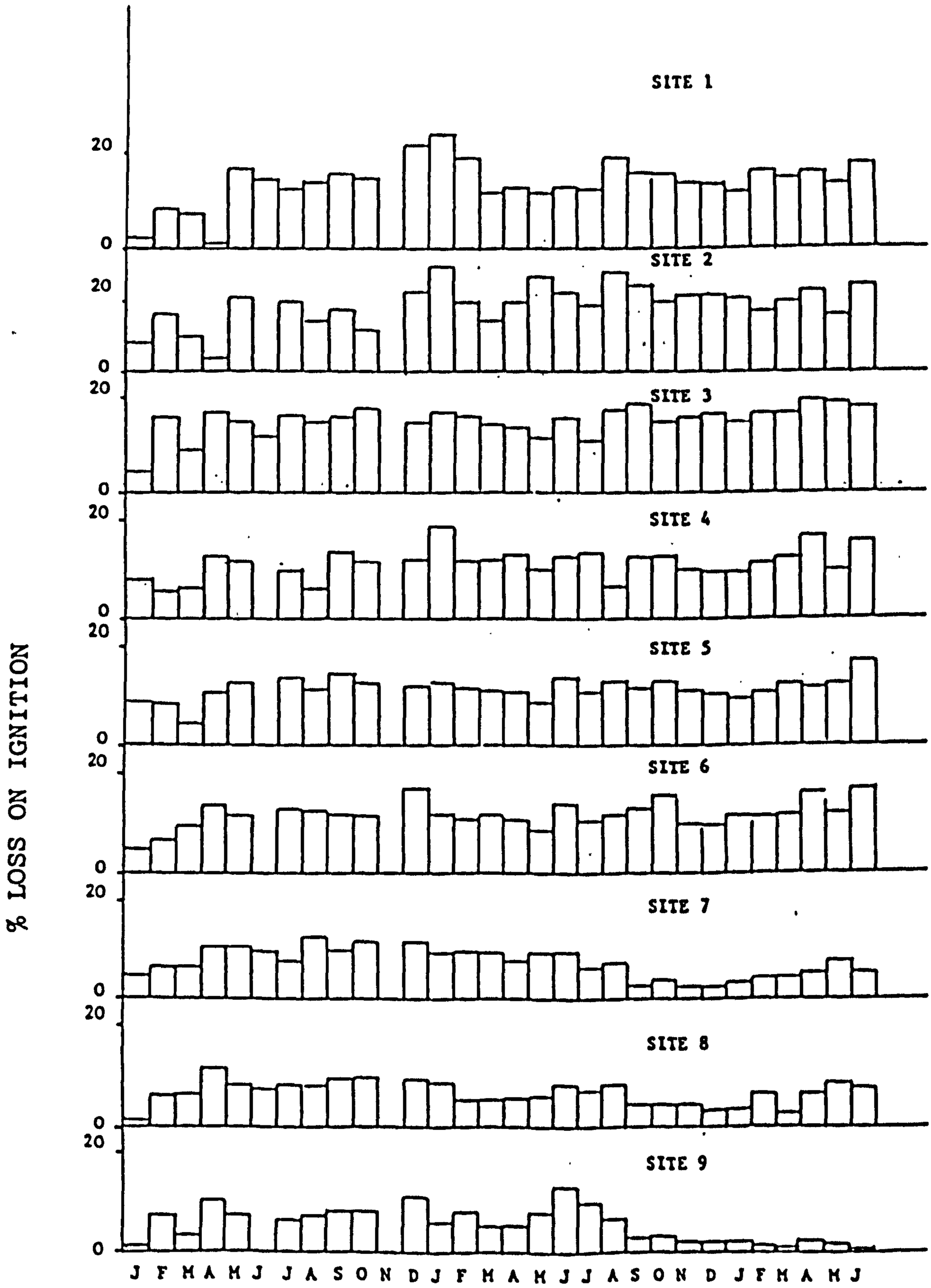


GRAPH 13

Spatial changes in levels of organic matter along the transect.

LEVELS OF ORGANIC MATTER VS. TIME

SALTMARSH SITES

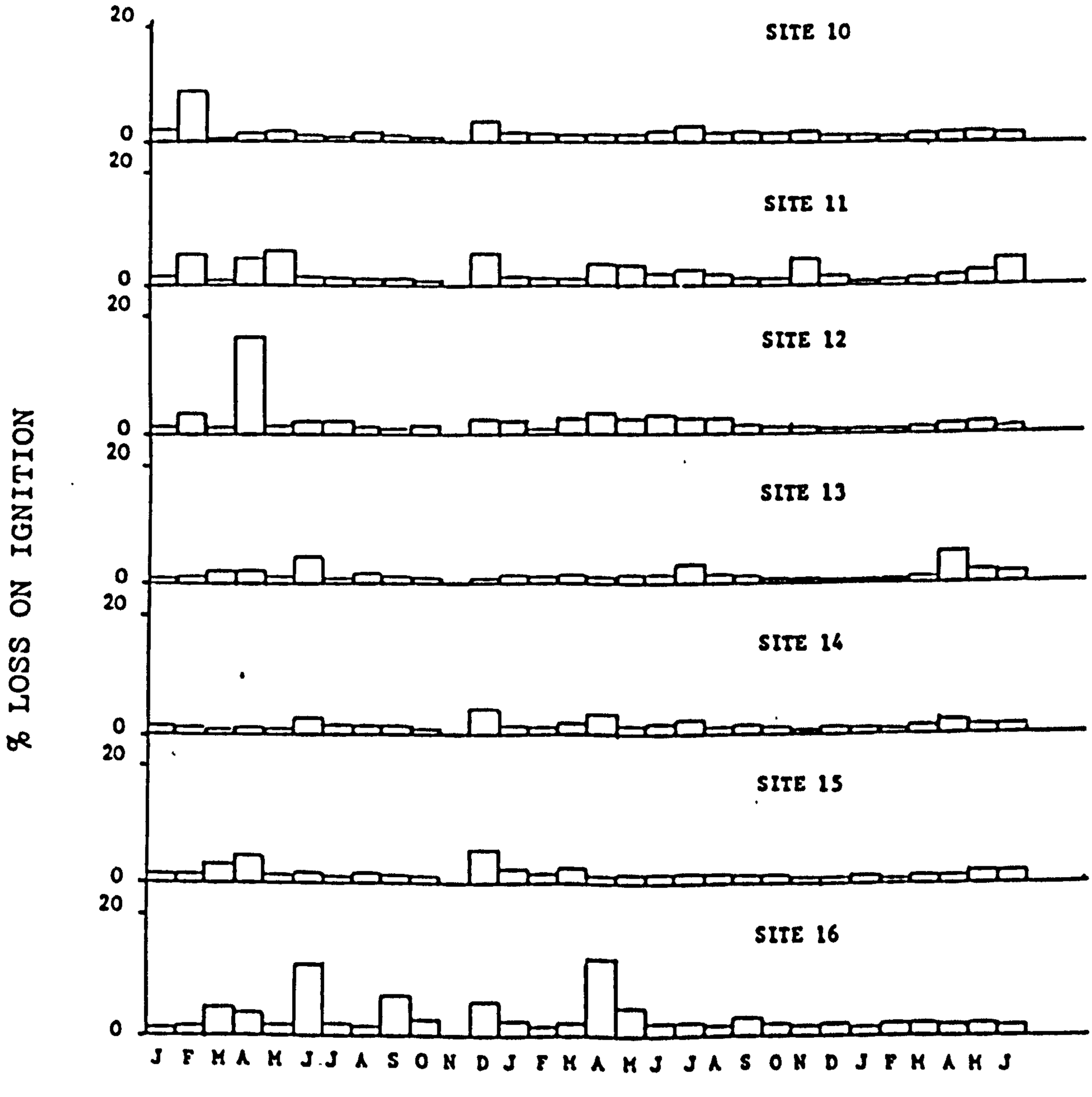


GRAPH 14

Temporal changes in levels of organic matter on the saltmarsh.

LEVELS OF ORGANIC MATTER VS. TIME

SANDFLAT AND MUDFLAT SITES



GRAPH 15

Temporal changes in levels of organic matter on the sandflat and mudflat.

at the mudflat were higher than at the sandflat with a range between 1.5-3.8%(see graph 13). The maximum ranges were approximately the same each year. The largest maximum ranges were observed in 1982. Mound sites (3, 6 and 9) had slightly higher levels of organic matter than other sites along the transect.

No seasonal pattern was observed. Graphs 14 and 15 show that the levels of organic matter oscillated about a mean level at each site. Increases and decreases in levels of organic matter seemed to occur synchronously at all sites on the saltmarsh, but this was not observed at sites 10-16.

Summary:

Levels of organic matter exhibited a gradient change along the transect with high levels of organic matter in the upper marsh,decreasing gradually in the middle and lower marsh. Very low levels of organic matter were recorded at the sandflat, but levels increased at the mudflat. No seasonal patterns were observed.

Discussion:

There appear to be two main habitats the saltmarsh, and the sandflat, whose differences are summarized in Table VI :

Table VI Summary of physical factors along the transect

Physical factor	Saltmarsh	Sandflat
Vegetation	Present	Absent
Light	Shade	No shade
Salinity	Freshwater-Brackish	Saline-Hypersaline
pH	Neutral	High (Alkaline)
Watercontent	High	Low
Organic matter	High	Low
Tidal innundation	Rare-Occasional	Daily

The presence of vegetation on the saltmarsh gives rise to a greater variety of microhabitats which in turn give rise to a greater range of physical

conditions. The mudflat (site 16) differed from the sandflat. Being the furthest site out towards the sea, it is exposed to more severe tidal disturbance. The sediments which were removed and deposited by tidal scour play a more significant role in determining the physical nature of the sediments at both the sandflat and mudflat.

Diatom populations inhabiting the surface sediments must tolerate extreme variability. The light intensity can be reduced to a small fraction of the full sunlight from shading by saltmarsh plants, while the sandflat offers no protection from very high light intensities. Although temperatures can rise to optimum levels for growth in the summer months, surface sediments were exposed to near freezing temperatures in winter. Changes in interstitial salinity were the most dramatic of all physical factors measured. A sandflat diatom assemblage grew in sediments ranging from freshwater conditions after rainfall to extreme hypersaline conditions of over 160‰. The pH also changed from neutral to high readings of 9.8. Other factors such as water content and levels of organic matter showed less extreme ranges. While the physical conditions changed at all sites each month, consistent gradients were maintained along the transect. These gradients can be inter-related.

As light intensity and temperature increase, water evaporates from the surface sediments, lowering the watercontent, and increasing the interstitial salinity and pH. The gradient change in watercontent and levels of organic matter, along the transect may be attributed to differences in particle size. Smaller particles of mud and clay were found in the upper marsh. These small particles have a higher surface area to volume ratio, and therefore may hold a larger surface water film mixed with organic material. As sediments become coarser, proportionally less

surface area becomes available, and larger gaps between the particles occur which may cause water moisture and organic material to sink lower down beneath the surface. This is speculation,further work on the micro-structure of the surface sediments is required.

Initial analysis of particle size using both a soil hydrometer and pipette method (as described in Avery & Bascomb 1974) have been undertaken. Initial results showed the bulk of the sediment at all sites to consist of sand-grains with a size range of 0.06-2 mm. Only 5-10% of the remaining sediment fraction consisted of a wide range of smaller silt and clay particles. Difficulties were encountered when sampling the sediment. This was due to stratification of the layers of different particle size. Due to the difficulties encountered, and the considerable amount of time required for analysis further work on particle size was discontinued. Particle size is a very important feature of the sediment because many physical factors can be associated with grain size.

Other important factors have not been analysed: such as chemical factors, nutrient availability, humidity, tidal innundation. It would be extremely desirable to obtain data on these and many other aspects. However, a three year project can only give a limited picture of events taking place in the field. Admiraal (1984b) has suggested that it is the physical factors which play a major role in determining diatom assemblage structure in estuarine mudflat ecosystems. Therefore these were the factors which were examined in this study.

3.2 FREQUENCY DISTRIBUTION STUDIES

3.2.1 Live and Dead Cells

The centrifugation and the coverglass techniques described, showed that the number of empty frustules at the sediment surface can be very large. By counting the number of diatom valves derived from empty frustules, as well as the number of live cells, the following questions can be answered: How does the proportion of valves from empty frustules or "dead valves" differ according to position along the transect? How does this proportion vary from season to season? Or year to year?

In addition to the live cell counts, the number of dead valves were also counted in each sample in order to answer these questions. The ratio of dead valves to valves from live cells could then be calculated. Seasonal means of these ratios could then be derived and drawn up in a graph (graphs 16 and 17).

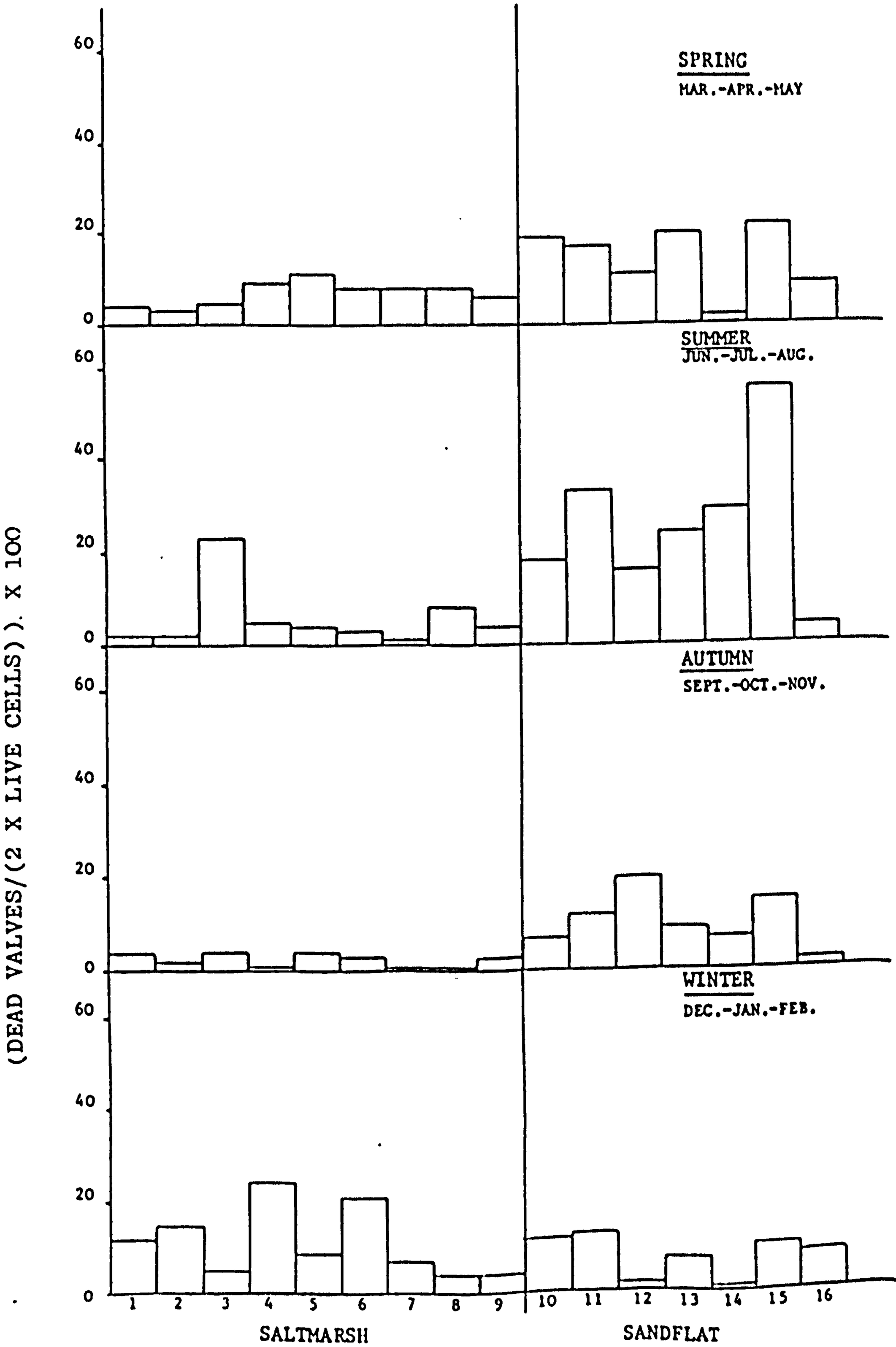
Graphs 16 and 17 show that higher ratios of dead valves to live cells occured at sandflat sites than at the saltmarsh. In 1982 (graph 16) the ratios at the sandflat sites were higher in spring and summer. While in the winter the ratios at the saltmarsh sites were higher than at any other season. The winter ratios of the saltmarsh sites were also higher than the sandflat sites.

GRAPH 16 (overleaf)

Ratios of dead valves to valves derived from live cells in 1982.

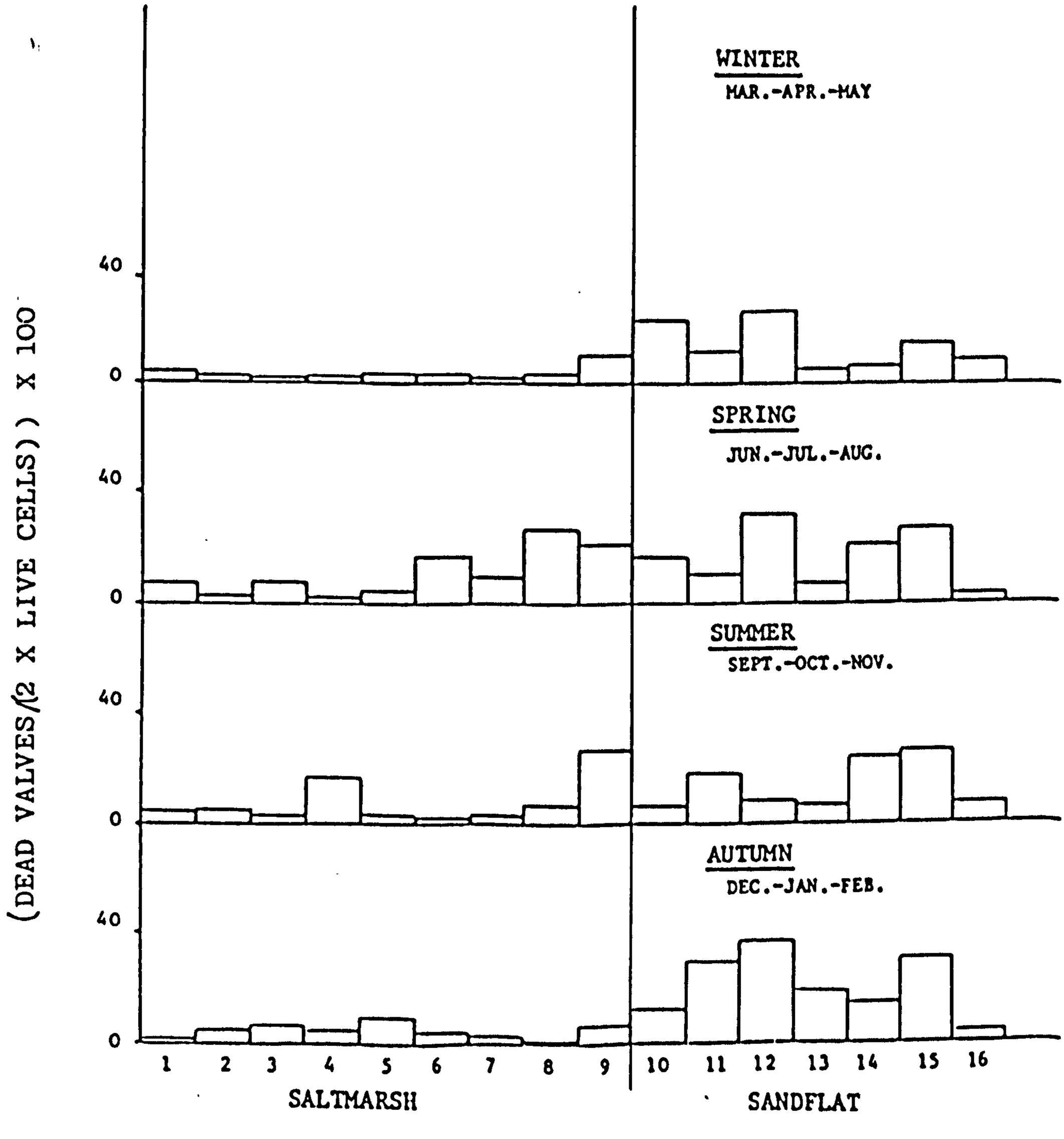
1982 RATIOS

DEAD VALVES



1983 RATIOS

DEAD VALVES



GRAPH 17

Ratios of dead valves to valves derived from live cells in 1983.

This seasonal pattern was not repeated in 1983 (graph 17). All ratios at sandflat sites were higher than at the saltmarsh. As the transect progresses out towards the sea, the ratios gradually increased.

Discussion

The proportion of dead valves does change according to the position of the sediment along the shore. The ratios can change seasonally, but the pattern of change is not necessarily repetitive from year to year. The proportion of dead valves was usually significantly high. Individual counts of dead valves can be as high as 86% of the total number of valves present. These results confirm that it is crucial to count live cells in any long term sampling strategy. Percentages of dead valves were consistantly high throughout the year:

Table VII Percentage of Counts with significant numbers of dead valves (>5%)

Month	Year	
	1982 %	1983%
January	31	44
February	58	35
March	37	13
April	35	58
May	23	71
June	56	52
July	44	41
August	42	46
September	25	62
October	23	47
November	40	53
December	27	38

Therefore an acid cleaning method would not give a simple picture of the actively growing diatom population.

Any available method of sampling the sediment surface would sample both live cells and empty frustules. Live cells would actively adhere to the undersurface of the sampling substrate (glass or lens tissue), by the secretion of mucilage. Empty frustules would also adhere to the sampling substrate due to the force of surface tension. The numbers of empty frustules adhering to lens tissue might be even greater due to the added force of absorbing interstitial water by capillary action. Any method sampling a volume of sediment will sample even greater numbers of empty frustules.

Why should greater numbers of empty frustules be found at sandflat sites? This might be an effect of tidal scour. The greater the tidal disturbance, the more reworking of the sediment,bringing more empty frustules to the surface.

3.2.2 Continuous Spatial Patterns

In order to consider the way a live population fluctuates, population density must be taken into account. Small organisms sampled in a comparatively large area are not necessarily evenly spaced. Organisms grouped in dense clusters will influence the fieldworkers choice of sampling strategy, and ultimately the final analysis.

What is the effect of patchiness? It affects the repeatability of a measurement. The more patchy the pattern of organisms in the field the less likely a repeated measurement will give the same answer. Most ecology text books recommend that a pilot study be undertaken in order to assess the degree of patchiness. It has been well documented in the literature that diatoms display an extremely patchy distribution (Aleem 1950, Eaton 1967). In order to quantify this observation, 10 coverglasses

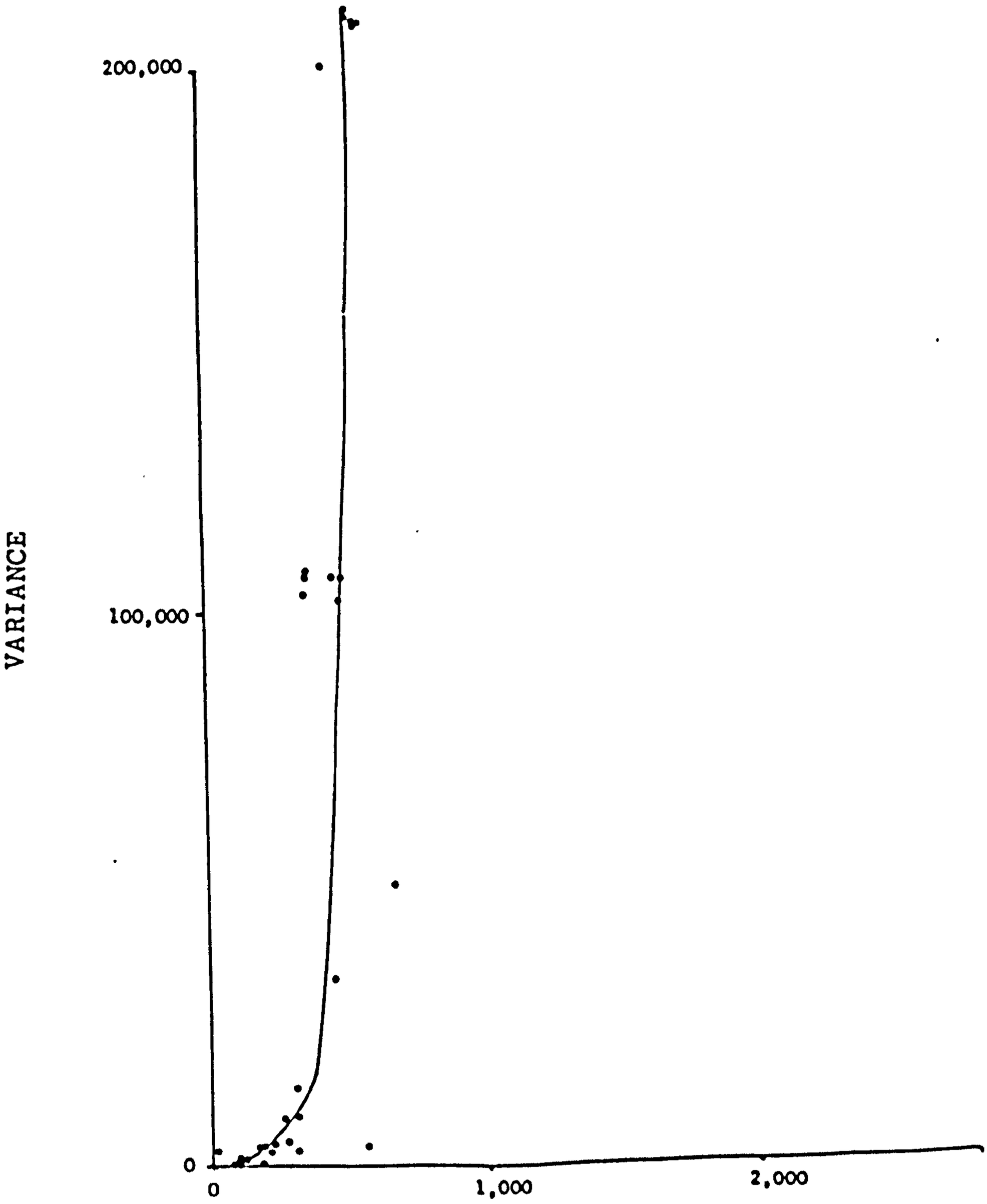
were placed on the sediment surface of mud that had been brought into the laboratory. Then they were mounted and counted as described in the methods section (Section 2.3). The mean and variance of the dominant species were then calculated.

Table VIII The mean and variance of 10 replicate counts of 2 co-dominants at two sites.

	Mean	Variance
Site 13		
Nitzschia vacillata	47.1	2,018
Nitzschia closterium	19.1	770
Site 4		
Nitzschia closterium	14.2	124
Anabaena cylindrica	239.6	67,436

These counts clearly show that the size of the variance exceeds the size of the mean. If the diatoms were randomly distributed in a Poisson distribution the variance would be the same size as the mean. In order to establish if any relationship between the variance and the mean exists, the two variables were plotted on a graph for both the live cell and dead valve counts, over a period of two years (graphs 19 and 20). For each scatter plot 64 means and their corresponding variance were calculated. Each mean represents duplicate counts for three months. So each point on the graphs represents the mean of six counts from a total of 768 different samples. Graph 18 shows that when the variance is plotted against the mean a curve is produced. In order to compare the relationship between the variance and the mean, with the slope of straight line of the Poisson distribution, a log-log plot of the data was produced. In all cases: both the live cell counts and the dead

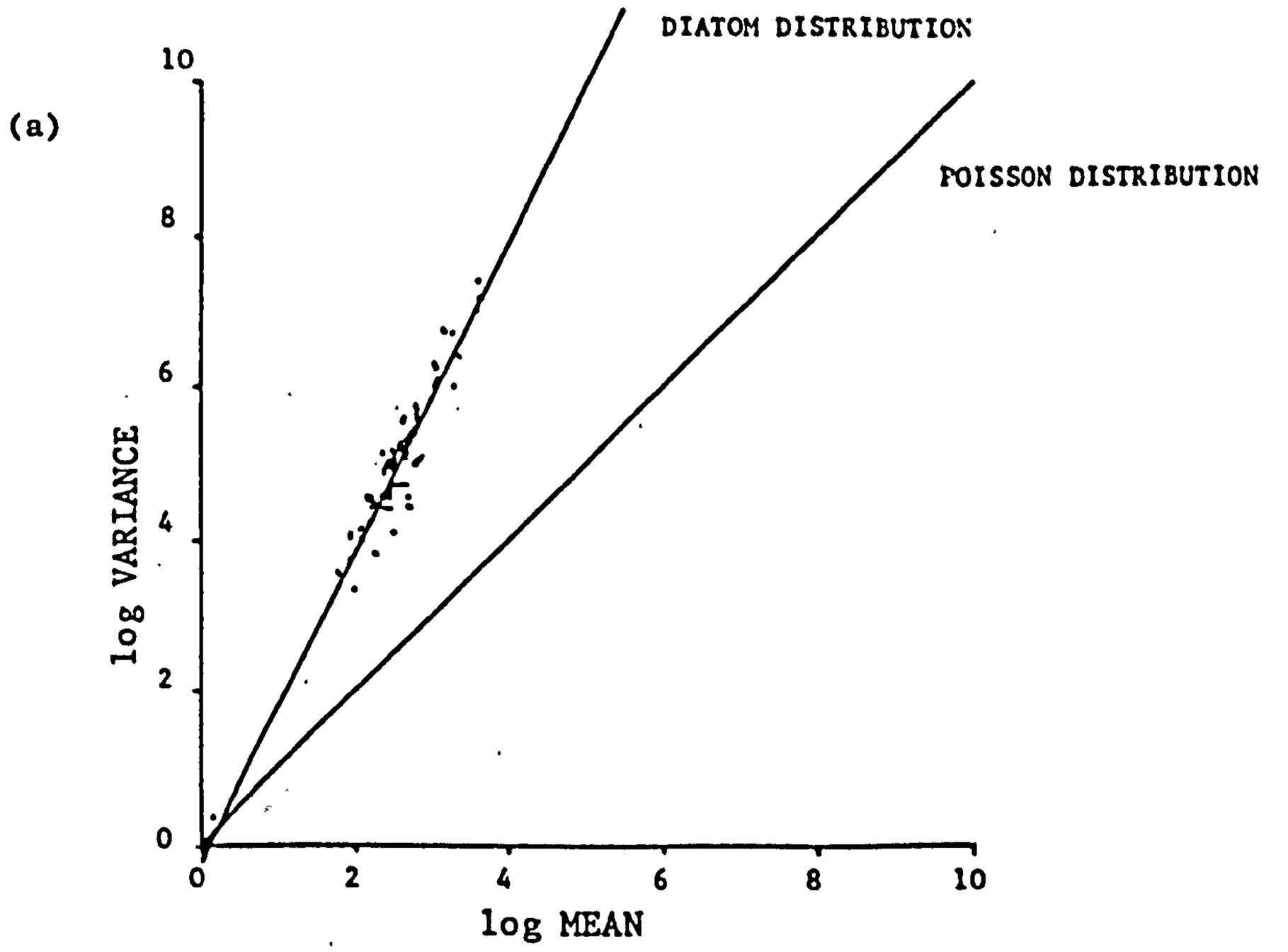
LIVE CELL DISTRIBUTION



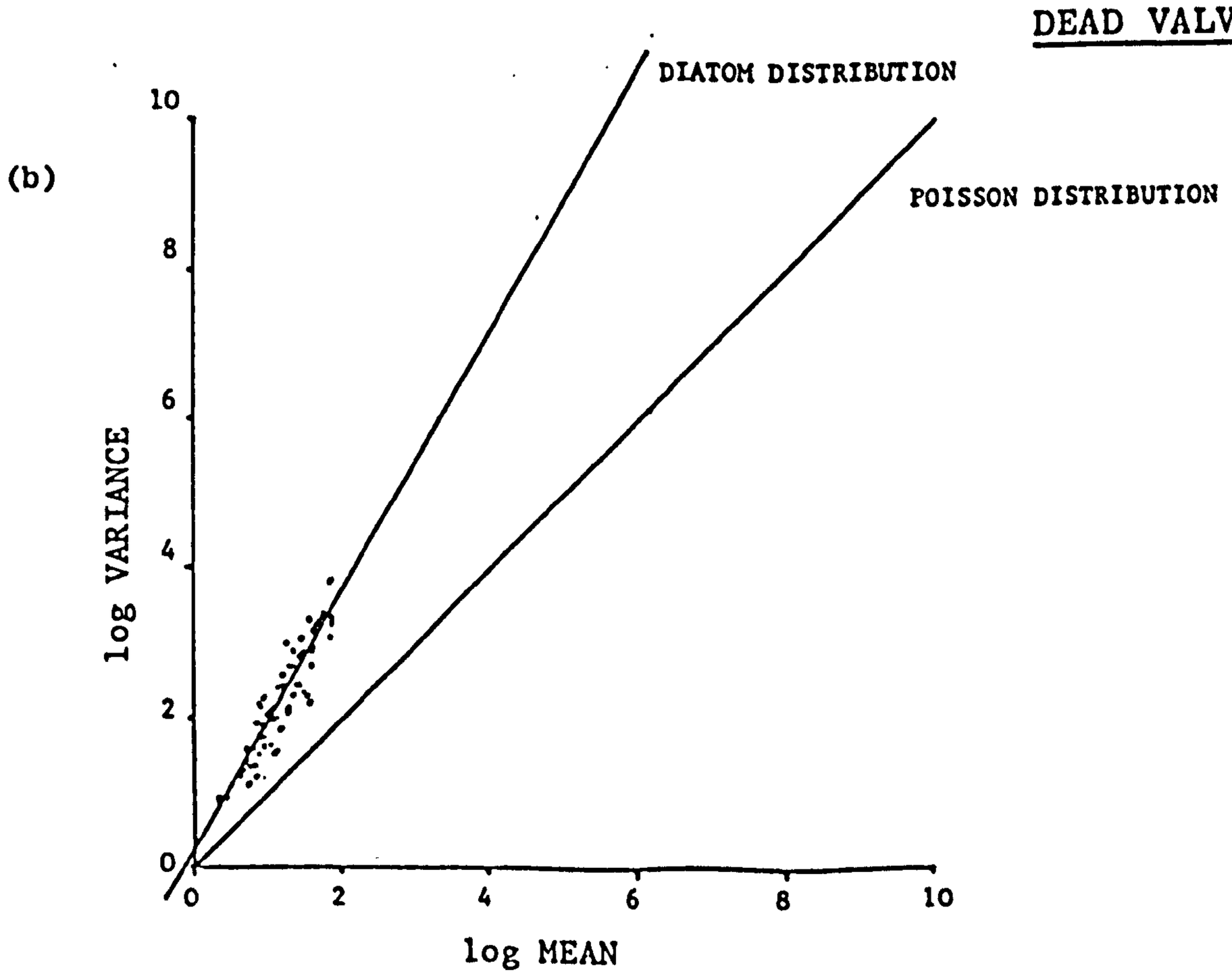
GRAPH 18

The Curve produced as the variance and mean increase.
Data from the 1982 live cell counts.

LIVE CELLS 1982



DEAD VALVES 1982

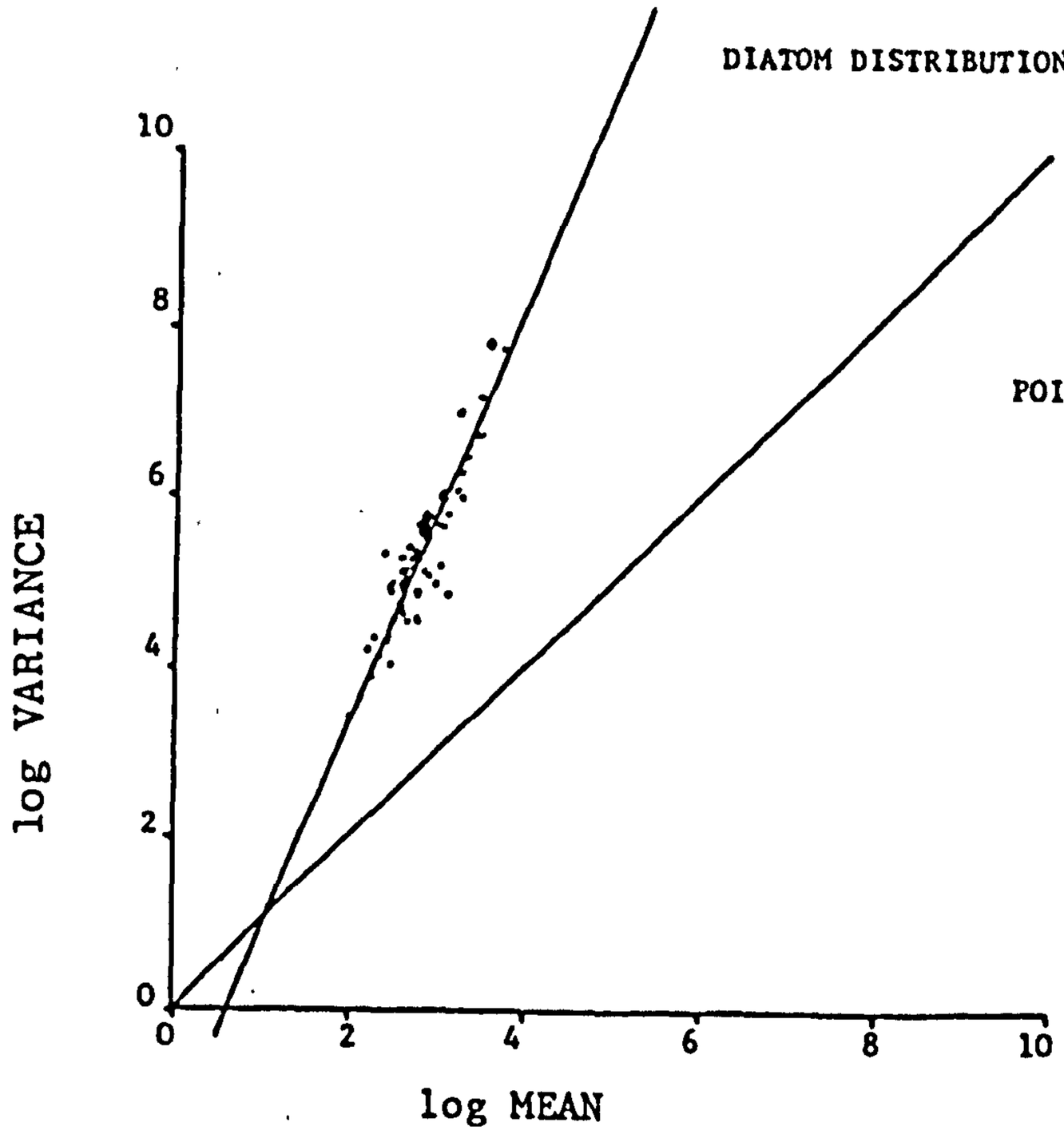


GRAPH 19

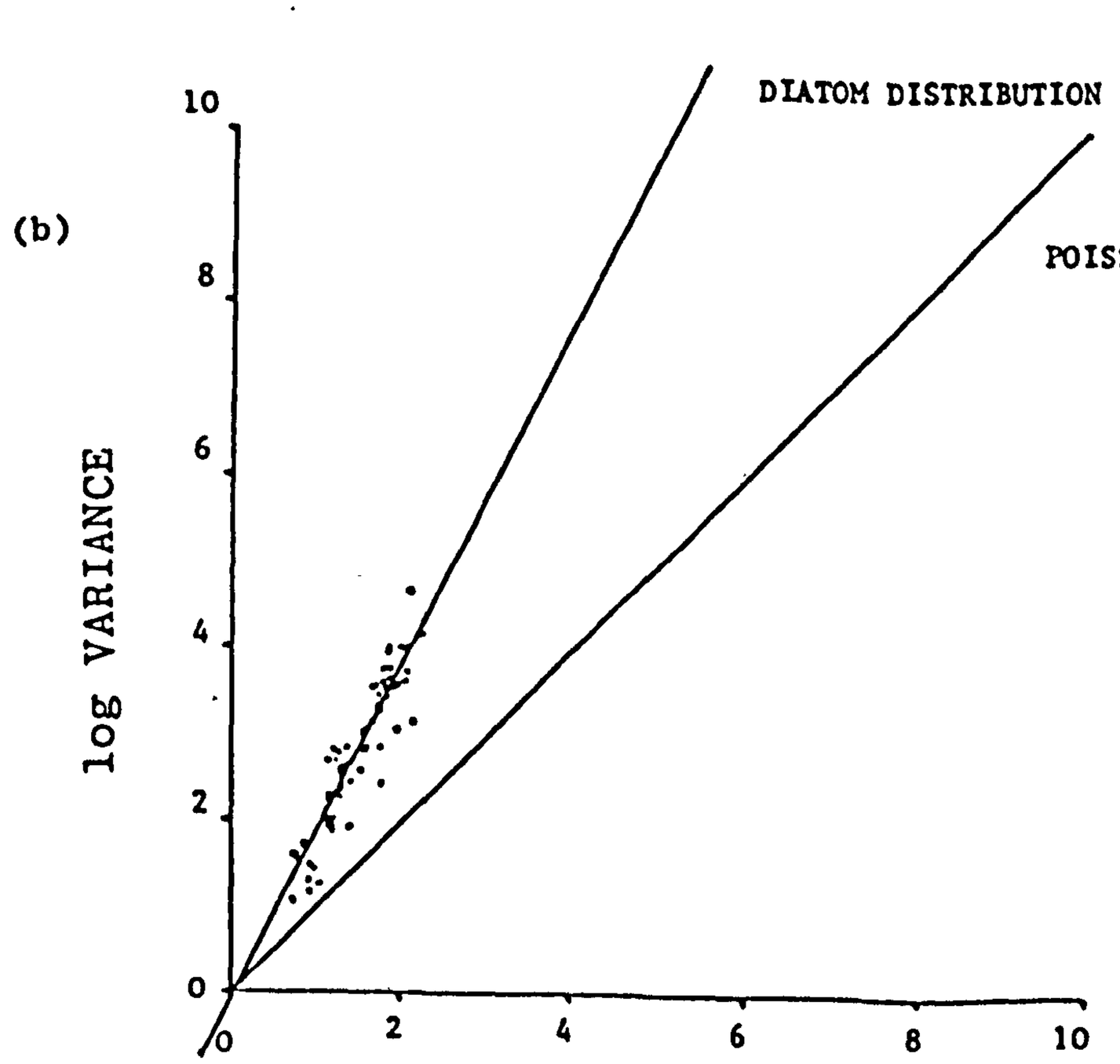
(a) Diatom distribution of the Live cell counts for 1982.

(b) Diatom distribution of the dead valve counts for 1982.

LIVE CELLS 1983



DEAD VALVES 1983



GRAPH 20

(a) Diatom distribution of the Live cell counts for 1983.

(b) Diatom distribution of the dead valve counts for 1983.

valve counts in 1982 and 1983, were straight line graphs of slope approximately 2. This means that the variance was proportional to the square of the mean. The data from 1984 showed the same relationship.

Discussion

This relationship was so consistent, and the regression line produced such a good fit, that an explanation was sought. The best model interpreting this phenomenon is a generalized distribution defined by the Neyman Type A equation:

$$Pr = e^{-\lambda_1} \frac{\lambda_2{}^r}{r!} \sum_{j=0}^{\infty} \frac{(\lambda_1 e^{-\lambda_2})^j}{j!} \cdot jr$$

(Pielou 1969)

r = The number of Individuals

Pr = The probability that a unit will contain r individuals

λ_1 = The mean number of clusters per unit area

λ_2 = The mean number of individuals per cluster

This model considers patchiness to be described by <u>two</u> main variables: the number of individuals within a cluster and the number of clusters per unit area.Pielou (1969) considers these two entities to have a specified pattern that is superimposed so that both variables will give rise to a Poisson distribution. Taking this assumption into account an expression of the mean can then be calculated:

$$\bar{x} = \lambda_1 \lambda_2$$

(Pielou 1969)

and an expression for the variance:

$$\text{Variance} = \lambda_1 \lambda_2 \cdot (1 + \lambda_2)$$

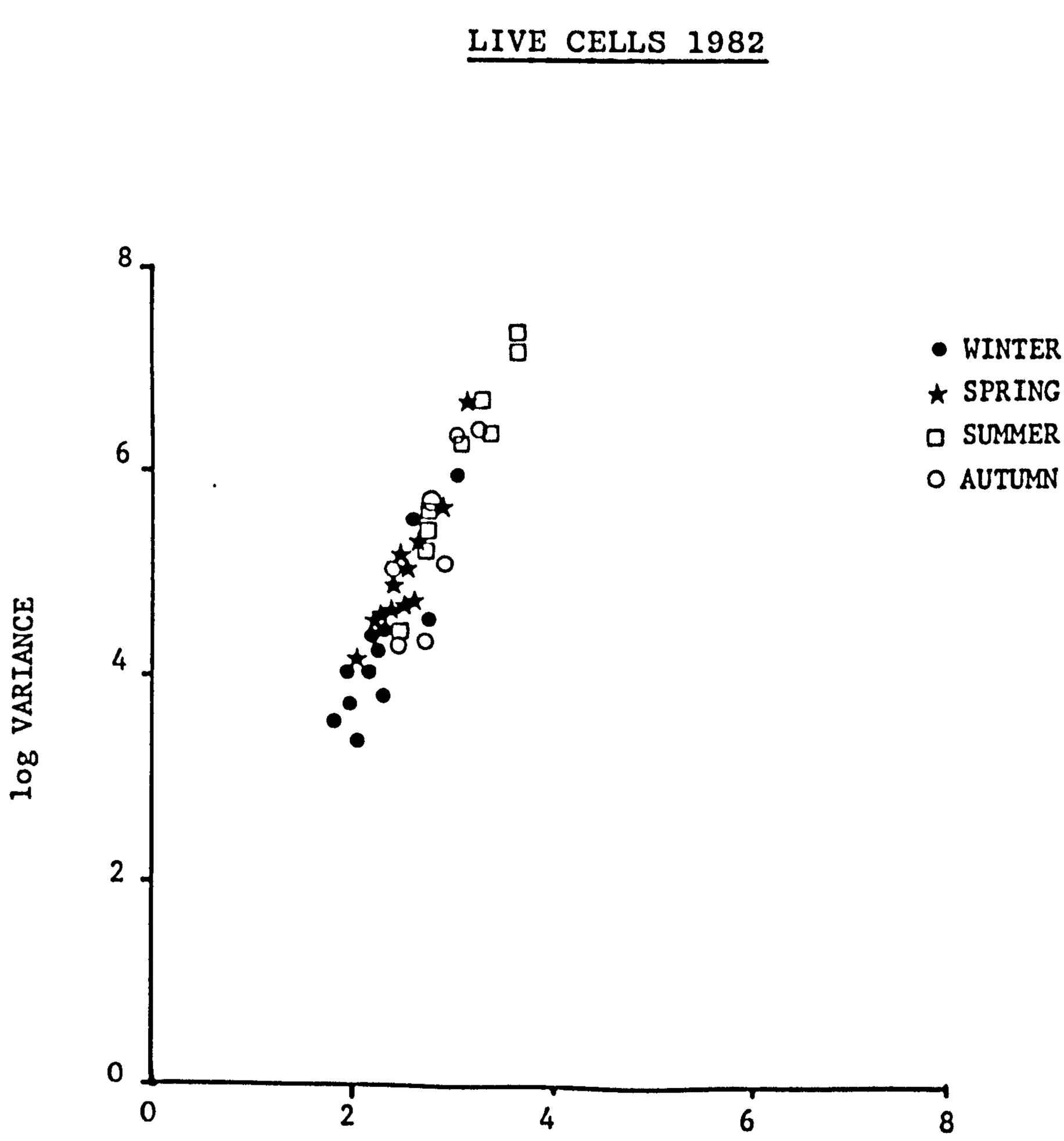
(Pielou 1969)

The equation for the variance will give values which obviously exceed the means. If λ_1 was a small value, and if λ_2 was a large value, then the variance could increase at a rate that is square to the mean.

Summarizing the explanation above in terms of diatom distribution the following events take place: a diatom moves up onto the sediment surface; it divides. Once division has taken place and the diatoms stick together and do not move as independent units, the diatoms display a non-random distribution. As diatom division continues and clusters form at the sediment surface two sources of variability arise; the mean number of diatom clusters per coverglass, and the mean number of diatoms within each cluster. The larger the clusters become,the more patchy their distribution over the sediment.

Since all the samples from the fieldwork of this project were counts of the total number of individuals per unit area, the data cannot be applied to the equations given above. There are many other factors which might influence diatom spatial patterns which have not been considered, such as varying birth and death rates, the effect of enviornmental factors such as tidal disturbance. Nor do these equations give a precise answer explaining the consistent slope of all the regression lines in graphs 19 and 20.

Nevertheless this model offers a start in the interpretation of a complex phenonmenon. Having gained some insight into the mathematics of diatom spatial patterns, more can be learned of their biology. If the individual points in these scatter plots are examined more closely (see graph 21), the points are positioned along the regression line according



GRAPH 21

Scatter plot examined more closely: ● Winter means, ★ Spring means, □ Summer means, and ○ Autumn means.

to season. Graph 21 shows the winter means (●) at the bottom of the scatter plot, while spring (★) and autumn (o) means are in the middle, and summer means (□) are at the top of the scatter plot. If a short term pilot study had been undertaken over a period of only a few months only a small range of variance would have been observed. If a pilot study had been undertaken in the winter months when the mean and variance are low, and appear proportional, the information would have been misleading.

There are two points which remain unexplained: why does the Y intercept of the regression lines change from one graph to the next if the slope is approximately the same. Why should the empty frustules not disperse in a random distribution within the sediment once the cells have died?

Further work is required in order to gain a better understanding of the spatial patterns being displayed. If the mean number of clusters, and the mean number of diatoms within each cluster could be counted then the data could be more rigorously analysed using the Neyman Type A equations.

Conclusions

As the variance changes with population density, no accurate measurement of the standing crop can be made with this technique. Therefore the graphs of the diatom assemblages discussed in later chapters show only relative fluctuations in temporal and spatial changes.

3.3 TEMPORAL CHANGES IN DIATOM ASSEMBLAGES

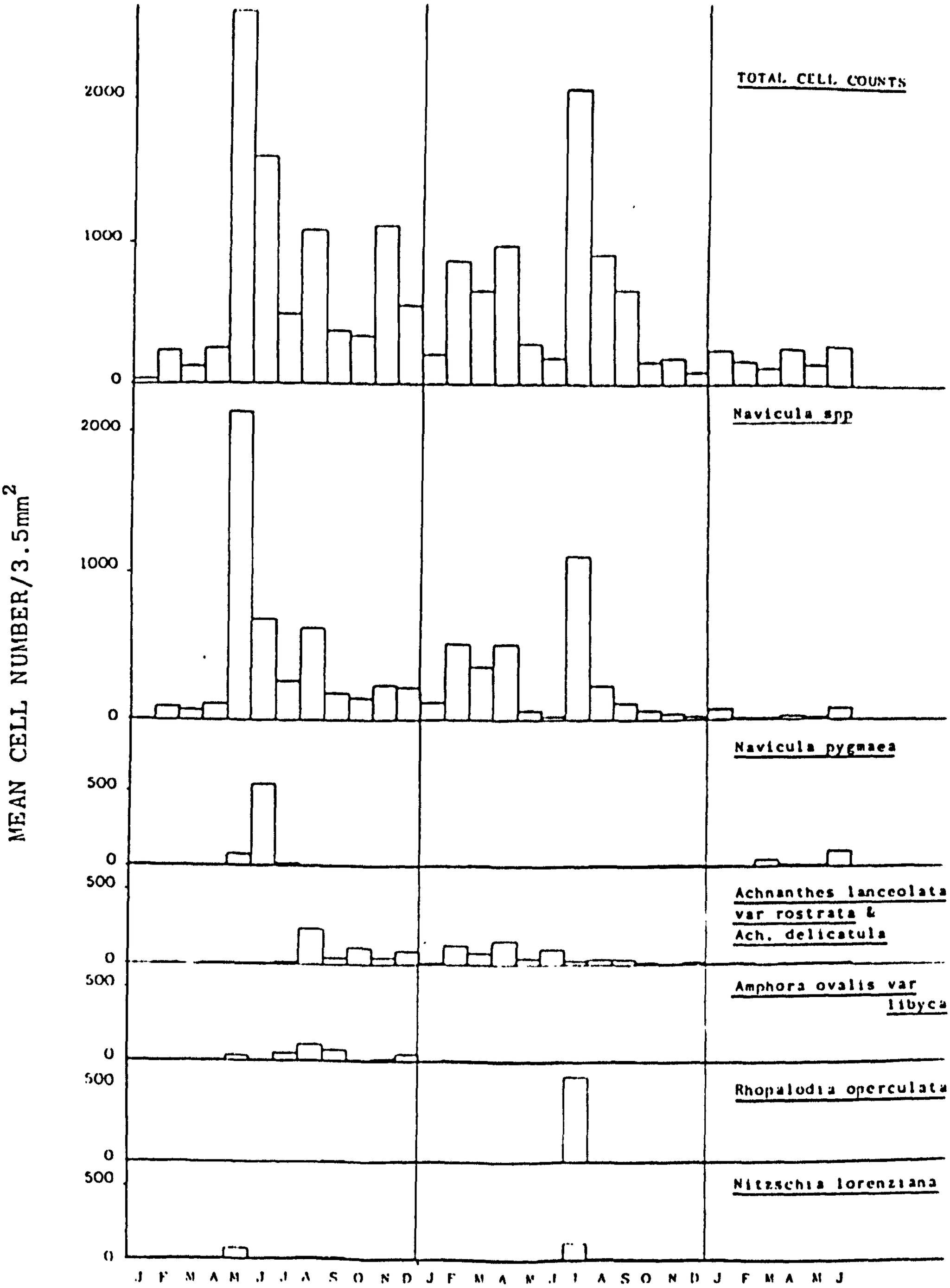
Like the physical factors, diatom assemblage structure changed in time and space. Temporal changes were analysed by plotting dominant monthly cell counts against time for each site (graphs 22-37).

3.3.1 THE UPPER MARSH

The total cell counts at site 1 (graph 22) showed a similar seasonal growth each year. Peak growth occured in May-June 1982 and July-August 1983. No peaks were observed in 1984. Each year's growth was the result of different dominant taxa blooming in different months. In May 1982 Navicula spp. (mostly Navicula cryptocephala and Navicula gregaria,) grew the most abundantly, followed by the growth of Navicula pygmaea in June. The lower cell counts recorded from August 1982 to June 1983 were predominantly composed of Amphora ovalis var. libyca from July-December 1982, Achnanthes lanceolata var. rostrata plus Achnanthes delicatula from August 1982 to June 1983. By July 1983 Navicula spp were again observed in high numbers and were accompanied by Rhopalodia operculata and Nitzschia lorenziana. The smaller growth in 1984 was due to fluctuating numbers of Navicula spp and N.pygmaea.

At site 2 (graph 23) the total cell counts displayed a large peak in June 1982, but no summer blooms were observed in the following years. This large June peak was again caused by the dominant growth of Navicula spp and to a lesser degree by Nitzschia vacillata. Although Navicula spp were largely responsible for the overall growth pattern of the total cell counts, Ach. lanceolata var. rostrata and Ach. delicatula became co-dominants from July-December 1982. Despite the lack of any seasonal peak in the total cell counts of 1983, a succession was observed: Navicula cincta, Navicula cari, Amphora exigua, and Nitzschia microcephala agg. were all sub-dominants of this assemblage at different months of the year. A. ovalis var.

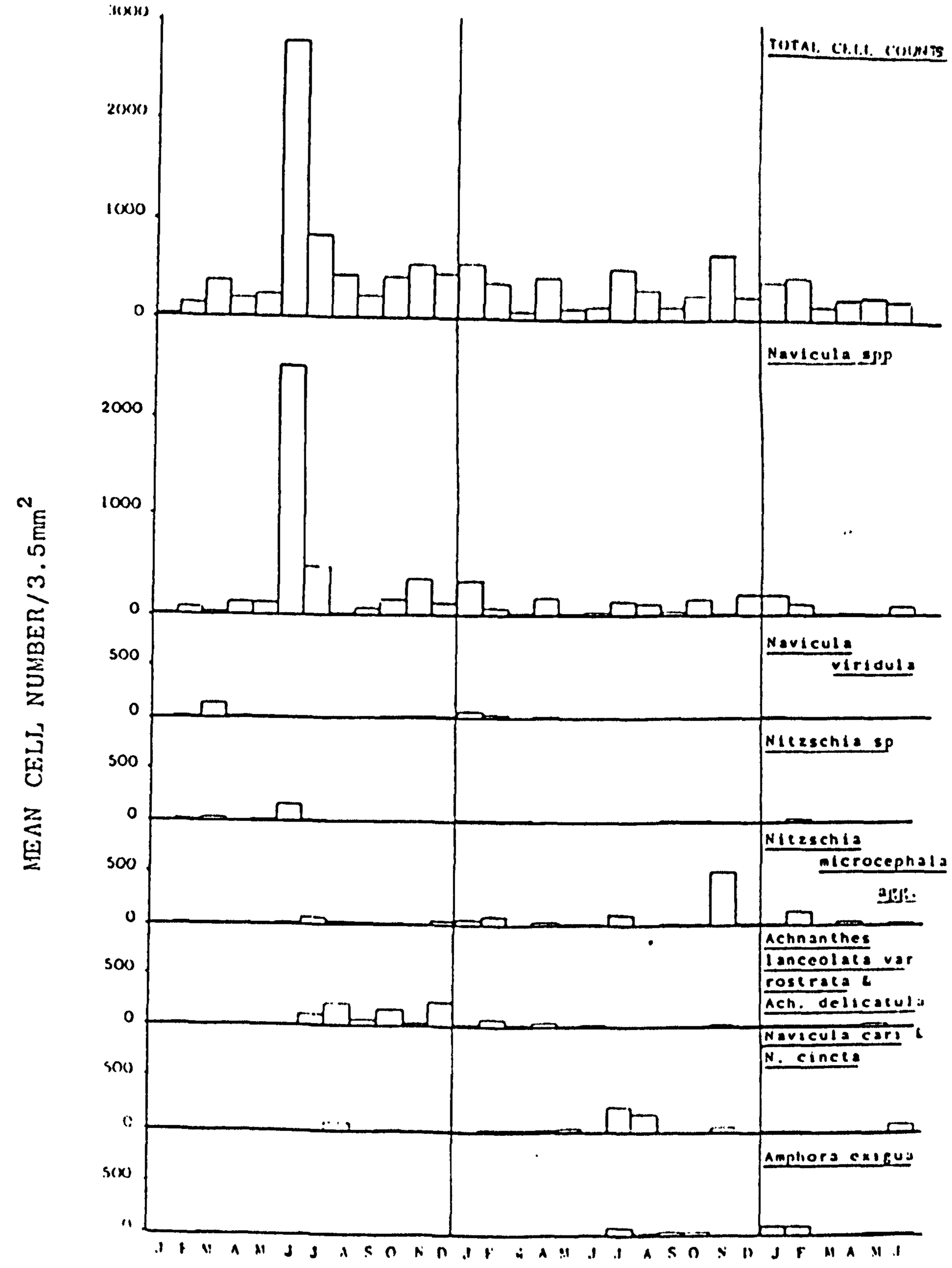
SITE 1 UPPER MARSH



GRAPH 22

Temporal changes in the assemblage structure of the pool site of the upper marsh.

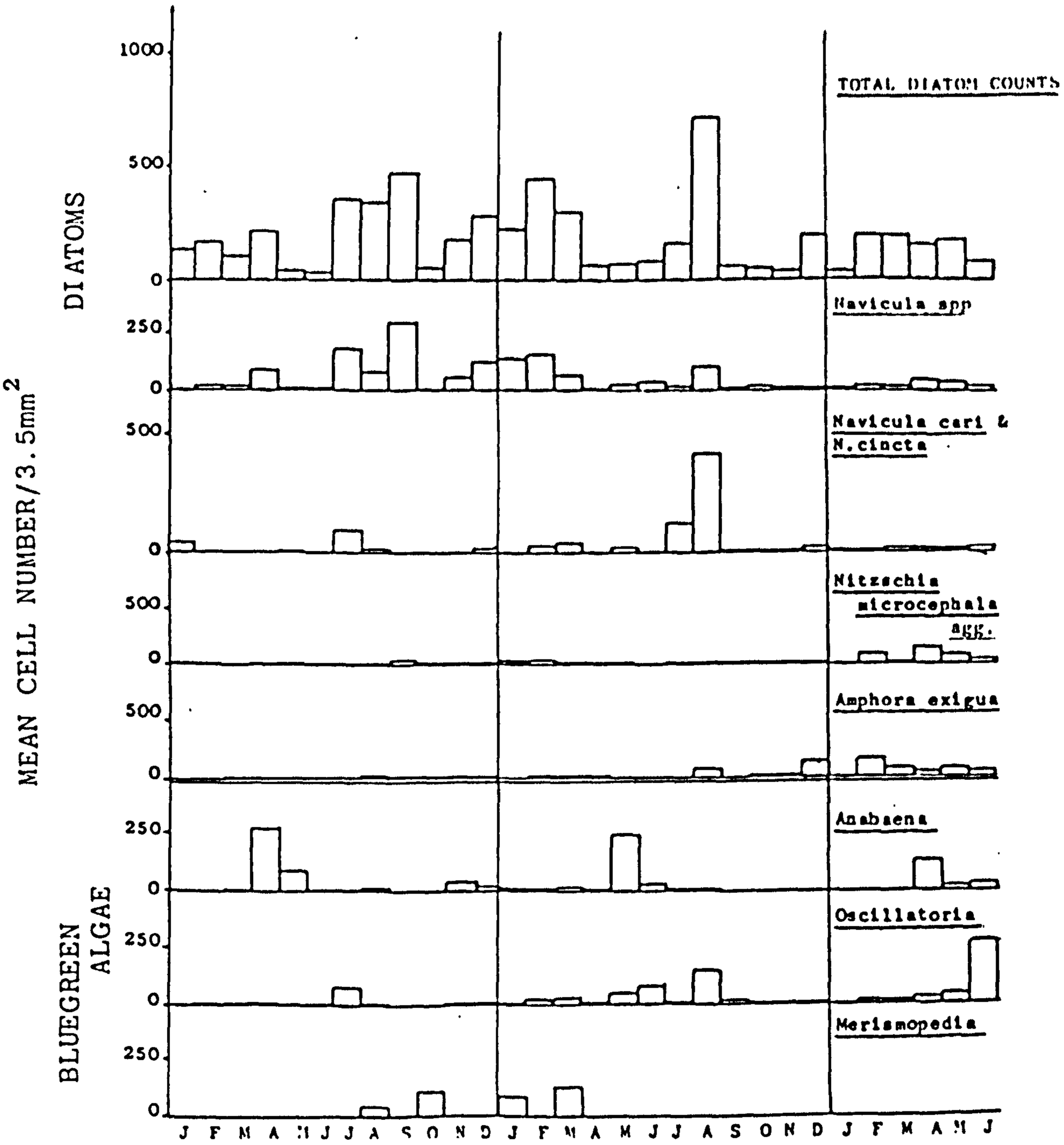
SITE 2 UPPER MARSH



GRAPH 23

Temporal changes in the assemblage structure of the slope site on the upper marsh.

SITE 3 UPPER MARSH



GRAPH 24

Temporal changes in the assemblage structure of the mound site on the upper marsh.

libyca was less abundant at site 2 than at site 1.

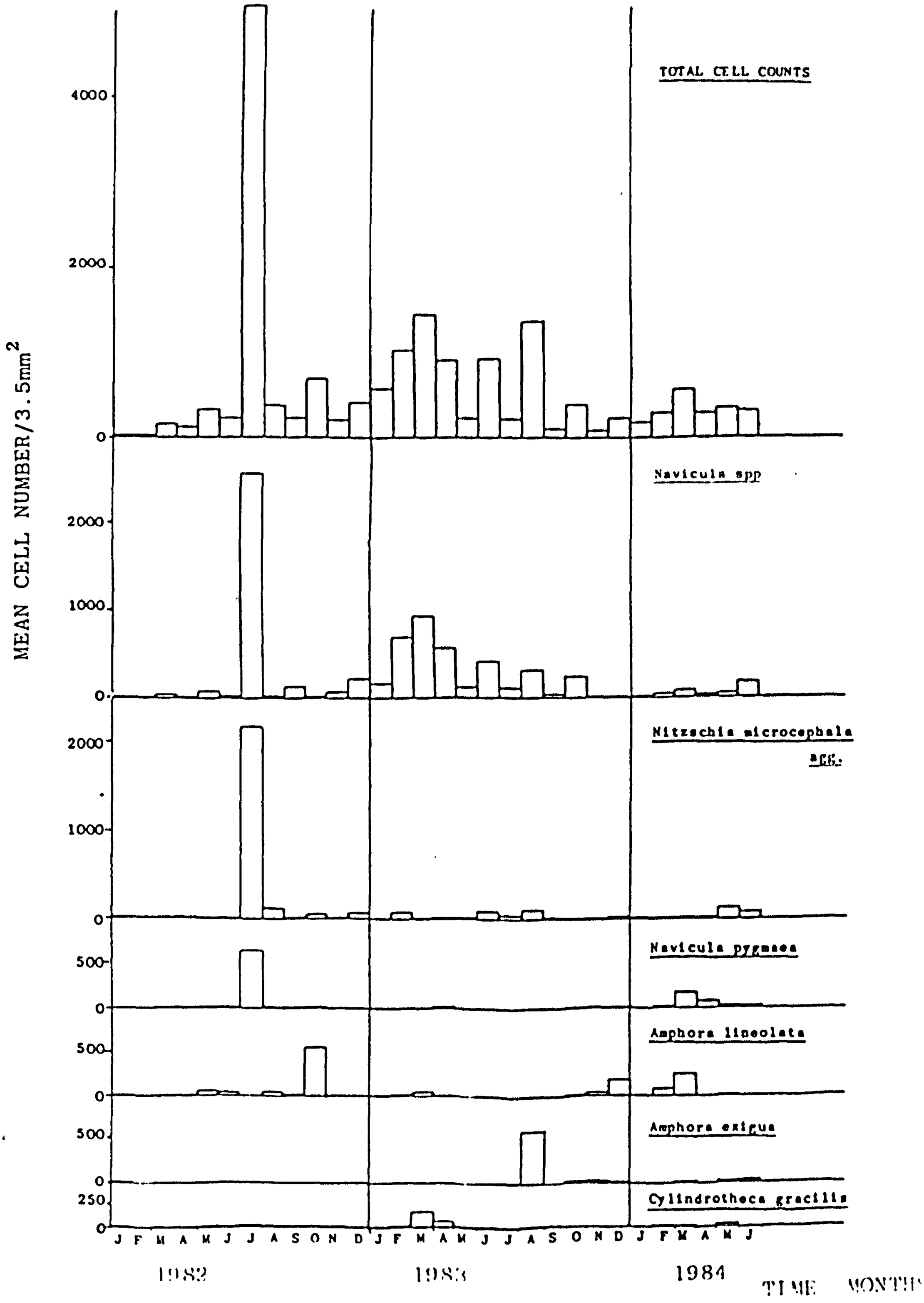
The number of cells counted at site 3 (graph 24) was much lower than at sites 1 and 2. However, small peaks were observed in July-September 1982, January-March 1983 and August 1983. As at sites 1 and 2 Navicula spp were largely responsible for the overall growth pattern of the total cell counts at site 3. Yet unlike sites 1 and 2, N. cari and to a lesser extent N. cincta became dominant members of the summer blooms in 1982 and 1983. Another new feature of site 3 was the more important influence of the blue-green algae. Prior to the diatom growth peak numbers of Anabaena spp followed by Oscillatoria spp and Merismopedia spp were recorded. Seasonal growths of Anabaena spp and Oscillatoria spp occured regularly each year, but the occurance of Merismopedia spp were more sporadic. By 1984 new diatom dominants: N. microcephala agg. and A. exigua were observed.

3.3.2 THE MIDDLE MARSH

The highest total mean cell count for the entire study period was observed in July 1982 at site 4 (graph 25). As in the upper marsh Navicula spp were the dominants over all months. However N. microcephala agg. reached equal numbers in July 1982 bloom, but decreased afterwards. Maximum numbers of N. pygmaea were also recorded in July 1982. A small growth was observed in October 1982. This was due to the sudden growth of Amphora lineolata. Cylindrotheca gracilis and A. exigua grew to small peaks in March and August 1983 respectively.

Maximum seasonal numbers of the diatom population were observed in August 1982, August 1983,and March 1984 at site 5 (graph 26). However the pattern of succession changed each year. As at all previous sites Navicula spp were largely responsible for the overall growth pattern. Yet in August 1982 there were 5 co-dominants: A. lineolata,Navicula spp,Nitzschia paleacea,

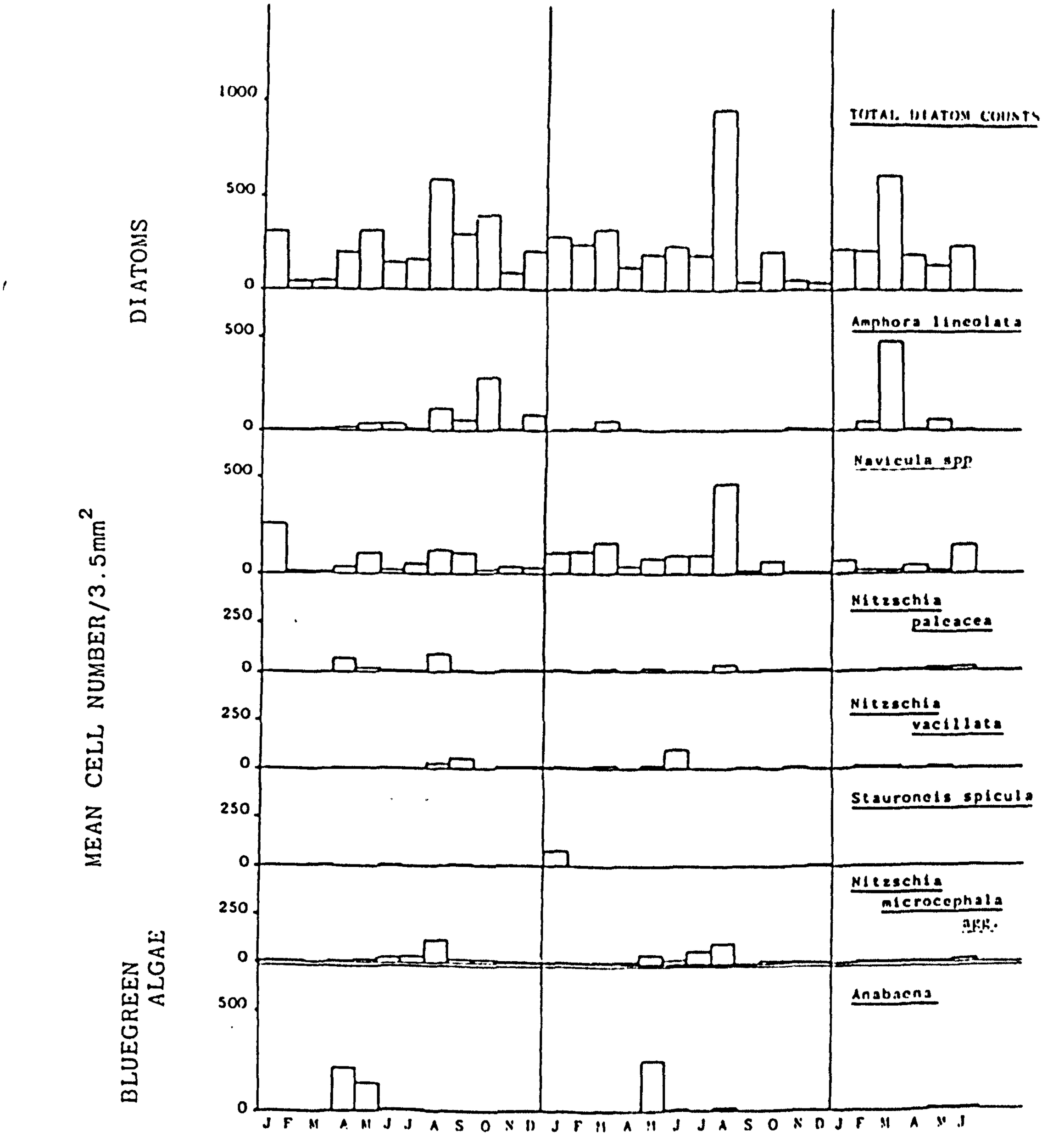
SITE 4 MIDDLE MARSH



GRAPH 25

Temporal changes in the assemblage structure of the pool site on the middle marsh.

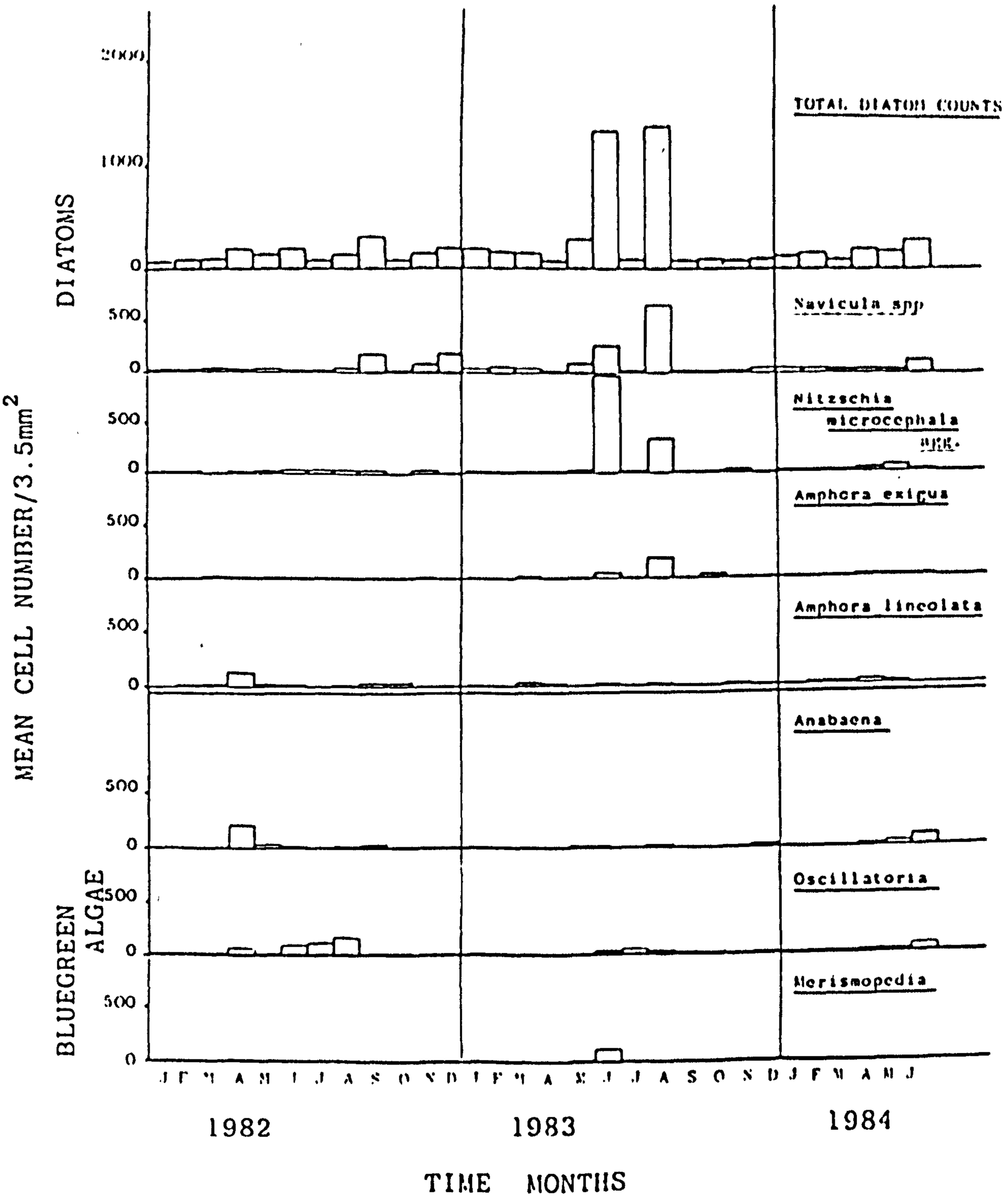
SITE 5 MIDDLE MARSH



GRAPH 26

Temporal changes in the assemblage structure of the slope site on the middle marsh.

SITE 6 MIDDLE MARSH



GRAPH 27

Temporal changes in the assemblage structure of the mound site on the middle marsh.

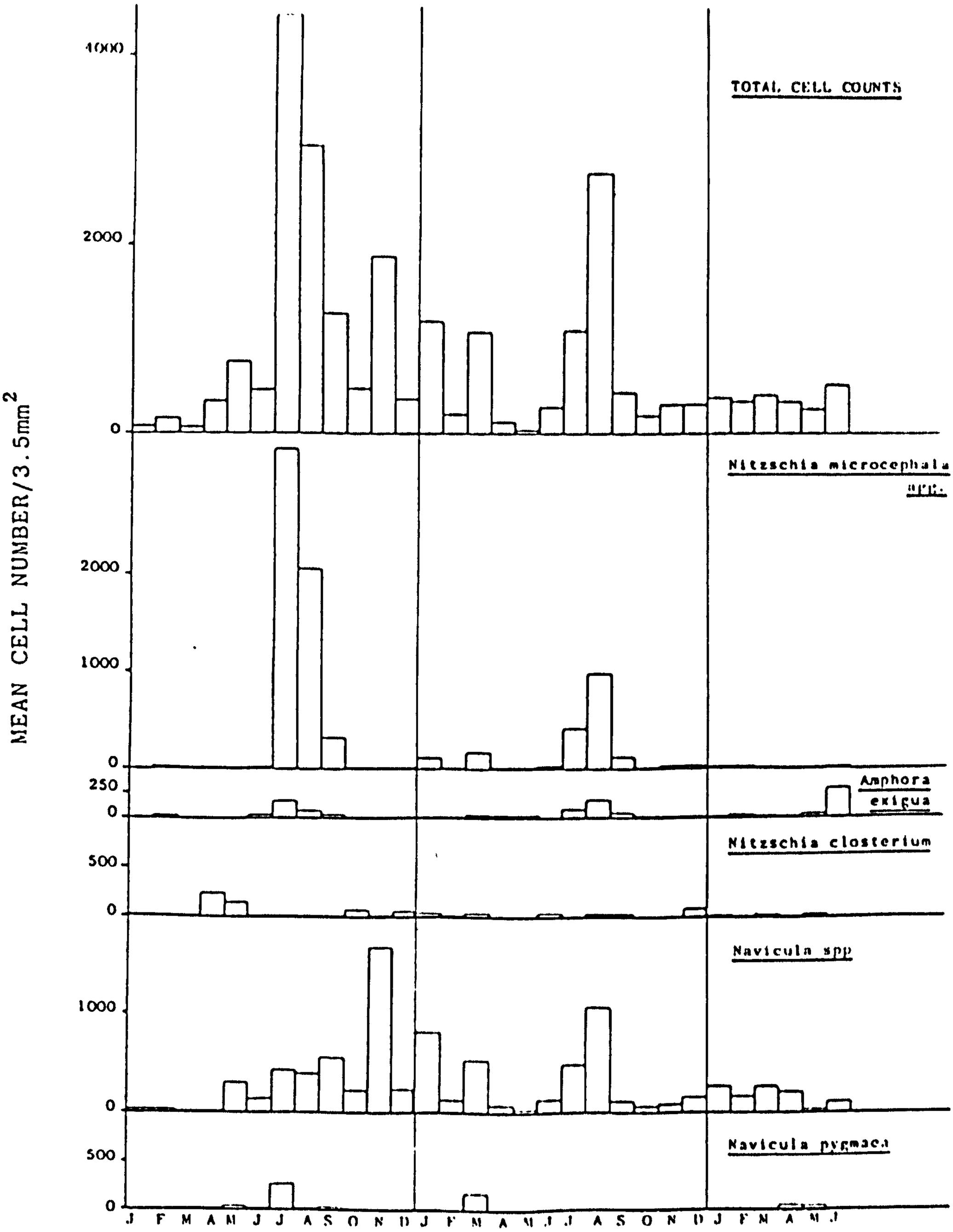
N. vacillata,and N. microcephala agg. A. lineolata was dominant in October 1982 and March 1984, while N.microcephala agg. and N.vacillata were less frequent memebers of the assemblage and only appeared during the summer months. Another species Stauroneis spicula suddenly grew in January 1983 and then rapidly disappeared. The blue-green algae, particularly Anabaena spp grew regularly each year from April-June and peak trichome counts occured prior to the maximum diatom growth.

The total cell counts at site 6 (graph 27) were smaller than at the pool or slope sites (4 and 5) of the middle marsh. The only notable growth at site 6 was observed in June and August 1983. Two aggregates of taxa were mainly responsible for these two peaks: N. microcephala agg.and Navicula spp; A. exigua also grew in smaller numbers in August 1983. The blue-green algae displayed a similar pattern of succession to those at site 3. Peak growth of Anabaena spp followed by Oscillatoria spp and Merismopedia spp occured over 2 years instead of 1.

3.3.3 THE LOWER MARSH

The major growth peaks occured in July-August 1982 and 1983 at site 7 (graph 28) and site 8 (graph 29). This time N. microcephala agg. was the dominant with peak numbers always occurring during summer months. Navicula spp played a much more subordinate role at these sites with maximal growth in November 1982, January,and March 1983. Nitzschia closterium was only present when the other two co-dominants decreased in cell numbers. A. exigua and N. pygmaea were less abundant species growing when total cell counts were high. Sites 7 and 8 displayed very similar patterns of succession. While Navicula spp still contributed to the overall biomass at the site, N. microcephala agg. grew in large numbers in August-September 1982, August-September 1983, and in May-June 1984. A.exigua grew in small numbers in the summer months; N. closterium and A. lineolata grew in months

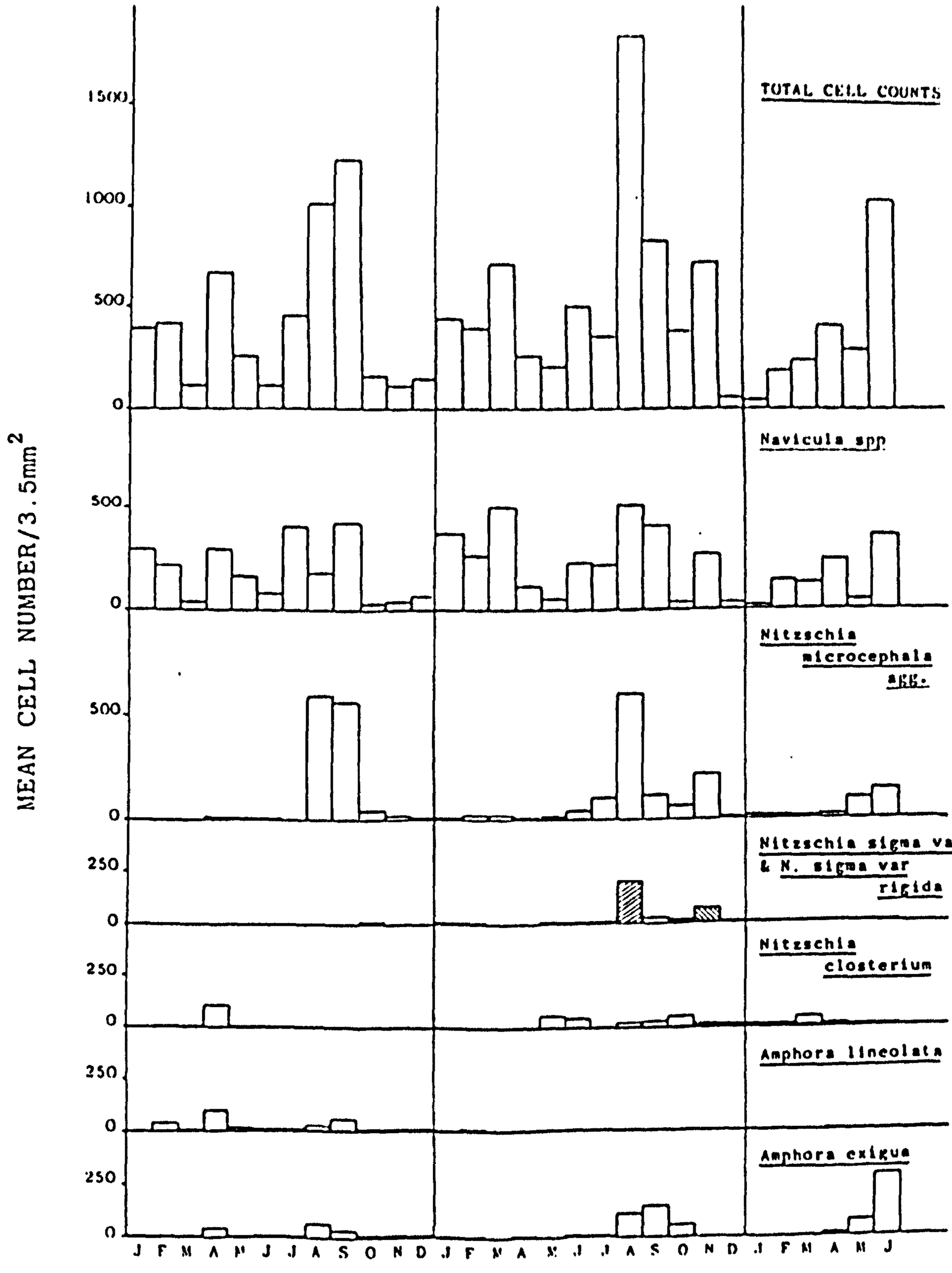
SITE 7 LOWER MARSH



GRAPH 28

Temporal changes in the assemblage structure of the pool site on the lower marsh.

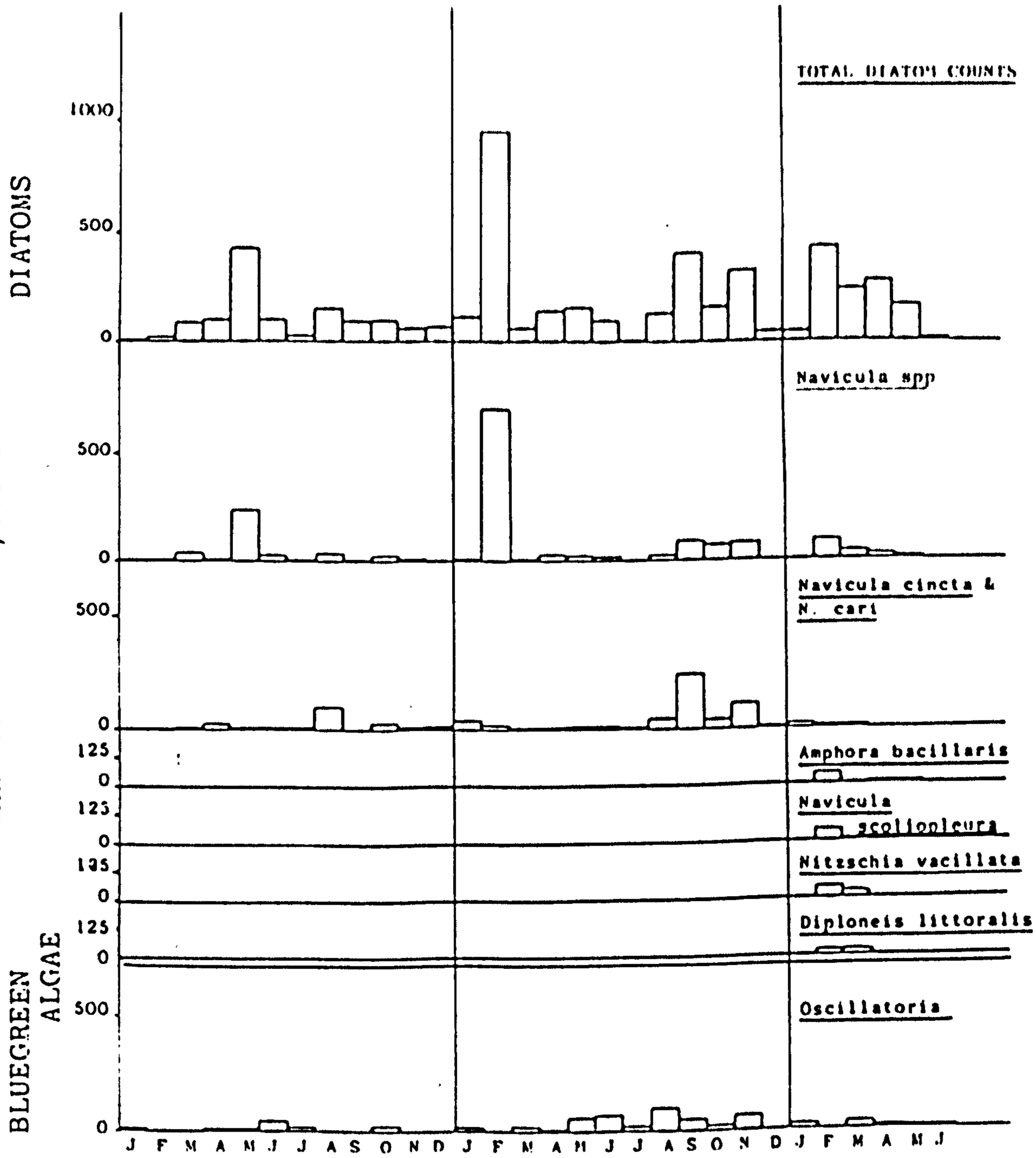
SITE 8 LOWER MARSH



GRAPH 29

Temporal changes in the assemblage structure of the slope site on the lower marsh. Nitzschia sigma var.

Nitzschia sigma var. rigida.



GRAPH 30

Temporal changes in the assemblage structure of the mound site on the lower marsh.

between the peaks of the other two.

New dominant diatoms appeared at site 8 viz Nitzschia sigma var. and Nitzschia sigma var. rigida. Although the live cell counts of these two varieties were indistinguishable; a parallel examination of the acid cleaned material showed that peak numbers of N. sigma var. occured in August 1983 and of N. sigma var.rigida in November 1983.

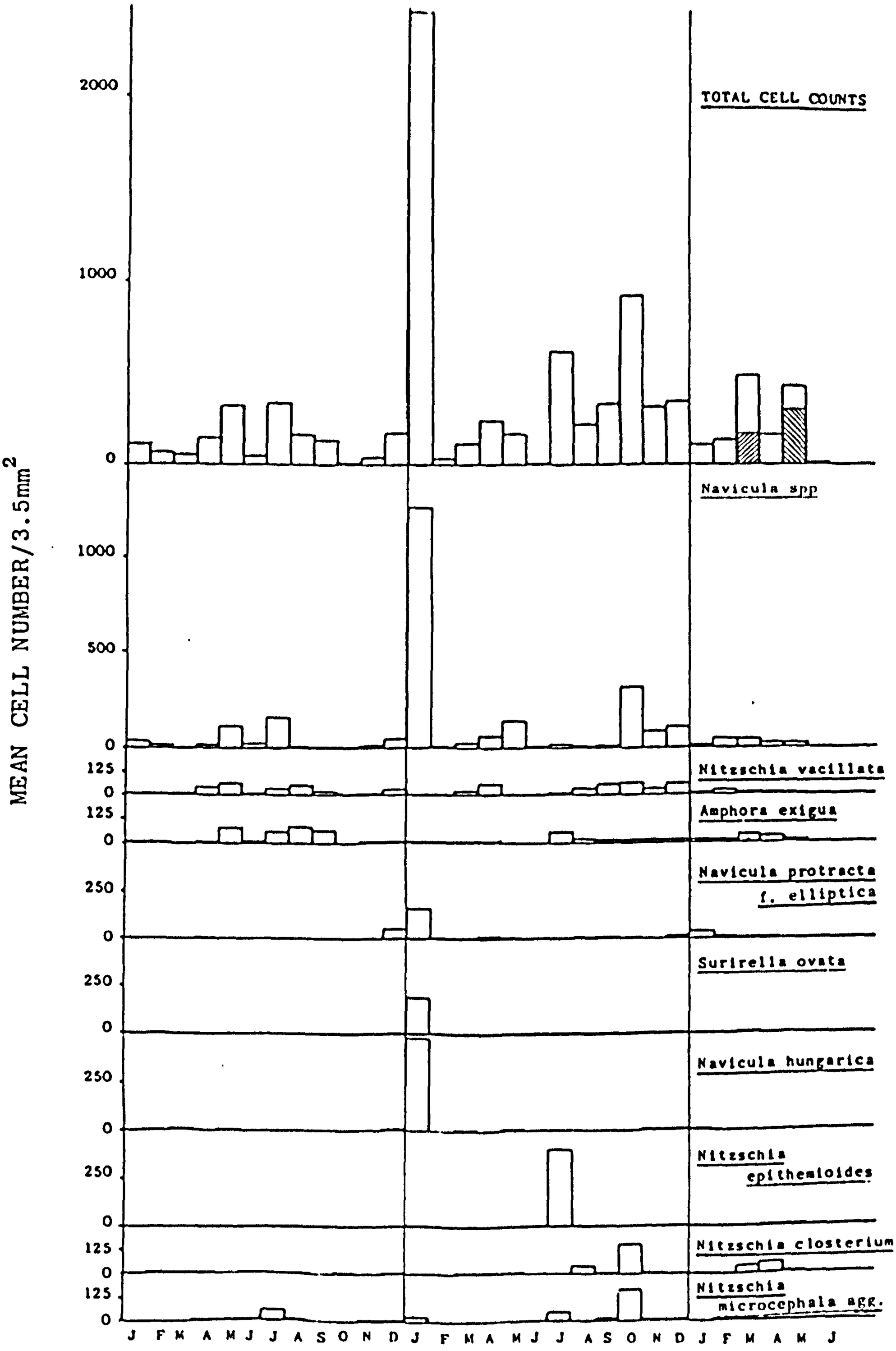
Site 9 (graph 30) was similar to other mound sites on the saltmarsh. The peak growths showed no regular pattern over each year. Navicula spp, N. cincta and to a lesser extent N. cari were largely responsible for the fluctuations in growth. Taxa which were usually found at sandflat sites were observed at site 9 from January-June 1984, when this site became innundated with sand. Oscillatoria spp grew in small numbers during low growth periods of the diatom population.

3.3.4 THE UPPER SANDFLAT

Cell counts of samples from the upper sandflat were lower than those in the saltmarsh. At site 10 (graph 31) one large peak in growth occured in January 1983. This was caused by the combined growth of Navicula spp, Stauroneis spp, Surirella ovata and Navicula hungarica f. elliptica. Even though Navicula spp produced the same growth pattern as the total cell count, many different species contributed to the overall growth pattern Navicula spp, N. vacillata and A. exigua were responsible for the major growth peaks in 1982, while Nitzschia epithemioides, N. closterium and N. microcephala agg. became important in the July and October blooms in 1983. By 1984 new dominants appeared: a Nitzschia sp bloomed in March 1984 and St. spicula in May 1984.

Maximum counts were recorded in April and June 1982, July and November 1983,

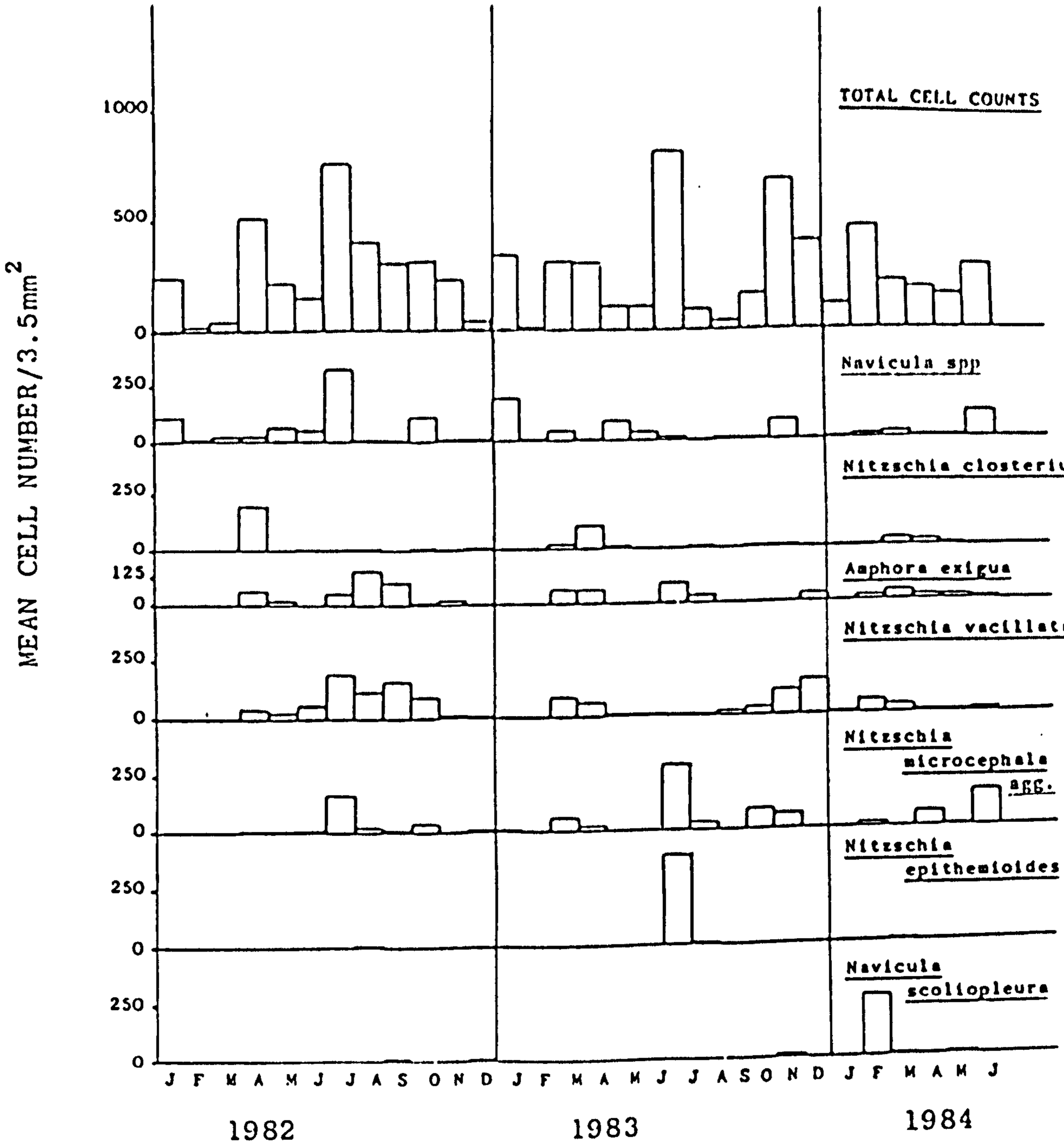
SITE 10 UPPER SANDFLAT



GRAPH 31

Temporal changes in the assemblage structure on the bottom of the stream channel at the supper sandflat ▨ Nitzschia sp, ▩ Stauroneis spicula.

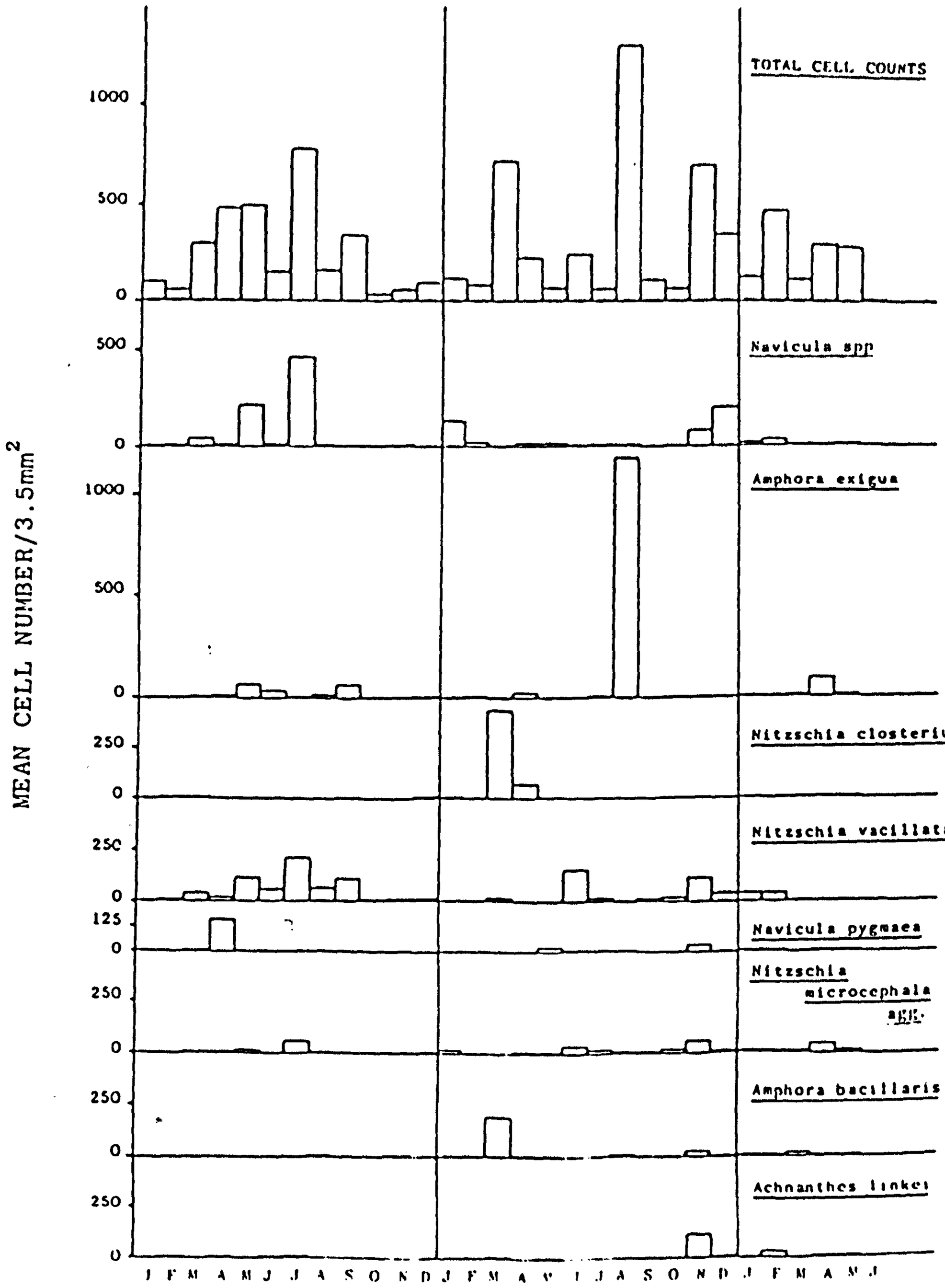
SITE 11 UPPER SANDFLAT



GRAPH 32

Temporal changes in the assemblage structure on the bank of the upper sandflat channel.

SITE 12 UPPER SANDFLAT



GRAPH 33

Temporal changes in the assemblage structure above the bank of the upper sandflat channel.

and February 1984 at site 11 (graph 32). Succession changed each year. In 1982 Navicula spp, A.exigua, N.vacillata and N.microcephala agg. were responsible for most of the total cell counts. In July 1983 N.epithemioides and N.microcephala agg. grew as co-dominants. In November many taxa became equally abundant. A new dominant Navicula scoliopleura was responsible for the smaller February peak in 1984.

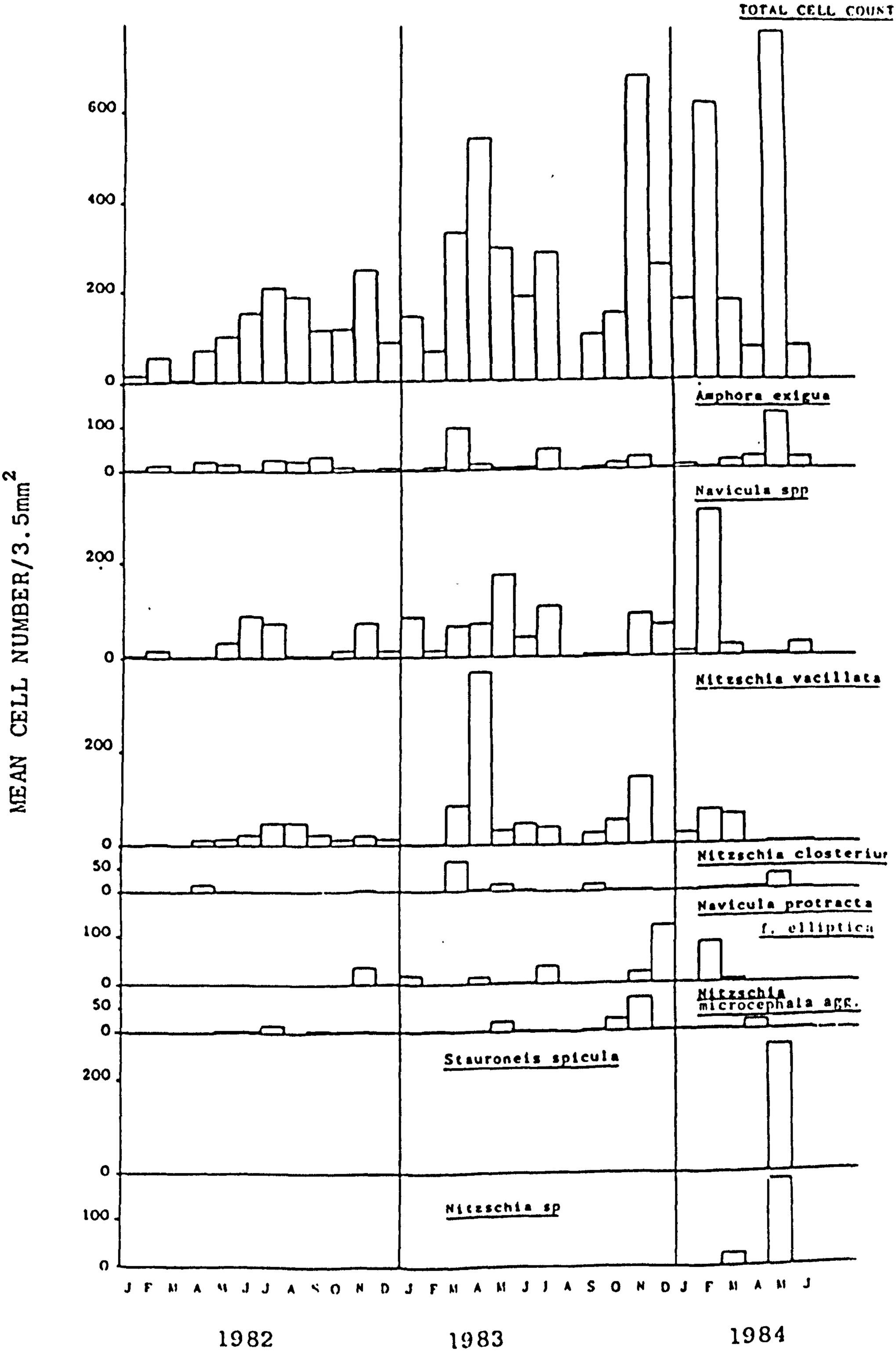
At site 12 (graph 33) growth increased to a maximum by summer each year. In 1982 the summer maximum was largely the result of growth of Navicula spp and N. vacillata. In 1983 major growth peaks were caused by blooms of N.closterium and Amphora bacillaris in March,and A.exigua in May. No particular species grew in significant numbers over others in 1984.

3.3.5 THE LOWER SANDFLAT

The total cell counts at all sites of the lower sandflat were smaller than at other sites. Seasonal peaks in growth were not easily recognised but a succession was observed at all three sites (graphs 34-36) . At site 13 A.exigua, Navicula spp and N.vacillata were co-dominants in 1982. Peak numbers of Navicula spp were observed in June and July 1982,prior to peak growth of N.vacillata in July-August 1982. By 1983 N.vacillata reached a maximum followed by a smaller growth of Navicula spp. In 1984 Navicula spp were dominant in February, followed by A.exigua, St.spicula,and a Nitzschia sp, in May. N.microcephala agg. Navicula protracta and N.closerium grew when the other taxa decreased in numbers.

At site 14 very small fluctuations in the total cell counts were recorded. In 1982 and 1983 Navicula spp and N.vacillata were largely responsible for the peaks. By 1984 A.exigua became dominant. N.closterium, N.epithemioides, Navicula rostellata, Achnanthes linkei,Navicula humerosa and N.scoliopleura all grew in succession but only produced low numbers from March 1983 to February 1984.

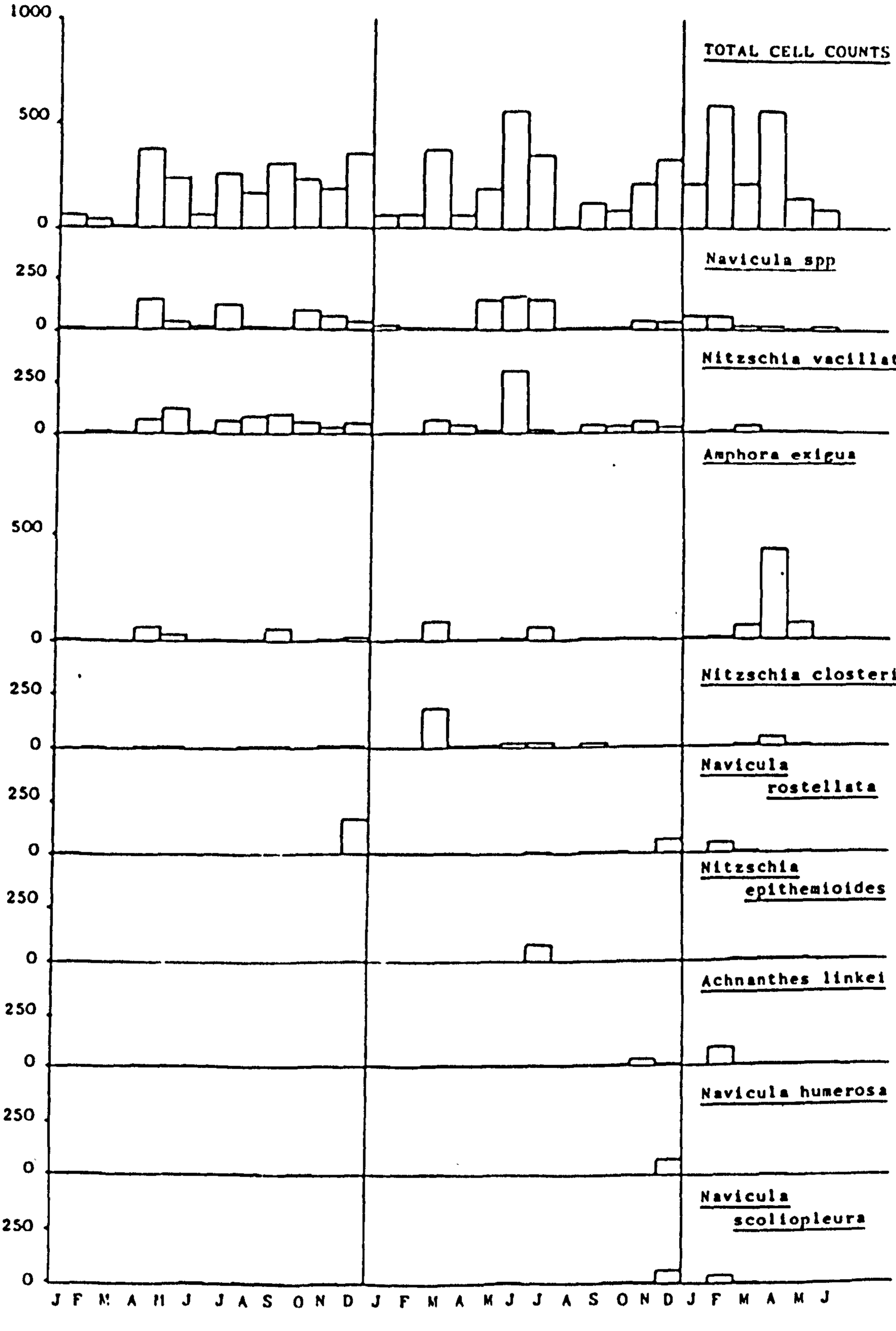
SITE 13 LOWER SANDFLAT



GRAPH 34

Temporal changes in the assemblage structure on the bottom of the stream channel at the lower sandflat

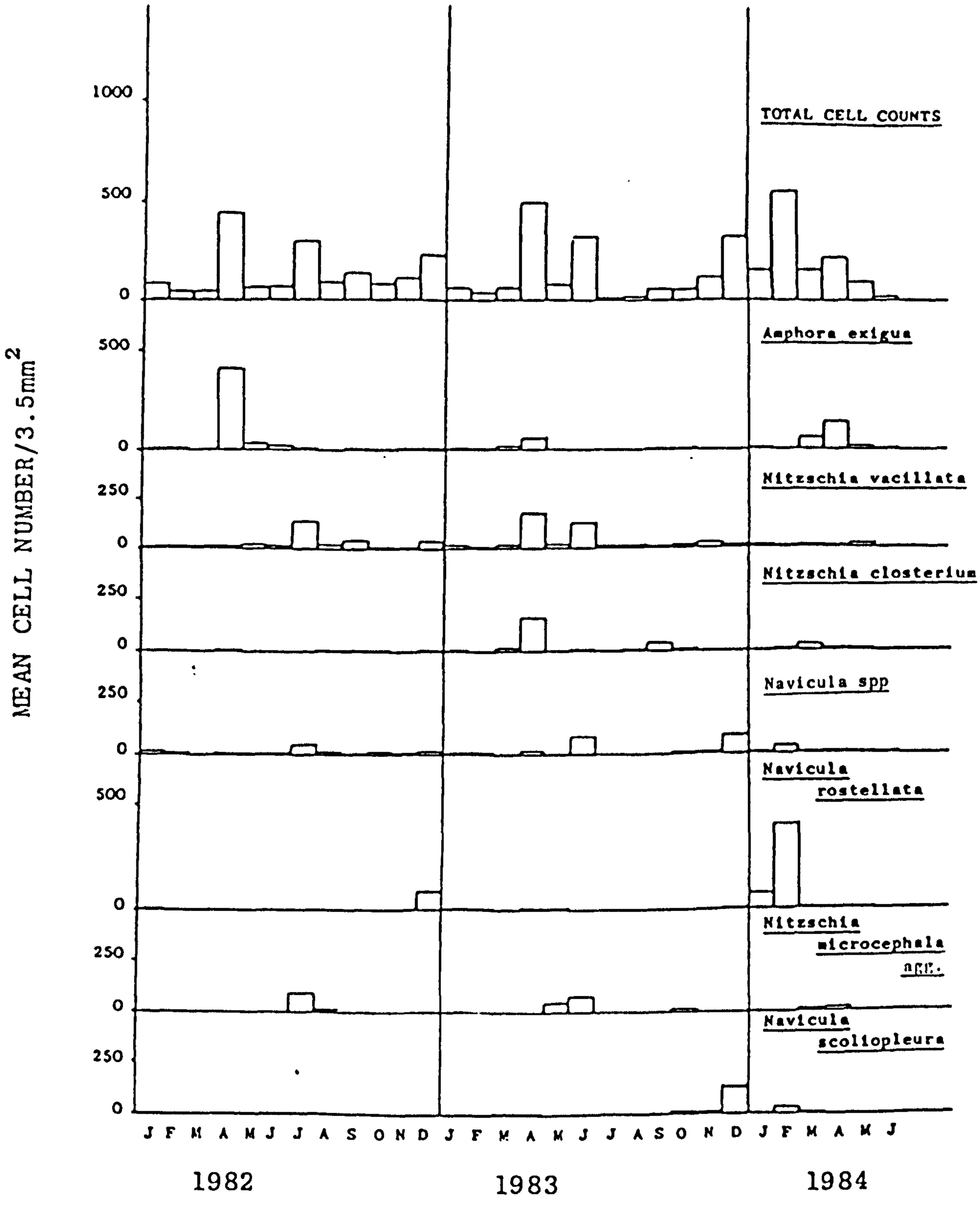
SITE 14 LOWER SANDFLAT



GRAPH 35

Temporal changes in the assemblage structure on the bank of the lower sandflat channel.

SITE 15 LOWER SANDFLAT



GRAPH 36

Temporal changes in the assemblage structure above the bank of the lower sandflat channel.

At site 15 no particular species became dominant. Different taxa grew to their maximal numbers over short periods of one or two months, with A.exigua dominant in April 1982, and N.rostellata in February 1984. Low numbers of all of the other taxa in succession were recorded over the 30 months studied.

3.3.6 THE MUDFLAT

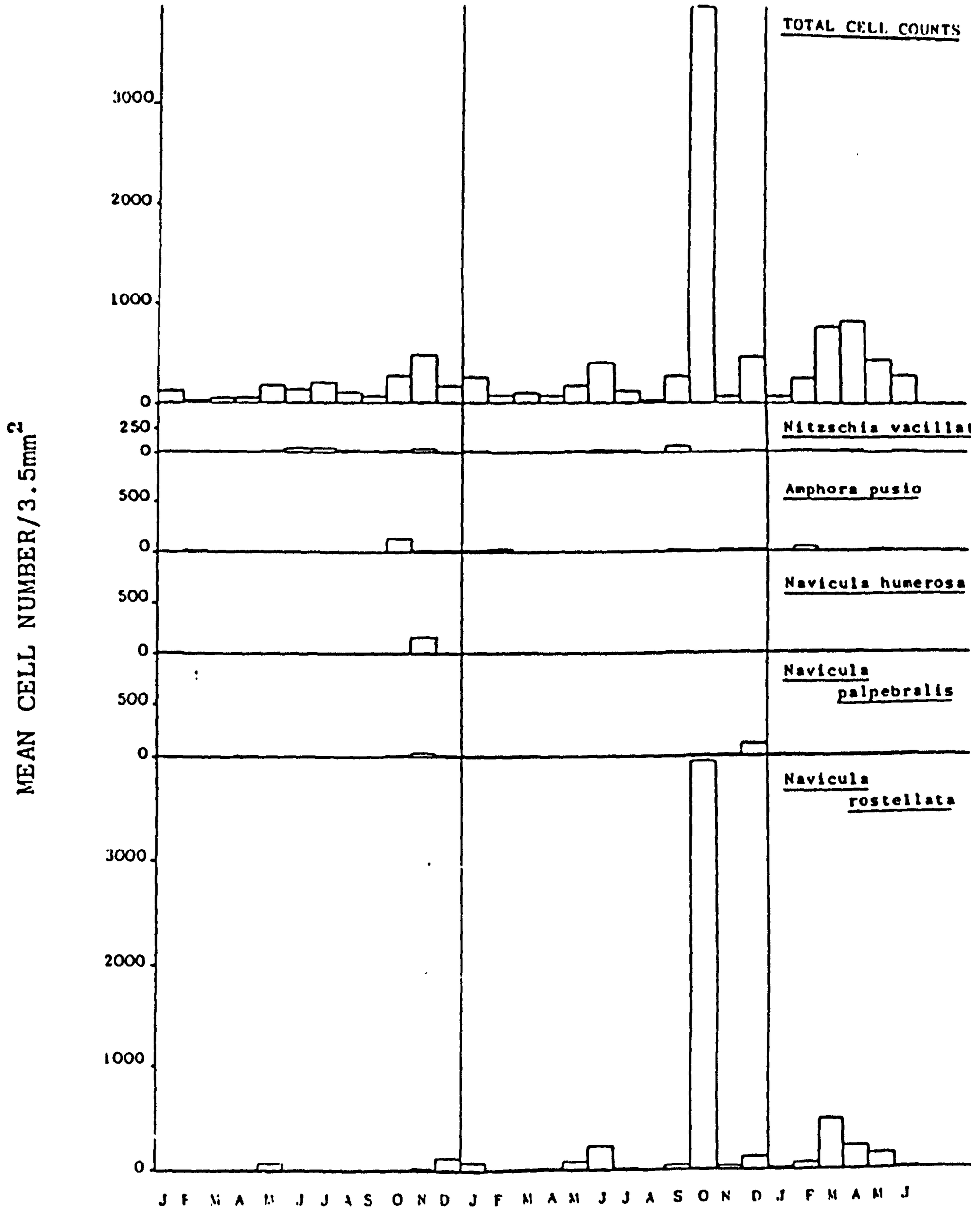
All the cell counts at site 16 (graph 37) were low with the exception of an enormous growth peak in October 1983. This large peak was caused by the growth of N.rostellata which grew as a surface film several cells thick. Therefore the coverglasses placed on its surface were only sampling a fraction of the total population present. N.rostellata was the dominant species over all 30 months studied. In addition Amphora pusio and Navicula palpebralis occured together in low numbers from October-December each year. Navicula humerosa was present in the late autumn months, but in decreasing numbers each year. N.vacillata occured in low numbers throughout the study period.

3.3.7 DISCUSSION

Every site along the transect displayed a clear pattern of succession. Seasonal fluctuations of the total cell counts were similar at most sites. Highest counts were recorded in the summer, decreasing by late summer, followed by smaller peaks in the autumn. Growth of the diatoms in the spring may have been prevented in some way by the abundant growth of blue-green algae. When and where blue-green algae were not observed in high numbers the summer peak of diatom growth occured earlier; e.g. site 1 where peak cell counts were observed in May 1982. When the mean cell counts were low a marked seasonal growth was more difficult to observe.

Sites on the sandflat generally had much lower total cell counts than on the

SITE 16 MUDFLAT



GRAPH 37

Temporal changes in the assemblage structure on the mudflat.

saltmarsh. This may be an effect of tidal disturbance and reduced light availability as suggested by Admiraal (1980). Tidal innundation occurs twice daily over the lower sandflat throughout the year and slightly less frequently over the upper sandflat. The summer tides are lower, and high tide does not always reach the seaward edge of the saltmarsh and therefore does not cover the upper sandflat twice daily. This may account for the slightly higher mean counts in the upper sandflat in contrast to the lower sandflat.

The mean cell counts from the mudflat (site 16) were mostly low. However disturbance of the sediments by the tide at this site were so severe that entire banks of sediment may be deposited or removed. Thus the diatom populations sampled are undoubtedly derived from different sediments. This far out on the shore, whole populations of diatoms may be swept up and down the estuary with the tidal currents. Therefore the diatom succession observed at the mudflat reflects the pattern of tidal currents rather than growth at the sediment surface.

One curious feature of the mudflat counts is the occasional occurance of an enormous mean cell count. If constant tidal disturbance maintains a low population density on most sediments how can such a very dense diatom film occur? Is it possible that the tidal currents are capable of continually depositing dense clusters of diatom cells onto the sediment surface? This phenomenon requires further investigation.

The diatom species themselves show different patterns of seasonal growth. Some species are present in low numbers throughout the year without any distinctive peaks in growth, an example is Nitzschia closterium growing at site 7. Other species or aggregates are present throughout the year and show a marked seasonal growth e.g. Navicula spp, Nitzschia microcephala agg.,

and Amphora lineolata. Others adopt more of an opportunist strategy appearing in one month over the 30 months studied and never recurring e.g. Nitzschia lorenziana, Rhopalodia operculata and Nitzschia epithemioides. The growth strategies of these diatoms are very similar to those previously reported (Round 1953).

A gradual change in spatial distribution is observed from pool to mound, and along the transect. Taxa which are major dominants in a pool site e.g. Navicula spp at site 1, have a much more subordinate position in the mound assemblage at site 3, where Navicula cari and Navicula cincta assume dominance. The assemblage at site 2 is intermediate between those of sites 1 and 3. These changes in assemblage structure correspond to changes in physical conditions. The assemblage transition from pool to mound is not as obvious in the middle marsh (sites 4-6) because no mound dominant at site 6 was observed. Sites 7 and 8 have very similar assemblages in the lower marsh. However the movement of sand at site 9 disturbed the assemblage structure, and any spatial relationships between the pool, slope, and mound sites became obscured.

A gradual transition in the spatial distribution of different taxa is observed along the transect itself. Species which are dominants in the upper marsh do not appear at sandflat or mudflat sites while the latter are inhabited by different dominants. This aspect will be more closely examined in the next section.

CONCLUSIONS

At each site along the transect a distinct pattern of seasonal growth, with a marked pattern of succession is observed. This pattern of succession is not usually repeated seasonally, therefore more than one year's field sampling is required to obtain any sort of detailed picture of temporal changes in diatom assemblage structure.

3.4 SPATIAL CHANGES IN ASSEMBLAGE STRUCTURE

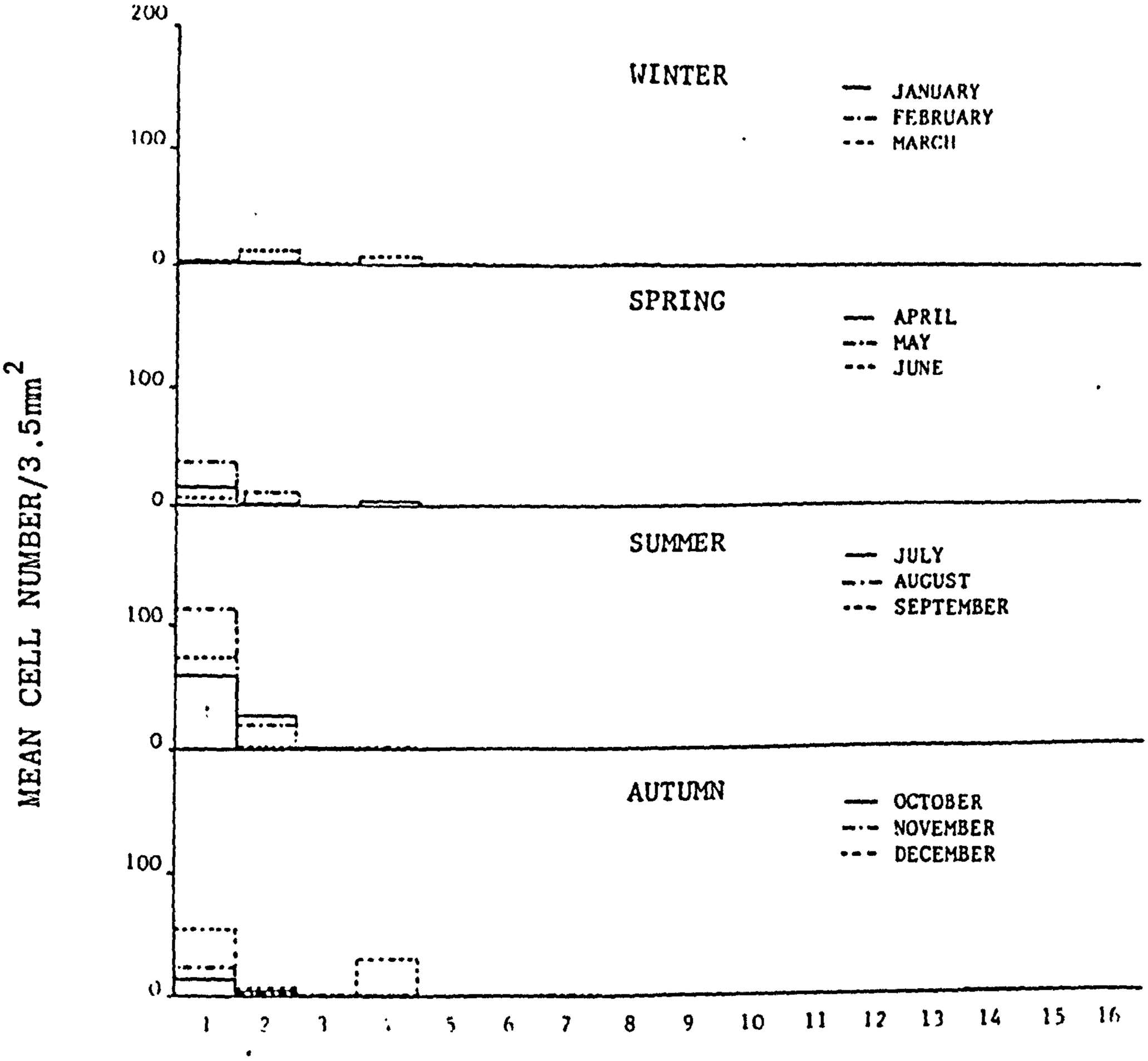
The results in the previous chapter indicated that the various diatom taxa occupy different spatial positions along the transect. Spatial position was analysed by graphing the mean monthly cell counts against distance. More than 2,450 computer plots were made using the mean monthly counts of 72 diatom and 10 blue-green algal taxa over the 30 month study. Then 300 plots were selected to describe the spatial positions of 10 taxa in detail. These 10 taxa were chosen because of their high abundance. Their high numbers not only made up the bulk of all cell counts, but their spatial positions displayed patterns that were representative of most taxa.

3.4.1 Amphora ovalis var. libyca (graphs 38-40)

In 1982 (graph 38) A. ovalis var. libyca grew in a confined area on the upper marsh, and to a lesser degree in the pool site of the middle marsh. Maximum numbers were recorded in the summer months, July-September. When the mean counts were high the spatial position did not extend beyond site 4. Only in winter months January-March, when numbers were low, were a small number of individuals observed at sites 5,6 and 7. In 1983 (graph 39) the spatial position changed. Maximum counts were recorded from site 4 although relatively high numbers were still observed from the upper marsh. When growth was low in winter and autumn more cells occured on the lower marsh and upper sandflat. By 1984 (graph 40) the distribution had shifted onto the middle marsh. A larger population grew in winter in 1984, than in previous years. Field observations agree with Hudstedt's (1939) conclusions that A. ovalis var. libyca is more of a widespread freshwater form.

DISTRIBUTION OF AMPHORA OVALIS VAR. LIBYCA

1982

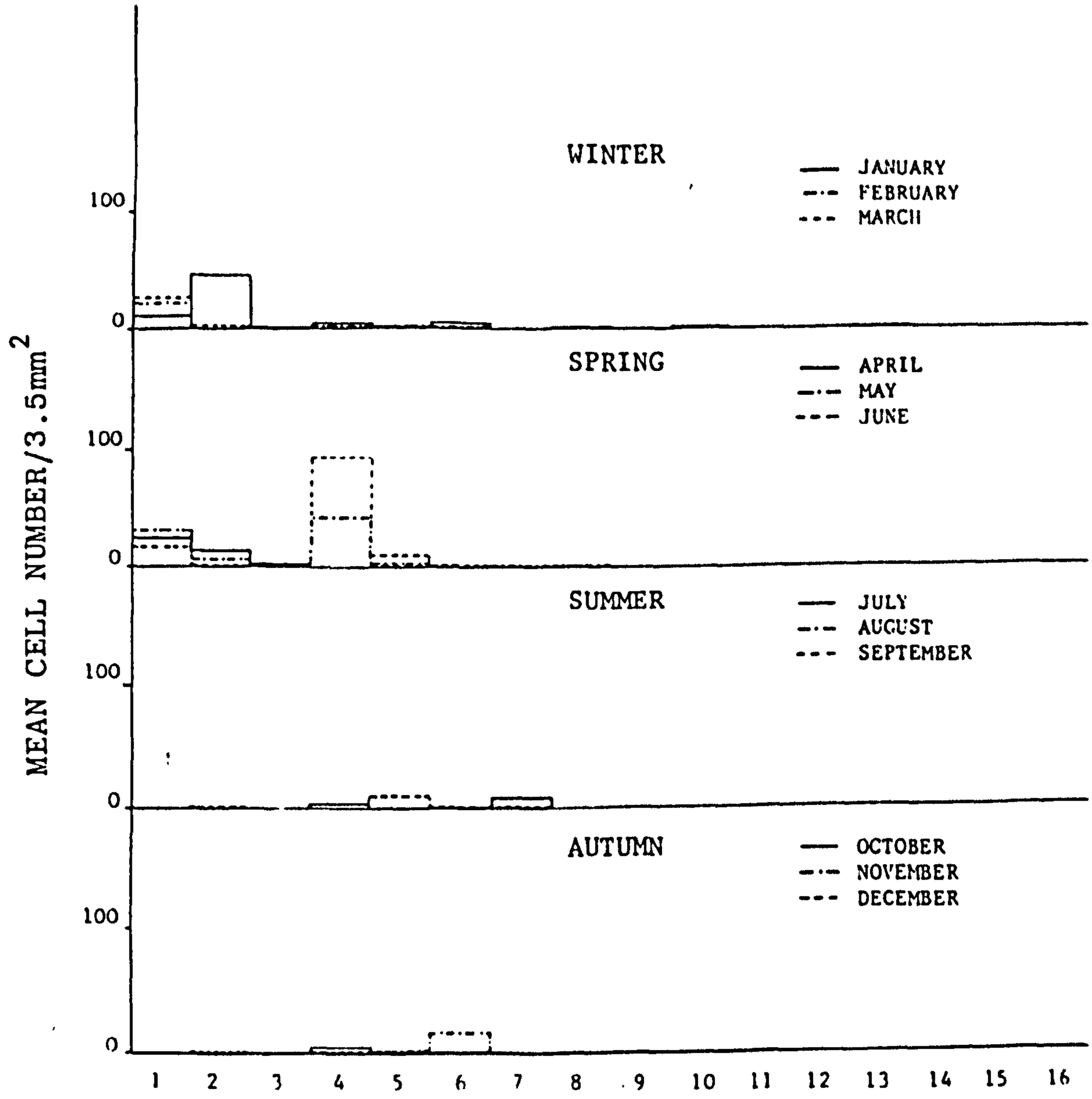


GRAPH 38

Spatial changes of A. ovalis var. libyca in 1982.

DISTRIBUTION OF AMPHORA OVALIS VAR LIBYCA

1983

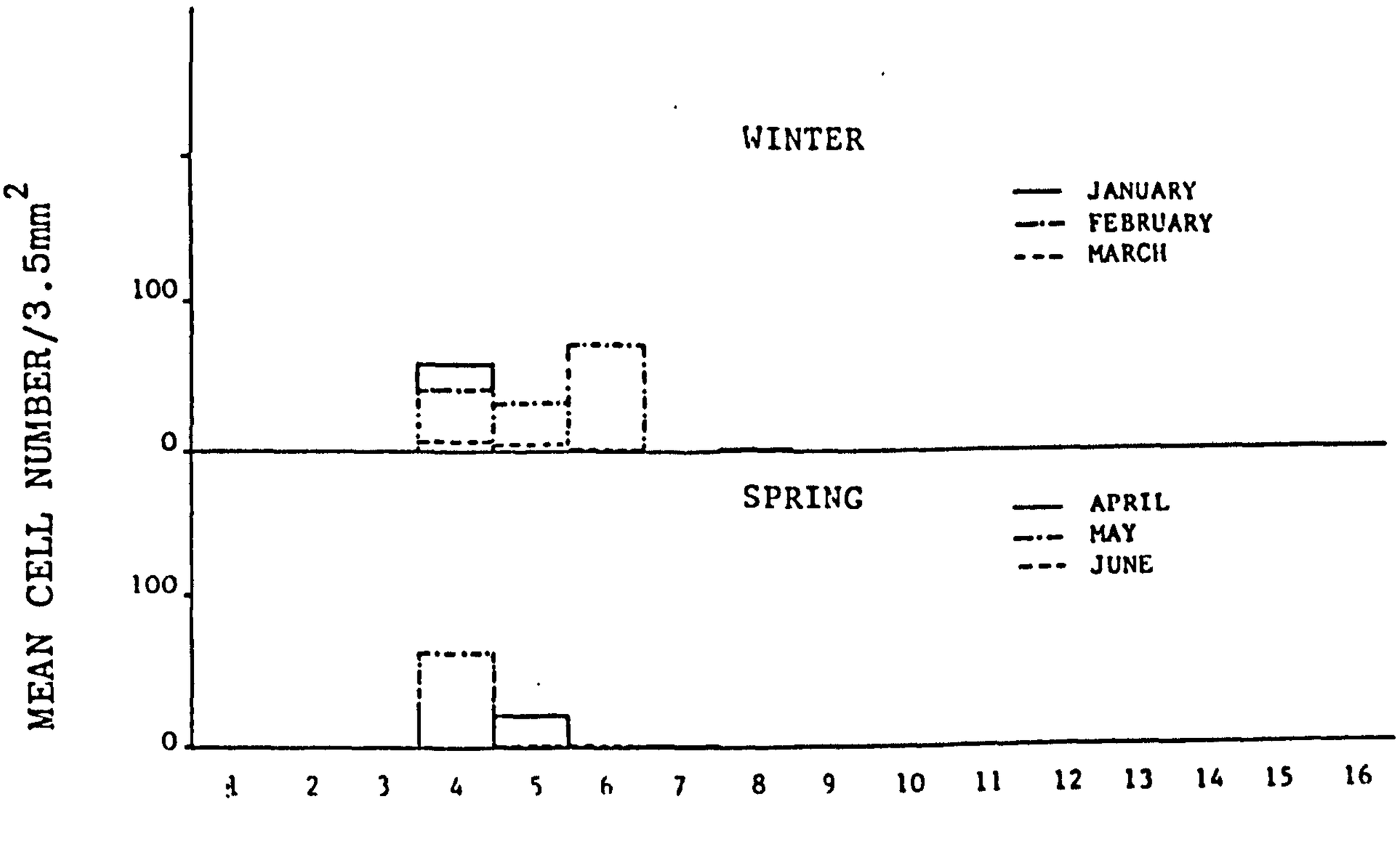


GRAPH 39

Spatial changes of A. ovalis var. libyca in 1983

DISTRIBUTION OF AMPHORA OVALIS VAR LIBYCA

1984



GRAPH 40

Spatial changes of A. ovalis var. libyca in 1984.

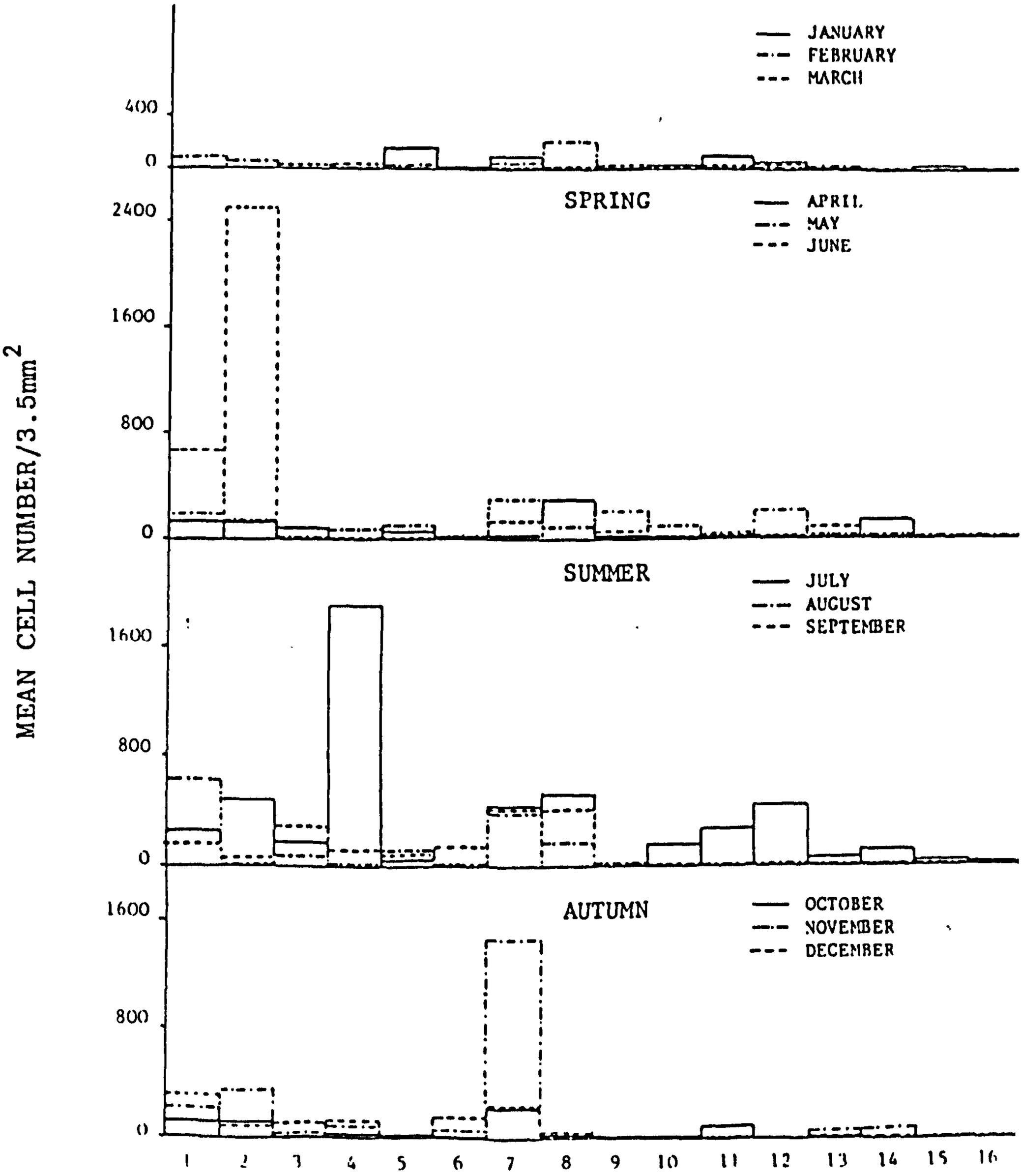
3.4.2 Navicula spp (graphs 41-43)

Although this aggregate has been observed at all sites,high counts were found on the saltmarsh. In 1982 (graph 41) maximum numbers were observed from site 2 in June. In the following month high numbers were recorded from site 4. The July mean count was lower than in June. By November a peak occured from site 7 which was lower than the June and July counts. Thus decreasing maxima appeared to shift outwards along the marsh over the year. This pattern was not repeated in 1983 (graph 42). The mean counts were generally much lower. Maxima appeared in winter and summer months on the lower marsh and upper sandflat. There was no distinctive spatial pattern observed by 1984 (graph 43). Navicula spp display a spatial pattern that is representative of most abundant taxa. Live cell counts are recorded at all sites along the transect with greatest abundance confined to a more restricted area.

3.4.3 Navicula pygmaea (graphs 44-46)

In 1982 (graph 44) N. pygmaea was only observed in high numbers in the summer months June-July. Maxima were observed from site 1, then site 4 and 7. Few counts were recorded in winter or autumn. Nevertheless low numbers occured over a broad range of sites along the transect. By 1983 (graph 45) abundance had decreased,with highest numbers recorded from samples taken from the lower marsh in September. Again low mean counts were found from a large number of sites along the transect. Abundance continued to decrease to even lower levels by 1984 (graph 46) with a larger proportion of the population inhabiting the saltmarsh. Within 30 months sampling, maxima had decreased from over 600 cells, to under 200. N. pygmaea is generally recognized as a brackish water form. Field observations of this species suggest that there must have been a

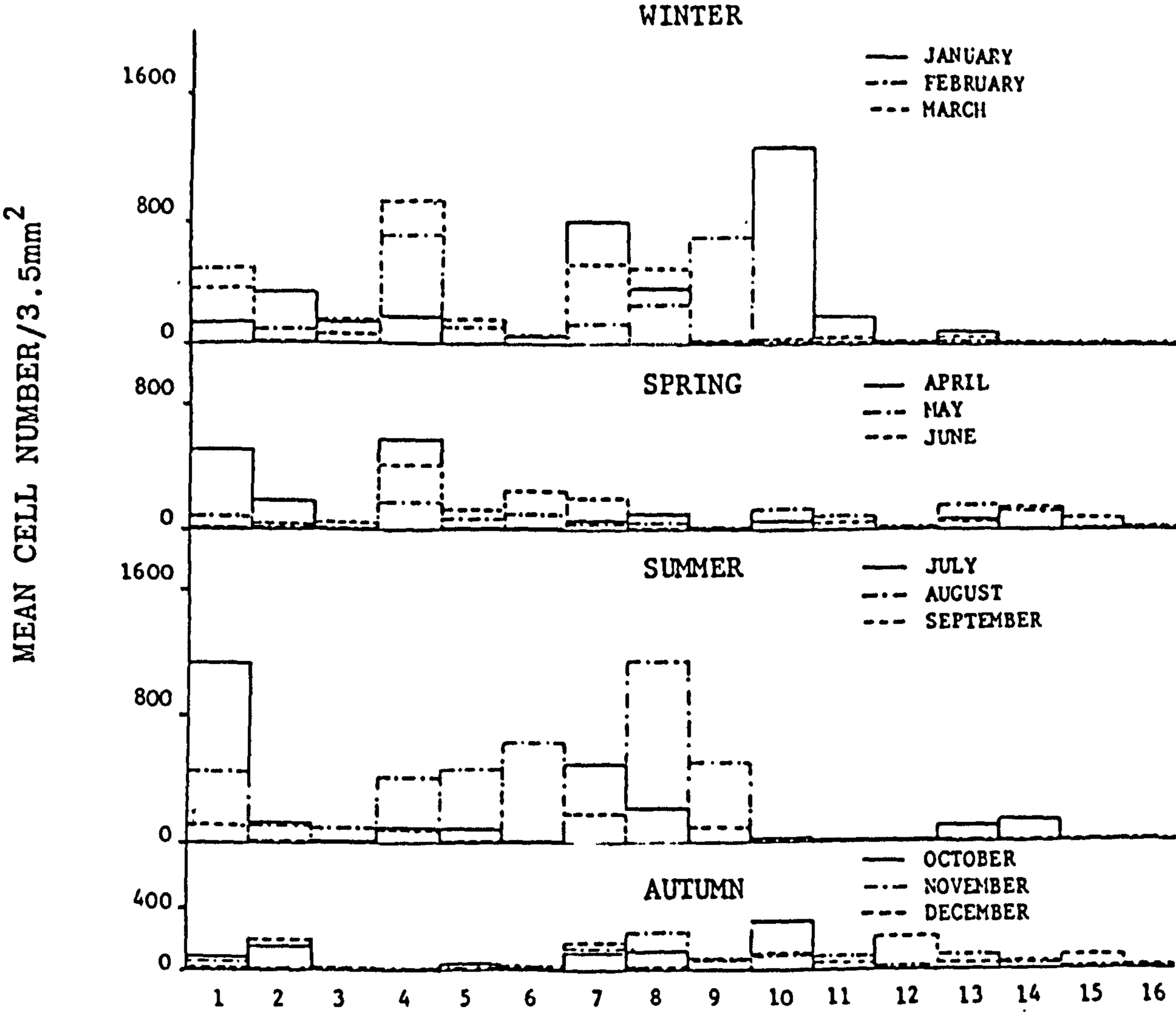
DISTRIBUTION OF NAVICULA SPP 1982



GRAPH 41

Spatial changes of Navicula spp in 1982

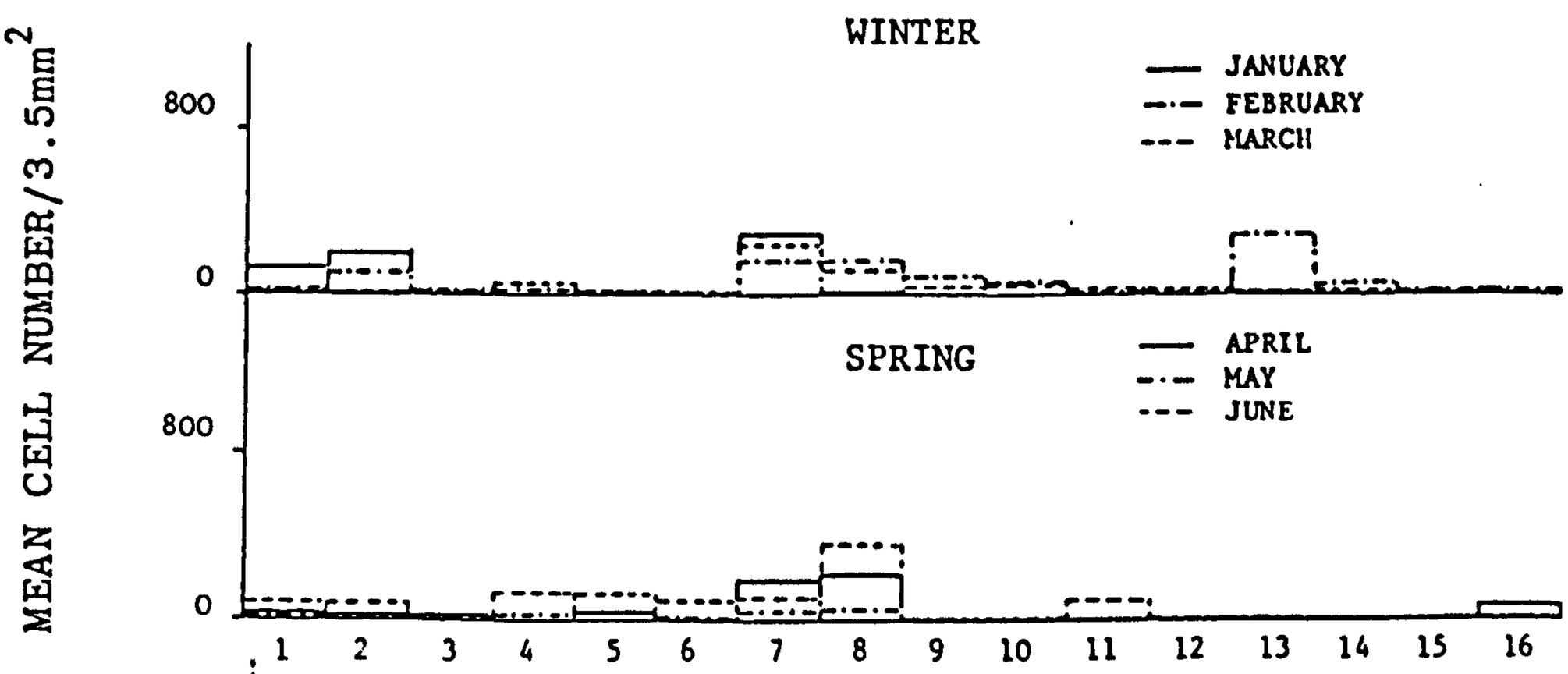
DISTRIBUTION OF NAVICULA SPP 1983



GRAPH 42

Spatial changes of Navicula spp in 1983.

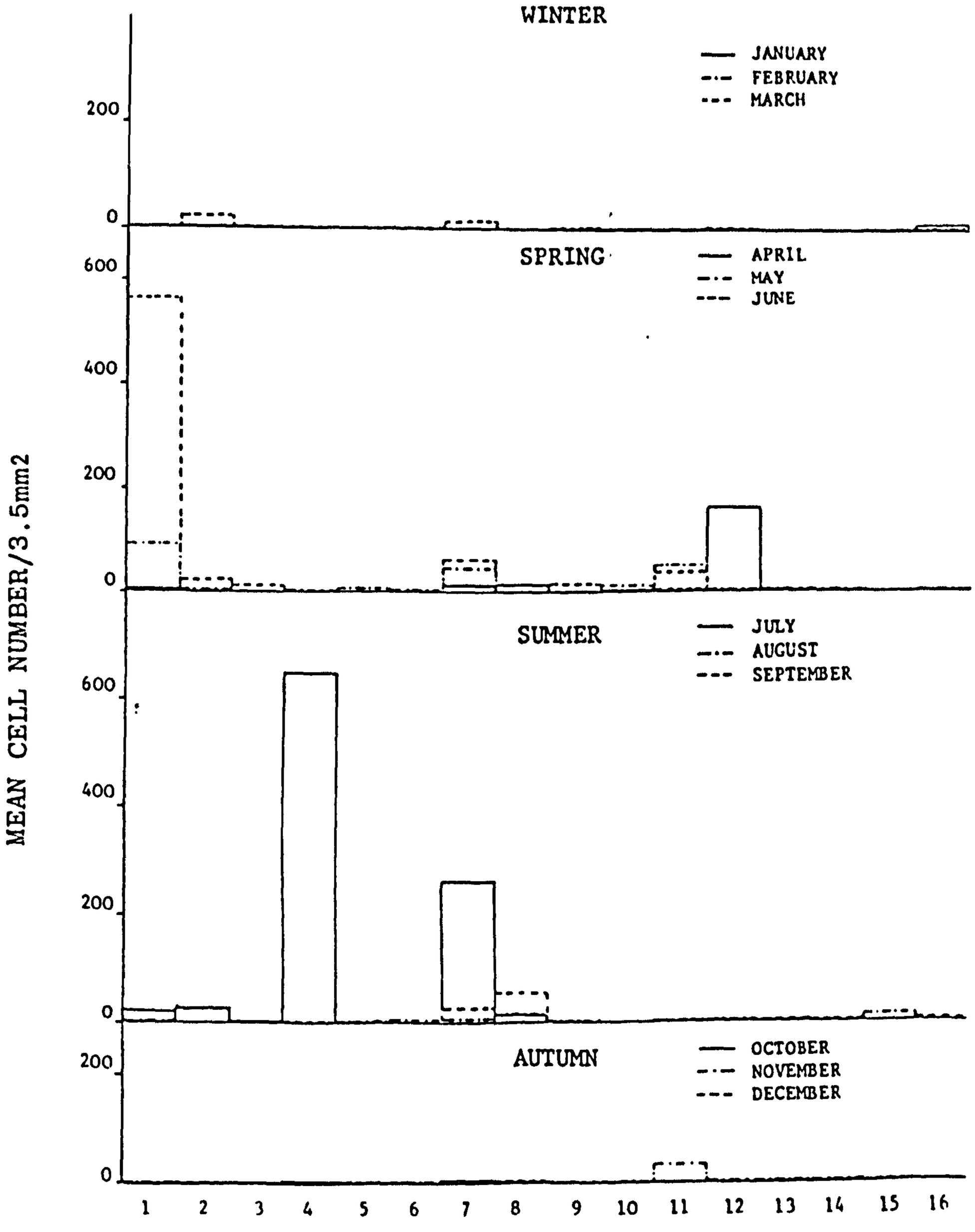
DISTRIBUTION OF NAVICULA SPP 1984



GRAPH 43

Spatial changes of Navicula spp in 1984

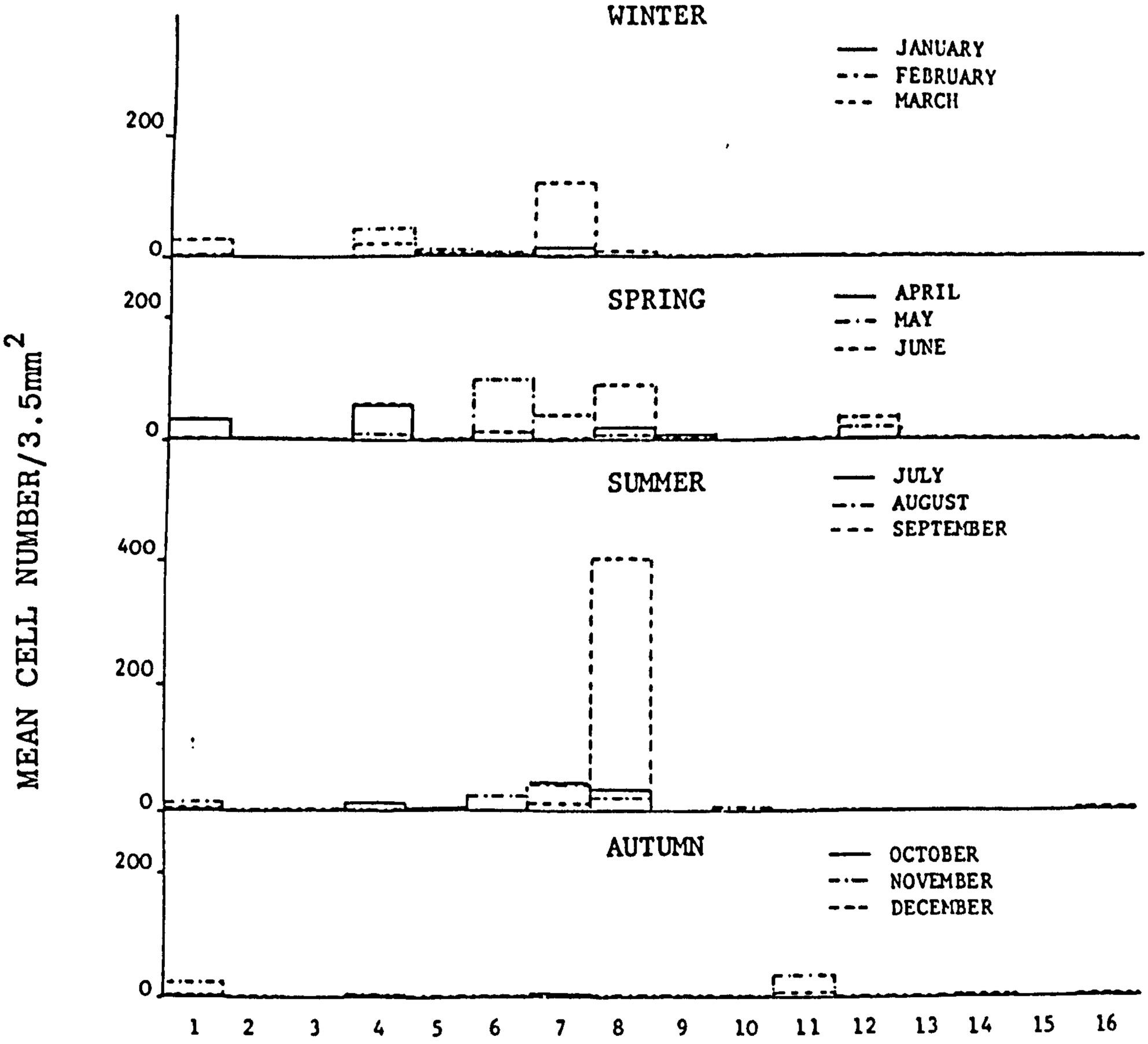
DISTRIBUTION OF NAVICULA PYGMAEA 1982



GRAPH 44

Spatial changes of N. pygmaea in 1982.

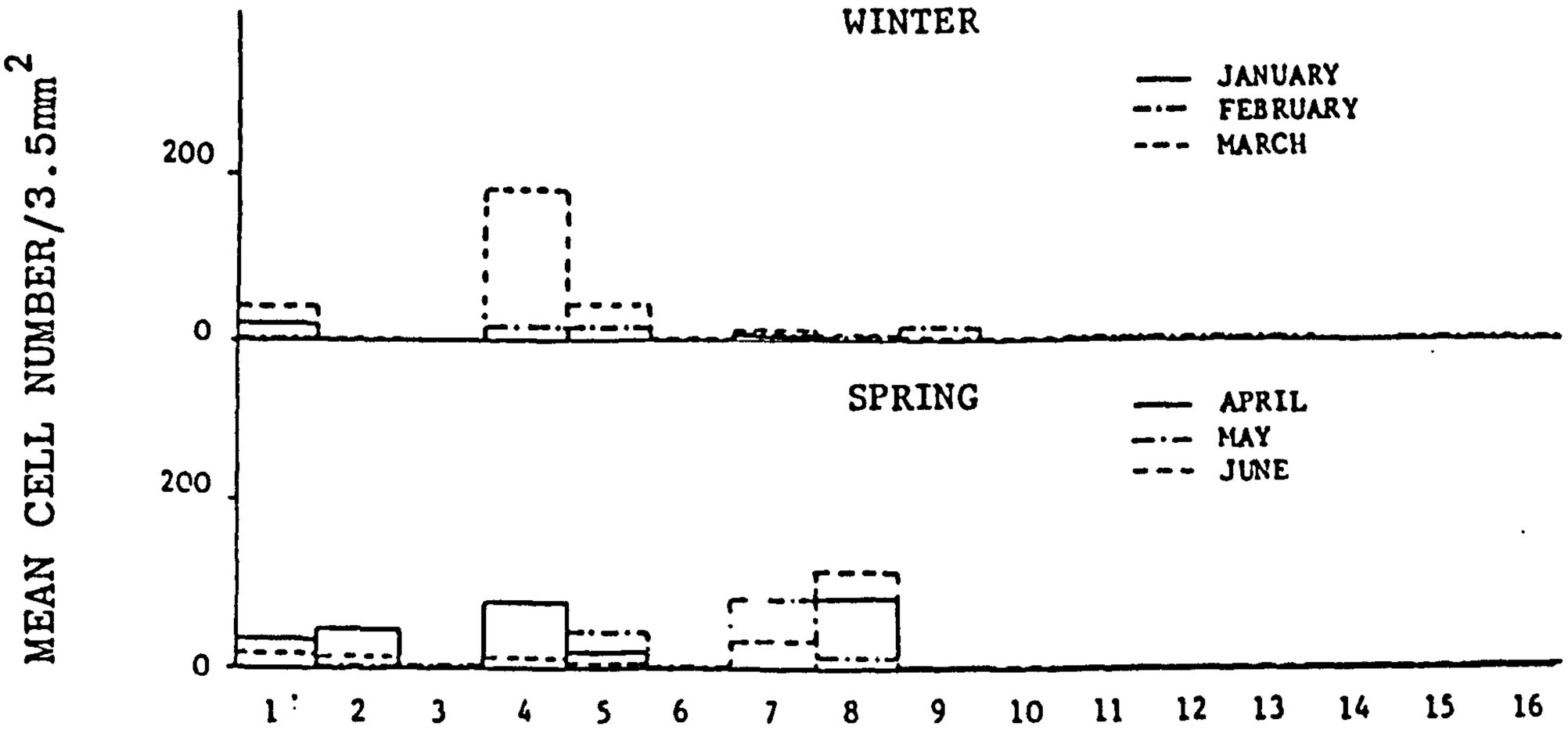
DISTRIBUTION OF NAVICULA PYGMAEA 1983



GRAPH 45

Spatial changes of N. pygmaea in 1983.

DISTRIBUTION OF NAVICULA PYGMAEA 1984



GRAPH 46

Spatial changes of N. pygmaea in 1984

slow change to more saline conditions in the saltmarsh over the 2½ years studied.

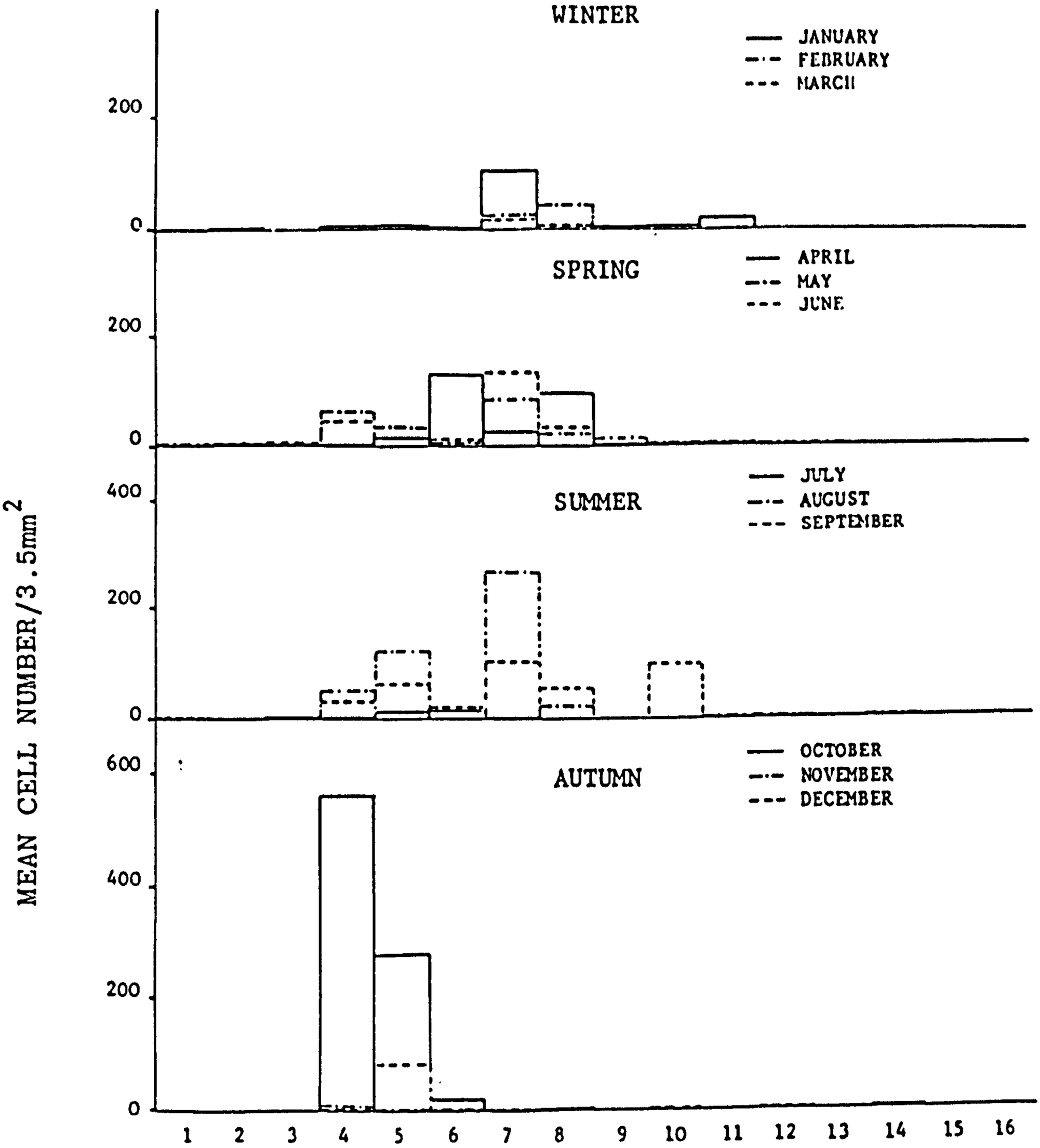
3.4.4 Amphora lineolata (graphs 47-49)

A. lineolata has a more restricted distribution than many taxa. In the winter, spring and summer of 1982 (graph 47) most mean counts were recorded from sites in the middle and lower marsh. Maximum counts in autumn were also noted at sites on the middle marsh. By 1983 (graph 48) and 1984 (graph 49) almost all growth occured at sites 4, 5 and 6. However peak growth was at different times each year. In 1982 a peak of 520 cells/3.5mm^2 was recorded from site 4 in October. The maximum in 1983 was under 200 cells/3.5mm^2 in December. By 1984 a maxima of 470 cells/3.5mm^2 was recorded in March. While a consistent seasonal growth does not occur, a confined distribution is maintained at brackish water sites along the transect. A. lineolata has also been classified as a brackish water form in Western Australia (John 1984).

3.4.5 Nitzschia microcephala agg. (graphs 50-52)

Like Navicula spp, N. microcephala agg.was found at all sites. Maximum numbers were found at specific sites. In 1982 (graph 50) high numbers were recorded from pool sites on the lower and middle marsh. Much lower counts were recorded from all other sites. The maxima recorded were some of the highest for any species, and occured during the summer months July-August. Very low numbers were observed in winter, spring,and autumn. Maximum growth was recorded in 1983 (graph 51) from June-August. The mean cell counts were much lower than in 1982, and maxima were recorded at a larger number of sites. Smaller populations grew on the sandflat and mudflat. Little growth was recorded in 1984 (graph 52).

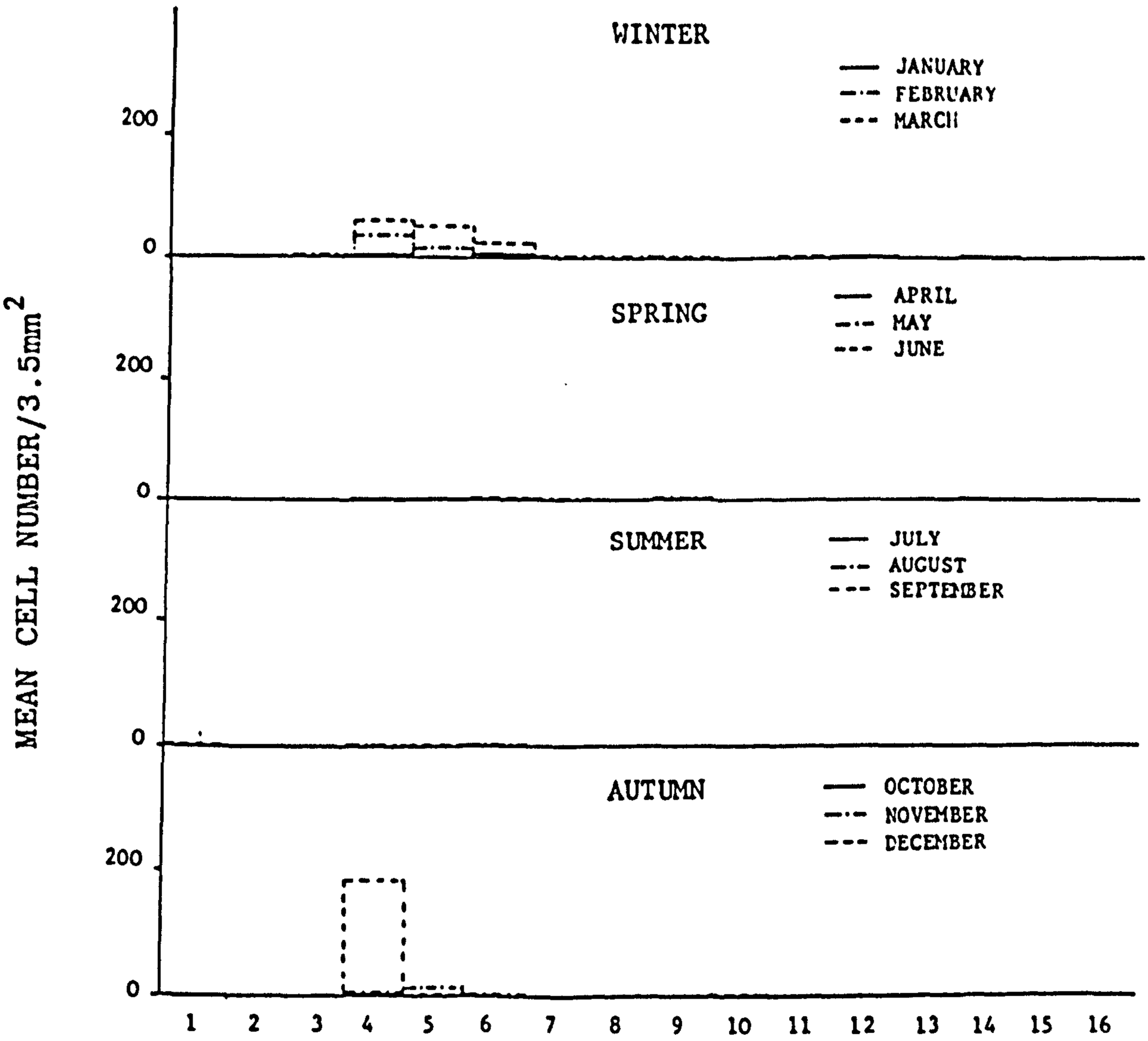
DISTRIBUTION OF AMPHORA LINEOLATA 1982



GRAPH 47

Spatial changes of A. lineolata in 1982.

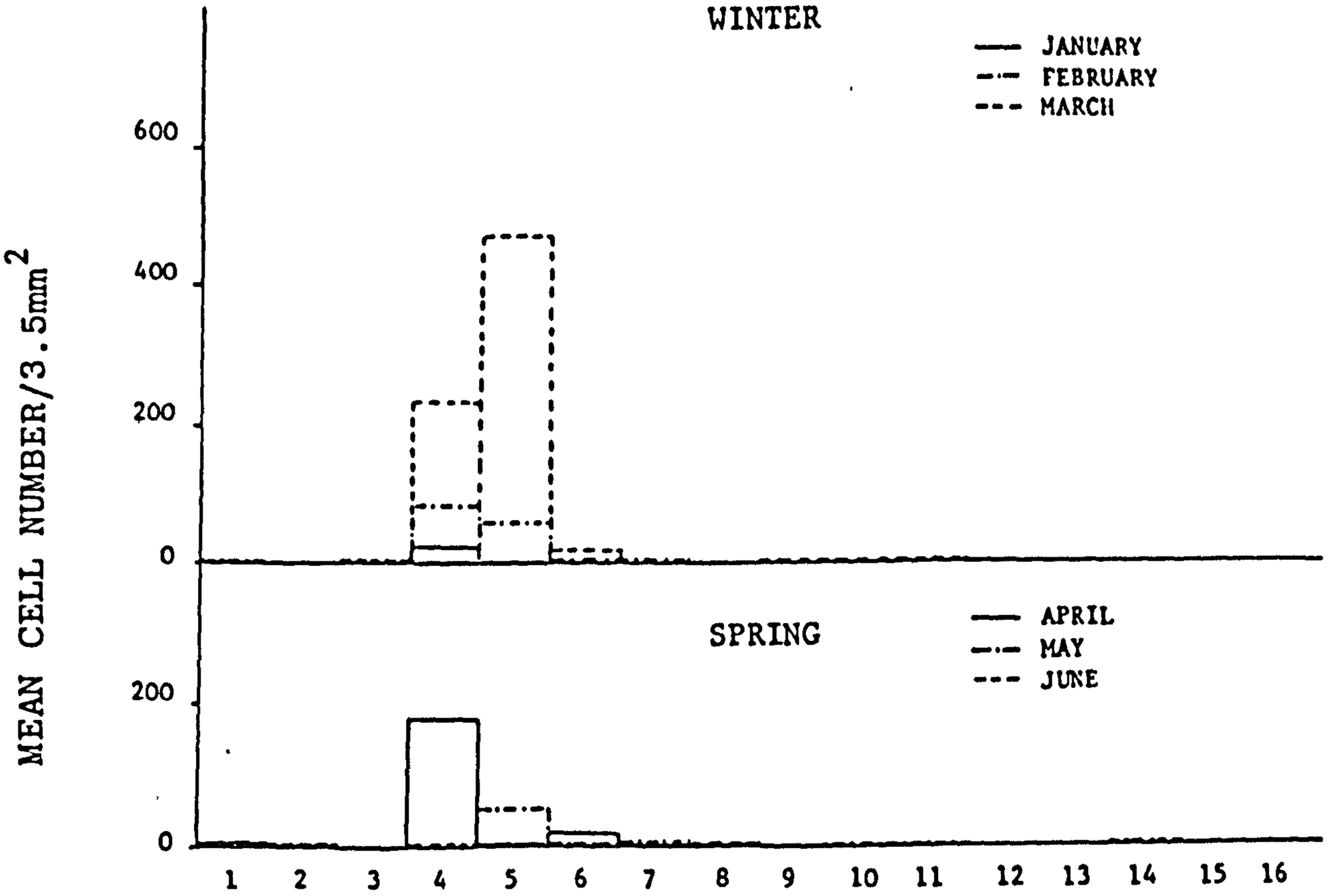
DISTRIBUTION OF AMPHORA LINEOLATA 1983



GRAPH 48

Spatial changes of A. lineolata in 1983.

DISTRIBUTION OF AMPHORA LINEOLATA 1984

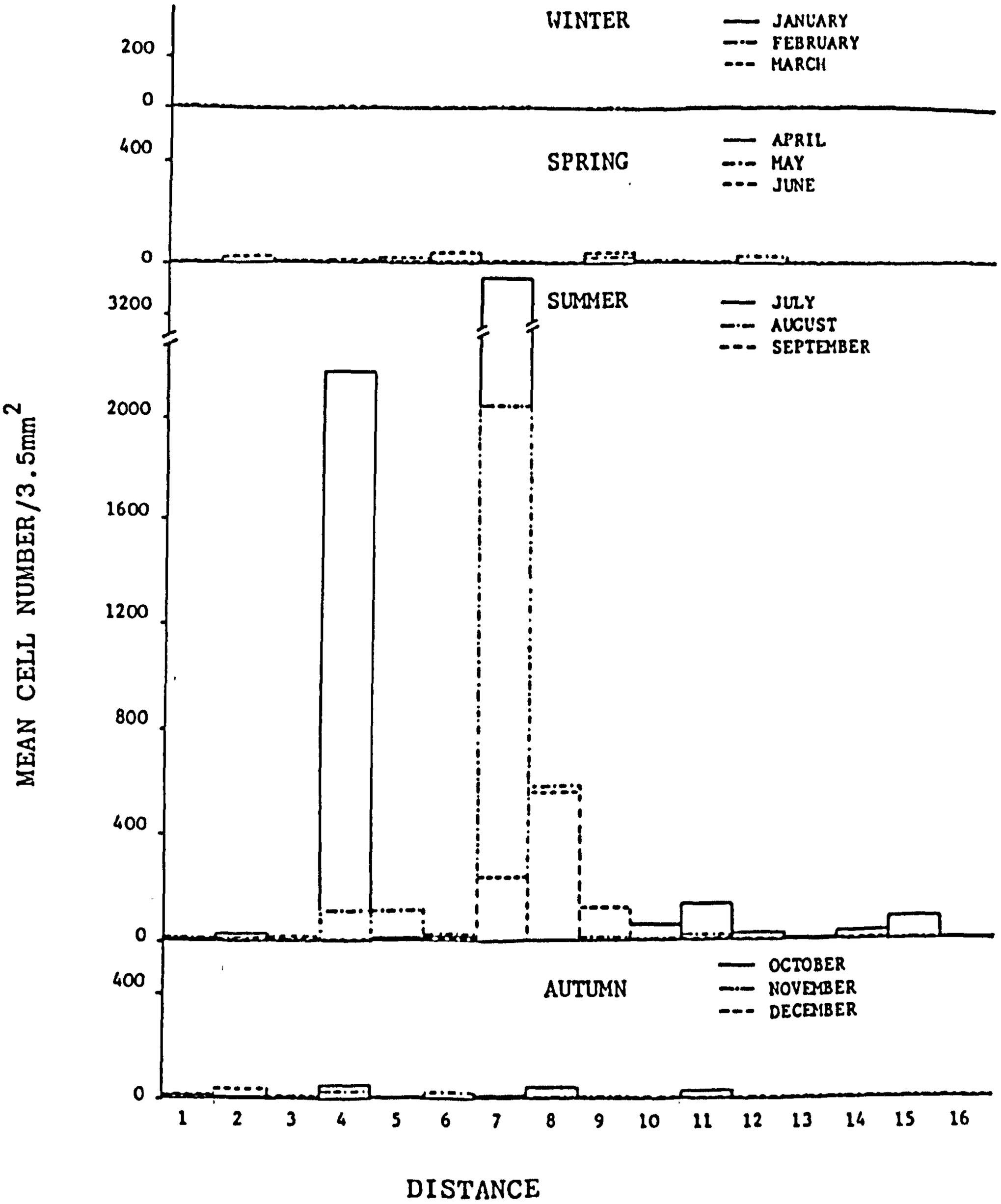


GRAPH 49

Spatial changes of A. lineolata 1984.

DISTRIBUTION OF NITZSCHIA MICROCEPHALA AGG.

1982

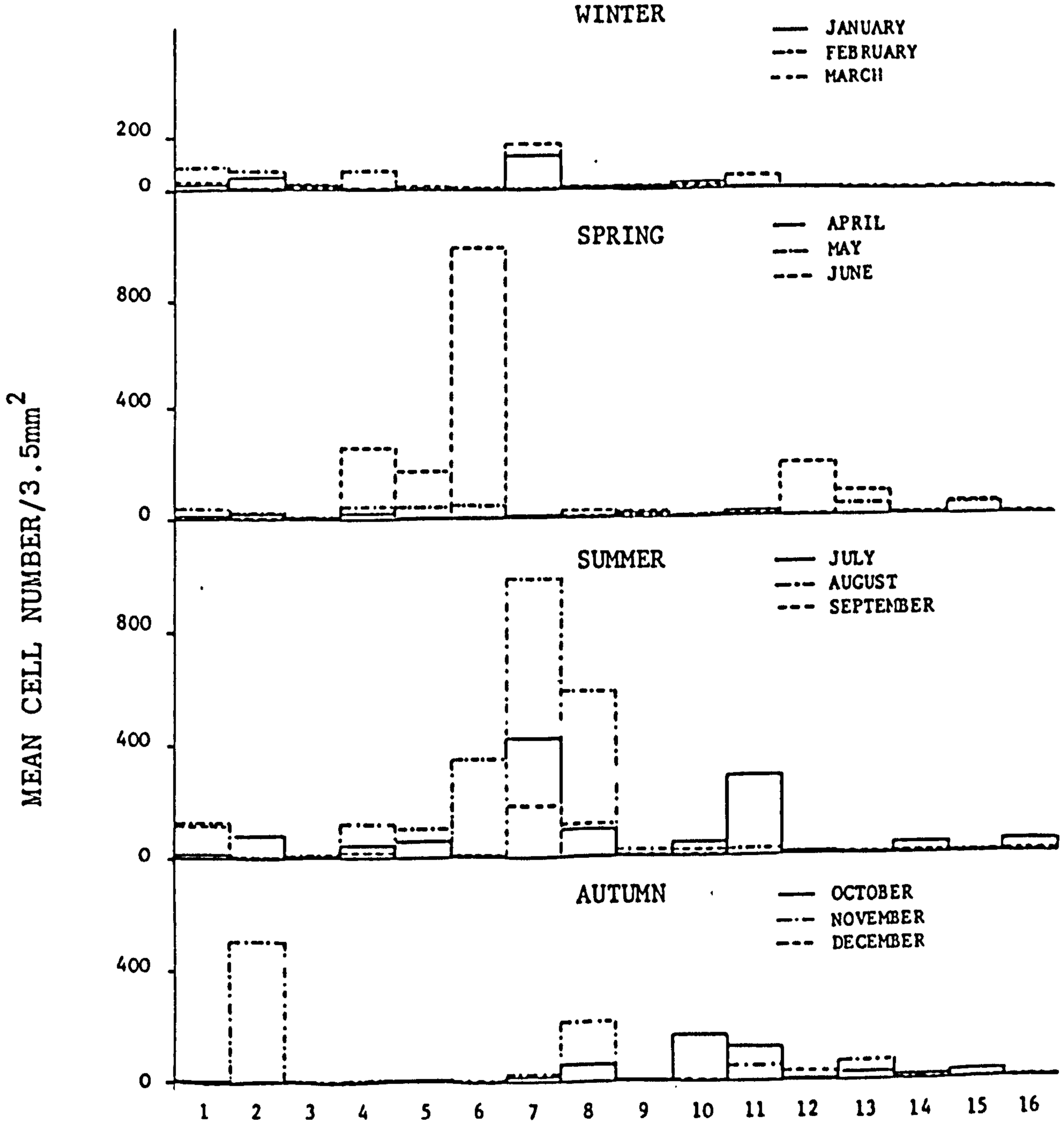


GRAPH 50

Spatial changes of N. microcephala agg. in 1982.

DISTRIBUTION OF NITZSCHIA MICROCEPHALA AGG.

1983

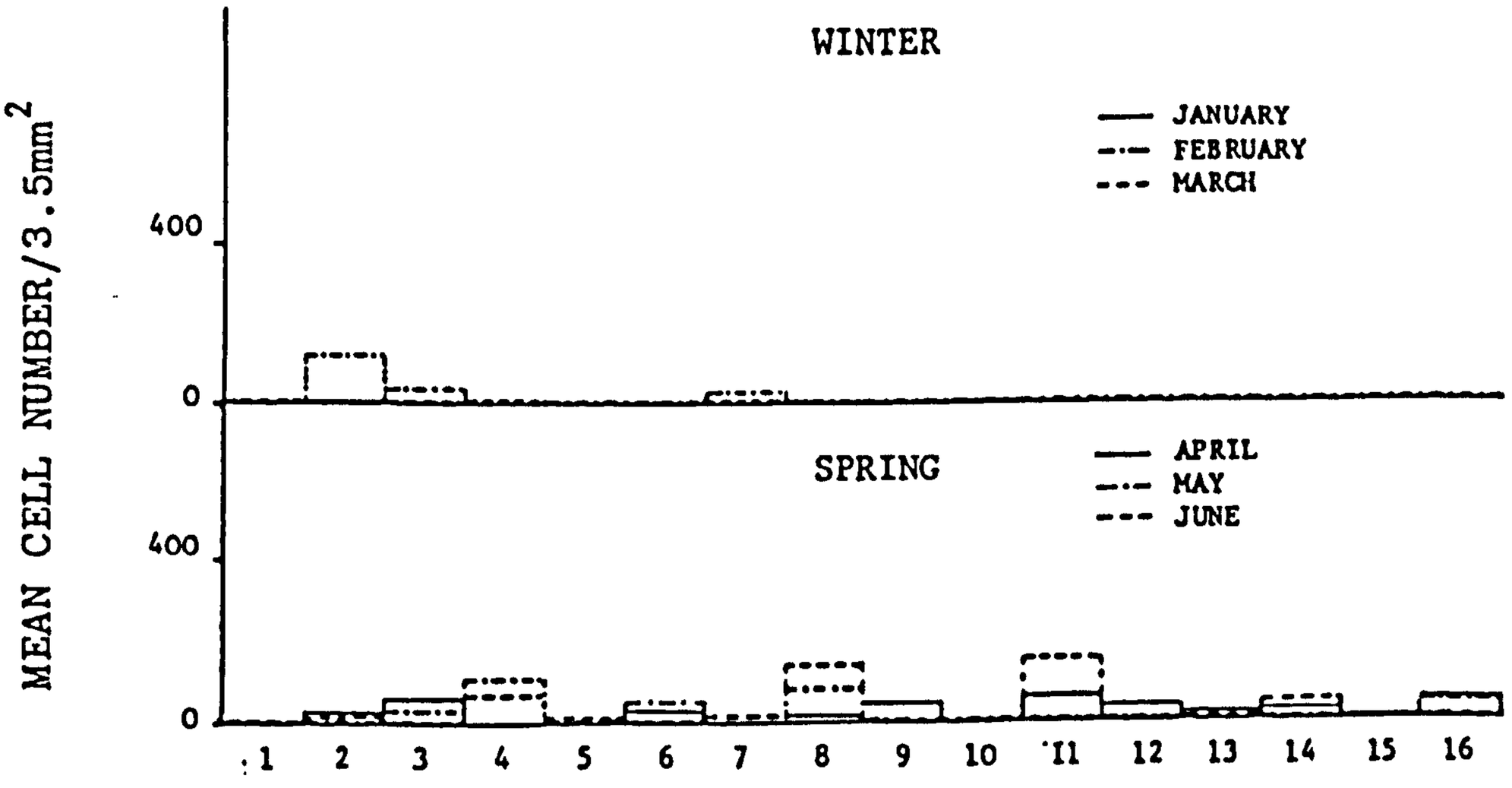


GRAPH 51

Spacial changes of N. microcephala agg. in 1983

DISTRIBUTION OF NITZSCHIA MICROCEPHALA AGG.

1984



GRAPH 52

Spatial changes of N. microcephala agg. in 1984.

3.4.6 Navicula cincta & Navicula cari (graphs 53-55)

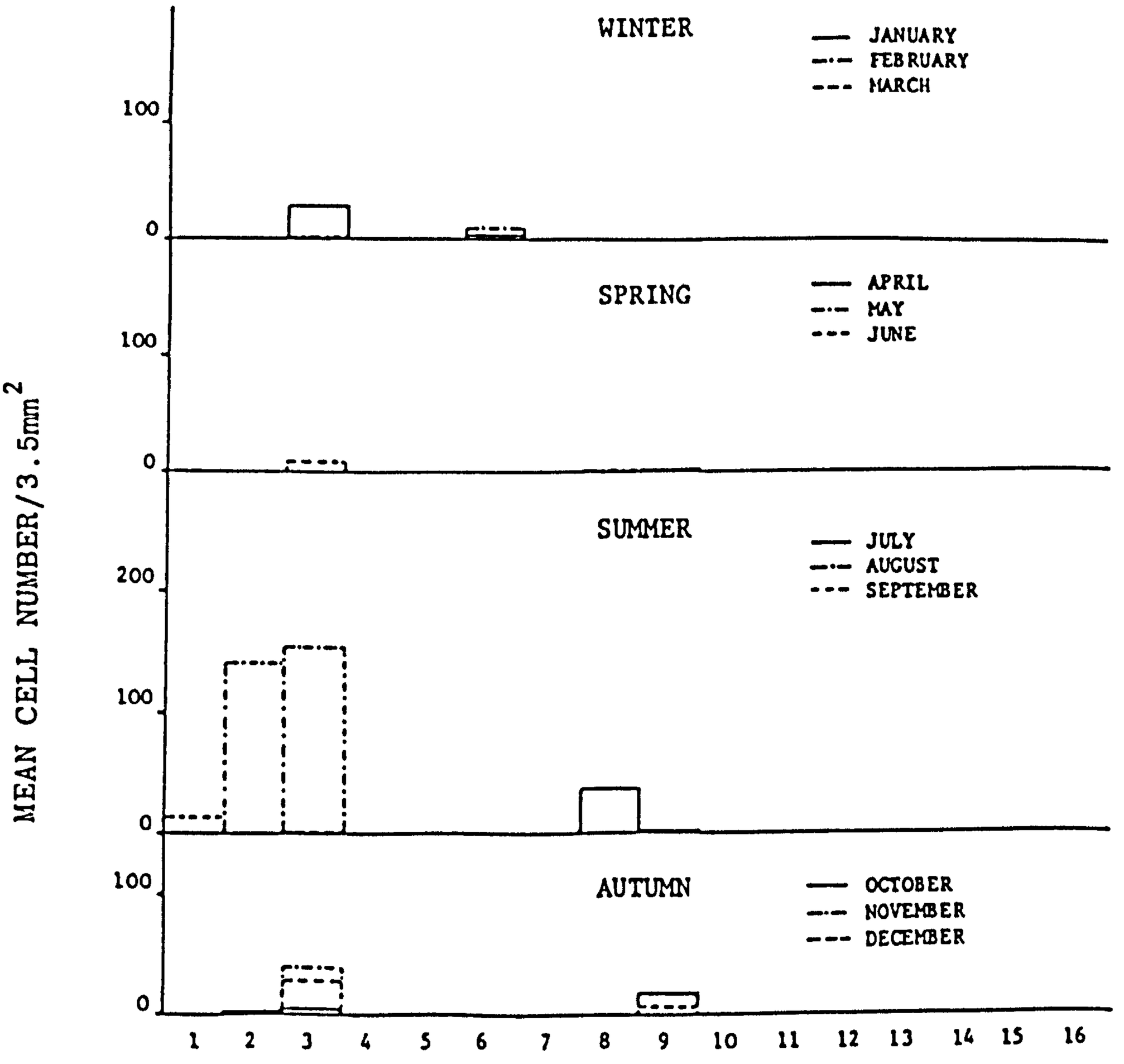
The combined counts of N. cincta and N. cari displayed a spatial pattern which differed from that of other taxa. These species were found at most sites on the saltmarsh. However maxima were recorded from samples taken at mound or slope sites. In 1982 (graph 53) a disjunct distribution was observed, the highest mean counts being recorded from sites 2 and 3, with lower counts at sites 8 and 9 in the summer. Very low counts were also recorded from site 6 in winter. These species were never observed on the sandflat or mudflat. By 1983 (graph 54) their distribution covered a more extensive area, and again maxima were recorded from mound or slope sites. Cell counts were higher, with maxima observed during the summer months July-September. Little growth was observed in 1984 (graph 55) and most counts were recorded from mound sites 3, 6 and 9.

Hudstedt (1939) classifies N. cari as a freshwater form and N.cincta as showing more of a preference for brackish waters. These conclusions are contrary to many field observations. N. cincta has been observed in hypersaline conditions in saline lakes in Israel (Erlich 1978) in hypersaline lakes in Western Australia (Johns 1984) and in the United States (Sullivan personal communication). N.cincta was observed in high numbers in hypersaline conditions in this study. Therefore the ecology of N. cincta must be re-assessed.

3.4.7 Nitzschia vacillata (graphs 56-58)

N. vacillata was also found at all sites. Maximum numbers were recorded from sandflat sites. In 1982 (graph 56) the higher mean counts were recorded from spring and summer samples with maxima at sites 11 and 12 in July. Lowest numbers were recorded during the winter. By 1983

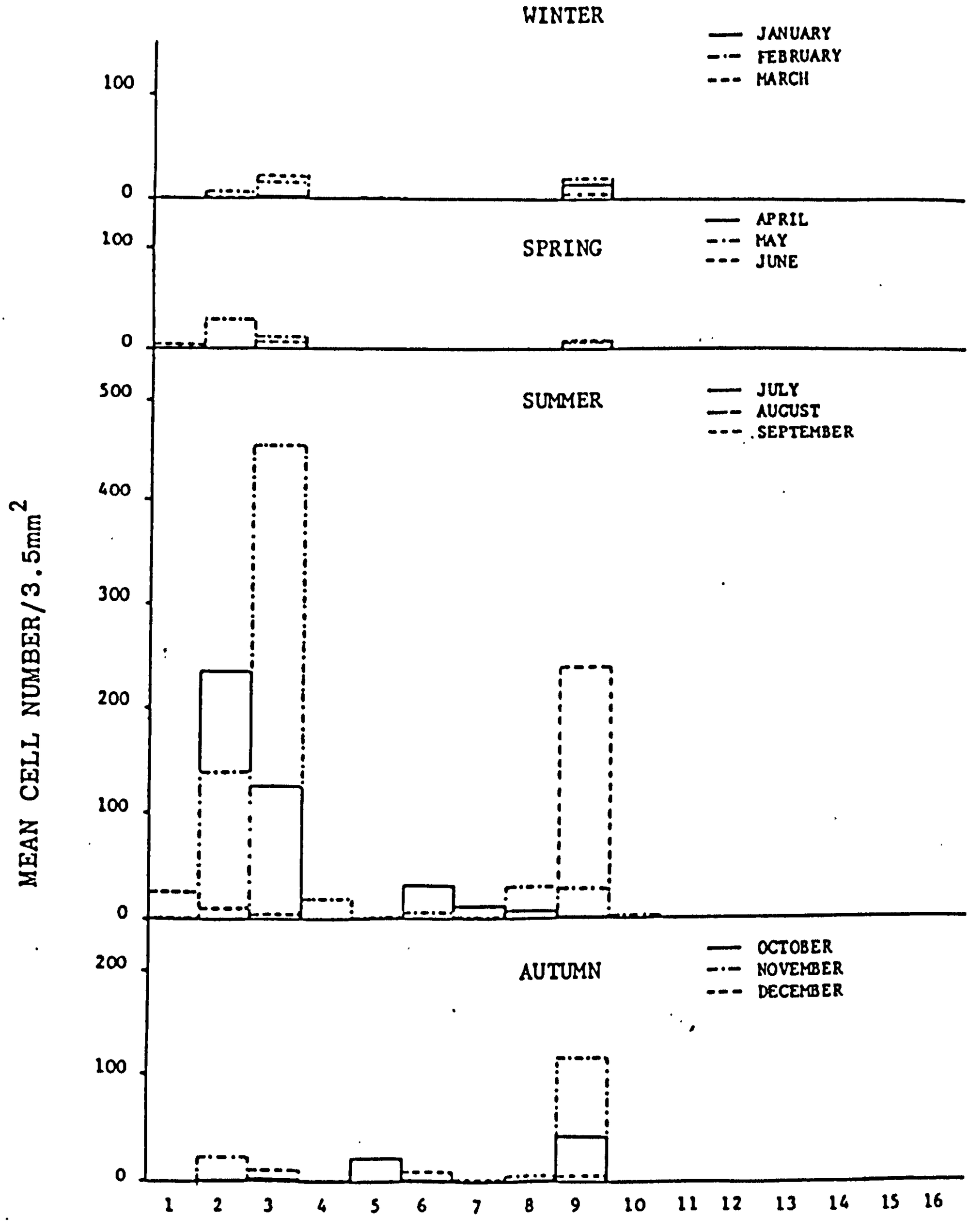
DISTRIBUTION OF NAVICULA CARI & NAVICULA CINCTA 1982



GRAPH 53

Spatial changes of N. cari & N. cincta in 1982.

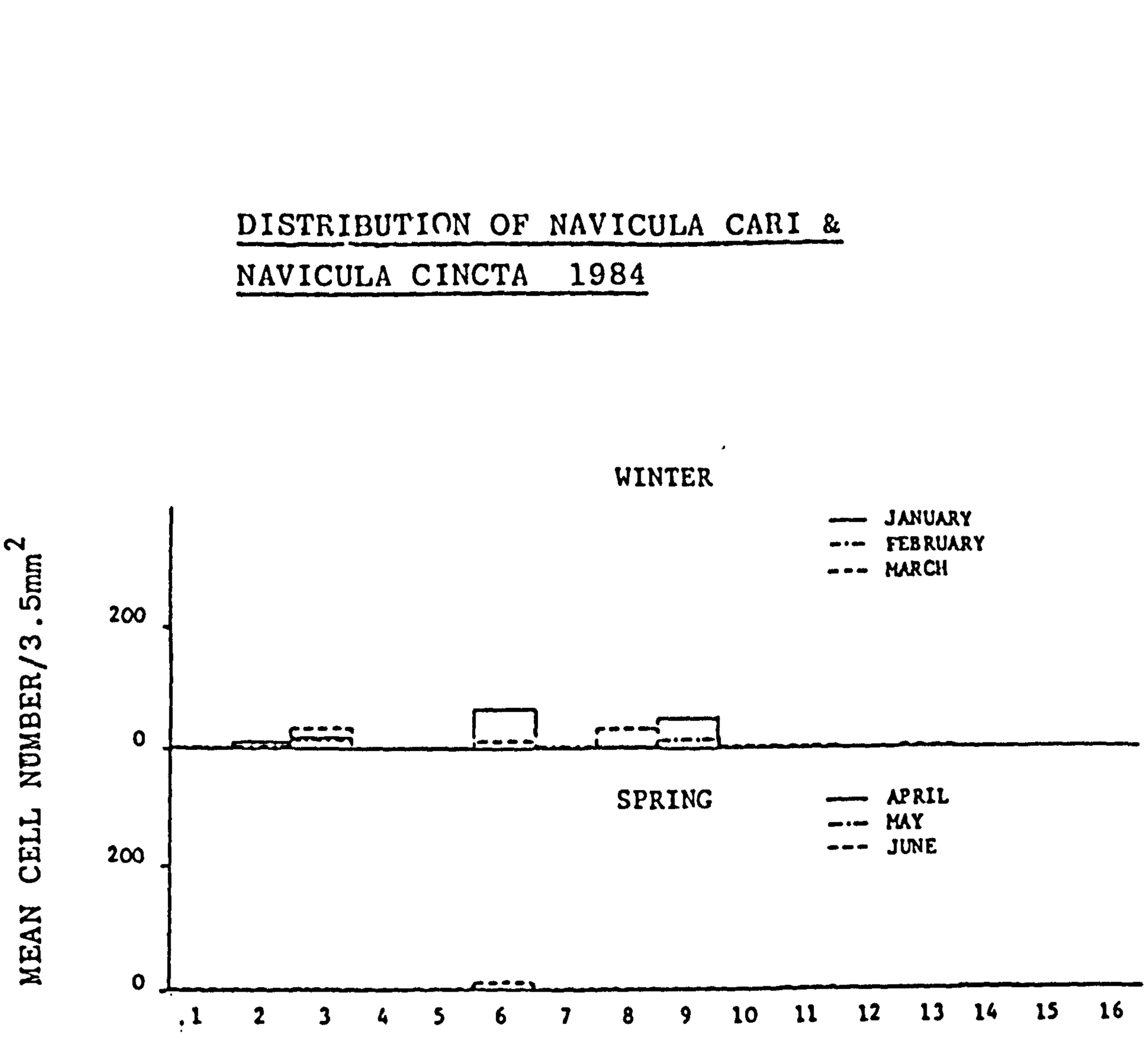
DISTRIBUTION OF NAVICULA CARI & NAVICULA CINCTA 1983



GRAPH 54

Spatial changes of N. cari & N. cincta in 1983.

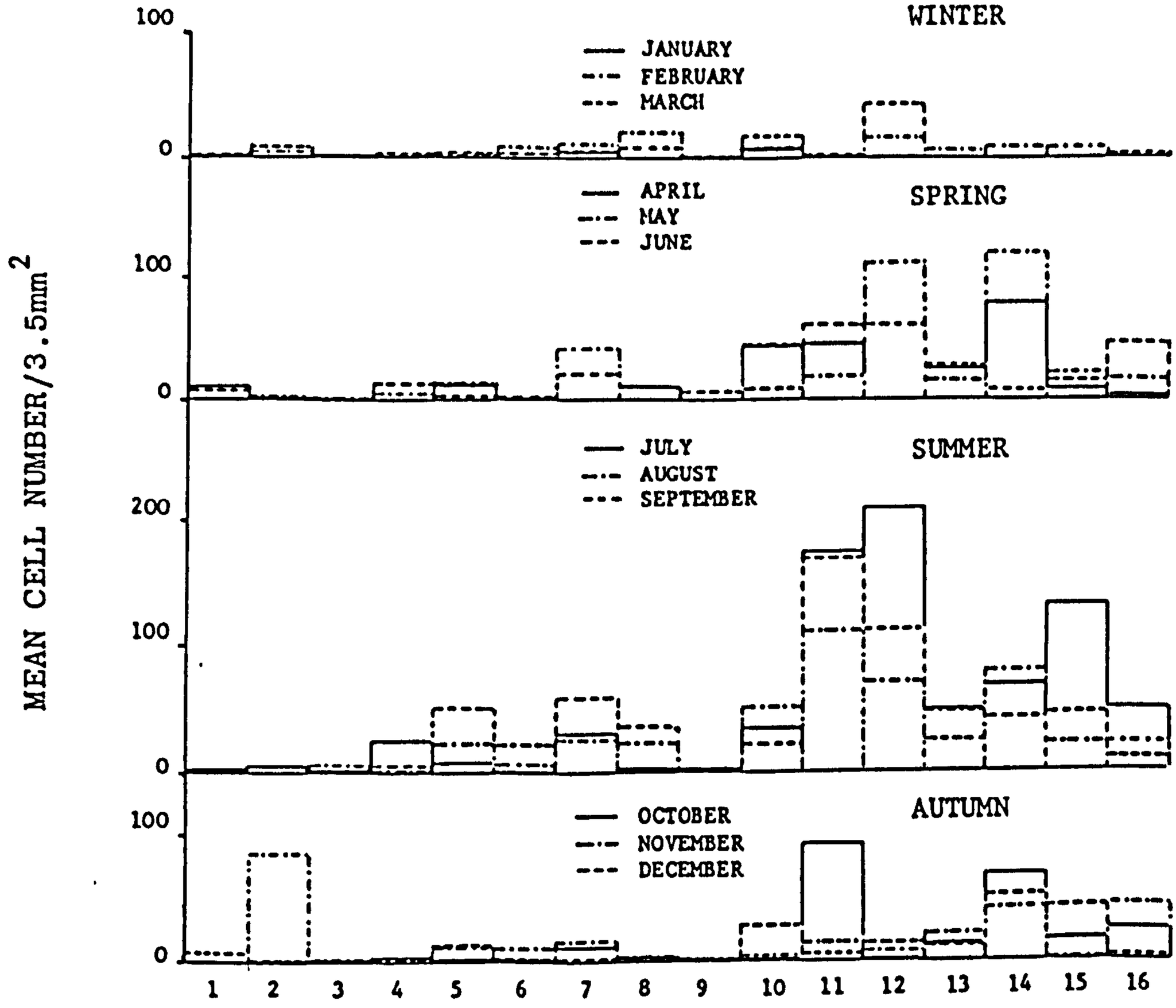
DISTRIBUTION OF NAVICULA CARI & NAVICULA CINCTA 1984



GRAPH 55

Spatial changes of N. cari & N. cincta in 1984.

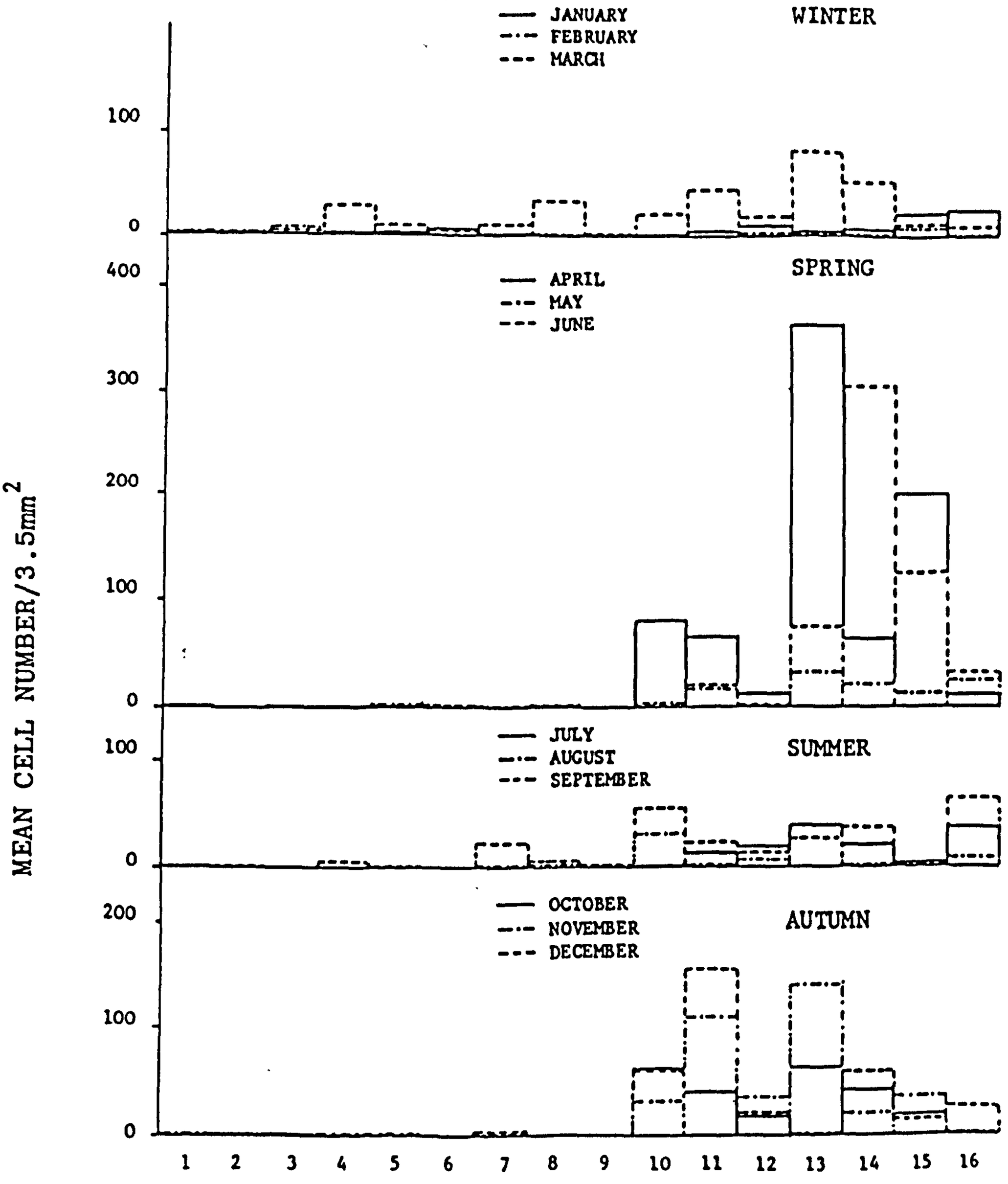
DISTRIBUTION OF NTZSCHIA VACILLATA 1982



GRAPH 56

Spatial changes of N. vacillata in 1982

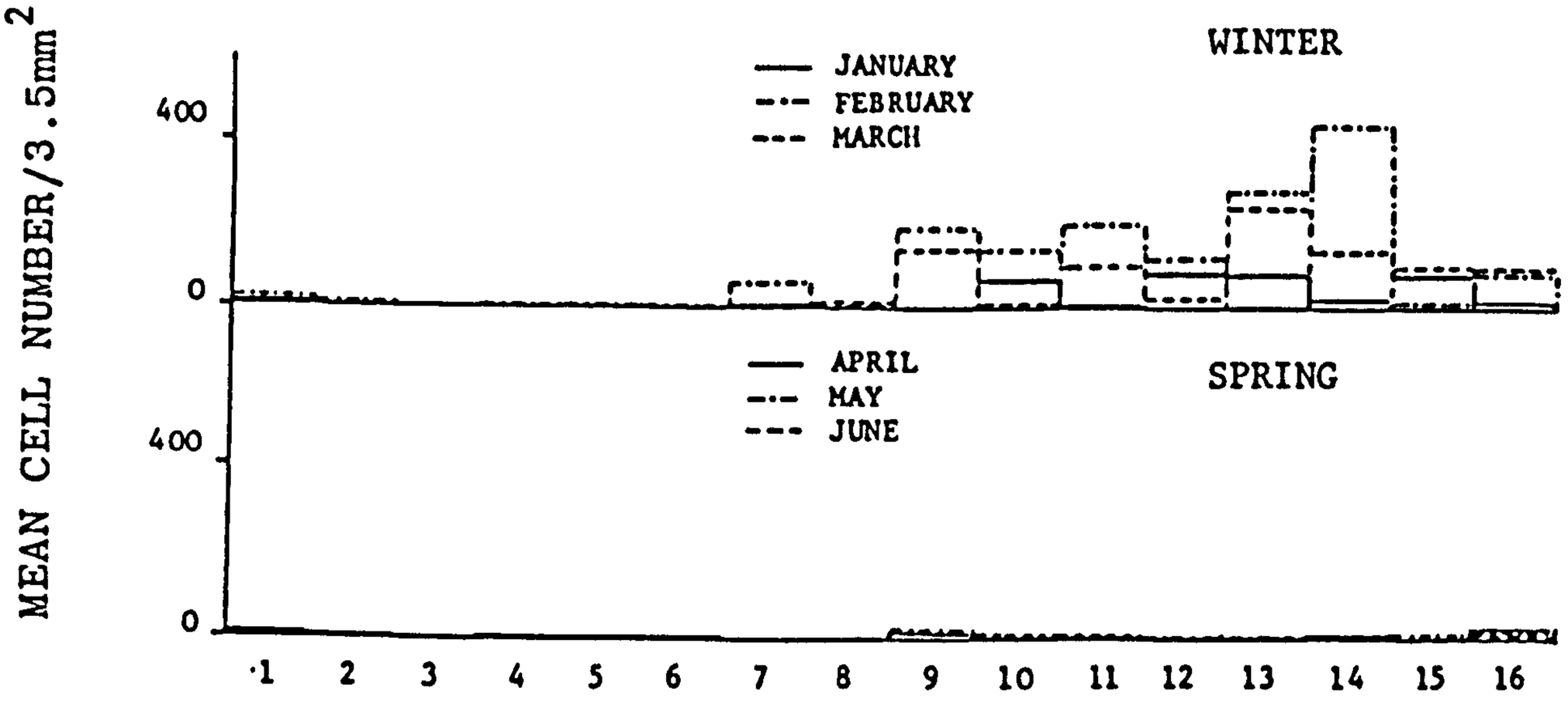
DISTRIBUTION OF NITZSCHIA VACILLATA 1983



GRAPH 57

Spatial changes of N. vacillata in 1983.

DISTRIBUTION OF NITZSCHIA VACILLATA 1984



GRAPH 58

Spatial changes of N. vacillata in 1984.

(graph 57) abundance doubled with highest counts occuring from April-June at sites 13, 14,and 15. Summer counts were much lower than in 1982, but higher in autumn. Few cells were observed at sites on the saltmarsh, and by 1984 (graph 58) no counts were recorded from saltmarsh samples. However a small population grew at sites 9-16 from January-March.

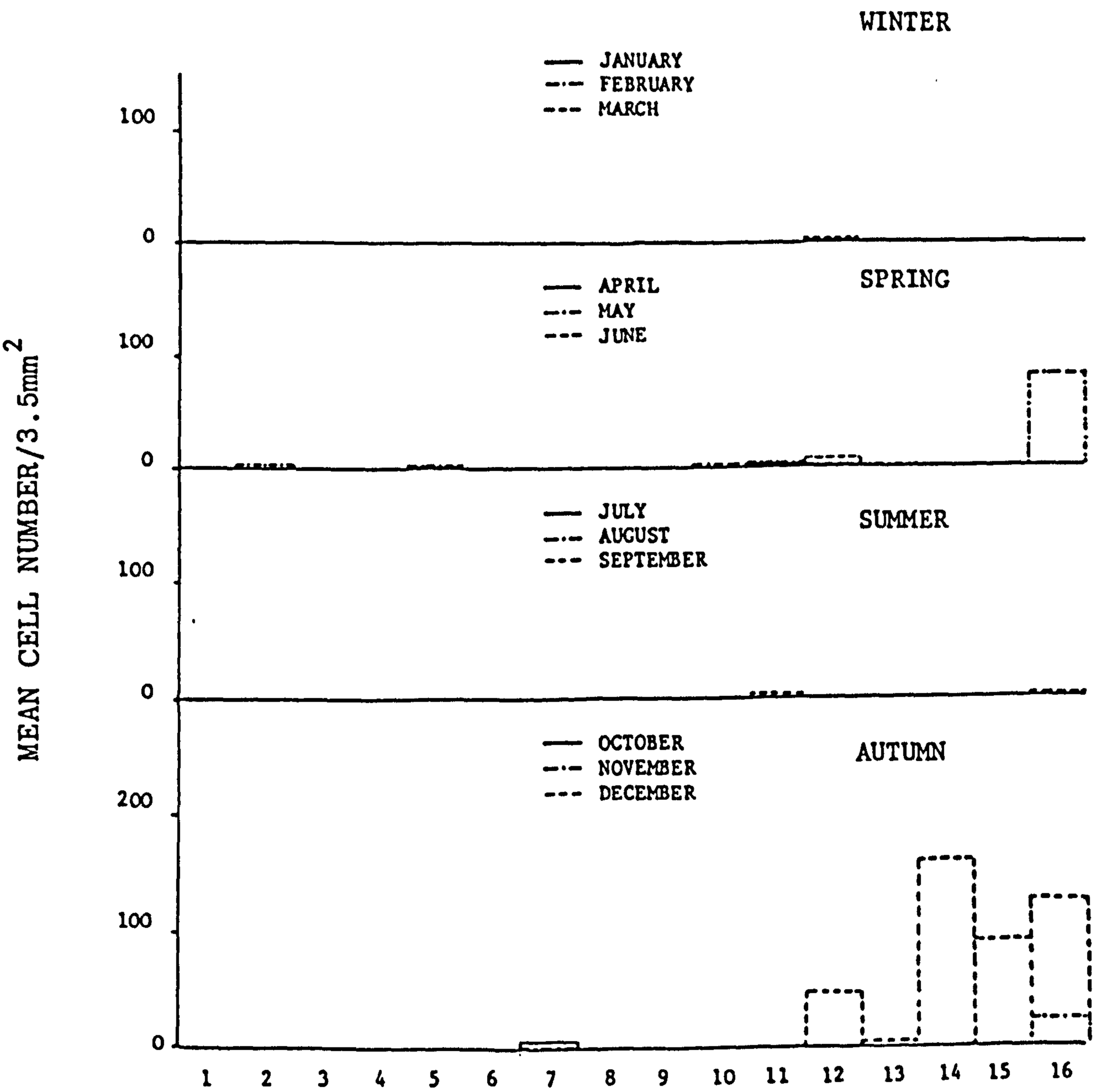
3.4.8 Navicula rostellata (graphs 59-61)

N. rostellata grew only on the sediments of the sandflat and mudflat. Only a small growth was observed in 1982 (graph 59) with maxima in autumn from the lower sandflat and mudflat. The lowest counts were on the sandflat. However population density changed dramatically by 1983 (graph 60). An enormous growth, the highest count for any individual species, occured in October from a sample taken from site 16. Population density gradually increased over the year on the mudflat while growth at other sites was minimal. In 1984 (graph 61) smaller counts were recorded from site 16, and maxima were observed from samples of the lower sandflat, during the winter. N. rostellata is a species typical of highly disturbed sediments.

3.4.9 Anabaena cylindrica (graphs 62-64)

A. cylindrica was the most abundant of the different species of Anabaena present. Like the diatoms a distinctive spatial position along the transect was observed. In 1982 (graph 62) A. cylindrica occupied an area of the upper and middle marsh. A preference for the more well drained sediments of the mound and slope sites was clear. In spring, maxima were observed from samples taken at sites 3, 5 and 6. Otherwise only low cell numbers were recorded. During periods of abundant growth, thick algal mats were observed which could be peeled off the

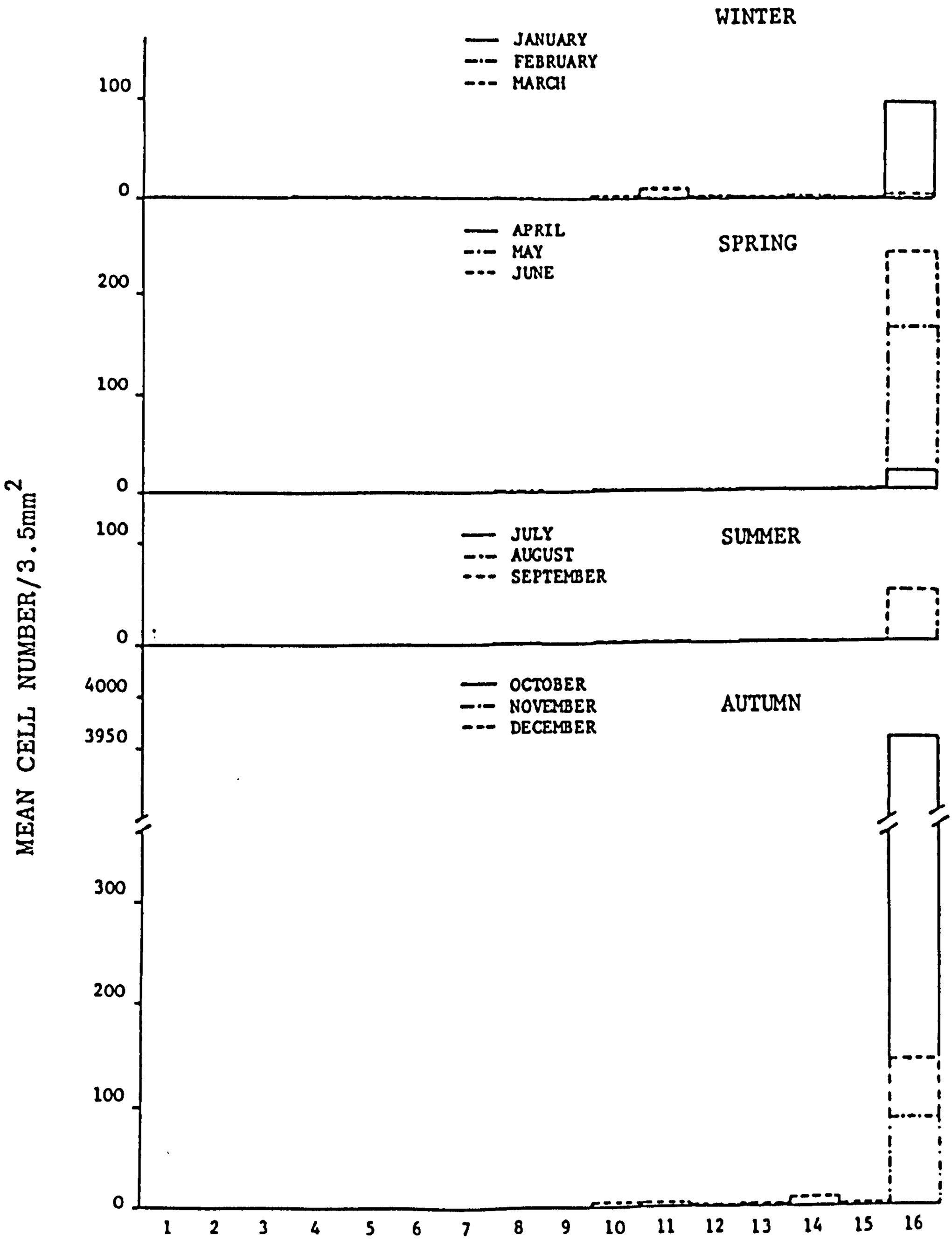
DISTRIBUTION OF NAVICULA ROSTELLATA 1982



GRAPH 59

Spatial changes of N. rostellata in 1982.

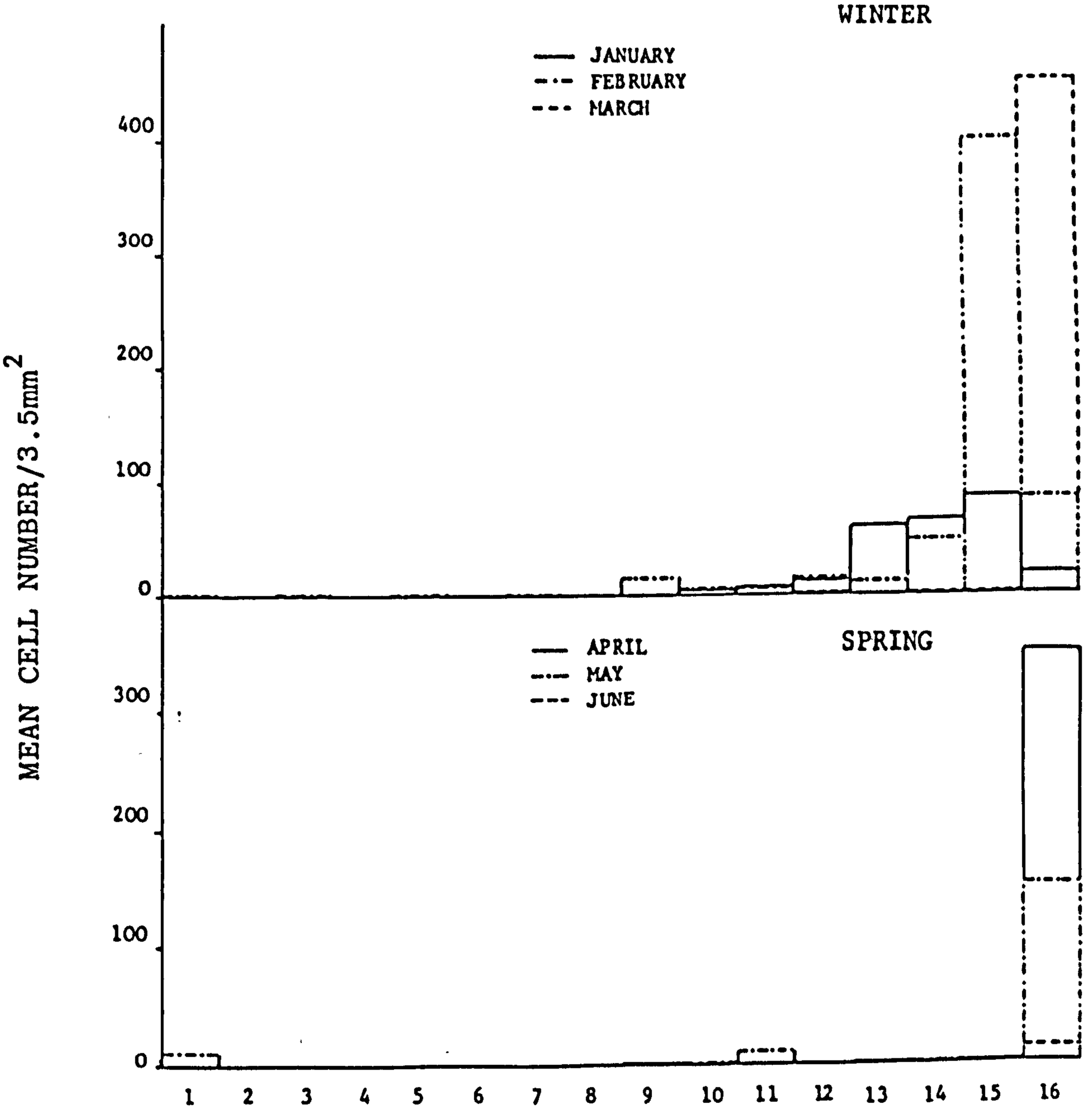
DISTRIBUTION OF NAVICULA ROSTELLATA 1983



GRAPH 60

Spatial changes of N. rostellata in 1983.

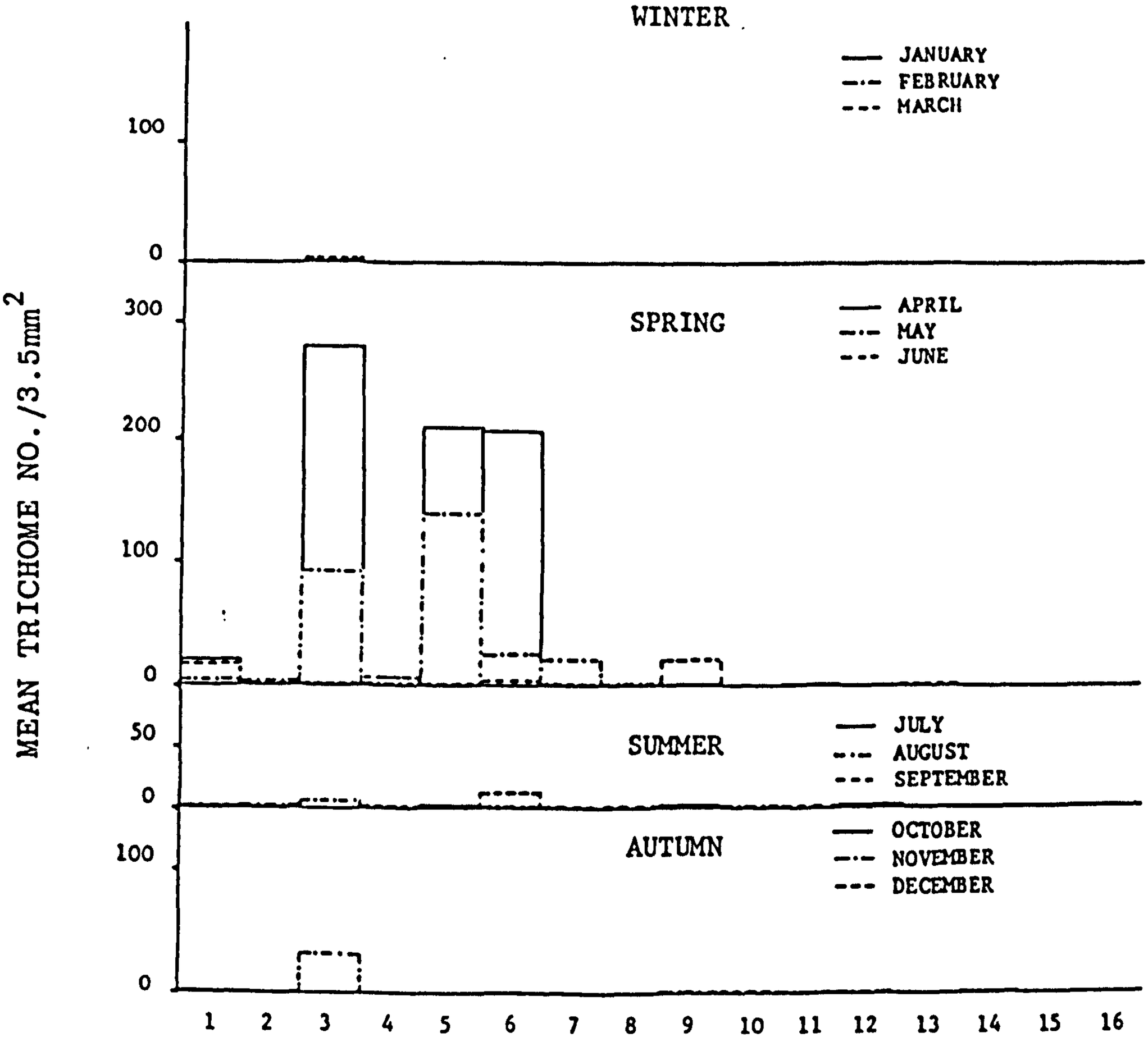
DISTRIBUTION OF NAVICULA ROSTELLATA 1984



GRAPH 61

Spatial changes of N. rostellata in 1984.

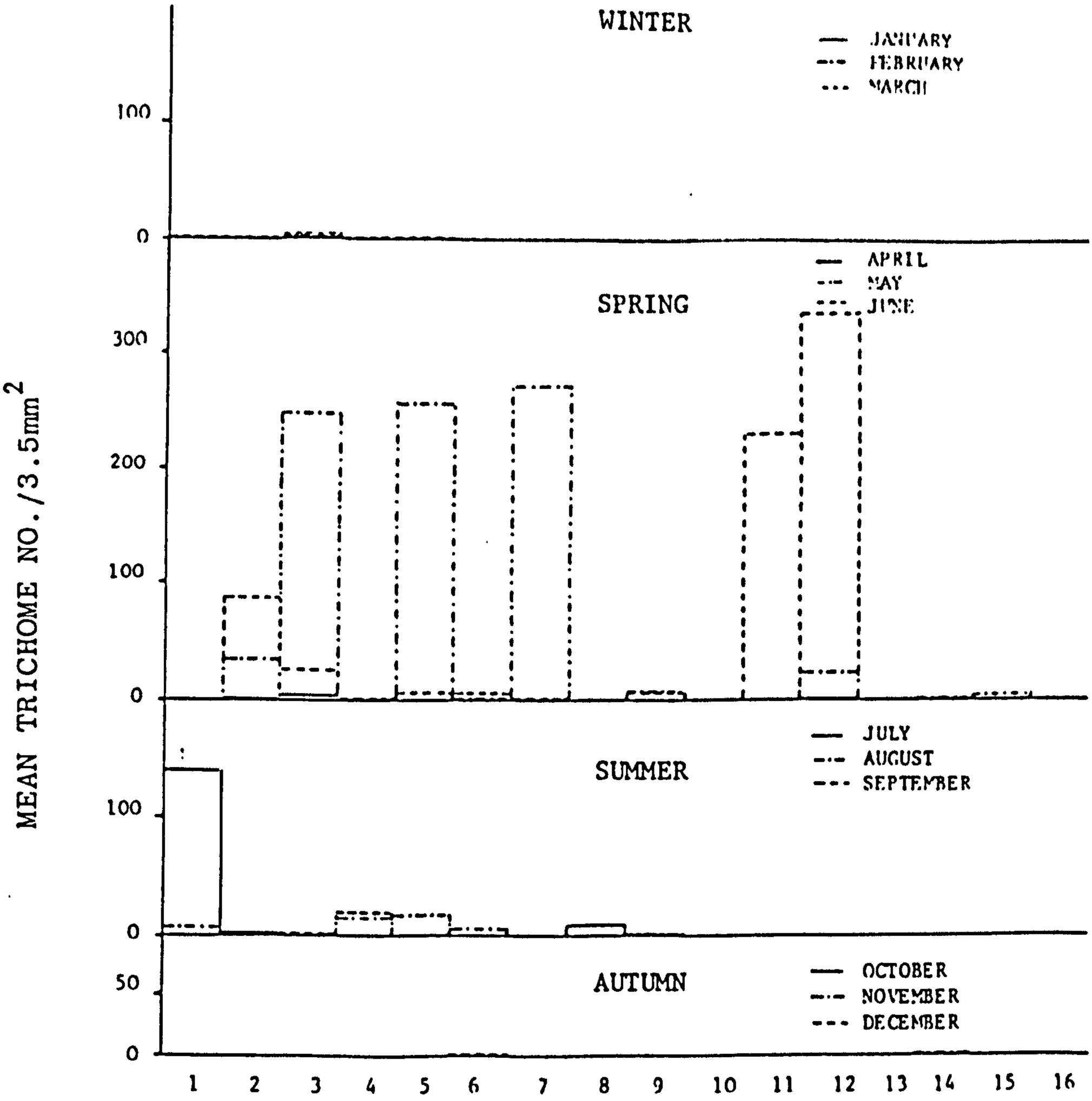
DISTRIBUTION OF ANABAENA CYLINDRICA 1982



GRAPH 62

Spatial changes of A. cylindrica in 1982.

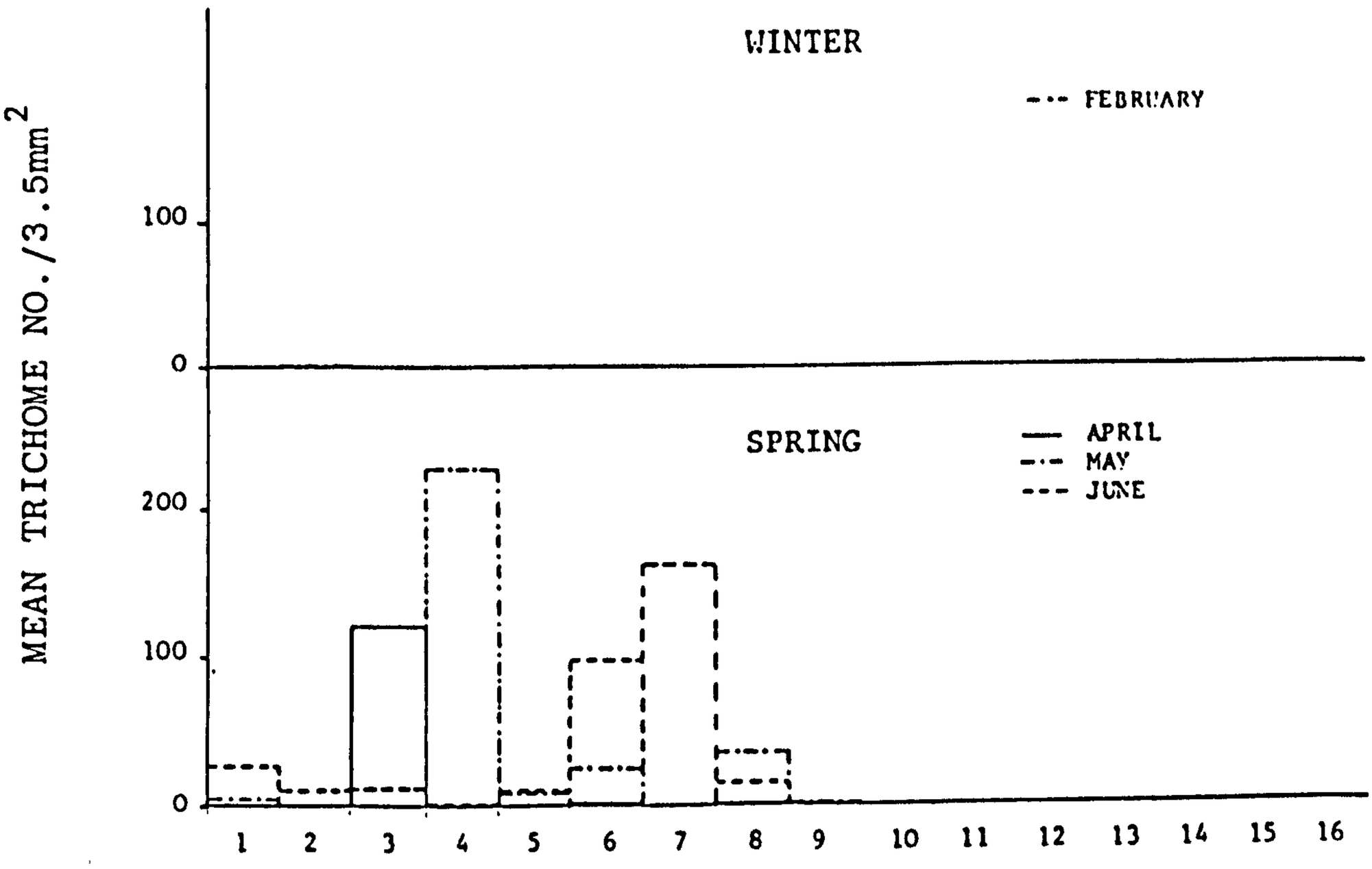
DISTRIBUTION OF ANABAENA CYLINDRICA 1983



GRAPH 63

Spatial changes of A. cylindrica in 1983.

DISTRIBUTION OF ANABAENA CYLINDRICA 1984



GRAPH 64

Spatial changes of A. cylindrica in 1984.

surface sediments. This only occured in 1982. By 1983 (graph 63) A. cylindrica had become more widespread along the transect. Large populations were recorded from slope and mound sites of the upper/ middle marsh and the upper sandflat in June. In July maxima were recorded from site 1. Otherwise all other counts were low. By 1984 (graph 64) peak numbers were observed in spring, and maxima occured on all slopes, as well as sites 4 and 7. Growth in the pool sites only occured during the drier months.

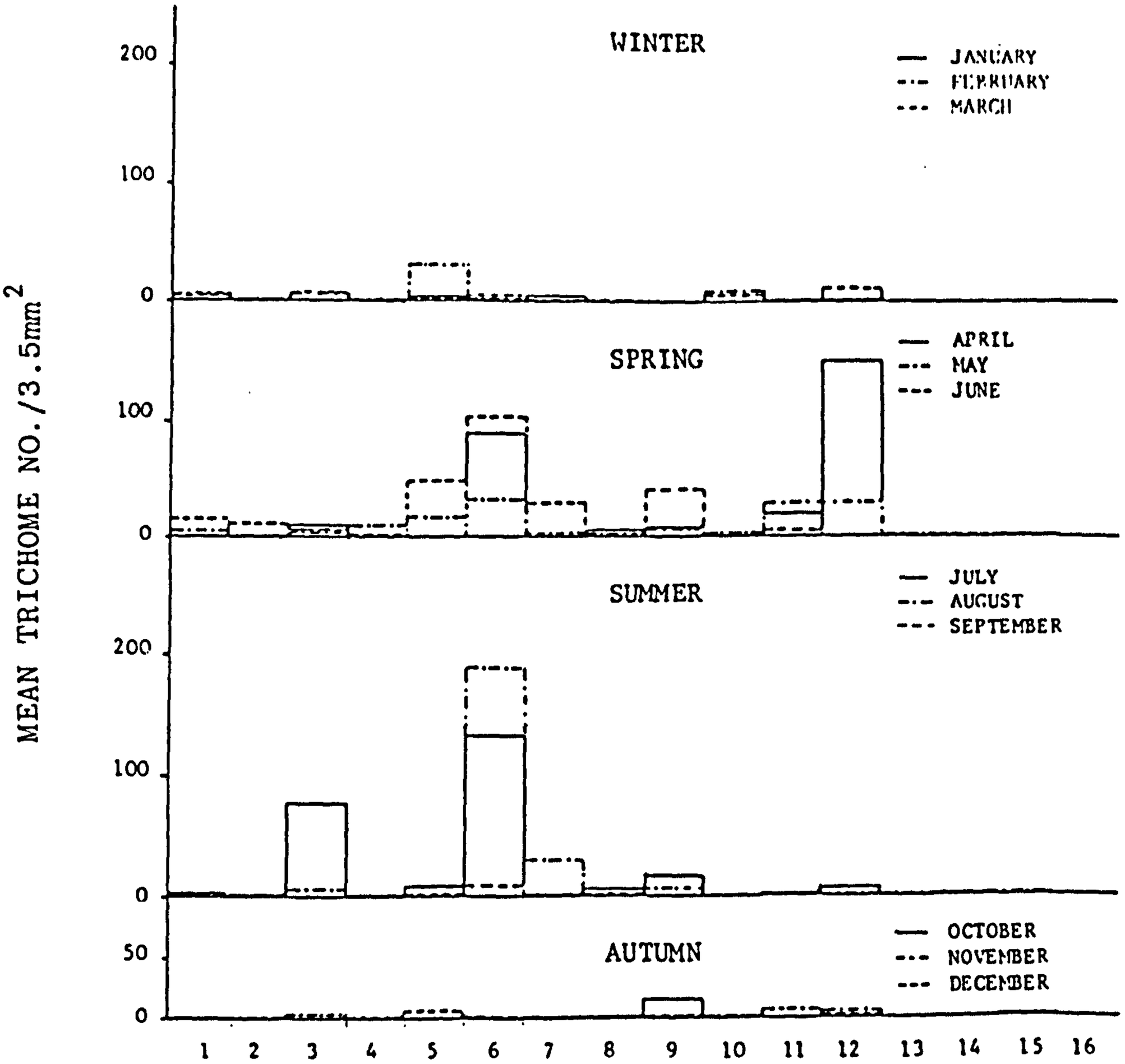
3.4.10 Oscillatoria spp (graphs 65-67)

Oscillatoria was represented by the largest numbers of species and varieties of all the blue-green algae. It was impossible to distinguish all the different forms in the time available, so all species and varieties were counted as one group. This grouping together of so many species and varieties would probably explain the broad distribution along the transect that was displayed. Like A. cylindrica larger populations grew at mound and slope sites on the saltmarsh and upper sandflat. In 1982 (graph 65) maxima occured during the spring and summer. Fewer trichomes were counted in winter or autumn. Maxima were recorded from sites 5, 6, 11,and 12. In 1983 (graph 66) abundant growth was observed in spring and summer from sites 2, 3, 4, 9,and 12. Maximum growth appeared to have shifted towards the upper marsh instead of the middle marsh. By 1984 (graph 67) larger populations grew once again on the upper/middle marsh (sites 3-6).

3.4.11 Summary Graphs (graphs 68-72)

So far the distributions of 10 different taxa have been described. Many more species have distinct positions along the transect. Each histogram on the summary graphs represents the mean of 60 different counts for each

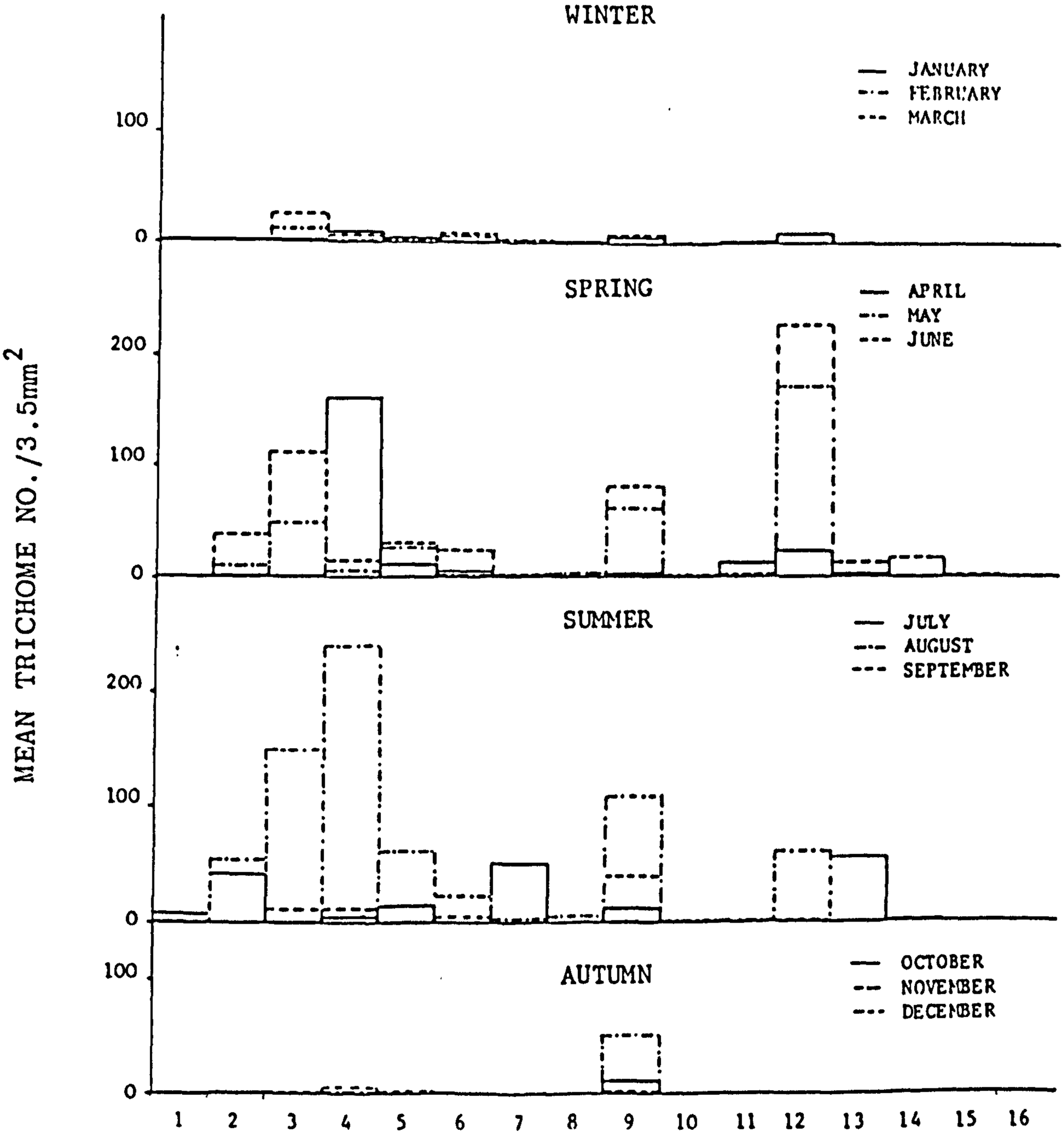
DISTRIBUTION OF OSCILLATORIA 1982



GRAPH 65

Spatial changes of Oscillatoria in 1982.

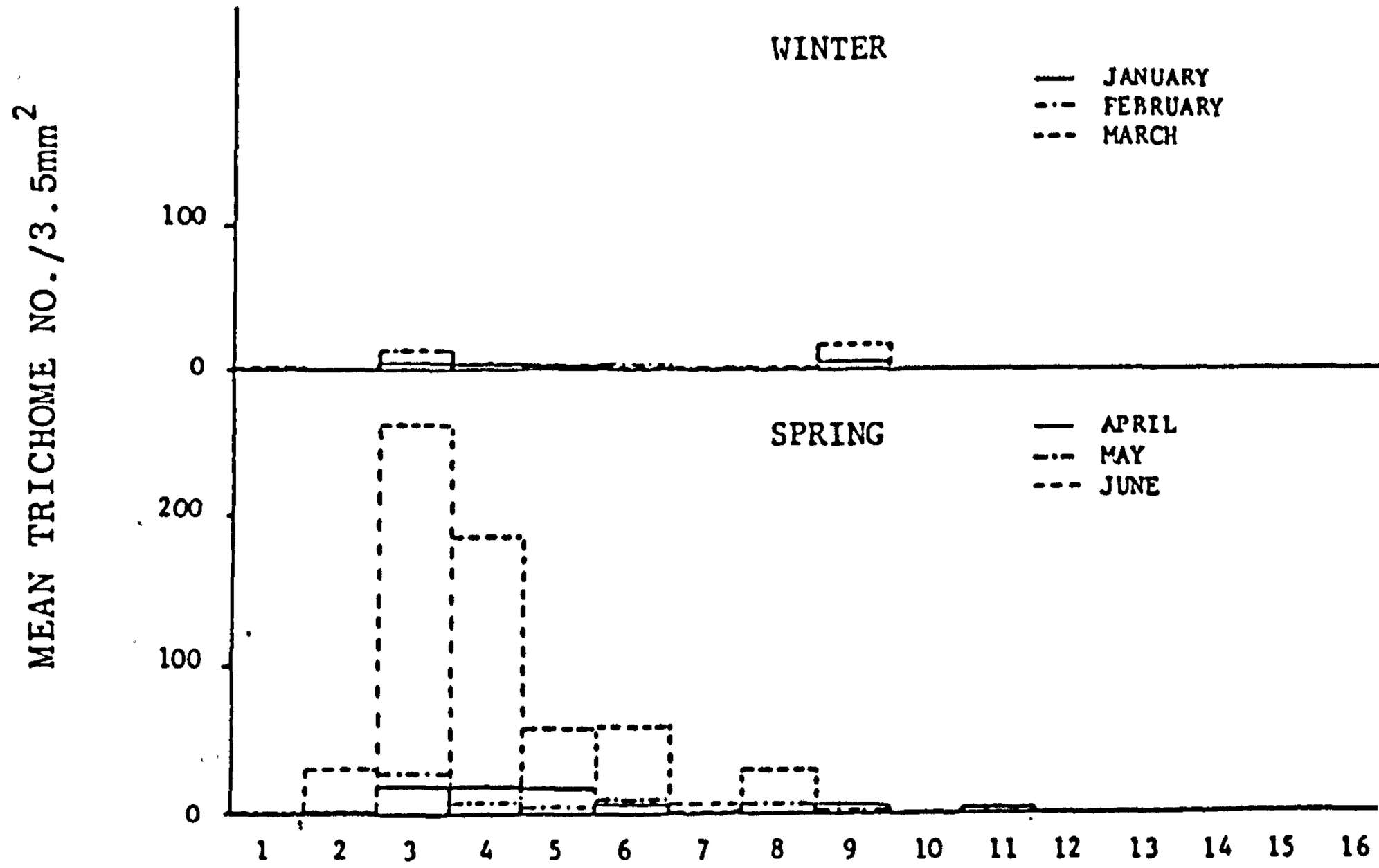
DISTRIBUTION OF OSCILLATORIA 1983



GRAPH 66

Spatial changes of Oscillatoria in 1983.

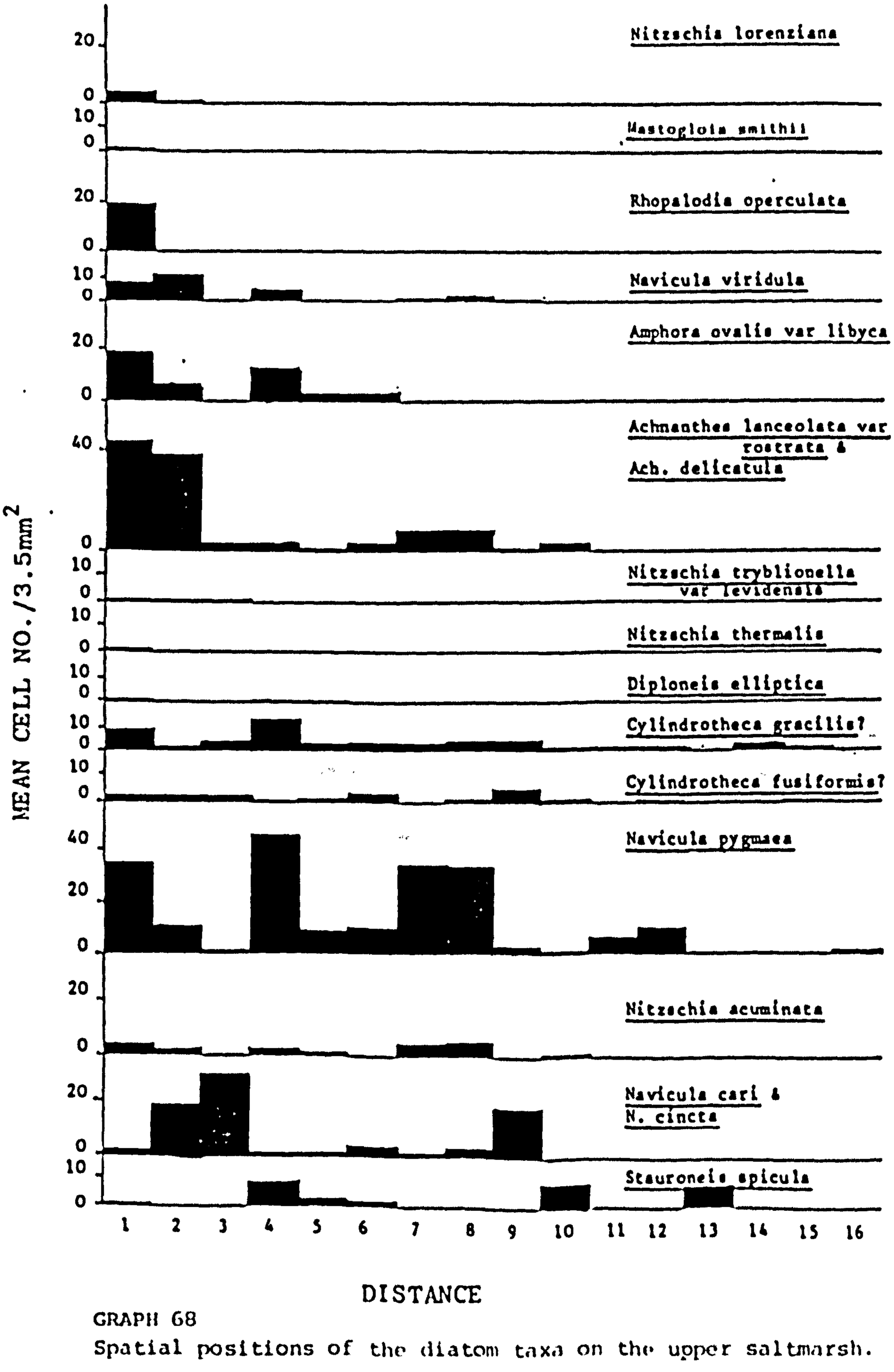
DISTRIBUTION OF OSCILLATORIA 1984



GRAPH 67

Spatial changes of Oscillatoria in 1984.

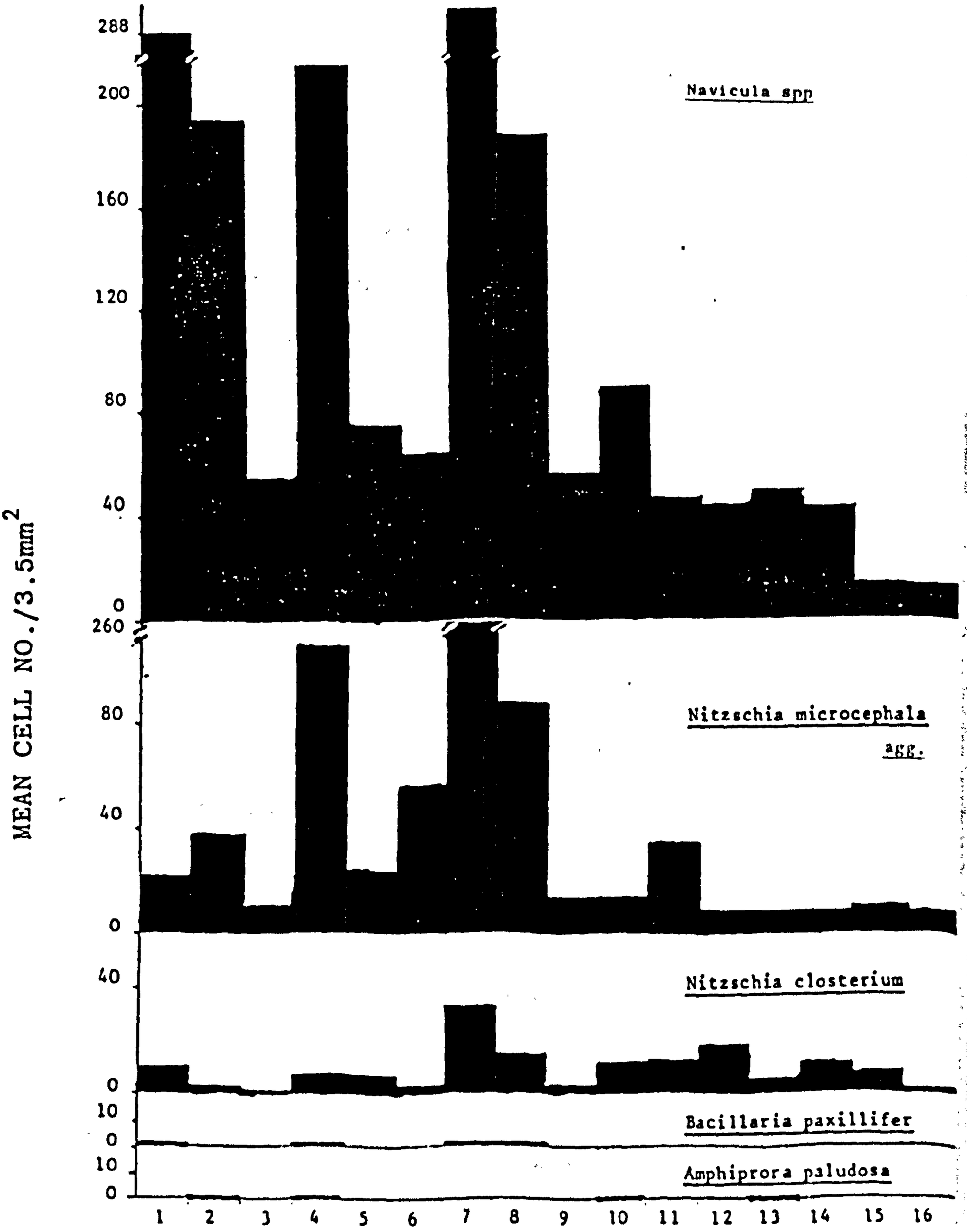
SUMMARY GRAPHS FOR THE SALTMARSH DIATOMS



GRAPH 68

Spatial positions of the diatom taxa on the upper saltmarsh.

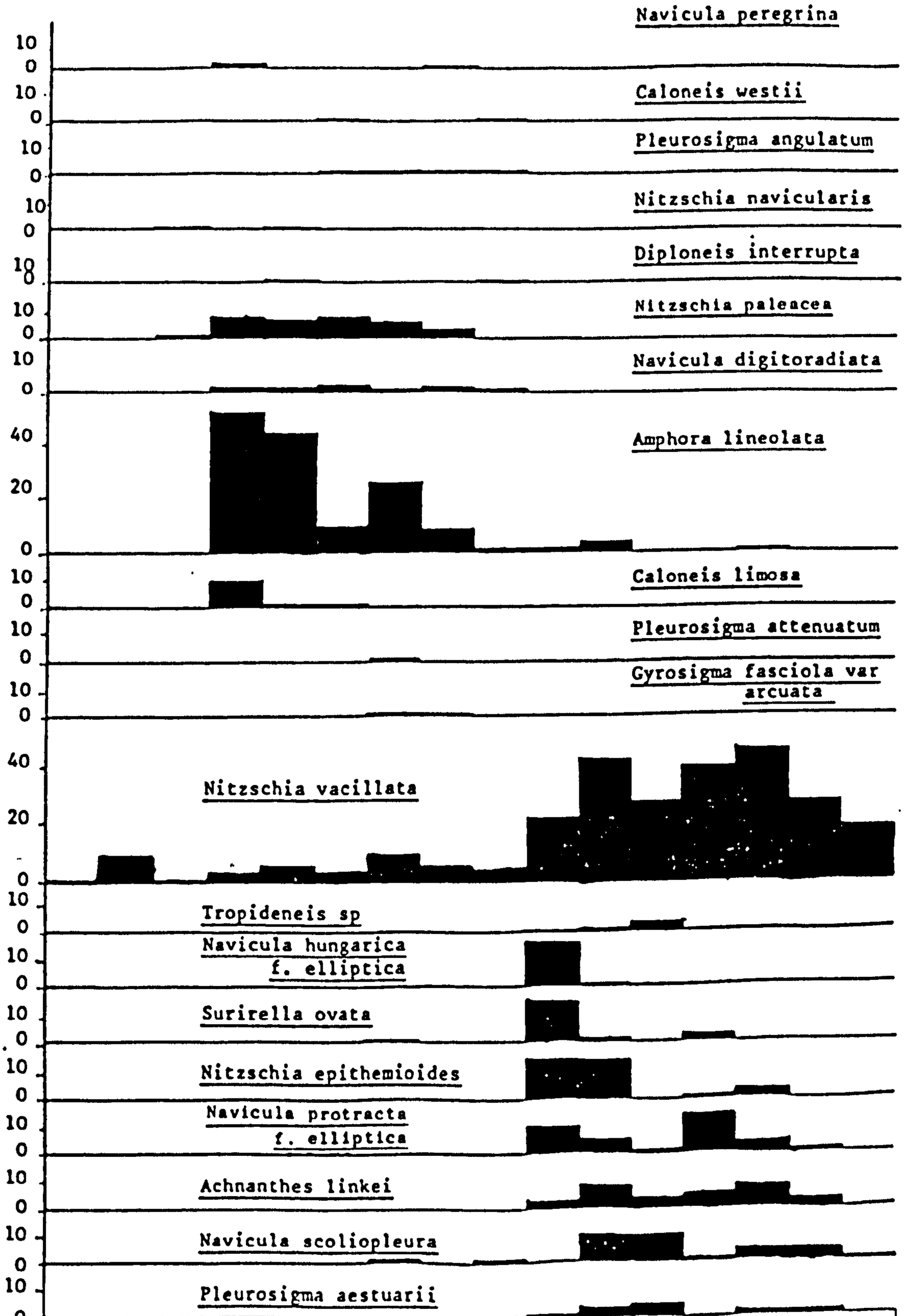
SUMMARY GRAPHS FOR THE SALTMARSH DOMINANT DIATOMS



GRAPH 69

Spatial positions of the diatom taxa which have been observed at all sites along the transect.

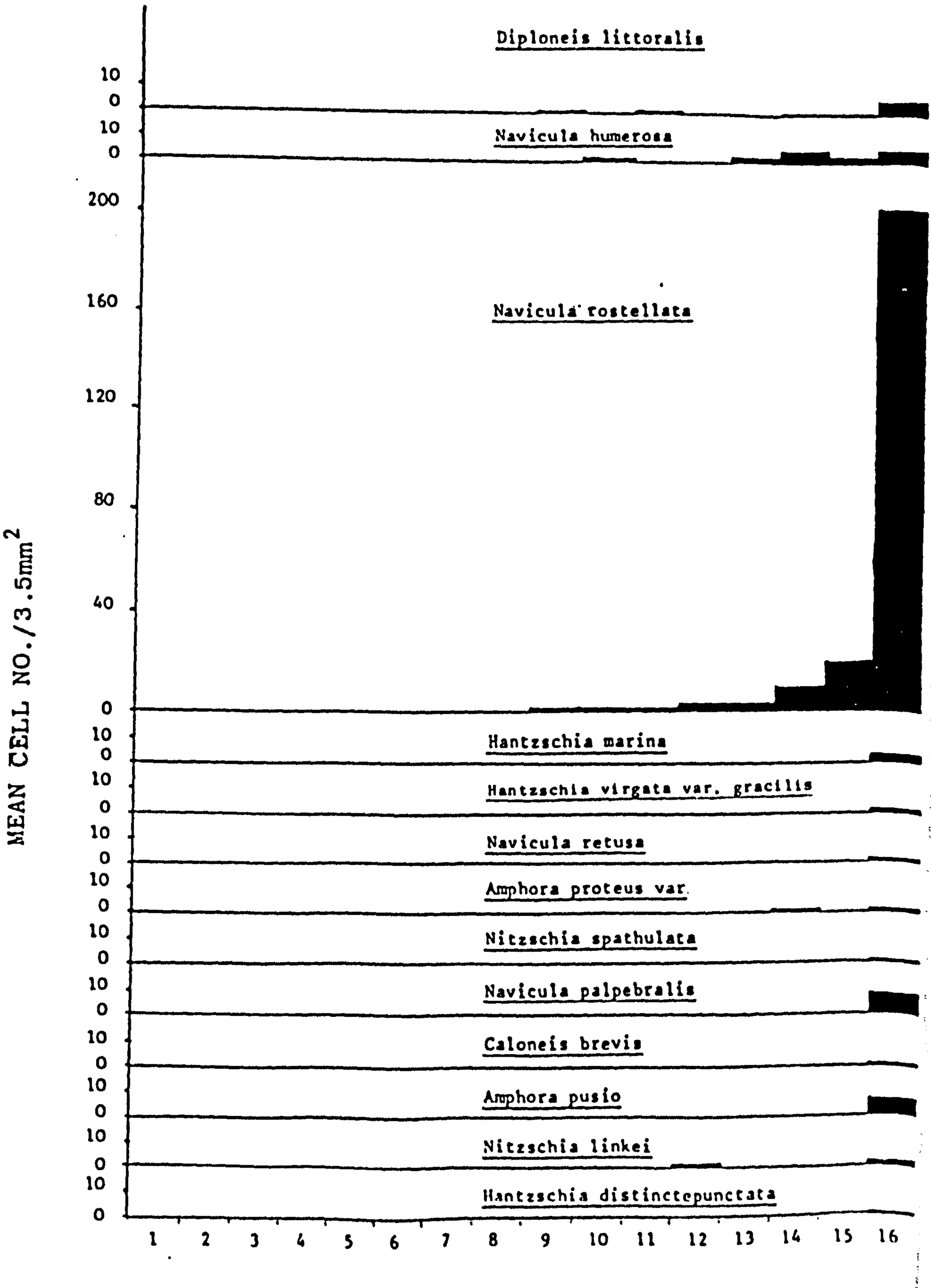
SUMMARY GRAPHS FOR THE MIDDLE/LOWER MARSH & SANDFLAT DIATOMS



GRAPH 70

Spatial positions of the diatom taxa of the middle marsh, lower marsh, and sandflat.

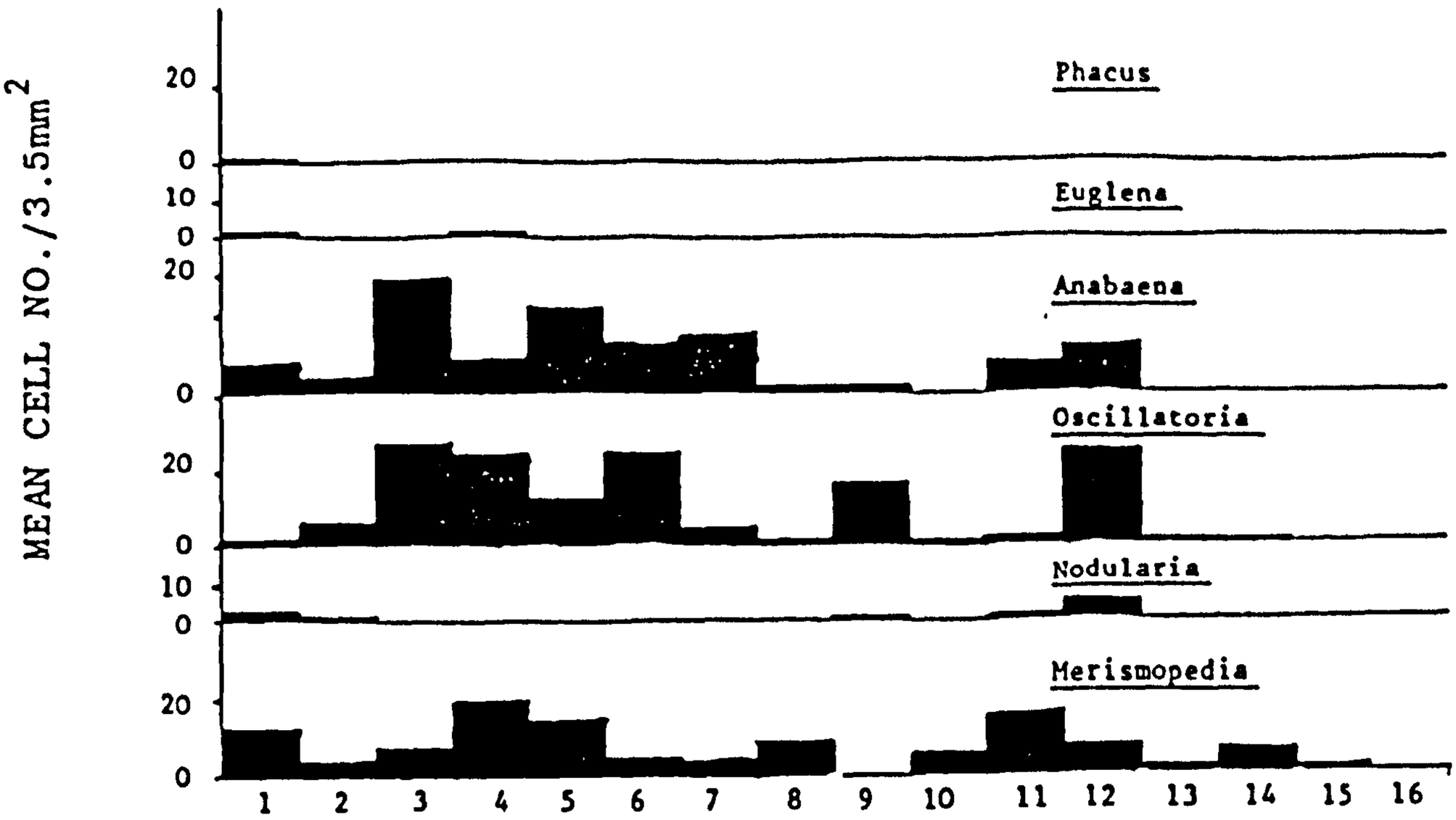
SUMMARY GRAPHS FOR THE MUDFLAT DIATOMS



GRAPH 71

Spatial positions of the diatom taxa of the lower sandflat and mudflat.

SUMMARY GRAPHS FOR THE BLUE GREEN ALGAE



GRAPH 72

Spatial positions of the abundant blue-green algal taxa.

taxa over the 30 months of counting. This larger mean should give a better overall picture of the position of each taxon along the shore.

The spatial positions of the 10 taxa so far described have showed a gradual shift in position from the upper marsh to the mudflat, for both the diatoms and the blue-green algae. Graph 68 shows the positions of the diatom taxa inhabiting the upper marsh area, Nitzschia lorenziana, Mastogloia smithii, and Rhophalodia operculata have only been observed at site 1. The diatom taxa further down the graph have progressively wider distributions.

Species which were found at all sites along the transect are illustrated on graph 69. While Navicula spp and Nitzschia microcephala agg. have been observed in higher numbers from saltmarsh sites, the distribution of Nitzschia closterium was more even, showing slightly higher abundance at sites 7, 8, 10, 11,and 12. Other species e.g. Bacillaria paxillifer and Amphiprora paludosa have only been observed in low numbers in samples from sites scattered along the transect.

Graph 70 shows the distribution of different diatom species in two main areas of the transect. The first 11 species drawn on the top half of the graph are all the diatom species which inhabited the middle to lower marsh area. Some species appeared to grow in higher numbers in the middle marsh such as Amphora lineolata and Caloneis limosa. Others have been observed in equal numbers across the middle and lower marsh such as Nitzschia paleacea and Navicula digitoradiata. While other taxa have been recorded in low numbers from scattered sites within the lower and middle marsh e.g. Navicula peregrina, Caloneis westii, Diploneis interrupta, Pleurosigma angulatum, and Gyrosigma fasciola var. arcuata.

The second main area of the transect occupied by a different group of taxa on graph 70, is that of the upper and lower sandflat. One species has been observed along the length of the transect, but only occured in high numbers on the sandflat viz Nitzschia vacillata. However most of the different sandflat species were usually only found at sandflat sites e.g. Nitzschia epithemioides, Achnanthes linkei and Pleurosigma aestuarii. Occasionally species observed at sandflat sites have been found in samples taken on the saltmarsh. This usually happened when samples were taken following a storm tide which had swept over the saltmarsh. At these times sediments innundated the saltmarsh.

Graph 71 shows all the diatom species which inhabit the lower sandflat and mudflat. Diploneis littoralis, Navicula humerosa and Navicula rostellata occupy a broader area of the sandflat. N. rostellata was only recorded in high numbers from the mudflat. All the other species listed on graph 71 were only found from samples taken at site 16.

Graph 72 summarises the distribution of some of the blue-green algal groups. The euglenoids were confined to the upper and middle marsh area. While other blue-green algal groups showed more widespread distributions. Both Anabaena and Oscillatoria were recorded from sites across the saltmarsh and uppersandflat. Slightly larger populations grew at sites 3-7. Oscillatoria has only been observed in slightly higher numbers than Anabaena from sites 9 and 12. Nodularia grew in two main areas of the transect: in the upper marsh and upper sandflat. While Merismopedia appeared to have a ubiquitous distribution from sites 1-15.

Discussion

All the graphs describing spatial positions of different taxa show a gradual transition along the transect. Approximately 4 different groups

can be distinguished, occupying 4 different areas. Two more groups of diatoms can be classified as having broad distributions. These are summarized in Table IX .

The spatial positions of the 10 different taxa (graphs 38-67), showed how niche space can vary seasonally and annually. As the population density of a given species decreases, a greater number of counts were recorded from a greater number of sites. This phenomenon seemed to occur regularly on many of the computer plots. Could this be a strategy which would maximize a taxon's chances of finding optimum conditions for growth? Further evidence is required to substantiate this hypothesis.

Furthermore maximum growth of a species does not always re-occur at the same site. Is this truely reflecting a shift in distribution? These shifting peaks are more likely to be a consequence of the variability of the sampling technique. A high mean count from one site, does not necessarily mean that a high density of diatoms is not present at another site. As shown in the frequency distribution studies the higher the population density, the more variable their distribution on the sediment, and the less repeatable the result becomes. Therefore finding large counts of a given species from a number of sites over 3 or 4 seasons is more likely to indicate a broad tolerance in its distribution.

However certain species such as Amphora ovalis var. libyca which have been counted in relatively low numbers also show a shift in position where maximum abundance was observed from year to year. Could this be associated with a change in the physical conditions? In July 1982

Table IX The spatial positions of 6 groups of taxa

UPPER MARSH	MIDDLE/LOWER MARSH
Nitzschia lorenziana	Navicula peregrina
Mastogloia smithii	Caloneis westii
Rhopalodia operculata	Pleurosigma angulatum
Navicula viridula	Nitzschia navicularis
Amphora ovalis var. libyca	Diploneis interrupta
Achnanthes lanceolata var. rostrata	Nitzschia paleacea
Nitzschia tryblionella var. levidensis	Navicula digitoradiata
Nitzschia thermalis	Amphora lineolata
Diploneis elliptica	Caloneis limosa
	Pleurosigma attenuatum
	Gyrosigma fasciola var arcuata
SANDFLAT	**LOWER SANDFLAT/MUDFLAT**
Tropideneis sp	Diploneis littoralis
Navicula hungarica f. elliptica	Navicula humerosa
Surirella ovata	Navicula rostellata*
Nitzschia epithemioides	Hantzschia marina
Navicula protracta f. elliptica	Hantzschia virgata var. gracilis
Achnanthes linkei	Navicula retusa
Navicula scoliopleura	Amphora proteus var.
Pleurosigma aestuarii	Nitzschia spathulata
	Navicula palpebralis
	Amphora pusio
	Nitzschia linkei
	Hantzschia distinctepunctata
ACROSS THE SALTMARSH	**ACROSS THE TRANSECT**
Cylindrotheca spp	Navicula spp*
Navicula pygmaea	Nitzschia microcephala agg*
Navicula hudsonis	Nitzschia vacillata*
Nitzschia acuminata	Nitzschia closterium
Navicula cari*	Bacillaria paxillifer
Navicula cincta*	Amphiprora paludosa
Stauroneis spicula	
Nitzschia microcephala*	
Achnanthes microcephala*	

* Species with broad distributions, but maximum counts are observed in specific areas.

when A. ovalis var. libyca was growing richly at site 1, the salinity recorded was 1‰, while the salinity was 4-22‰ at sites 4-6. In June 1983 when peak numbers of A. ovalis var. libyca were recorded from site 4 the salinity reading was 1‰, while at sites 1-3 the salinity ranged between 2-4‰. This would indicate that A. ovalis var. libyca changed position where localized changes in the physical conditions occured.

The summary graphs give a much better overview of how the different species are positioned along the transect. The degree of overlap in the range of sites occupied by different species across the saltmarsh is high. Whereas there is little overlap between taxa growing on the saltmarsh and the sandflat. If different diatom species are positioned in such a varied way along the shore, it would seem likely that the taxa can be associated together into distinct groups.

Conclusions:

Each diatom species inhabits a specific range of sites along the transect. The degree of overlap of sites occupied by different species varies. Since these positions are maintained from year to year it would seem likely that the diatoms are positioned along the transect according to the physical gradient conditions that are most suitable for growth.

3.5 STATISTICAL ANALYSIS

3.5.1 Assemblage Composition Measures

Of the 120 different diatom taxa identified (Appendix A), 72 different species and varieties were chosen for computer analysis. Of these 72 taxa only 13 accounted for just over 80% of the total number of cells counted.

Table X Percentage of the total cell counts of the dominant taxa.

Species	1982 %	1983 %
Navicula spp	39.59	37.48
Nitzschia microcephala agg.	19.40	12.31
Navicula rostellata	0.01	7.62
Nitzschia vacillata	6.36	5.34
Amphora exigua	4.37	4.92
Amphora lineolata	3.37	0*
Navicula pygmaea	2.76	2.73
Achnanthes lanceolata var.rostrata & Achnanthes delicatula	2.70	2.14
Nitzschia closterium	2.62	1.03
Rhopalodia operculata	0.02	5.33
Navicula cari & Navicula cincta	0.86	2.89
Amphora sp	0*	2.32
Total	82.06	84.11

* The percentage was so small that a zero was derived once the values had been calculated to the second decimal place.

Certain species which appeared in one month at one site (e.g. Mastogloia smithii) were not included in the computer analysis. All taxa used in the analysis accounted for approximately 90% of the total cell counts. While it is recognised that a certain amount of information was not analysed, general and repeatable relationships between the more abundant taxa could be determined.

Niche Breadth

The niche breadth values (Bj) for the 72 diatom taxa analyzed displayed

a large range, with a minimum Bj of 1.29 (Rhopalodia operculata) and a maximum of 14.18 (Navicula spp). The most common range of Bj values was between 5-6, and the overall spread appeared to be random, resembling that of a Poisson variate. This result is not unexpected because different taxa possess a range of competitive strategies.

What is interesting is that the most common range of Bj (of 5-6) was so high. The fact that most diatoms can compete equally successfully at 5 to 6 different sites shows their tolerance of a wide range of physical conditions, and that a wide tolerance is a strategy adopted by most taxa.

The results of the Bj calculated, are listed in Appendix B. These results agree with the direct analysis of spatial positions in the previous section. Taxa with broad distributions along the transect had high Bj values, while the taxa with restricted positions had small values.

3.5.2 Cluster Analysis

Contrary to initial expectations the cluster analysis did not produce associations of discrete assemblages changing along the transect. All three years analysis emphasized strong associations between specific pairs or triplets of taxa. These associations were observed each year.

Centroid Cluster Analysis 1982 (Figure 2)

In 1982 two strongly associated pairs were observed 1) Amphora pusio and Amphora proteus var., 2) Diploneis littoralis and Navicula palpebralis. Both pairs were associated at the 85th level. Both pairs also

CENTROID CLUSTER ANALYSIS 1982

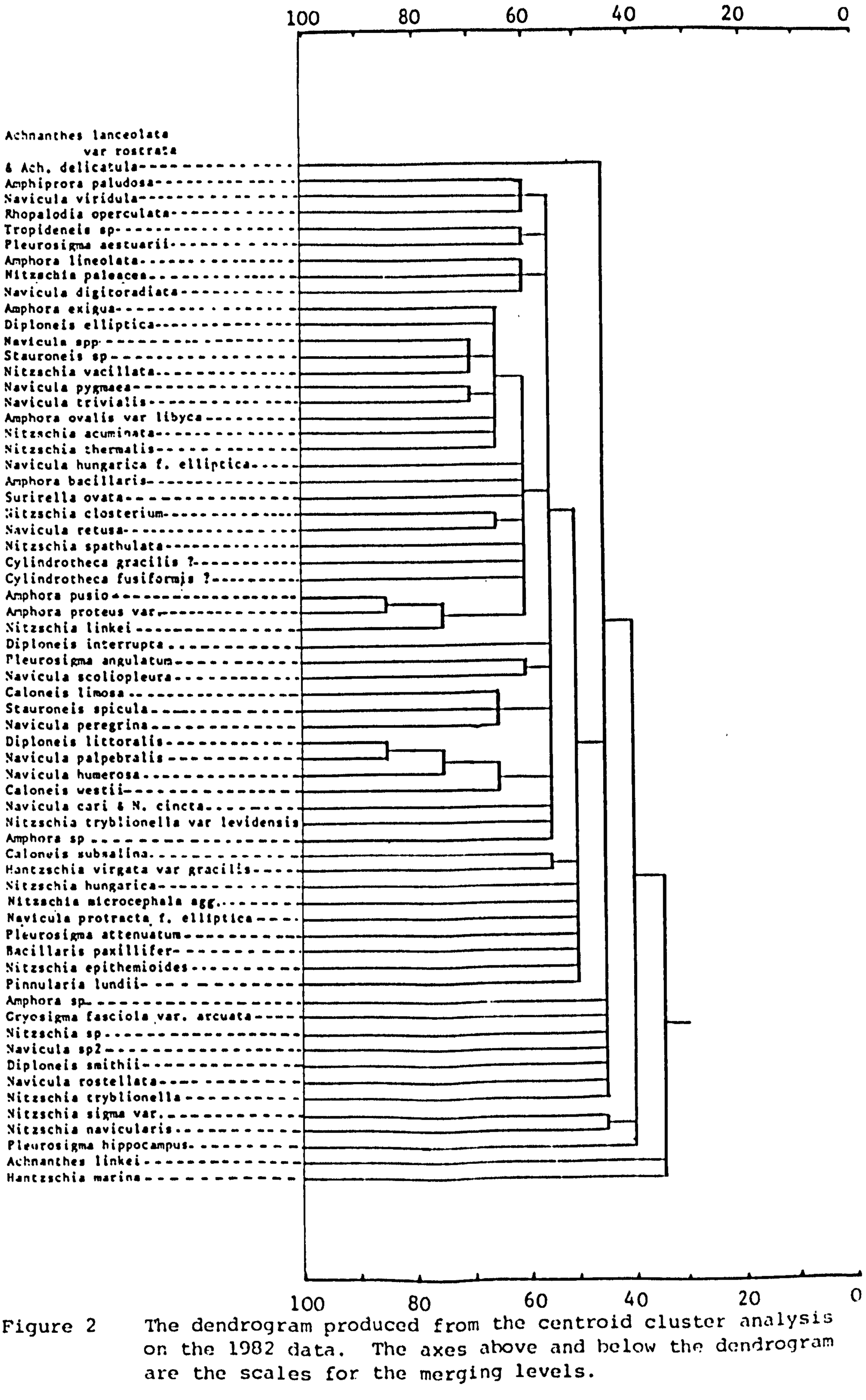


Figure 2 The dendrogram produced from the centroid cluster analysis on the 1982 data. The axes above and below the dendrogram are the scales for the merging levels.

became associated with other species at more distant levels: Nitzschia linkei joined the first pair at the 75th level; Navicula humerosa joined the second pair at the 75th level then Caloneis westii associated with the second triplet at the 65th level. All these species live on the mudflat, site 16. The two most strongly associated pairs were observed at only one site over a period of 1-2 months. The species which joined onto these pairs at more distant levels in the dendrogram, were species which were also found on the mudflat. They were present over a longer period of time. The association of C. westii with D. littoralis, N. palpebralis, and N. humerosa is confusing, as C.westii was rarely observed, and was generally found at sites on the saltmarsh.

Other pairs and triplets were grouped at more distant levels: Navicula spp, Stauroneis spp, and Nitzschia vacillata were associated at the 70th level; as were Navicula pygmaea and Navicula trivialis. All these taxa were found at most sites along the transect with highest cell numbers observed on the saltmarsh. N. vacillata was one exception, as it was abundantly recorded on the sandflat. However in 1982 higher numbers of N. vacillata occured on the saltmarsh than in any other year.

Other pairs or triplets of taxa were those which displayed broad distr-
ibutions, but were recorded in high numbers at specific sites:

Table XI Pairs and triplets of taxa with strong associations in 1982.

Merging level	Taxa	Location at which max. no.s observed
65th	Caloneis limosa Stauroneis spicula Navicula peregrina	Middle marsh
60th	Amphiprora paludosa Navicula viridula Rhopalodia operculata	Upper marsh
60th	Tropideneis sp Pleurosigma aestuarii	Sandflat
60th	Amphora lineolata Nitzschia paleacea Navicula digitoradiata	Middle marsh

The triplet which merged at the 65th level was observed as a group in high numbers following a storm tide, otherwise it was rarely observed.

There was also a larger group of 10 different taxa merging at the 65th level (Amphora exigua ... Nitzschia thermalis) were all taxa with broad distributions on the saltmarsh.

Groups of taxa formed at the 55th and lower levels were so distant that little meaning can be drawn from the data. However most taxa merging at distant levels were those species and varieties with either broad distributions; or they occured in such low numbers that no seasonal pattern could be discerned.

Centroid Cluster Analysis 1983 (Figure 3)

The most strongly associated pair was N. linkei and N. palpebralis which merged at the 95th level. These two mudflat species again occured for a short period (1-2 months). The previously closely associated species A. pusio, now grouped together with Amphora bacillaris, Navicula

CENTROID CLUSTER ANALYSIS 1983

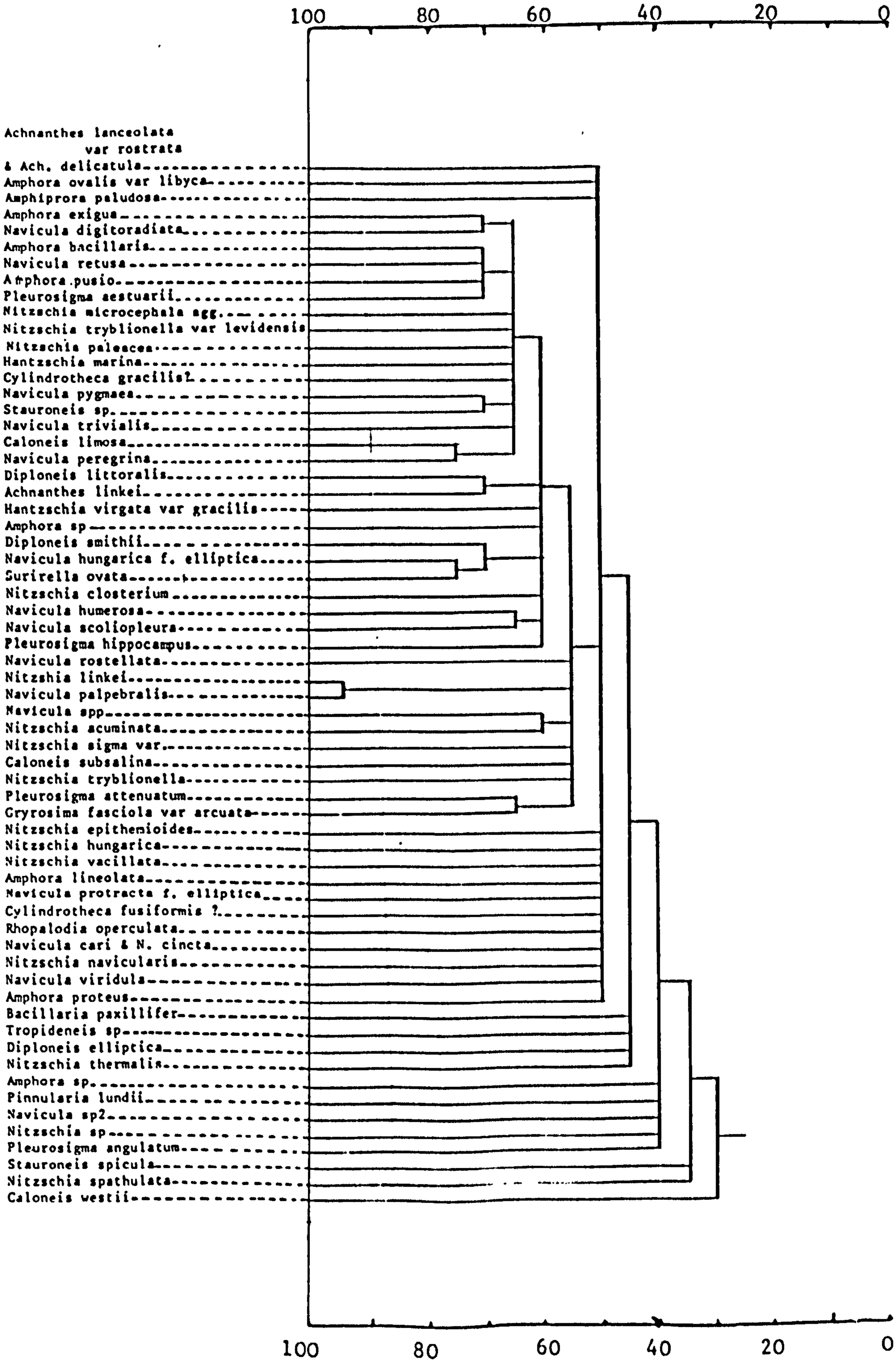


Figure 3 The dendrogram produced from the centroid cluster analysis on the 1983 data. The axes above and below the dendrogram are the scales for the merging levels.

retusa, and Pleurosigma aestuarii at the 70th level. A. pusio was observed in lower numbers in 1983, while the other species grouped with it occured in higher numbers. A sandflat species D. littoralis now grouped together with Achnanthes linkei at the 70th level.

Some associated pairs reappear in 1983 such as C. limosa and N.peregrina which grouped at the 75th level. This pair was only present in low numbers at many sites on the saltmarsh, while a new pair grew abundantly following the storm tides viz Navicula hungarica f. elliptica and Surirella ovata which merged at the 75th level. Diplonels smithii merged with the latter pair at the 70th level.

As in 1982, other pairs of taxa were recorded from a number of sites, but grew abundantly in specific areas, and the associations formed were the following:

Table XII Pairs of taxa with strong associations in 1983.

Merging level	Taxa	Location at which max. no.s observed
70th	Amphora exigua Navicula digitoradiata	Lower saltmarsh & Mudflat
70th	Navicula pygmaea Stauroneis spp	Saltmarsh
65th	Navicula humerosa Navicula scoliopleura	Sandflat
65th	Pleurosigma attenuatum Gyrosigma fasciola var.arcuata	Saltmarsh
60th	Navicula spp Nitzschia acuminata	Saltmarsh

A.lincolata does not pair with N. paleacea and N. digitoradiata in 1983. Both A. lincolata and N. paleacea were observed in much lower numbers in this year.

As in 1982 all groups at, and below the 55th level were so distant that little meaning could be drawn from that part of the dendrogram. Unlike the results from 1982, there were species e.g. Navicula rostellata, Navicula cari, and Navicula cincta, which were observed in maximum numbers at specific sites, yet were not associated with another taxon. However most other species grouping at low levels within the 1983 dendrogram were observed in low numbers, or displayed broad distributions.

Centroid Cluster Analysis 1984 (Figure 4)

Again N. linkei and N. palpebralis were the first pair to group together at the 90th level. This pair became associated with A. pusio at the 60th level. Another strong association not previously observed was the pairing of N. acuminata with Nitzschia hungarica at the 85th level. A. paludosa grouped together with this pair at the 80th level, and N. trivialis at the 75th. These 4 species were found on the saltmarsh.

Grouped at the 80th level were A. bacillaris, Ach. linkei, A.proteus var, with N. digitoradiata grouping with the triplet at the 75th level. Again the same mudflat and sandflat taxa formed close associations. Other mudflat species observed in higher numbers in 1984 were Nitzschia spathulata and Stauroneis amphioxys var. obtusa pairing at the 75th level.

CENTROID CLUSTER ANALYSIS 1984

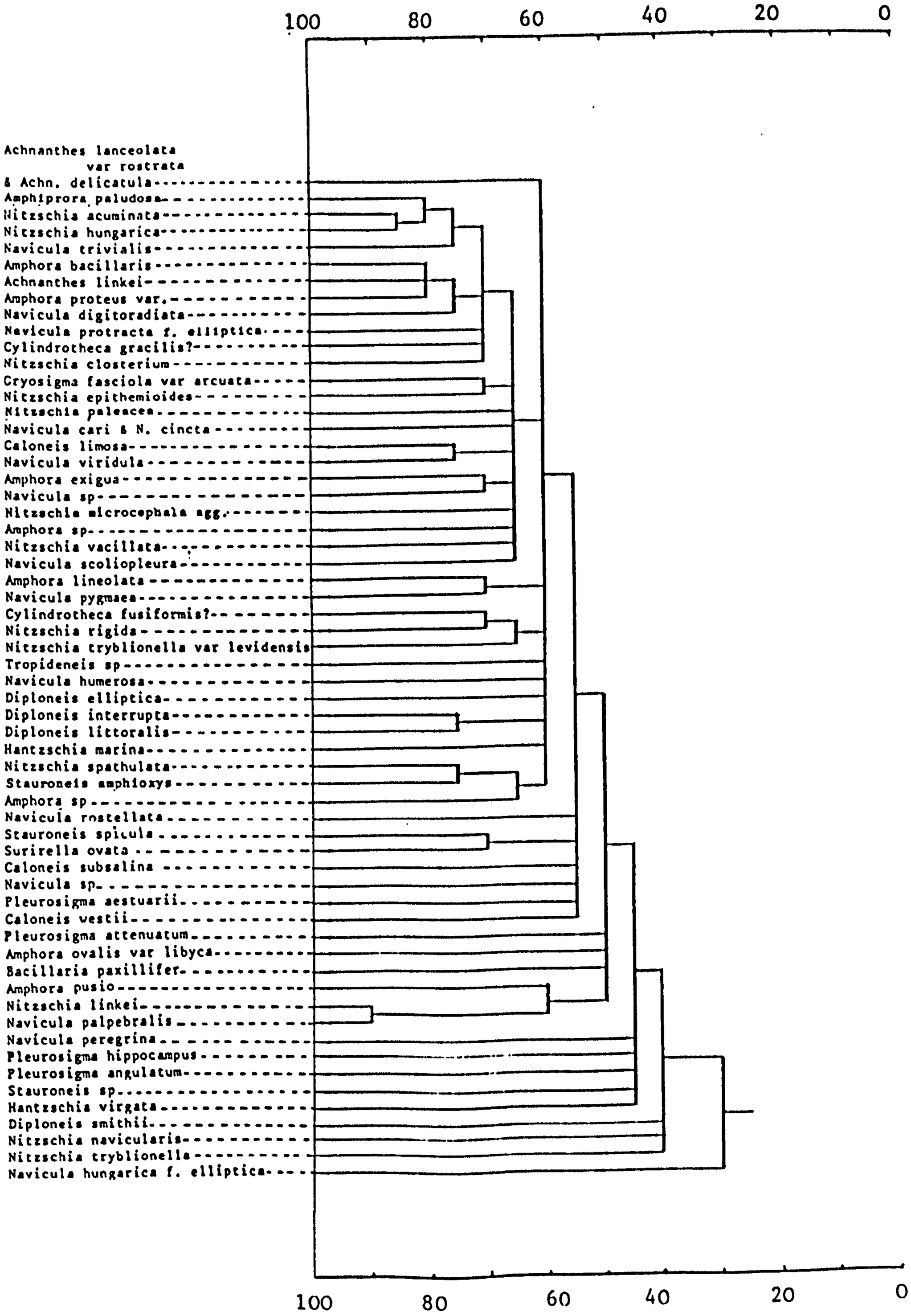


Figure 4 The dendrogram produced from the centroid cluster analysis on the 1984 data. The axes above and below the dendrogram are the scales for the merging levels.

Table XIII New pairs observed in 1984

Merging level	Taxa	Location at which max. no.s observed
75th	Caloneis limosa Navicula viridula	Saltmarsh
75th	Diploneis interrupta Diploneis littoralis	Lower Marsh
70th	Gyrosigma Fasciola var.arcuata Nitzschia epithemioides	?
70th	Navicula spp Amphora exigua	Saltmarsh
70th	Amphora lineolata Navicula pygmaea	Middle Marsh
70th	Stauroneis spicula Surirella ovata	Uppersand flat
65th [70th [	Cylindratheca fusiformis Nitzschia rigida Nitzschia tyblionella var. levidensis	Saltmarsh

By 1984 larger numbers of N. pygmaea occured together with A. lineolata in the middle marsh. This corresponds with the shift in distribution of N. pygmaea shown in graphs 44-46, D. littoralis and D. interrupta were recorded together due to the innundation of the lower marsh with sand, which caused a mixture of different assemblages. St. spicula and S. ovata grew in abundant numbers in the upper sandflat following a period of rainfall after more saline and dry conditions in previous months. One inexplicable association was that Gyrosigma fasciola var. arcuata and Nitzschia epithemioides. These two taxa have very different spatial positions, yet a similarity measure of 71% was calculated in 1984.

Principal Coordinate Analysis

Little information was derived when a principal coordinate analysis was attempted on each of the 3 years counts. Only 10-20% of the total variance was accounted for in the first 3 dimensions.

Discussion:

All three centroid cluster analyses showed consistent and repeatable associations between pairs of taxa from the same areas along the transect. Varying abundance of a given species appeared to alter its associations slightly from one closely related taxa to another. However the most strongly associated species all reappeared each year. The more distantly grouped taxa at the 55th and lower merging levels, remained distantly related each year.

There are 3 possible interpretations explaining why some taxa will not group together. First, a species may be observed in equal numbers at many sites, thereby associating equally with many species, and therefore group into a large cluster at a distant level within the dendrogram e.g. Nitzschia closterium. Secondly, other taxa may be observed in low numbers over a scattered area, so that no association with any particular taxon will emerge viz Pinnularia lundii. Thirdly a particular taxon may grow in such high abundance, that it outcompetes any other member of the assemblage, and therefore is not associated with any other taxon: Navicula rostellata.

Perhaps more associations between taxa could have been revealed if all cell counts had been considered. However new pairs emerged in each successive years counts, with the limited data analysed, and these new pairs might be indicating changes in the physical conditions.

A clear pattern can be detected in those taxa which were strongly associated. These pairs or triplets of taxa were forms with specific spatial positions along the transect, and they displayed a marked seasonal growth. Some of these pairs were opportunists, which grew abundantly following a storm tide or a period of stressed physical

conditions.

The cluster analysis gives a limited picture of some of the relationships between the more abundant taxa. The small fraction of the total variance accounted for in the principal coordinate analysis emphasizes the point that there are many factors influencing the associations between taxa, and one or two types of multivariate statistical analysis cannot present a detailed interpretation to the complex relationships between different diatom assemblages.

Conclusions:

Many factors influence the associations between different diatom taxa. In order to obtain a greater understanding of the many factors involved, a variety of techniques must be used. Different techniques should include different types of computer analysis, as well as physiological experiments using diatom cultures in the laboratory.

CHAPTER 4 TAXONOMY

Identification was determined from 3 approaches: (a) examination of valve morphology including details of the valve face and mantle; (b) measurements of the valve dimensions and specific mantle features and (c) where the above information did not suffice, details of girdle band structure and number were also examined. In almost all cases 15 individuals of each taxon were measured in every detail. The mean, and confidence limits (95%)were calculated to give an idea of the average size range. Then 100 individuals were examined and the smallest and largest individuals were measured to give a full range in each description. When fewer than 100 individuals have been measured due to lack of cleaned material, the individual measurements are given.

No single taxonomic source covered all the different species observed at Berrow. Therefore a variety of sources were referred to. Each identification was cross referenced, and the best description matching the material identified is referenced in each description.

In addition to the identification of each species, any variation in morphology was noted and discussed. The autoecology of each taxon is also briefly given. This information was interpreted from the spatial distribution graphs described in section 3.4. Finally the nomenclature of all species has been checked in Vanlandingham (1975). All terminology for the siliceous components of the diatom cell correspond to the terms given in Ross et al. (1979) and Simonsen (1975).

The descriptions that follow are not intended to be full or detailed. The accounts of each species is meant to compliment and supplement the

information given in the referenced description.

ORDER: ACHANANTHALES

FAMILY: ACHNANTHACEAE

GENUS: Achnanthese

Achnanthes delicatua Kütz. PLATE 3 Figs.1-4

sensu Hustedt (1930) p.201-202, Fig.293

Length: 11 µm - (13.93 µm ± 0.77 µm) - 18 µm

Width: 6 µm ± 0

No. of Striae in 10 µm on the epivalve: 14-16

No. of Striae in 10 µm on the hypovalve: 16-18

The valve is elliptic-lanceolate with rostrate ends. The hypovalve has a slightly greater number of striae in 10 µm than the epivalve. Not a great deal of variation has been observed in the valve morphology.

This species has been confused with Achnanthes lanceolata var. rostrata in the live cell counts. This is due to the similarity between the live cell types. The marginal sinus of Ach.lanceolata var. rostrata could not always be observed during the live cell counting. Examination of the acid cleaned material revealed the presence of the two species living together in one sample.

The striae on the epivalve and hypovalve of Ach.delicatula radiate more; and the value outline is rounder than that of Ach.lanceolata var.rostrata. Ach. delicatula does display a slightly different spatial distribution along the transect compared with Ach. lanceolata var. rostrata. Ach. delicatula has been observed at most sites on the saltmarsh (Stations I to III). It has a wider distribution range than Ach. lanceolata var. rostrata.

Achnanthes lanceolata var. rostrata Hust. PLATE 3 Figs. 5,6

sensu Germain (1981) p.115-116, pl.44, Fig.11-16

Length: 7 µm - (12.4 µm ± 0.98 µm) - 18 µm

Width: 5 µm - (5.53 µm ± 0.35 µm) - 7 µm

No. of Striae in 10 µm : 14 - (14.73 ± 0.53 um) - 16

This species is easy to identify in the cleaned material due to the marginal sinus arising on one side, in the middle of the epivalve. The valve outline is narrowly elliptic - lanceolate. The valve apices are strongly rostrate. The smaller valves become rounder in valve outline. The number of striae were recorded for both the epivalve and hypovalve, and the ranges were the same, therefore only one range is given above. The variety differs from the type species in its shape and smaller size range.

It is difficult to establish the exact spatial and temporal distribution of this variety. The chief reason being, because of the difficulty in distinguishing the live cells from Ach. delicatula (see explanation in Ach. delicatula). Closer examination of the acid cleaned material revealed that the distribution of Ach. lanceolata var. rostrata is generally confined to Station I, greatest numbers of Ach. lanceolata var. rostrata were recorded in the spring and summer months.

Achnanthes linkei Hust. PLATE 3 Figs. 7-9

sensu Hustedt (1939) p.607-608, Fig. 28-32.

Length: 23 µm - (29.67 µm ± 1.59 µm) - 44 µm

Width: 11 µm - (12 µm ± 0.36 µm) - 13 µm

No. of Striae in 10 µm : 10 ± 0

Hustedt (1939) gives a good description and series of illustrations

describing the variability that can be encountered for both the epivalve and the hypovalve. Both valves are very similar. The striation on both valves is almost the same. The only difference between the epivalve and hypovalve is in the shape of the hyaline area. The hyaline area of the epivalve of Ach. linkei extends to one side in the middle of the valve (see Fig. 7-9).

This species shows a uniform distribution at all sandflat and mudflat sites (Stations IV to VI), and has been found most abundantly in late autumn to early winter (Nov.-Feb).

ORDER: NAVICULALES

FAMILY: NAVICULACEAE

GENUS: Mastogloia

Mastogloia Smithii var. lacustris Grun. PLATE 4 Figs. 1,2

sensu Germain (1981) p.124, pl.45, Fig.1

Length: 33 µm - (37.93 µm ± 0.90 µm) - 42 µm

Width: 11 µm - (11.60 µm ± 0.28 µm) - 12 µm

No. of Striae in 10 µm : 16 - (16.60 ± 0.46) - 18

No. of locules in girdle band in 10 µm: 8-9

All the features in Germains' (1981) description can be observed: the elliptic lanceolate outline of the valve, the punctate striae, the sinuous raphe complex, and a broad loculate girdle band attached beneath the valve mantle. The Berrow material differs very slightly in that the valve apices are more rounded than those in the figure given in Germain (1981).

This species is not very variable. It is rarely observed on the salt-marsh. All counts of this taxa have been recorded at site 1 only, where it was the third most abundant member of the assemblage at site 1 in July 1983, blooming at the same time as Rhopalodia operculata and Nitzschia lorenziana (see the description of Rh. operculata for more details).

GENUS: Pleurosigma

Pleurosigma aestuarii (de Brébisson ex Kützing) Wm. Smith

PLATE 4 Fig. 3

sensu Hendey (1964) pl.36 Fig.5

Length: 58 µm - (65.13 µm ± 2.36 µm) - 79 µm

Width: 17 µm - (17.87 µm ± 0.41 µm) - 19 µm

No. of oblique transverse striae in 10 µm : 20

The size range is somewhat smaller than reported by Hendey (1964). However the sigmoid shape of the raphe, which lies along the mid-line valve at the centre, becomes eccentric towards the ends of the valve, as Hendey (1964) described. The degree of curvature of the raphe varies according to the size of the valve. However 20 transverse striae were counted in 10 µm.

This species is found at all sandflat and mudflat sites (Stations IV to VI). It is not an uncommon species. It is found in the live cell counts very frequently, but it has never been observed in very high numbers. Peak numbers were recorded in the summer months (May-Sept) at Stations IV and V.

Pleurosigma angulatum Wm. Smith PLATE 4 Fig.4

Sensu Hendey (1964) p.245-246, Pl.35, Fig. 1-3

Length: 118 µm - (140 µm ± 7.27 µm) - 167 µm

Width: 29 µm - (30.47 µm ± 0.66 µm) - 32 µm

No. of oblique transverse striae in 10 µm: 16 - (18.40 ± 0.88) -20

(Only 15 individuals were measured to give the size ranges above).

Two main features make the identification of this species clear: (a) The valves are rhombic-lanceolate in shape, and the valve margin is angular in the middle of the valve, (b) The terminal striae form parallel rectilinear lines at the valve apices, while the striae are oblique in orientation in the middle.

The valve outline can vary from being slightly to distinctly angular. Peragallo (1891) gives a good series of illustrations showing the range in variation of valve outline (Peragallo 1891 Plate 24 Figs. 3-5).

This species is generally found in the pool sites along the saltmarsh. Unfortunately too few individuals were encountered in order to establish any pattern in seasonal growth or spatial distribution. However, it is interesting to note that this species was much more commonly observed 3 years ago before continual sampling was undertaken. This species has decreased in abundance over the last 3 years, and is presently almost completely absent from all the sites.

Pleurosigma elongatum Smith PLATE 4 Fig.5

sensu Peragallo (1891) p.7, Pl.3, Fig.5

Length: 195 µm - (232.73 µm ± 9.51 µm) -257 µm

Width: 20 µm - (24.50 µm ± 1.53 µm) - 28 µm

No. of oblique transverse striae in 10 µm : 18-20

Only 50 valves measured.

The valve is elongated and narrow,with valve apices that are almost acute. The raphe is central along the length of the valve. Peragallo (1891) illustrates a range in valve shape. However figure five of Peragallo's illustrations (1891) illustrates the valve outline that matches the material measured.

This species has been observed both at Station II and Station III.

Highest counts were recorded at site 7 in the spring months (March-May).

GENUS: Gyrosigma

Gyrosigma fasciola (Ehr.) Griffeth & Henfrey PLATE 5 Fig.1

sensu Peragallo & Peragallo (1897-1908)

Pleurosigma fasciola Sm. p.173, pl.34, Fig. 30,31

Length: 81 µm - (88.93 µm ± 2.21 µm) - 95 µm

Width: 11 µm - (12.93 µm ± 1.31 µm) - 14 µm

No. of longitudinal striae in 10 µm : 22-(22.80 ± 0.48) - 24

Only 15 valves measured

The valve outline is sigmoid with long attenuated valve ends. The raphe is central, and the striae are fine but easily counted.

Gyrosigma fasciola has been observed at most sites on the saltmarsh, and occasionally on the upper sandflat. This species does not occur in dry situations such as sites 3 and 9. Highest numbers have been observed at Station II and III. Higher counts were observed in 1982 than 1983. By 1984 this species was almost absent from all cell counts. This might possibly be a sign that conditions on the saltmarsh were becoming more saline.

Gyrosigma peisonis (Grun.) Hustedt PLATE 5 Fig.2

sensu Germain (1981) p.132, pl.48, Fig.4

Van der Wuerff (1957) P.D.G. XVI 120

Length: 66 µm - (84.14 µm ± 8.98 µm) - 121 µm

Width: 9 µm - (10 µm ± 0.42 µm) - 11 µm

No. of Longitudinal striae in 10 µm : 21 - (23.73 ± 0.57) - 26

No. of Horizontal striae in 10 µm: 20 - (21.53 ± 0.59) - 22

The valve is linear/sigmoid in shape. The raphe is S-shaped, and curves at more of an angle than the valve outline.

This species is not very abundant in terms of cell number. However it has been recorded at a large number of sites on the saltmarsh. This species shows a preference for drier mound sediments.

This species was not sampled in sufficient numbers in the live cell counts. Nevertheless an examination of the computer plots revealed that this species only occurs at sites on the saltmarsh (Stations I, II and III).

GENUS: Entomoneis

Entomoneis paludosa var. hyperborea Grunow PLATE 5 Fig.3

sensu Poulin & Cardinal (1983) p.116 Fig.30

Valve length: 33 µm - (43.40 µm ± 4.04 µm) - 77 µm

Valve width: 9 µm - (10.47 µm ± 0.5 µm) - 12 µm

Striae in 10 µm: 20 - 30

No. of Fibulae in 10 µm: 9-10

This is a very delicately silicified valve, strongly waisted in the middle. The keel is sigmoid in valve view, and has a very fine pattern of striae.

There is a row of fibulae that are irregularly spaced just beneath the raphe canal running along the margin of the keel. The junction line forms a smooth arc. Poulin & Cardinal (1983) report that the junction line can be sinuous to arcuate. Only arcuate forms were observed at Berrow.

This species was not observed in the first two years of fieldwork. Then in spring of 1984 (March to May), this species bloomed. The bloom was in relatively small numbers at Station IV, however this species has been observed at other sites on the sandflat.

GENUS: Amphiprora

Amphiprora paludosa Sm. PLATE 6 Fig.1

sensu Peragallo & Peragallo (1887-1908) p.184, pl.38, Fig.14,15

Length: 40 µm (54 µm ± 3.84 µm) - 69 µm

Frustule width in girdle view: 34 µm - (35.70 µm ± 2.80 µm) - 42 µm

Striae in 10 µm: 18 -(24 ± 2.90) - 26

There seems to be much confusion in the description of this species in the literature. However, the diagram and size ranges given in Peragallo & Peragallo (1897-1908) match the dimensions given above. There seems to be a great deal of variation in the shape of the keel but two of Peragallo & Peragallos' (1897-1908) figures given above, match the most abundant forms in the Berrow material.

When using pahse contrast illumination, at 1000 x magnification, with oil immersion objectives on a compound microscope; a single row of dots can be observed along the length of the raphe canal on the margin of the keel. These represent a single row of fibulae. The junction line is very sinuous and is clearly seen in girdle view. Insufficient material was observed in valve view in order to measure valve width.

This species is widely distributed along the saltmarsh and occured in low

numbers at Stations I to IV. Highest numbers were recorded at Station IV (from Oct.-Dec.).

Amphiprora paludosa var. duplex Donkin PLATE 6 Fig.2

sensu Peragallo & Peragallo (1897-1908) p.185, pl.38, Fig.18, 19

Length: 54 µm - (67.07 µm ± 4 µm) - 86 µm

Frustule width in girdle view: 39 µm - (43.13 µm ± 1.69 µm) -48 µm

No. of striae in 10 µm: 20 - (22.93 ± 0.80) - 24

This variety is also very common at Berrow. It differs from A. paludosa by its slightly larger size range. The junction between the keel and the valve is less curved. The striae are somewhat finer and six slightly sigmoid shaped girdle bands can be counted on the frustule.

The distribution of this variety differs only slightly from A. paludosa in that most counts were observed on the upper sandflat (Station IV).

GENUS: Tropideneis

Tropideneis sp nov. PLATE 6 Figs. 3,4

Length: 47 µm - (53.67 µm ± 1.38 µm) - 63 µm

(Valve in girdle view) width: 7 µm - (7.93 µm ± 0.33 µm) - 9 µm

No. of striae in 10 µm: 22 - (23.93 ± 0.25) - 24

There is much confusion in the literature between the two genera: Amphiprora and Tropideneis, and many descriptions do not clearly provide any guidelines which the reader may use to differentiate between them. Paddock (personal communication), describes the following distinctions: (1) In Amphiprora there is no basal siliceous layer thickening at the valve apices, while Tropideneis has distinctive helictoglossae which glow brightly, when using phase contrast illumination under the compound microscope. (2)

In Amphiprora the shape of the keel in valve view is sigmoid, while in Tropideneis the keel is straight. (3) In Amphiprora single or multiple rows of fibulae are present inside the keel, in Tropideneis fibulae are absent.

The Tropideneis sp described, has all three features which Paddock considers to be associated with this genus. Having established in which genus to place this taxa, the problems of identification only just begin.

Different species of Tropideneis have a double flap of silica on the keel which appears as a "lip" bending back over the waisted centre of the valve. Tropideneis sp, has no such structure. There appears to be no fibulae inside the raphe canal, or at the margin of the keel. Both the raphe canal and terminal nodules glow brightly using 1000 x magnification, and phase contrast illumination. The keel has a fine pattern of striae forming a continuous band along its length. The valve face and mantle are very delicate hyaline areas of silica which curve out gently. The frustule is rectangular in girdle view, but has a central contriction. Although there is not a great deal of variation in the length and width of the valve, the degree of constriction in the centre of the valve can vary a great deal. The two extremes are illustrated in Figures 3 & 4 (Plate 6).

The description of Tropideneis sp does not fit into any single category. The most closely allied forms are: (1) Tropideneis lepidoptera var. minor (Peragallo & Peragallo 1897-1908) (2) T. semistriata (Cleve 1894) and (3) T. vitrea (Hendey 1964).

T. lepidoptera var. minor has the same valve and frustule shape as Tropideneis sp. The keel consists of only a single flap of silica. How-

ever the size range described in Peragallo & Peragallo (1897-1908) is two times larger than the size ranges described above. Peragallo & Peragallo (1897-1908) also reports a maximum of 20 striae in 10 µm whereas the range in Tropideneis sp is 21-24.

T. semistriata has a keel which is somewhat eccentric (Cleve 1894 p.27) Tropideneis sp shows perfect symmetry. Cleve (1894) also reports 19 striae in 10 µm which is fewer than in the measurements of Tropideneis sp given above. However at certain angles T. semistriata appears very similar in girdle view. T. semistriata also appears to have a second flap of of silica lying over the waisted centre of the valve, which is sometimes seen in girdle view. This has never been observed in Tropideneis sp.

T. vitrea as described in Hendey (1964) is also very similar to Tropideneis sp. T. vitrea has rounded and more truncate apices as does Tropideneis sp, but Hendey (1964) only records 17 transverse striae in 10 µm on the keel. The size ranges for T. vitrea are also much larger.

Cells of Tropideneis sp are usually solitary. One interesting feature of the live cells is the common appearance of bacteria growing within the cup-shaped infolds of the chloroplast. This has been observed in fresh material from the field as well as older material.

Tropideneis sp can be found at all sites on the sandflat and mudflat (Stations IV to VI). It has only been observed in high numbers in one month (May 1984). This was a month of high temperature, low salinity and low levels of organic matter. Interestingly these conditions represent a marked contrast to the conditions of hypersalinity recorded at the same sites in the previous month. Generally the occurrence of this species is rare.

GENUS: Diploneis

Diploneis elliptica Kütz. PLATE 7 Fig. 2.

sensu Patrick (1966) p.414, Pl.38, Fig.10

Length: 23 µm - (32.70 µm ± 2.41 µm) - 47 µm

Width: 17 µm - (20.5 µm ± 1.79 µm) - 23 µm

No. of costae in 10 µm: 8 - (8.3 ± 0.35) - 9

No. of alveoli in 10 µm: 19 - (20.8 ± 0.94) - 22

As described in Patrick (1966). Found in low numbers all year round on the saltmarsh. Highest numbers recorded in the upper and middle marsh areas (Stations I and II). This species was much more abundant in 1981 before regular field sampling was undertaken.

Diploneis littoralis (Donkin) Cleve PLATE 7 Fig.2

sensu Hendey (1964) p.226, pl.32, Fig.9

Length: 23 µm - (30.33 µm ± 1.98 µm) - 60 µm

Width: 15 µm - (17.47 µm ± 0.96 µm) - 20 µm

No. of costae in 10 µm: 11 - (12.13 ± 0.29) - 13

This valve outline is elliptic in shape. The silicified ridges that run on either side of the raphe are prominent. The costae are straight in the middle of the valve and curve radially towards the valve apices.

One interesting feature about Diploneis littoralis, is that it exhibits a marked vertical migration rhythm that appears to be linked with light and tide cycles. Preliminary observations showed that during the period of low tide, D. littoralis migrated to the surface of the sediment in the morning and returned beneath the surface by early afternoon while other species succeeded it's place on the surface sediments (Oppenheim 1981).

D. littoralis can be found at all sandflat and mudflat sites (Stations IV VI). Highest numbers have been recorded in the late autumn and winter months from Nov. - Jan. at Station V. This species has been slowly decreasing in abundance over the last 4 years. Dominant blooms with cell counts in the thousands of this single species were recorded in 1981. This species has never been observed in such large numbers since that time.

GENUS: Stauroneis

Stauroneis spicula Hickie PLATE 7 Fig.3

sensu Germain (1981) p.168, pl.63, Fig.6

as Navicula spicula Cleve

Length: 58 µm - (63.20 µm ± 1.15 µm) - 66 µm

Width: 8 µm - (8.93 µm ± 0.39 µm) - 10 µm

No. of striae in 10 µm: 40

The valve is linear lanceolate with acute apices. The central hyaline area is narrow and runs transapically across the raphe at a right angle. The striae are so fine that an extremely high resolution compound lens on a Zeiss Jena compound microscope was required to measure them. This valve is very delicately silicified and breaks easily in the acid cleaning preparation.

This species was observed in high numbers at two sites only on two separate occasions. Once a smaller bloom was observed in association with Caloneis limosa following a storm tide on the saltmarsh. The second bloom occured on the upper sandflat (at Station IV) in May 1984. This latter bloom occured when the site had a low salinity readings following conditions of hypersalinity in the previous month. During the 2½ years of fieldwork this species was confined to the middle marsh area (Station II).

Stauroneis amphioxys var. obtusa Gregory PLATE 7 Figs.4,5

sensu Hendey (1964) p.219, pl.37, Fig. 13,14

Length: 51 µm - (58.40 µm ± 3.19 µm) - 84 µm

Width: 12 µm - (12.93 µm ± 0.33 µm) - 15 µm

No. of striae in 10 µm : 19 - (19.87 ± 0.29) - 21

The valve is linear lanceolate with a large central hyaline area. In girdle view the frustule is rectangular with a constriction in the central areas of both valves. The valve thus appears concave in valve view. The hyaline area is rectangular, but expands slightly towards the margin of the valve face. The striae are easily measured, and end unevenly adjacent to the raphe on the valve face. The striae continue over the valve mantle. Shorter rows of striae can be seen on the valve mantle beneath the central hyaline area.

This variety can be found on the sandflat and mudflat (Stations IV to VI). Although this is not an uncommon diatom (i.e. it is found at many sites), no more than one or two cells were observed during the live cell counts. Highest numbers were recorded in May, 1984 at Station IV.

GENUS: Navicula

GROUP 1: Orthostichae

Navicula cryptocephala Kütz. PLATE 8 Figs. 1-4

sensu Hudstedt (1930) p.295, Fig.496

Length: 12 µm - (19.47 µm ± 1.98 µm) - 27 µm

Width: 6 µm - (6.40 µm ± 0.28 µm) - 7 µm

No. of striae in 10 µm: 18 - (19.87 ± 0.81) - 22

The valve is linear-lanceolate widening towards the middle of the valve. The axial area is narrow expanding centrally to form a small circular area around the central nodule. The striae are curved and radiate in the middle of the valve becoming convergent towards the valve apices. The valve apices vary considerably; from acute to rostrate. This is illustrated in figures 1 to 4 (PLATE 8). Using phase contrast illumination at 1000 x magnification the striae appear as single rows of punctae.

This species is the most dominant representative of a group of lanceolate naviculoid cells called Navicula spp in the live counts. Navicula spp are the most abundant group in terms of cell number of all the live cell counts. It also represents the largest number of taxa placed together in a single aggregate. The second most abundant memember of Navicula spp is N. gregaria. The live cells of N. cryptocephala and N. gregaria were indistinguishable during the live cell counts. It was also difficult to separate the two species when examining the cleaned material. The variation observed of both species seemed to overlap to such a degree that separation of the two taxa became unclear. Far more work using a variety of microscopic techniques needs to be done in order to classify and count the different lanceolate naviculoid species separately.

N. cryptocephala can be found at all sites along the transect throughout the year. Higher counts were recorded on saltmarsh sites, than on the sandflat. A large number of Navicula spp were observed at Station I which was equally dominanted by N. cryptocephala and N. gregaria. However N. gregaria was the more dominantof the two atStations II and III. For a fuller description of the spatial distribution see Section 3.4.

GROUP 2: Lineolatae

Navicula cari Ehr. PLATE 8 Fig. 5

sensu Hustedt (1930) p.299 Fig.512 N. cari var. PLATE 8 Fig.6

Length: 17 µm - (24.27 µm ± 2.19 µm) - 40 µm

Width: 5 µm - (5.47 µm ± 0.29 µm) - 6 µm

No. of Striae in 10 µm: 18 - (20.20 ± 0.60) - 22

The valve is linear lanceolate. The striae are strongly radial in the centre of the valve becoming slightly convergent towards the valve apices. The identification is easily confused with Navicula cincta. Differences that distinguish the two species are: (a) A greater number of striae are recorded in 10 µm in N. cari. Also the striae are more curved in N. cari. (b) Mean size length is slightly larger in N. cari. (c) The valve outline in N. cari tends to be more narrow and the valve apices more acute.

The live cell counts of N. cincta and N. cari have been grouped together. This is because the live cells were of the two species were indistinguishable. Examination of the cleaned material, showed that both species (including different varieties of N. cari which are also placed within the same group in the live cell counts), occured together at the mound sites 3 and 9. Closer observation revealed spatial differences. N. cari and N. cari var. were less dominant than N. cincta at most months of the year. N. cari occured in its greatest numbers at site 3. While N. cincta was usually dominant at site 9. Hustedt (1930) describes N. cari as more common in freshwater, see section 3.4 for spatial distribution.

Navicula cincta (Ehr.) Kützing PLATE 8 Fig. 7

sensu Hustedt (1930) p. 298, Fig. 510

Length: 17 µm - (26.13 µm ± 3.08 µm) - 43 µm

Width: 5 µm - (6 µm ± 0.31 µm) - 7 µm

No. of Striae in 10 µm: 10 - (12 ± 0.47) - 14

The valve is linear-lanceolate, with radial striae becoming convergent towards the valve apices. The raphe is simple and is surrounded by a narrow hyaline area. The hyaline area widens to a circle around the central nodule.

Details of the spatial distribution of this species is described in section 3.4. When examining the mean salinity readings over the year at the sites where N. cincta occurs, the salinity can be considered brackish to saline. However when the highest counts of this species have been observed the individual salinities were hypersaline (65-75 ‰). Such readings were recorded in July - Sept, at site 9 (Station III).

Navicula digito-radiata (Gregory) Ralfs. PLATE 8 Figs.8,9

sensu Hendey (1964) p.202, pl29 Fig.8

Length: 35 µm - (50.33 µm ± 5.30 µm) - 89 µm

Width: 11 µm - (12.07 µm ± 0.44 µm) - 14 µm

No. of Striae in 10 µm: 9 - (10.27 ± 0.39) - 12

The species illustrated on Plate 8 Fig. 9 matches Hendeys (1964) illustration and description. This species is very variable. The valve shape is broadly elliptic to elliptic-lanceolate. Of the two illustrations given in Hendey (1964) only one figure corresponds to the Berrow material.

The distribution of N. digito-radiata is unusal. Throughout the year N. digito-radiata was found on the salt-marsh, and was abundant on the

middle and lower marsh sites (Stations II and III), in late summer (July-Aug.). N. digito-radiata was also common on the mud-flat (site 16) during the winter months, and was observed in relatively high numbers together with Amphora pusio, A. proteus var. impressa, Navicula palpebralis, and Nitzschia linkei.

Navicula hungarica f. elliptica Schulz PLATE 8 Figs. 10,11

sensu Cleve-Euler (1951-1955) p.137-138, Fig. 782 b

Length:	13 µm - (21.33 µm ± 2.14 µm) - 32 µm
Width:	6 µm - (6.93 µm ± 0.33 µm) - 8 µm
No. of Striae in 10 µm:	8 - (9.87 ± 0.46) - 11

The valve is broadly elliptic with rounded valve ends and course striae. The striae are radial in the middle of the valve, becoming convergent towards the valve ends. The raphe is simple, lying within a narrow hyaline area. The valve face is very curved and is usually seen lying to one side in the acid cleaned material.

Its distribution is uniform throughout the year. It has been observed in low numbers at most of the sites along the transect. High numbers were recorded following a storm tide in January 1983 at Station IV.

Navicula palpebralis de Brébisson ex. Wm. Smith PLATE 9 Figs. 1,2

sensu Hendey (1964) p.216-217 pl.34, Figs. 13-19

Length:	24 µm - (38 µm ± 3.78 µm) - 67 µm
Width:	13 µm - (14.6 µm ± 1.04 µm) - 20 µm
No. of Striae in 10 µm:	10-11

As described in Hendey (1964). N. palpebralis shows a high degree of variability in morphology. The shape and size of the hyaline area is the most

variable freature. Hendey (1964) gives an excellent series of illustrations showing this. The valve apices can be apiculate, apiculate and produced, to broadly cuneate.

This species was recorded in highest numbers from October to December. Its distribution along the transect was restricted to the outer most station (Station VI), where the sediments are the most disturbed, and the mean salinity readings are the high.

Navicula peregrina (Ehr.) Kütz. PLATE 9 Fig. 3

sensu Hustedt (1930) p.300, Fig. 516

Length:	82 µm - (103 µm ± 5.23 µm) - 123 µm
Width:	19 µm (20 µm ± 0.43 µm) - 21 µm
No. of Striae in 10 µm:	6 - (6 ± 0.34) - 7
No. puntae in 10 µm:	18 - (20 ± 0.27) - 21

As described in Hustedt (1930). The variability in valve shape is well illustrated in Germain (1981 p.178, pl.66, Figs. 1-3). The range in length is smaller than the measurements given in Hustedt (1930) or Germain (1981).

N. peregrina is found in small numbers along the saltmarsh, throughout the year. Highest counts were recorded at Station II in January 1983.

Navicula rostellata Kütz. PLATE 9 Fig.4

sensu Hendey (1964) p.200, pl.30, Fig. 11

Length:	30 µm (43.13 µm ± 2.69 µm) - 52 µm
Width:	8 µm (8.33 µm ± 0.27 µm) - 9 µm
No. of Striae in 10 µm:	11 - (12.20 ± 0.48) - 14

The valve is linear lanceolate with rostrate apices. The striae are radial becoming convergent towards the valve apices. The axial area is narrow with a central hyaline area widening to form an elliptic area at the central nodule.

The size range given in Hendey (1964) for valve length is larger (40 - 75 µm). Otherwise the dimensions and general morphology correspond to his discription. For an account of its spatial distribution see section 3.4.

This species also appears to display a distinct vertical migration rhythm linked with daylight and tidal cycles (Oppenheim 1981).

Navicula viridula Kütz. PLATE 9 Figs.5,6

sensu Germain (1981) p.178, pl.67, Fig. 1,2

Length:	33 µm (39.13 µm + 2.39 µm) - 57 µm
Width:	11 µm (11.67 µm ± 0.4 µm) - 13 µm
No. of Striae in 10 µm:	9 - (9.67 ± 0.4) - 11
No. Punctae in 10 µm:	20 - (23.87 ± 1.12) -28

The overall morphological features match Germain's (1981) description. However the range for valve length recorded by Germain (1981) is larger. Also the valve is broader in the middle. Cleve-Euler (1951) quotes a smaller size range and the Berrow measurements corresponds with hers.

The distribution of N. viridula extends over the saltmarsh. However it occurs in its greatest numbers in the pools on the upper and middle marsh (from Feb.-Apr.).

GROUP 3: Retusae

Navicula retusa Breb. PLATE 10 Figs. 1,2

sensu Peragallo & Peragallo (1897-1908) p.102, pl.13, Fig.11

Length: 39 µm, 30 µm, 45 µm, 35 µm, 39 µm, 31 µm

Width: 7 µm, 6 µm, 7 µm, 6 µm, 7 µm, 6 µm

No. of Striae in 10 µm: 8, 7, 7, 8, 8, 8

The valve is elliptic-lanceolate. The frustule is rectangular in shape in girdle view, and is waisted in the middle. Thus the valve is concave at the centre. The raphe is sinuous, and is surrounded by a broad hyaline area. The striae are broad and parallel.

This species has been observed at sandflat and mudflat sites (Stations IV to VI in low numbers and on few occasions. However in recent winter months (Jan-Feb. 1984) it has occured in greater numbers.

GROUP 4: Punctatae

Navicula humerosa Brébisson PLATE 10 Fig. 3

sensu Hustedt (1930) p.311 Fig. 559

Length: 33 µm - (46.67 µm $\pm$ 4.55 µm) - 84 µm

Width: 21 µm - (24.20 µm $\pm$ 0.87 µm) - 27 µm

No. of Striae in 10 µm: 10 - (12.0 $\pm$ 0.47) - 14

No. of Punctae in 10 µm : 10

This is a very variable species. The valve outline shows a range of form: the sides of the valves may be parallel or slightly waisted. The valve apices can be rostrate, or broadly rounded. The striae are usually of unequal length and the punctae are easily visible.

This species has an ubiquitous distribution along the sandflat and

mudflat stations (Stations IV to VI). It appears in high numbers in the late autumn and winter and was extremely abundant in 1981. However its growth has continuously declined over the last four years.

GROUP 5: Lyratae

Navicula forcipata Greville PLATE 10 Fig.4

sensu Hustedt (1930-1966) Band VII, Teil 3, p.531, Figs.a,b

Length:	11 µm - (32.60 µm ± 3.46 µm) - 52 µm
Width:	10 µm - (14.67 µm ± 2.09 µm) - 26 µm
No. of Striae in 10 µm:	14 - (15.60 ± 0.41) - 16

The valve outline is broadly elliptic in the smaller forms, to almost lanceolate-elliptic in the larger individuals.

N. forcipata is characterized by coarse striae. Punctae are easily visible. The most important features are the central striate areas on either side of the raphe. These central striate areas can often be asymmetrical as reported by Hustedt (1930-1966). The range in length observed in the Berrow material is much smaller than the ranges given in Hustedt (1930-1966).

N. forcipata was not an abundant form. The live cell counts of this and Navicula pygmaea have been combined, since living cells of the two species were indistinguishable. However it is important to note that N. forcipata was only observed in small numbers on one occasion (Nov. - 82 at site 16), otherwise only single valves were observed.

Navicula pygmaea Kütz. PLATE 10 Fig.5

sensu Hustedt (1930) p.312, Fig.561

Length:	18 µm - (28.73 µm + 3.49 µm) - 39 µm
Width:	9 µm - (10.67 µm ± 0.58 µm) - 12 µm

No. of Striae in 10 µm : 23 - (24.07 ± 0.39) - 26

N. pygmaea is very similar to N. forcipata except the former is more narrowly elliptic in valve outline, and the striae are much finer. No punctae are visible on the valve and its size range is smaller.

This species has been observed at all sites along the transect, but grows in highest numbers on the saltmarsh (Stations I to III). It shows great variability in size which changes in time. Small sized valves are found in spring prior to the summer bloom, when the largest cells are observed. For a more detailed description of the spatial distribution see section 3.4.

GROUP 6: Microstigmaticae

Navicula protracta forma elliptica Gallik. PLATE 10 Figs. 6-10

sensu Hustedt (1930-1966) p.316, Fig. 1435

Length: 12 µm - (17.40 µm ± 1.55 µm) - 26 µm

Width: 5 µm - (5.67 µm ± 0.27 µm) - 6 µm

No. of Striae in 10 µm: 23 - (24.13 ± 0.29) - 25

The valve is elliptic to elliptic-lanceolate. The smaller valves are more broadly elliptic. As the valve increases in size the valve outline narrows. The central hyaline area widens and is slightly asymmetrical. The striae are radial, and each consists of a single row of punctae. This can be seen using phase contrast illumination, at 1000 x magnification. In girdle view the frustule, is wide and rectangular, the striae can be seen on the valve mantle, which is very wide. The valve face is curved, therefore the frustule tends to appear in girdle view in the live cell counts.

This species is found in small numbers at all sandflat sites (Stations IV

and V) throughout the year, but high numbers were recorded together with abundnant growth of Navicula hungarica f.elliptica in January 1983 at Station IV following a storm tide.

Navicula scoliopleura A. Schmidt PLATE 10 Figs.11,12

sensu Van der Werff (1957-1974).P.D.G. XVI 109

Length:	22 µm -(30.87 µm ± 3.10 µm) - 43 µm
Width:	6 µm -(7.00 µm ± 0.21 µm) - 8µm
No. of Striae in 10 µm:	9 - (9.67 ± 0.27) - 10

The valve is linear-lanceolate. The frustule is rectangular in girdle view with a central constriction so the valve is concave in valve view. The apices can be rostrate to broadly apiculate. The striae are broad and strongly radial becoming slightly convergent towards the valve apices. The central hyaline area is rectangular expanding towards the margin. Two striae much shorter in length than the other striae on the valve, lie just beneath the hyaline area on the valve mantle.

This species is found in low numbers at all sandflat sites (Stations IV to V) throughout the year. Highest numbers were recorded on the lower sandflat (Station V) during the winter months.

GENUS: Caloneis

Caloneis brevis (Gregory) Cleve PLATE 11 Fig.1

sensu Peragallo & Peragallo (1897-1908) p.80, pl.10, Fig.13

as Navicula brevis Greg.

Length:	38 µm-(43.33 µm ± 1.75 µm) - 62 µm
Width:	17 µm -(18.20 µm ± 0.52 µm) - 20 µm
No. of Striae in 10 µm:	15 - (16.07 ± 0.25) - 17

Only 30 individuals were measured.

The valve is elliptic with rounded valve apices. The alveolate striae are radial, and a single longitudinal line can be observed adjacent to the valve margin. Although much of this information is missing in Peragallo & Peragallo's (1897-1908) description, the main morphological features are discussed.

There is some variation in the shape of the hyaline area, which is usually circular, however broader, larger, elliptic shapes have been observed.

This species has only been observed at Stations V and VI since the winter months of 1984 (Jan.-Mar). No previous observations of this form were made before this time.

Live cell counts were rare, therefore there is insufficient data to determine any temporal patterns in growth.

Caloneis limosa (Kütz) Patrick PLATE 11 Figs.2,3

sensu Patrick (1966) p.587, pl.54, Fig.10

Length:	20 µm - (25.53 µm ± 1.11 µm) - 53 µm
Width:	7 µm - (7.73 µm ± 0.33 µm) - 9 µm
No. of Striae in 10 µm:	16 - (19.53 + 1.02) - 21

This was a very difficult species to identify, mainly because the dimensions given above correspond exactly to the dimensions of Caloneis ventricosa (Ehr.) Meister in Germain (1981), C. silicula (Ehr.) Cléve and C. silicula var. truncatula Grun. in Hustedt (1930). Two distinguishing features make the identification of this species match Patrick's (1966) description (a)

the presence of a small pair of crescent shaped areas of striae in the central hyaline area on either side of the central nodule, (b) two submarginal longitudinal lines are present on each side of the valve as shown in Patricks' diagram (1966).

The crescent-shaped area of striae can only be observed when focusing on the uppermost surface of the valve. The longitudinal lines can only be resolved when focusing on the lower valve mantle.

The larger valves show the biconstricted or triundulate outline clearly. The smaller the valves, the more elliptic its shape. Also the cresent shaped area of striae are much more difficult to see in the smaller forms.

There is further confusion in the nomenclature of this species. Vanlandingham (1975) considers C. limosa to be an incorrect identification of C. silicula var. limosa (Kütz) Vanlan. This is incorrect since the description of the type species C. silicula gives no description of the crescent shaped area of striae, or the presence of 2 longitudinal lines. Therefore Patricks (1966) classification is used above.

C. limosa shows a fairly restricted distribution. It is usually found on the middle marsh (Station II) and blooms in winter months. High numbers have been observed after storm tides.

Caloneis subsalina (Donkin) Hendey PLATE 11 Figs.4,5

sensu Hendey (1964) p.230, pl.29, Fig.4

Length:	49 µm - (62.07 µm ± 4.04 µm) - 94 µm
Width:	23 µm - (25 µm ± 0.66 µm) - 29 µm
No. of Striae in 10 µm:	12 - (13.07 ± 0.53) - 14

As described in Hendey (1964). The valve shows great variability in length and outline. Large size forms are elliptic with sub-apiculate apices. As valve size decreases the sides of the valve become parallel and the apices more rostrate. The larger sized forms were observed on all saltmarsh sites, while the smaller size valves were found on sandflat sites (Station IV & V).

This species was not sampled in sufficient numbers during the live cell counts to determine any patterns in temporal growth.

Caloneis westii (Wm. Smith) Hendey PLATE 11 Fig.6

sensu Hendey (1964) p.230-231, pl.44, Figs.5-10 & pl.45, Figs. 1-13

Length: 58 µm - (87.93 µm ± 9.24 µm) - 128 µm

Width: 16 µm - (19.80 µm ± 1.01 µm) - 23 µm

No. of Striae in 10 µm: 12 - (12.33 ± 0.27) - 13

As described in Hendey (1964). This is a very variable species, the variation is excellently figured in Hendey (1964).

The distribution extends over the saltmarsh (Stations I to III) in low numbers throughout the year. Insufficient numbers were observed in order to determine any patterns of seasonal growth.

GENUS: Pinnularia

Pinnularia lundii Hust. PLATE 11 Fig.7

sensu Germain (1981) p.246, pl.89, Fig.11

Length: 41 µm, 41 µm, 36 µm, 41 µm, 39 µm.

Width: 10 µm, 11 µm, 11 µm, 10 µm, 11 µm.

No. of Striae in 10 µm: 10, 10, 10, 11, 12

The sides of the valve are parallel with very broad capitate ends. The central hyaline area occupies a large area on the valve face. The striae are strongly radial in the middle of the valve becoming convergent towards the apices. The dimensions given above are twice as large as the size ranges given in Germain (1981). Nevertheless, the morphological features of the raphe complex, and striae measurements correspond to Germains' (1981) description.

Vanlandingham (1975) reclassifies P. lundii as P. interrupta var.crassior (Grun.) Cleve. The morphological features described above do not match the original description of P. interrupta var.crassior in Grunow & Cleve (1880, then identified as Navicula globiceps var. crassior.), therefore the nomenclature given in Germain (1981) is maintained.

This species was rarely recorded during the live cell counts. Small numbers of this species have been observed at most pool and slope sites along the salt marsh. This species was more abundant 3 years ago before regular sampling was undertaken.

FAMILY: CYMBELLACEAE

GENUS: Amphora

Amphora bacillaris Greg PLATE 12 Fig.1

sensu Cleve (1895) p.127, pl.4, Figs.40,41

Length:	30 µm - (38.87 µm ± 2.86 µm) - 57 µm
Width:	5 µm - (5.27 µm ± 0.33 µm) - 6 µm
No. of Striae in 10 µm:	18 - (19.33 ± 0.65) - 21
No. of Girdle bands:	7-8

The frustule is almost rectangular in shape. Each girdle band has a single row of punctae. The valve morphology is as described in Cleve (1895),

very narrow, and somewhat variable in length.

This species has only been observed at sandflat and mudflat sites (Stations IV to VI). Highest numbers have been observed at Station V during the winter months (Jan.-Mar.). However, this species is commonly observed in low numbers from Oct.-Mar.

Amphora exigua Greg. Cleve PLATE 12 Fig.2

sensu Peragallo & Peragallo (1897-1908) Plate 50 Figs. 30,31

Length:	18 µm - (24.91 µm ± 1.89 µm) - 40 µm
Width:	4 µm - (4.67 µm ± 0.51 µm) - 6 µm
No. of Striae in 10 µm:	22-24

As described in Peragello & Peragallo (1897-1908). The valve is semicircular, the ventral edge is gibbous, and the valve ends curve. Striae are transapical, becoming slightly radiate towards the ends, the raphe curves slightly in the centre, and at the apices. The frustule is rectangular with slightly protruding ends.

Live cells grew at all sites along the transect, throughout the year. Highest numbers were recorded during dry conditions, when the intersitial salinity was high.

Amphora lineolata Ehr. PLATE 12 Fig.3

sensu Hustedt (1930) p.346 Fig. 636

Length:	26 µm - (34.71 µm ± 3.28 µm) - 53 µm
Width:	6 µm - (7.17 µm ± 0.44 µm) - 9 µm
No. of Striae in 10 µm:	22 - (23.21 ± 0.52) - 24

As described in Hustedt (1930). The frustule is elliptic, and is very delicately silicified. It is easily damaged in the acid cleaning preparation. A.lineolata shows great variability in length during peak growth periods. The chloroplast structure is also very distinctive. Two lobed chloroplasts lie at each end of the cell. Each chloroplast may have 2-4 lobes extending into the middle of the cell.

As shown in section 3.4 A. lineolata has a restricted distribution on the middle marsh (Station II).

Amphora ovalis var. libyca (Ehr.) Cleve PLATE 12 Fig.4

sensu Hustedt (1930) p.342, no fig.

Length:	18 µm - (29.73 µm ± 2.67 µm) - 47 µm
Width:	6 µm - (7.7 µm ± 0.38 µm) - 10 µm

No. of Striae in 10 µm: 10-13

As described in Hustedt (1930). This species is a good example of a taxon which changes size with time. In January 1983 the length range of 15 individuals had a mean of 34.73 µm ± 2.80 µm, while in March 1983 the mean decreased to 24.73 µm ± 2.85 µm at site one.

As shown in section 3.4. A. ovalis var.libyca occurs at the upper end of the transect (Stations I and II).

Amphora proteus var. PLATE 12 Fig.5

sensu Cleve-Euler (1951) p.92, Fig. 673(f)
Brockmann (1950) p.22, pl.4, Figs. 16,17

Length: 17 µm - (40.19 µm ± 5.84 µm) - 64 µm

No. of Striae in 10 µm: 12 - (12.13 ± 0.23) - 13

As described in Cleve-Euler (1951). The valve is extremely curved. Therefore it is very difficult to record valve width. The coarse punctae can be easily observed. The valve morphology has been described as very variable in the literature. However the most closely related variety is A. proteus var. impressa A.Cl. nach Brockmann. This species occurs at the lower sandflat and mudflat sites (Stations V and VI). Highest numbers were observed in October and March.

Amphora pusio Cl.N. Nach Cleve PLATE 12 Fig.6

sensu Cleve-Euler (1951) p.92, Fig. 670 (c & d)

Length: 17 µm - (22 µm ± 1.71 µm) - 34 µm

Width: 3 µm - (3.67 µm ± 0.27 µm) - 4 µm

No. of Striae in 10 µm: 14-16

As described in Cleve-Euler (1951). This species occurs most abundantly

in October. It can be found throughout the winter months at Station VI. It usually seems to occur in association with: Amphora proteus var. Navicula palpebralis, Nitzschia linkei and N. spathulata var. hyalina.

FAMILY: EPITHEMIACEAE

GENUS: Rhopalodia

Rhopalodia operculata (C.A. Agardh) Håkansson PLATE 13 Fig.1

sensu Håkansson (1979) p.166

Length: 23 µm - (35 µm ± 0.99 µm) - 38 µm

Width: 8 µm - (9.40 µm ± 0.35 µm) - 10 µm

No. of transapical ribs in 10 µm: 3 -(4.20 ± 0.37) -5

No. of striae between the transapical ribs in 10 µm: 12-14

The valve is a semi-circular crescent shape. The transapical ribs are thickly silicified and irregularly spaced across the valve. This species does not show a great deal of variability.

The spatial changes in growth have been discussed in section 3.4. As shown in section 3.2 peak numbers were recorded in July 1983 at site 1. This was at a time when the marsh was very dry. The pool at Station I had dried out completely, and salinity readings were at their highest ever recorded for that site. Peak numbers of Nitzschia lorenziana and Mastogloia smithii were also observed at the same time.

FAMILY: NITZSCHIACEAE

GENUS: Cylindrotheca

Cylindrotheca gracilis (Breb. ex Kütz) Grun. PLATE 13 Fig.2

sensu Reimann and Lewin (1964) p.290, pl.127, Fig.1

Length: 90 µm - (104 µm ± 2.53 µm) - 153 µm

Frustule width: 6 µm - (6.07 µm ± 0.14 µm) - 8 µm

No. of spirals: 2½

No. of Fibulae in 10 µm: 19-20

The measurements given above correspond to the description of Cyl.gracilis var. gracilis given in Reimann and Lewis (1964). However it would be misleading to identify all cells as this variety, for the following reasons: (1) these measurements have only been recorded from one sample, (2) the frustules of Cylindrotheca sp are largely made up of organic matter and therefore break up completely using acid cleaning methods, and even using the more delicate peroxide treatments. Therefore only a very limited amount of cleaned material could be examined.

When measuring the live cells, the size range varied from 30 µm to 300 µm. This suggests that more than one variety, and possibly several species of Cylindrotheca sp were present on the saltmarsh. Two size ranges were recorded from repeated measurements from the living material: a small size range from 30 µm - 90 µm, and a larger size range from 90 µm - 300 µm. This would suggest that at least 2 species of Cylindrotheca sp were present.

Due to the difficulties of obtaining cleaned material for a more critical examination of valve morphology, it is impossible to make any conclusive statements. In order to establish a clearer picture of the variability observed, it would be necessary to carry out a detailed examination of Cylindrotheca using scanning and transmission electron microscope techniques.

GENUS: Bacillaria

Bacillaria paxillifer (O.F.Müller) Hendey PLATE 13 Fig.3

sensu Hendey (1964) p.274 pl.21 Fig.5

Length: 71 µm - (87 µm ± 7.24 µm) - 120 µm

Width: 5 µm - (5.73 µm ± 0.33 µm) - 7 µm

No. of Striae in 10 µm: 20 - (21.47 ± 0.72) - 24

No. of Keel punctae in 10 µm: 6 - (6.33 ± 0.34) - 7

As described in Hendey (1964). Colonies are generally found on pool and slope sites along the saltmarsh (Stations I, II, and III), throughout the year. Highest counts were recorded in the winter on the middle and lower marsh areas (Stations II, III).

GENUS: Hantzschia

Hantzschia marina (Donkin) Grunow PLATE 13 Figs.4,5

sensu Hendey (1964) p.285, pl.39, Fig.12

Length: 40 µm - (48.07 µm ± 3.27 µm) - 77 µm

Width: 6 µm - (7.47 µm ± 0.35 µm) - 8 µm

No. of Fibulae in 10 µm: 6 - 8

No. of Punctae in 10 µm: 18-20

As described in Hendey (1964), although the full length range (80-100 µm) was not recorded in the Berrow material, the rectangular shape of the frustule and the obvious fibulae which extend to form transverse costae and cross the valve, made its' identification clear. Double rows of punctae can be seen between the costae.

This species can be found at all sites on the sandflat and mudflat (Stations IV to VI). It is generally observed in low numbers. Highest numbers have been recorded at Station VI in the late summer and early autumn (Sept.-Nov.).

Hantzschia virgata var. gracilis Hustedt PLATE 13, Figs.6,7

sensu Mann (1981) p.385-387, Fig. 6 a-d, Fig. 2c,d.

Length: 37 µm - (53.43 µm ± 4.60 µm) - 79 µm

Width: 5 µm - (6 µm ± 0.30 µm) - 7µm

No. of Striae in 10 µm: 15-16

No. of Fibulae in 10 µm: 4-6

The valve is very narrow and slightly arcuate. The valve apices are obtuse and slightly produced. Mann (1981) gives a detailed description. The arcuate shape of the valve may vary slightly according to each individual.

This variety was more common than H. virgata var. virgata. H.virgata var. gracilis was observed at all sandflat and mudflat sites (Stations IV to VI). Highest counts were recorded at site 16 in the winter months (Dec-Mar).

Hantzschia virgata (Roper) Grunow var. virgata PLATE 13 Fig.8

sensu Mann (1981) p.379 - 384, Figs. 2a, b, Fig. 3 a,e

Length: 85 µm - (97.07 µm ± 5.28 µm) - 113 µm

Width: 9 µm - (13.1 µm ± 1.99 µm) - 17 µm

No. of Striae in 10 µm: 8 - (9 ± 0.3) - 10

No. of Punctae in 10 µm: 18

No. of Fibulae in 10 µm: 4-5

Only 15 individuals have been measured.

As described in Mann (1981), this variety is considered to be more common than other varieties. The transapical costae are wider and deeper than in other related taxa. This is easily observed using the light microscope.

This is a rare variety in the Berrow material. No more than one or two individuals have been recorded in any live cell count. This species has only been observed on sandflat and mudflat sites. Highest numbers were recorded on the mudflat (site 16).

Hantzschia weyprechtii Grun PLATE 13 Fig.9

sensu Mann (1978) p.70-79, pl.122-137, Figs. 131-137

Length: 38 µm - (51.53 µm ± 4.26 µm) - 60 µm

Width: 5 µm - (5.93 µm ± 0.49 µm) - 8 µm

No. of Striae in 10 µm: 30 - (31.40 ± 0.55) - 33

No. of Fibulae in 10 µm: 7 - (8.20 ± 0.52) - 10

Only 15 individuals measured.

The valve is semi-lanceolate, with extremely produced ends. The keel forms a thickened margin. Fibulae are irregularly spaced along the keel. The transverse costae are parallel. The frustule is rectangular widening in the middle.

This species was recorded on all sandflat and mudflat sites (Stations IV to VI). Only a few individuals were usually observed in any given count. Highest numbers were recorded in the winter months of 1984.

GENUS: Nitzschia

GROUP 1: Tryblionellae

Nitzschia acuminata (Smith) Grun. PLATE 14 Fig.1

sensu Hustedt (1930) p.401, Fig. 764

Length: 28 µm - (32.40 µm ± 1.77 µm) - 53 µm

Width: 6 µm - (6.33 µm ± 0.27 µm) - 7 µm

No. of Striae in 10 µm: 12 - (13.67 ± 0.83) - 16

As described in Hustedt (1930) although the sizes for valve length and width are larger than those measurements given above. The shape of the valve is linear-lanceolote and is slightly waisted in the middle. The striae are parallel, with a hyaline area just off centre on the valve face.

Live cells were recorded in cell counts at nearly all the sites along the transect. However its distribution is generally confined to the saltmarsh and upper sandflat (Stations I - IV). Highest counts were recorded in the summer months (July-Aug.) at Stations I and II.

Nitzschia debilis (Arnott) Grunow PLATE 14 Fig.2

sensu Germain (1981) p.334, p.126, Figs 7-10

as Nitzschia tryblionella var. debilis (Arnott.) A. Mayer

Length: 12 µm - (16.47 µm ± 1.43 µm) - 23 µm

Width: 6 µm - (7.13 µm ± 0.55 µm) - 9 µm

No. of Fibulae in 10 µm : 9-10

No. of Striae in 10 µm: 16-17

The valve is elliptic-lanceolate, and smaller in length than closely allied forms: N. tryblionella and N. tryblionella var. levidensis. A fine striation, can be seen on the valve surface, and the fibulae are widely spaced.

This variety is frequently found on the mound sites along the saltmarsh, although it has been recorded from most sites of Stations I to III. This species was not observed very frequently until the early spring of 1984 (Mar).

Nitzschia hungarica Grun. PLATE 14 Figs.3,4

sensu Hustedt (1930) p.401 Fig.766

Length: 36 µm - (48.27 µm ± 7.52 µm) - 106 µm

Width: 8 µm - (9.53 µm ± 1.09 µm) - 10 µm

No. of Striae in 10 µm: 15 - (16.53 ± 0.55) - 18

No. of Keel punctae in 10 µm: 8 - (8.47 ± 0.51) - 10

As described in Hustedt (1930). This is one of the species showing the greatest degree of variability in time. The size range of the valve clearly varies from month to month. When peak numbers were observed, the average valve length ranged from 65 to 74 µm. The length range given above was measured from a number of different slides. Therefore a mean range taken from a larger sample would have been larger.

This species can be found at most pool and slope sites along the salt-marsh. Highest counts were recorded on sites 1 and 2 (Station I) during the summer months (July-Sept.).

Nitzschia navicularis (Bréb. ex. Kütz.) Grunow PLATE 14 Fig.5

sensu Hendey (1964) p.276 pl.39 Fig. 3-5

Length: 21 µm - (44.14 µm ± 7.71 µm) - 73 µm

Width: 15 µm - (17.87 µm ± 1.06 µm) - 21

As described in Hendey (1964) This species shows a great deal of variability in valve length and in many aspects of its morphology. The smaller valves are elliptic, and the larger its size, the more elliptic-lanceolate the valve outline.

Hendey's (1964) figures shows some of the variation in valve shape. The

double rows of small punctae forming the striae at the valve margin often penetrate the central hyaline area, forming continuous rows of punctae across the valve.

Although this species can be found at any site on the saltmarsh, it is most abundant on the upper and middle marsh. Highest counts have been recorded from March-April.

Nitzschia tryblionella Hantzsch in Rabenhorst PLATE 14 Fig.6

sensu Hendey (1964) p.276-277, pl.44, Fig. 2,3

Length: 56 µm - (67.93 µm ± 8.73 µm) - 204 µm

Width: 15 µm - (20.93 µm ± 1.60 µm) - 25 µm

Only 15 individuals measured.

As described in Hendey (1964). The median fold in the apical axis of the valve is clearly visible. The valve surface is finely striate, with 6-10 striae in 10 µm. There is enormous variability in valve size. The larger valves are slightly waisted in the centre.

Although this species has been observed at all sites along the saltmarsh, it is more common in the pools of the upper marsh (Station I).

Nitzschia tryblionella var. levidensis (Wm. Smith) Grun. PLATE 14 Fig.7

sensu Hustedt (1930) p.399, Fig. 760

Length: 25 µm - (50.47 µm ± 5.55 µm) - 60 µm

Width: 8 µm - (9.73 µm ± 0.49 µm) - 12 µm

No. of Transapical ribs in 10 µm: 9-10

The valve is widely lanceolate with slightly apiculate valve ends. This

species also shows some degree of morphological variation. This variation is expressed spatially. Large sized valves are found in pools and at sites with high water content. While small sized valves tend to occur on mound sites. The possibility of 2 different varieties being present was investigated. However, the differences in morphology did not deviate from the range of features described for N. tryblionella var. levidensis.

This species may be found along the saltmarsh (Stations I to III) Large counts were recorded at Station I in spring (March-May).

GROUP 2: Dubiae

Nitzschia dubia Wm. Smith PLATE 15 Fig. 1

sensu Germain (1981) p.338, pl.123, Fig. 1,2

Length:	109 µm - (127.60 µm ± 7.48 µm) - 170 µm
Width:	12 µm - (14.07 µm ± 0.53 µm) - 15 µm
No. of Fibulee in 10 µm:	8 - (9.6 ± 0.66) - 11
No. of Striae in 10 µm:	20 - (21.80 ± 0.70) - 25

As described in Germain (1981). This species was observed infrequently. It was found in low numbers along the saltmarsh (Stations I to III). Highest numbers were recorded in pool sites at Stations I-III.

GROUP 3: Costatae

Nitzschia epithemioides Grun. PLATE 15 Fig. 2

sensu Hustedt (1930) p.407, Fig. 779

Length:	27 µm - (39.40 µm ± 4.05 µm) - 53 µm
Width:	8 µm - (9.53 µm ± 0.48 µm) - 10 µm
No. of Keel punctae in 10 µm:	8 - (8.20 ± 0.25) - 9
No. of transapical ribs in 10 µm:	3 - (4.07 ± 0.53) - 6

The dimensions and valve morphology correspond to Hustedts' (1930) description. This species is a typical example of diatoms which do not reappear each year. In 1982 single live cell counts were recorded less than half a dozen times. However in the month of July 1983 N. epithemiodes was counted in large numbers at all the sandflat sites (Stations IV and V). Highest counts were recorded on the upper sandflat (Station IV). Since this time N. epithemioides has only been observed in smaller numbers. Hypersaline conditions were recorded during periods of peak growth.

GROUP 4: Spathulatae

Nitzschia linkei Hustedt PLATE 15 Fig. 3,4

sensu Hustedt (1939) p.661 Fig.114

Van der Werff (1957-1974) PD1 XXI 138

Length: 41 µm - (49.47 µm ± 2.26 µm) - 61 µm

Width: 7 µm - (8.20 µm ± 0.43 µm) - 9 µm

No. of Keel punctae in 10 µm: 10-10.80 ± 0.52 - 12

N. linkei was very difficult to identify. It is easily confused with Nitzschia cursoria and different varieties of Nitzschia socialis. The valve outline matches exactly that of N. cursoria. Two features distinguish N. linkei from N. cursoria: (1) N. linkei has very fine striae which are parallel on either side of the mid-rib which are fine, but can be observed at 1000 x magnification using phase contrast illumination under a compound microscope. The striae of N. cursoria are much finer. (2) N. linkei does not possess two longitudinal lines that run parallel to the central mid-rib.

The differences from N. socialis are more obvious. N. linkei has a small range in valve length, and it has a greater number of keel punctae in 10 µm than the varieties of N. socialis.

The chains of cells of N. linkei can lie side by side, or end to end like the chains of Pseudo-nitzschia, Van Der Werff (1957-1974) gives a good series of illustrations which show the different positions of this colonial form.

The striae of N. linkei, can be observed, but are extremely difficult to count. Approximately 28 striae have been measured in 10 µm. Hustedt (1939) records 33 in 10 µm.

This species has only been observed at Station VI. Its distribution is restricted to this area. Highest numbers were recorded in October.

Nitzschia spathulata var. hyalina Greg. PLATE 15 Fig.5

sensu Peragallo & Peragallo (1897-1908) p.285, Pl.73, Fig.5

Length: 29 µm - (34 µm ± 2.08 µm) - 43 µm

No. of keel punctae in 10 µm: 6 - (6.47 ± 0.29) - 7

Only 50 individuals measured.

This species is very distinctive. The apices are clearly spathulate in girdle view, and the valve curves outwards in the middle of the valve. N. spathulata var. hyalina is an uncommon form at Berrow. The valve width could not be measured because is was not clearly distinguishable from other Nitzschia sp in the acid cleaned material.

Peragallo & Peragallo (1897-1908) records a slightly larger number of keel punctae in 10 µm for N. spathulata var. hyalina (7-8). However the length measured in the Berrow material was too small to classify it as N. spathulata Bréb.

This variety has only been recorded in very low numbers. Live cells were observed at all sandflat and mudflat sites. Highest numbers have been recorded at Station VI in the late summer to autumn (Aug.-Nov.).

GROUP 5: Lanceolatae

Nitzschia microcephala Grun PLATE 15 Figs.6-8

sensu Peragallo & Peragallo (1897-1908) p.286-287, pl.73, Figs.23,24

Length: 9 µm - (15.80 µm ± 3.38 µm) - 30 µm

Width: 3 µm - (3.33 µm ± 0.34 µm) - 5 µm

No. of keel punctae in 10 µm : 12-13

No. of striae in 10 µm: ?

This species is an aggregate of different taxa. The most abundant form resembles Nitzschia microcephala. This aggregate is the most abundant group in terms of cell number. It is also the most difficult to identify. More detailed classification and identification of the different valves is required. It is unfortunate that such a detailed taxonomic study is beyond the scope of this project. However the morphological variability can be described.

The large valves are linear-lanceolate with acute apices. Small sized valves are lanceolate with captate ends. The valve ends of the small sized valves can be broadly capitate to subcapitate. The two extremes of valve shapes just described are classified as different species or varieties in the literature. An examination of a range of material reveals a continuum of change in valve shape from the large form to the small form.

These valves are very delicately silicified and rarely survive the acid cleaning treatment. Striae are not visible on the valve surface, using

1000 x oil emmersion objectives under a compound microscope.

A larger number of keel punctae in 10 µm was measured than the dimensions given in Peragallo & Peragallo (1897-1908), and Hustedt (1930). Giffen (1967) describes a small linear lanceolate form: N. perindistincta which he reports as being delicately silicified. However the size range is smaller, and a captate form is not described.

Despite the taxonomic problems of this group, a distinct spatial distribution along the transect was observed. Large valves were observed in small numbers at any given site on any particular occasion. The capitate form was the most numerous (see section 3.4).

Nitzschia paleacea Grun. PLATE 15 Fig.9

sensu Germain (1981) p.349, pl.132, Fig.23

Length: 22 µm - (36.67 µm ± 1.49 µm) - 43 µm

Width: 3 µm - (3.93 µm ± 0.14 µm) - 4 µm

No. of Keel punctae in 10 µm: 12 ± 0

The valve is linear-lanceolate with a slight constriction on one side of the valve. The frustule appears sigmoid in girdle view. The keel punctae are regularly spaced along the valve margin. The two central punctae are spaced wider apart, at the point of constriction. There appear to be no striae on the valve surface using 1000 x oil immersion objectives, valve apices are acute.

This species is commonly found at most sites along the saltmarsh. High numbers were recorded at Station II in spring and summer months (Apr-Aug).

Nitzschia vacillata Giffen PLATE 16 Figs.1-4

sensu Giffen (1964) p.279, pl.4, Fig. 8,9

Length: 23 µm - (25.60 µm ± 1.22 µm) - 42 µm

Width: 3 µm - (3.67 µm ± 0.27 µm) - 4 µm

No. of keel punctae in 10 µm: 12 - (14.33 ± 0.98) - 18

The valve is linear lanceolate. The keel is thickly silicified and the degree of curvature can vary. Keel punctae are easily observed in an irregular array along the length of the keel. The curvature of the outer margin of the valve is also variable. Valve apices are acute and produced in varying degrees, according to the curvature of the keel, and the distal valve margin. In girdle view the shape of the frustule is rectangular with convex sides. Striae are not visible on the valve face or mantle.

This is a very difficult specimen to clean and mount even with the hydrogen peroxide treatment. The valves always appeared broken and chipped.

N. vacillata is a very common species at all sites on the sandflat and mudflat (Stations IV to VI), and occurs in high numbers at most times of the year. Peak numbers were recorded at Station V (from Apr-Jun).

Nitzschia sp PLATE 16 Fig.5

Length: 34 µm - (44.40 µm ± 2.84 µm) - 59 µm

Width: 5 µm - (5.67 µm ± 0.27 µm) - 6 µm

No. of Fibulae in 10 µm: 9 - (9.93 ± 0.25) - 11

The valve is linear-lanceolate with acute apices. Fibulae are

irregularly spaced, and run along the length of the keel. The keel is the most thickly silicified part of the valve. The valve face and mantle is hyaline and very delicate, and is easily broken.

This taxon has been found at all sandflat and mudflat sites (Stations IV to VI). Highest numbers have been recorded at Station V in May 1984.

GROUP 6: Sigmoideae

Nitzschia sigma var. PLATE 16 Fig.6

sensu Germain (1981) p.368, pl.139, Fig.3 as N. Sigma(Kütz)Wm. Smith

Length: 48 µm - (60.6 µm ± 3.73 µm) - 94 µm

Width: 5 µm - (5.47 µm ± 0.29 µm) - 6 µm

No. of keel punctae in 10 µm: 9 - (10.07 ± 0.25) - 11

No. of striae in 10 µm: 25-35

The shape of the valve and frustule is the same as that of N. sigma var. rigida. N. sigma var. is smaller in length. The striae are easily seen in N. sigma var. under 1000 x magnification, oil immersion objectives and phase contrast illumination. The striae are irregular and punctate. The irregular pattern of striae make an accurate measurement difficult. The number of striae counted in 10 µm in the Berrow material is greater than the type species described in Germain (1981). Therefore this taxon was classified as a variety.

The ecology of this species is discussed in the description of N. sigma var. rigida.

N. sigma var. rigida (Kütz) Grunow PLATE 16 Fig.7

sensu Peragallo & Peragallo (1897-1908) as N. rigida Kütz p.291,pl.74, Figs. 8,9.

Length: 55 µm - (96.80 µm ± 10.44 µm) - 129 µm

Width: 5 µm - (6.40 µm ± 0.46 µm) - 8 µm

No. of keel punctae in 10 µm: 9 - (10.27 ± 0.44) - 12

No. of striae in 10 µm: ?

The valve is slightly sigmoid in valve view with slightly attenuated ends. The striae are barely discernable using 1000 x oil immersion objectives and phase contrast illumination. Therefore an accurate measure of the number of striae in 10 um could not be made.

Peragallo & Peragallo (1897-1908) describe a variety N.rigida var. rigidula Grun. which is only considered different by its smaller size.

The size range of N. sigma var. rigida spans the size range of both N. rigida and N. rigida var. rigidula in Peragallo & Peragallos' (1897-1908) descriptions. There appears to be no discontinuity in variation from the larger valves to the smaller valves, using light microscopy. Therefore it is not possible to establish whether both the species N. rigida and the variety N. rigida var rigidula are present. A more critical examination using scanning and transmission electron microscopes is required.

There is further confusion in the live cell counts because the live cells of N. sigma var. and N. sigma var rigida could not be distinguished. Upon examination of the acid cleaned material temporal differences between N. sigma and N. sigma var. rigida could be established. Both taxa have completely overlapping spatial positions along the transect. For further details see section 3.3. (lower marsh).

Nitzschia vermicularis f. genuina mh.. PLATE 16 Figs.8,9

sensu Cleve-Euler (1951) p.72, Fig.1468, a,b

Length in µm: 264, 245, 254, 243, 256, 240

Width in µm: 9, 8, 8, 9, 9, 9

No. of keel punctae in 10 µm: 8, 8, 8, 8, 7, 8

No. of striae in 10 µm: 22, 22, 22, 22, 24, 22

The frustule is strongly sigmoid in girdle view, while in valve view it is linear. The valve ends are acute and slightly prolonged. Striae are coarse and punctate. The keel punctae are regularly spaced along the valve margin.

This species can be found in the pools sites of the saltmarsh. It does not occur on drier surface sediments. The method used for counting did not sample this species in sufficient numbers in order to determine any patterns in seasonal growth.

GROUP 7: Nitzschiellae

Nitzschia closterium (Ehr.) W. Smith PLATE 16 Fig.10

sensu Hustedt (1930) p.424 , Fig. 822

Length: 38 µm - (43.80 µm ± 2.60 µm) - 66 µm

Width: 3 µm - (3.73 µm ± 0.25 µm) - 4 µm

Valve length without spines: 15 µm - (19.80 µm ± 1.48 µm) - 25 µm

No. of keel punctae in 10 µm: 12-16

The valve is curved, and expands in the middle. Both the valve face and spines have a single row of keel punctae. No striae can be seen on the surface using 1000 x oil immersion objectives. This species shows considerable variation in spine length. The degree of curvature of the spine is also variable. The valve length measured excluding spine length

gives a much more consistent measure. The size range for valve length given in Hustedt (1930) is much larger than what is given above.

Reimann and Lewin (1964) report a strain of Cylindrotheca closterium where the keel punctae form a half spiral around the valve which is illustrated in an electronmicrograph (Plate 125, Fig.2). Nothing of this nature was observed under the light microscope in the Berrow material.

This species is very common in the live cell counts. Frustules rarely survive the acid cleaning or hydrogen peroxide preparations. Therefore all measurements were taken from living material.

This species is common at all sites along the transect. Peak numbers were recorded at Stations III, IV and V (Oct-Apr.).

Nitzschia lorenziana Grun. PLATE 16 Fig.11

sensu Peragallo & Peragallo (1897-1908) p.293, pl.74, Fig.25

Length: 86 µm - (164 µm ± 23.01 µm) - 222 µm

Width: 5 µm - (5.20 µm ± 0.23 µm) - 6 µm

No. of Striae in 10 µm: 14 - (14.27 ± 0.33) - 16

No. of keel punctae in 10 µm: 5 - (5.80 ± 0.31) - 7

The size ranges of N. lorenziana Grun seems to vary from description to description:

Table XIV Size ranges recorded from different sources

Reference:	Length µm:	Width µm:	No. of Striae in 10 µm	No.of keel in 10 µm
Hustedt (1930)	65-160	3-5	17-19	6-8
Germain (1981)	66-160	6-8	15-19	6-8
Peragallo & Pergallo (1897-1908)	130-220	6-7	13-14	6-7
Van Heurk (1896)	130-190	6-7	13.5-14	6-7
Cleve-Euler (1952)	65-235	-	14-20	6-8.5

The description from Peragallo & Peragallo (1897-1908) best matches the measurements recorded in the Berrow material. Perhaps one reason for the variability encountered in the descriptions is due to the variability in valve morphology. The frustule of N. lorenziana is sigmoid. The numbers of striae in 10 µm is higher towards the valve apices. As the valve narrows sharply towards the ends, an accurate measurement of the striae becomes more difficult.

N. lorenziana is only occasionally seen on the saltmarsh, and in very small numbers. Only on one occasion (July 1983 at site 1) was this species observed as a dominant member of an assemblage. This was at a time when the salinity was at its highest ever recorded at this site. The other co-dominants of the assemblage at this time were: Rhopalodia operculata and Mastogloia smithii.

FAMILY: 'SURIRELLACEAE

GENUS: Surirella

Surirella ovata Kütz PLATE 16 Fig.12

sensu Hustedt (1930) p.442, Fig. 863-864

Length: 18 µm - (31.33 µm ± 3.67 µm) - 67 µm

Width: 14 µm - (22.20 µm ± 2.31 µm) - 34 µm

No. of aloe . . in 10 µm: 5 - (5.80 ± 0.31) - 7

As described in Hustedt (1930). The size ranges (the length and width measurements) were variable. This species was recorded in high numbers on the upper sandflat (Station IV), but has been observed at all sites along the transect. Highest numbers have been recorded in late autumn and winter months (Sept.-Jan).

DISCUSSION

Two main features emerge from the descriptions just given: one is the large variety of taxa identified, and second is the enormous variation in morphology that can be observed for any single taxon. How can such diversity be accounted for?

First consider the former. The identification of a large number of different genera has been observed in other estuarine studies (Round 1960, Gargari 1980). Perhaps one explanation is that constantly changing conditions provide a large number of microhabitats. Hence there is a greater potential for the exploitation of a larger number and variety of niches by a wide range of taxa.

Intraspecies variation can be explained in more than one way. The initial step is to try and establish if morphological variation is an expression of genotypic, phenotypic, or environmental variation. First consider the division cycle of the diatom cell. Following auxospore formation the diatom undergoes a series of vegetative divisions. This leads to a gradual reduction in the size of the diatom valve. Cox (1984) suggests that in addition to reduction in valve size, there occurs a concurrent change in valve outline, which can be observed when sampling in the field.

This reduction in cell size could account for the temporal changes observed in valve length, as in the case of Amphora ovalis var. libyca, or Nitzschia hungarica. The decrease in valve length and change in valve shape with time could just be a reflection of the division cycle.

However this does not account for spatial differences in morphological variation of a single species. Why for example, do small sized valves of Nitzschia tryblionella var. levidensis occur on mound sites along the saltmarsh,while large sized valves are observed at the pool sites? This could be more of an effect of environmental stress. When a diatom species is occupying an area at the extreme of its niche, only certain extreme morphological forms will tolerate the stressful environmental conditions.

Why do larger diatom frustules and very delicately silicified cells inhabit coarse disturbed sediments in the sandflat, and generally smaller sized cells are found in the finer sediment of the saltmarsh? Could this be a response to the environmental limitations imposed by the habitat?

Finally one must consider differences in growth rate. Why do some taxa grow regularly in a cyclic pattern each year, while others which are rare, suddenly bloom in one month and rapidly disappear again. There are those species whose numbers rise and fall more gradually over a period of 3 years or more. It is tempting to interprete varying growth rates in terms of each taxons competative ability as defined by the differential equations of Lotka and Volterra (1925-1926 from Odum 1971). However it would be dangerous to apply this model beyond the theoretical scope for which it was intended.

The selection pressures caused by the abiotic and biotic environment, may give rise to two types of growth strategies. The r- selected taxa, are those opportunist forms which grow rapidly after a sudden change in the physical environment. Take for example seasonal events which trigger a sudden change in the physical conditions of a microhabitat : a storm tide, a dry day which causes the interstitial water to become hypersaline,

or a period of rainfall following conditions of hypersalinity. In each of these circumstances new conditions prevail, allowing rapid exploiters to invade and die as quickly as the new conditions appear. This situation is very similar to the rapid colonizers which only survive in the early uncrowded stages of succession as described by MacArthur & Wilson (1967 from Odum 1971).

K-selected species might be the larger sized cells. The division cycle is considerably slower, but they have better capabilities for competative survival under the equilibrium phase in succession when many different organisms co-exist (Odum 1971).

It is unfortunate that the different types of variation encountered has been described in only 70 taxa. This is by no means a comprehensive list of the diatom taxa observed at Berrow. A more detailed species list is given in Appendix A. In addition to these diatom species, far more work on the taxonomy of the following genera is required: Amphora, Navicula, Nitzschia, Gyrosigma, Pleurosigma and Stauroneis.

Thus possible sources of abiotic variation can arise in many different ways, and the response and expression of morphological variation differs from species to species. It is necessary to emphasize at this point, that all the above explanations for variation are pure speculation. This project has not attempted to confirm hypotheses made from observations in the field.

The next step is to attempt to understand and establish what the possible causes of variability are. It is crucial to attempt to understand the causes and responses of variability both in the environment and in the

morphology of the diatom valve. Otherwise it would be very difficult to use diatoms as indicators of environmental conditions. It is also necessary to recognize morphological variation within a species if an accurate quantitative field sampling strategy is to be achieved.

PLATE 3

ORDER: ACHNANTHALES

FAMILY: ACHNANTHACEAE

GENUS: Achnanthes

Figs. 1-2 Achnanthes delicatula Kütz. hypovalve

Figs. 3-4 A. delicatula Kütz. epivalve

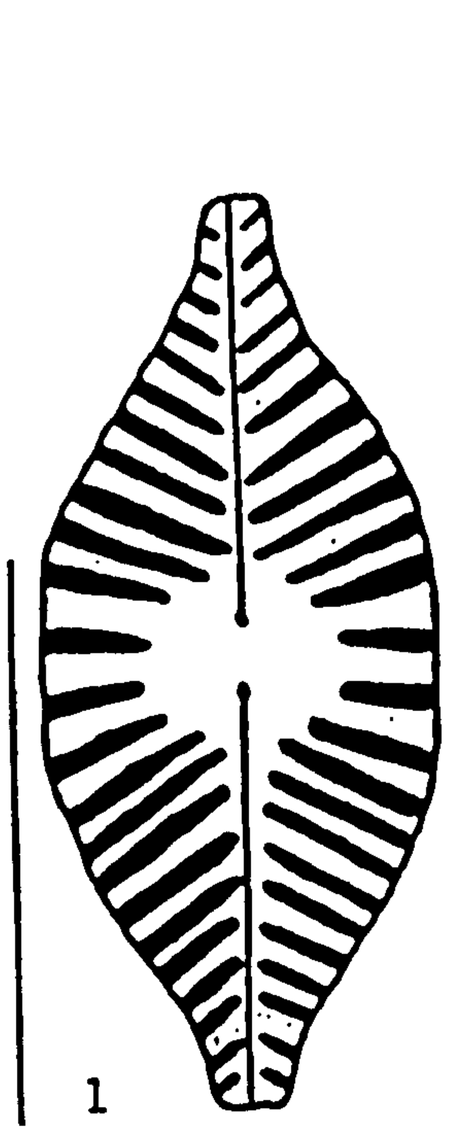
Fig. 5 A. lanceolata var. rostrata Hust. epivalve

Fig. 6 A. lanceolata var. rostrata Hust. hypovalve

Fig. 7 A. linkei Hust. epivalve

Figs. 8-9 A. linkei Hust. hypovalve

PLATE 3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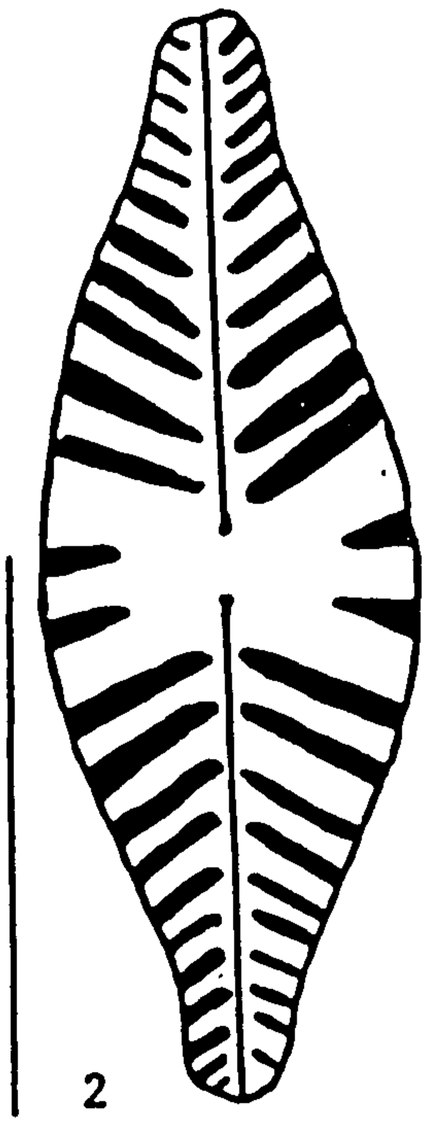
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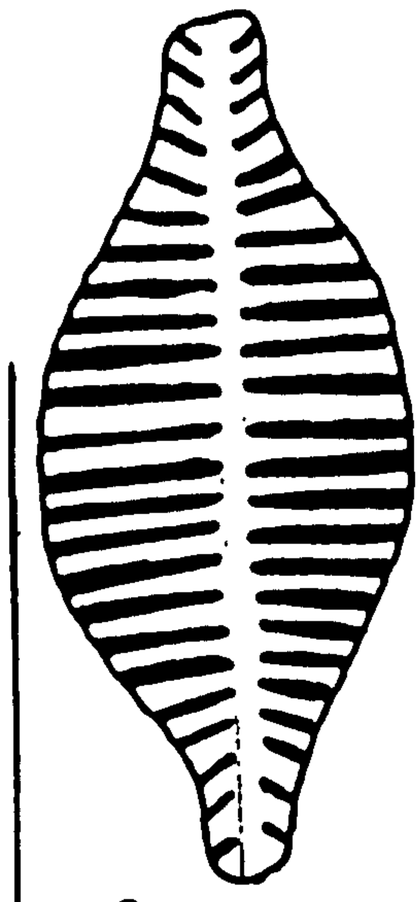
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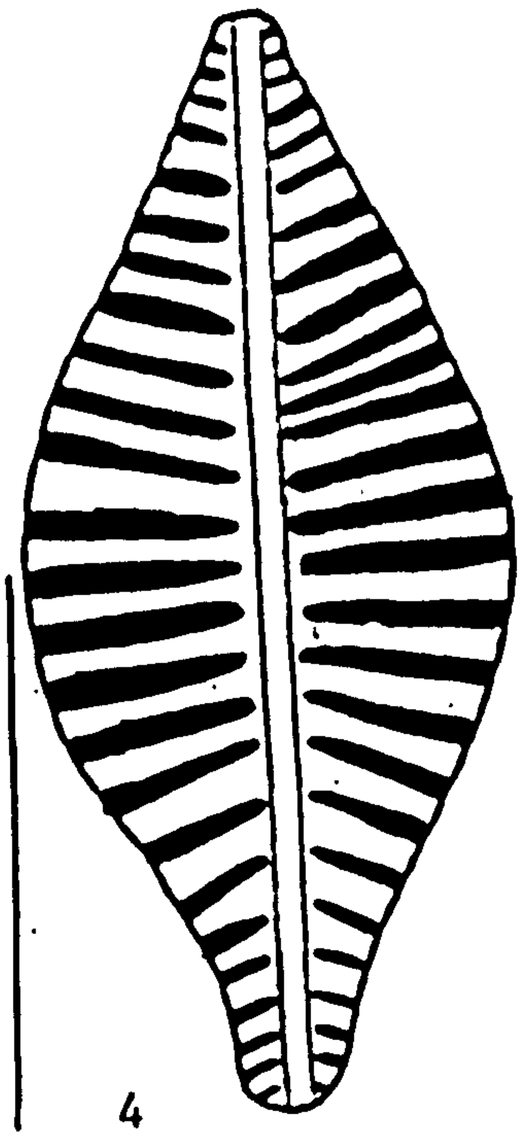
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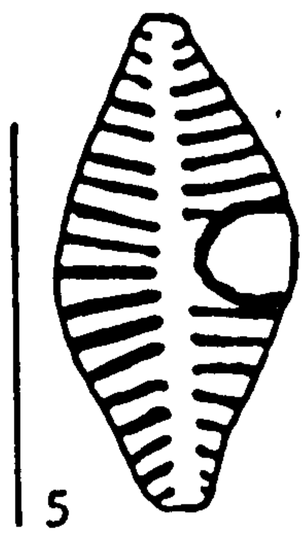
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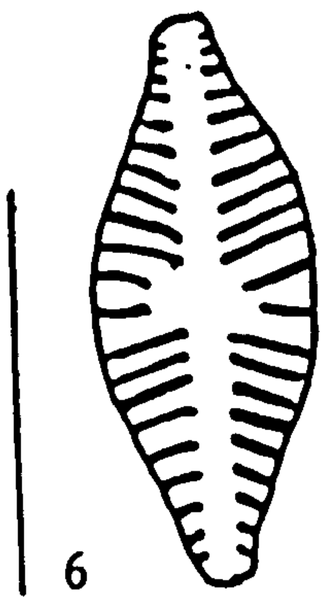
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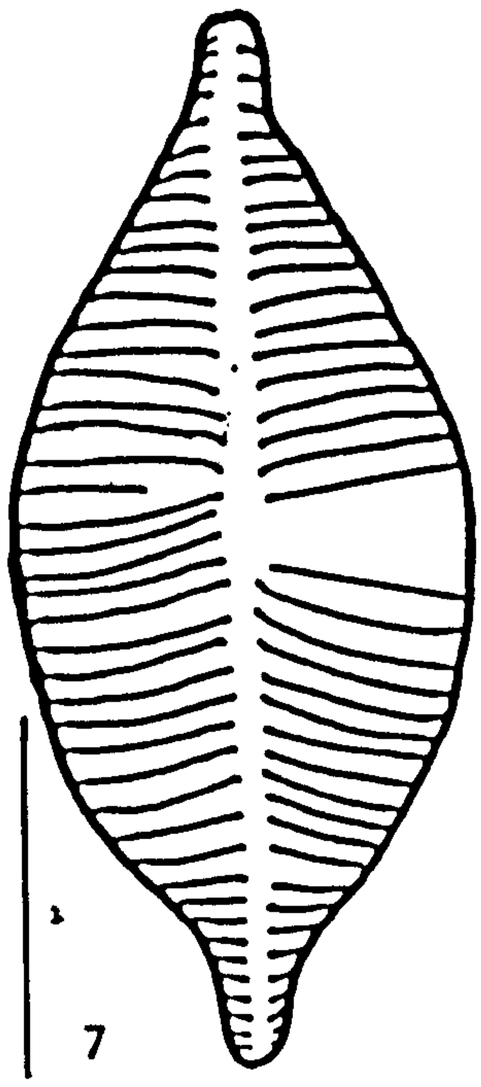
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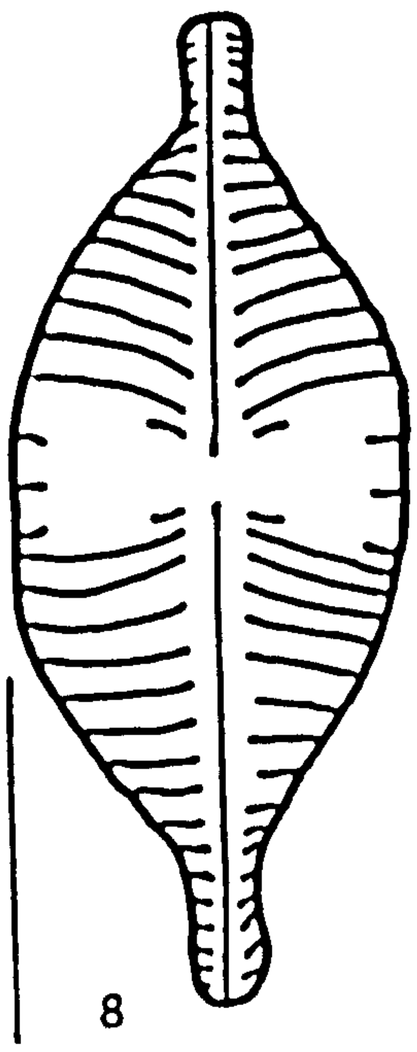
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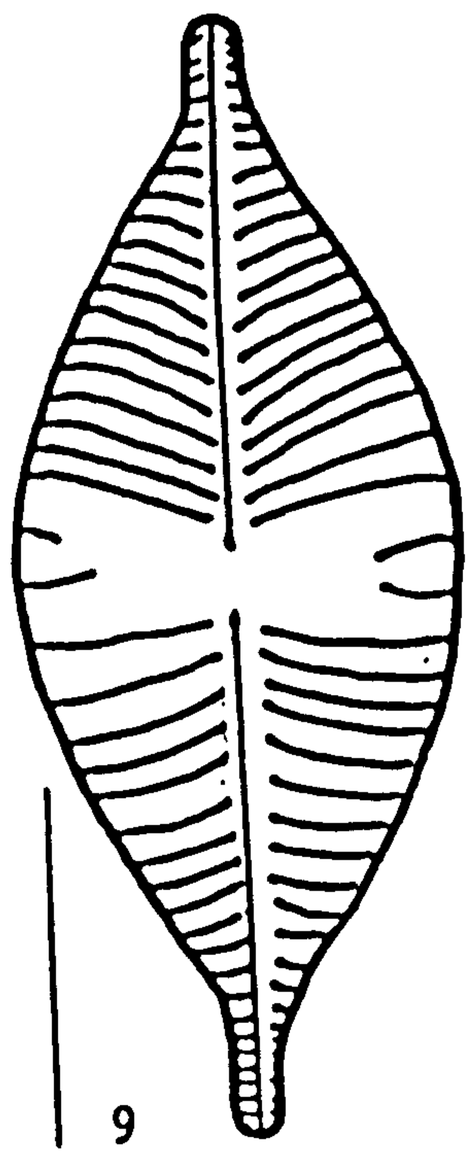
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PLATE 4

ORDER: NAVICULALES

FAMILY: NAVICULACEAE

GENUS: Mastogloia

Fig. 1 Mastogloia smithii var. lacustris Grun. undersurface showing loculate girdle band

Fig. 2 M. smithii var. lacustris Grun. valve view

GENUS: Pleurosigma

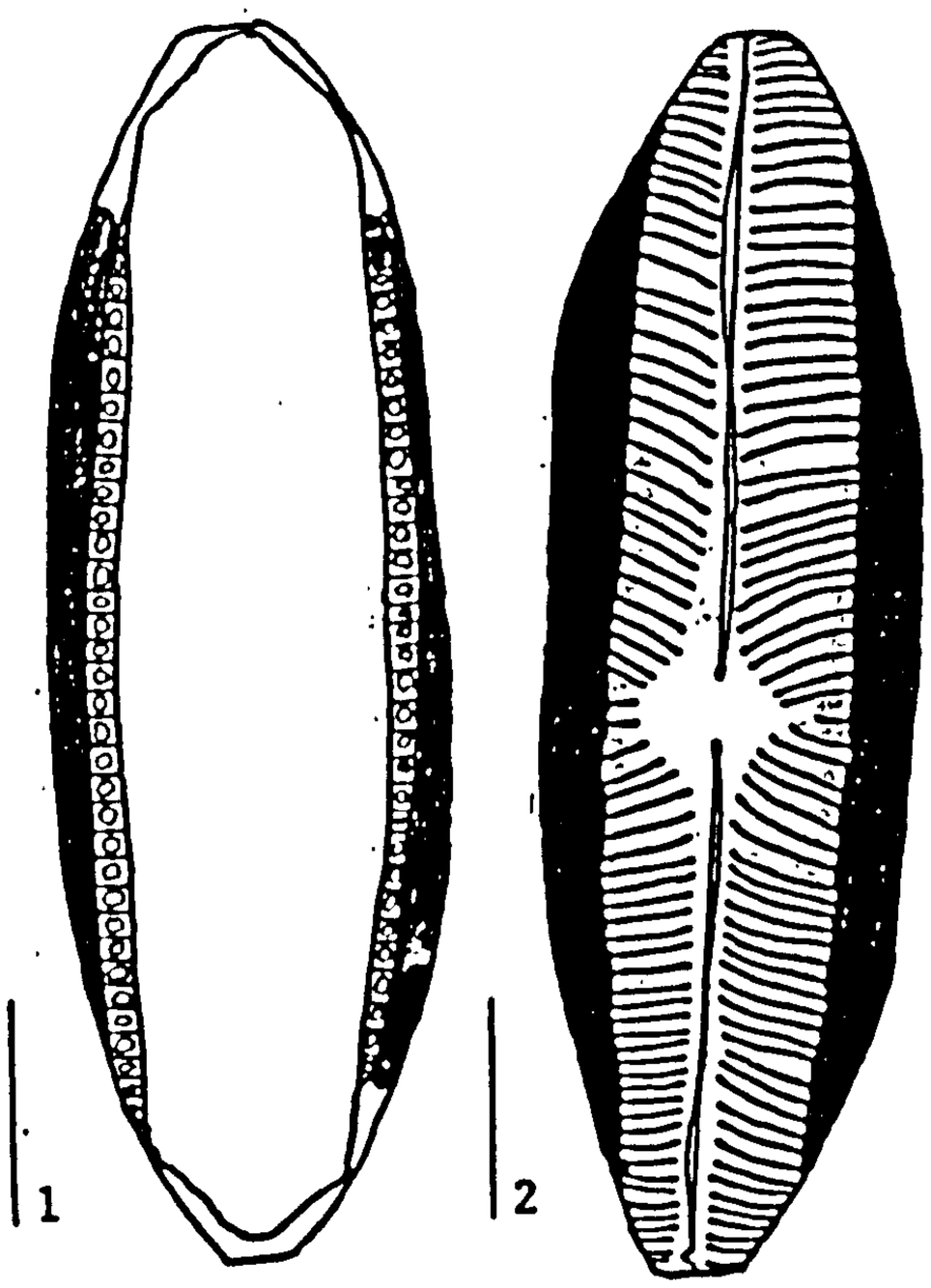
Fig. 3 Pleurosigma aestuarii (Bréb.ex Kütz) Smith

Fig. 4 Pl. angulatum Wm. Smith

Fig. 5 Pl. elongatum Smith

Fig. 5(a) & 5 (b) enlargement of Valve apices showing raphe ends of Pl. elongatum Smith

PLATE 4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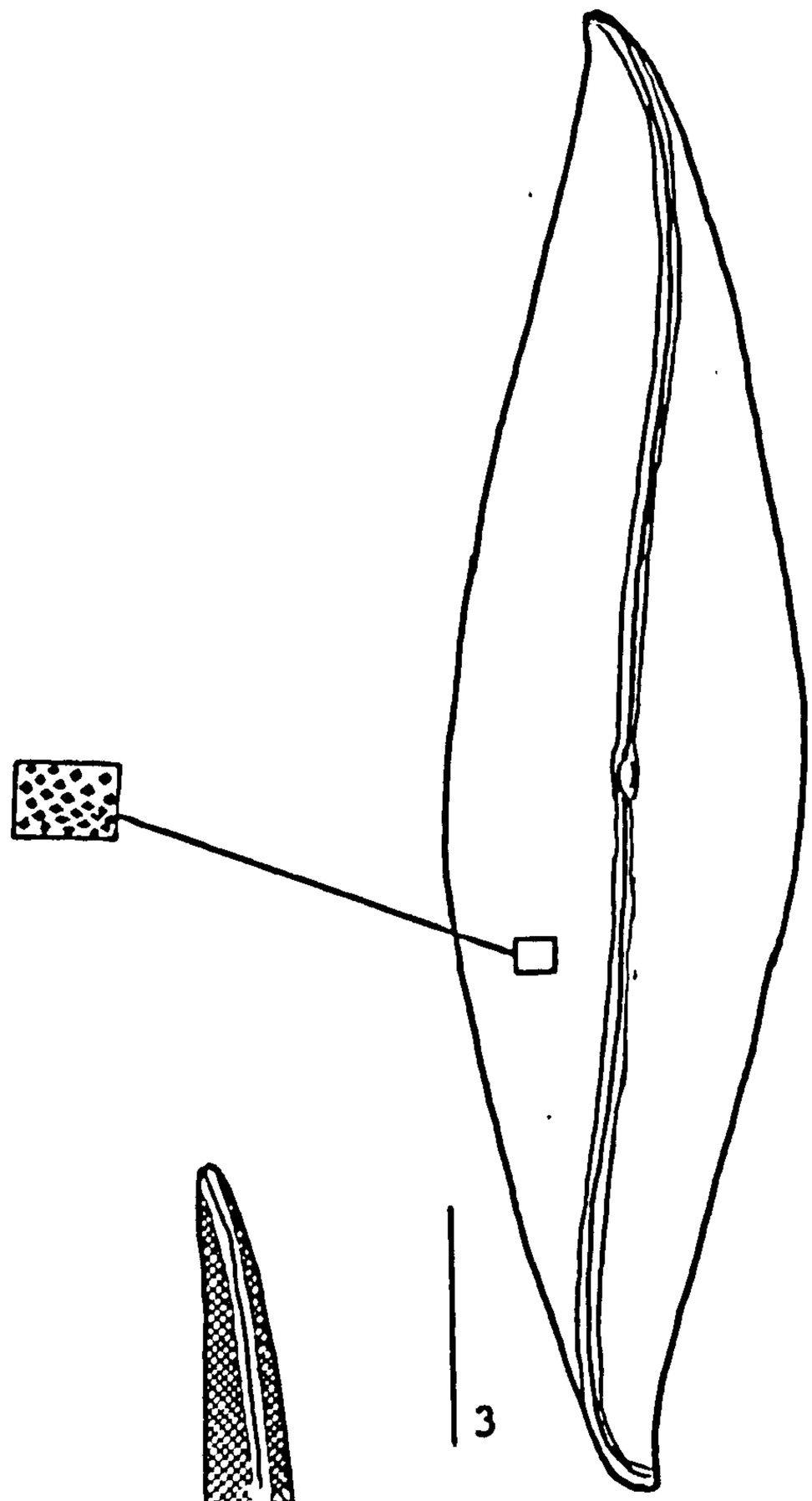
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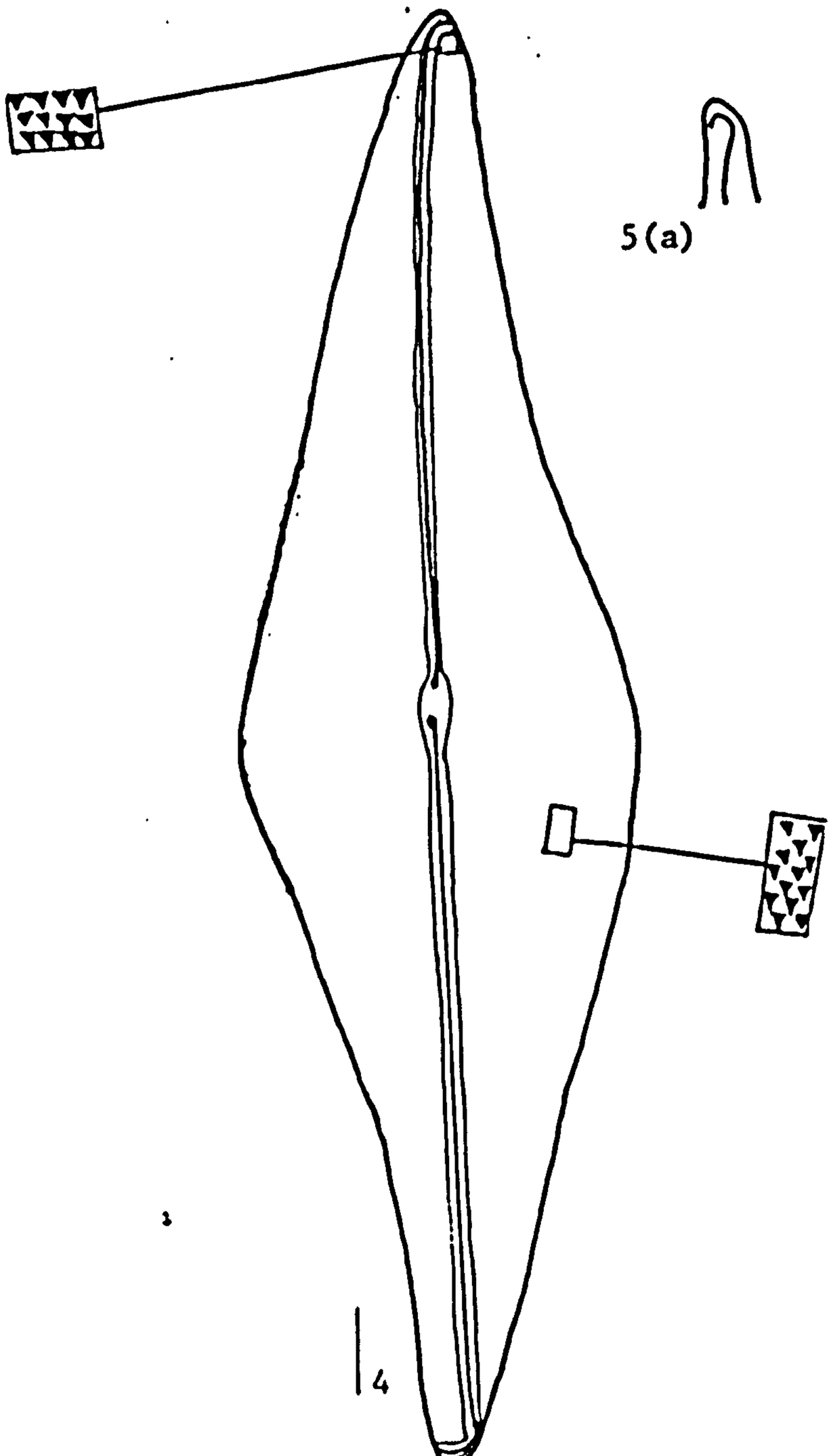
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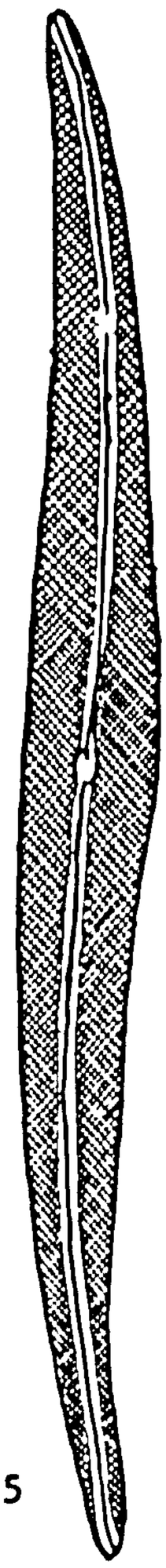
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5(b)

PLATE 5

GENUS: Gyrosigma

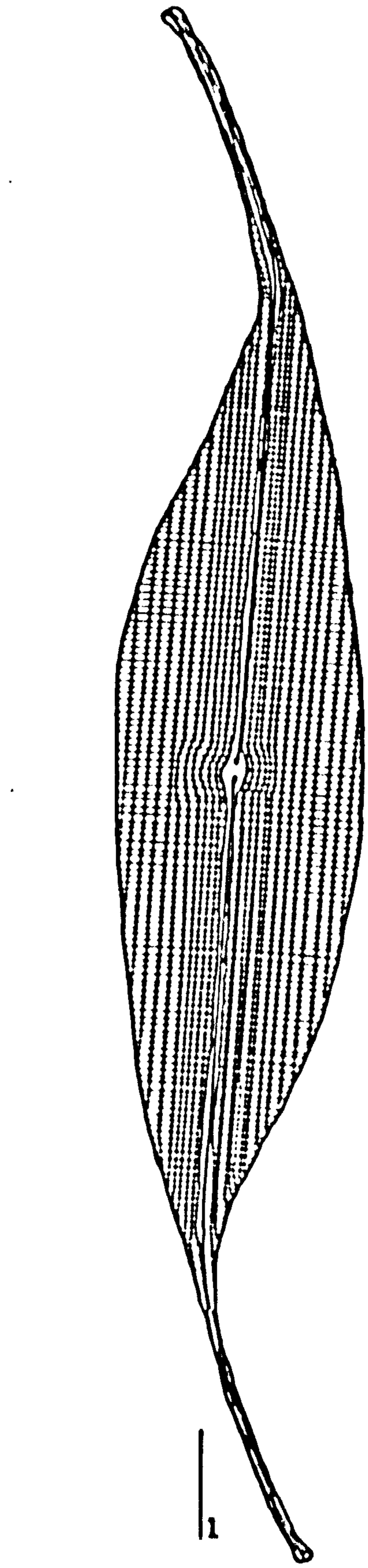
Fig. 1 Gyrosigma fasciola (Ehr.) Griffeth & Henfrey

Fig. 2 Gyr. peisonis (Grun.)Hust.

GENUS: Entomoneis

Fig. 3 Entomoneis paludosa var. hyperborea Grunow

PLATE 5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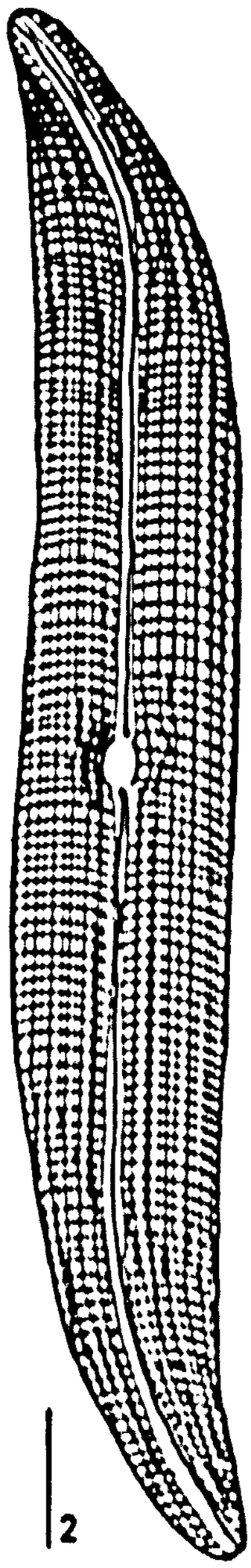
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3

PLATE 6

GENUS: Amphiprora

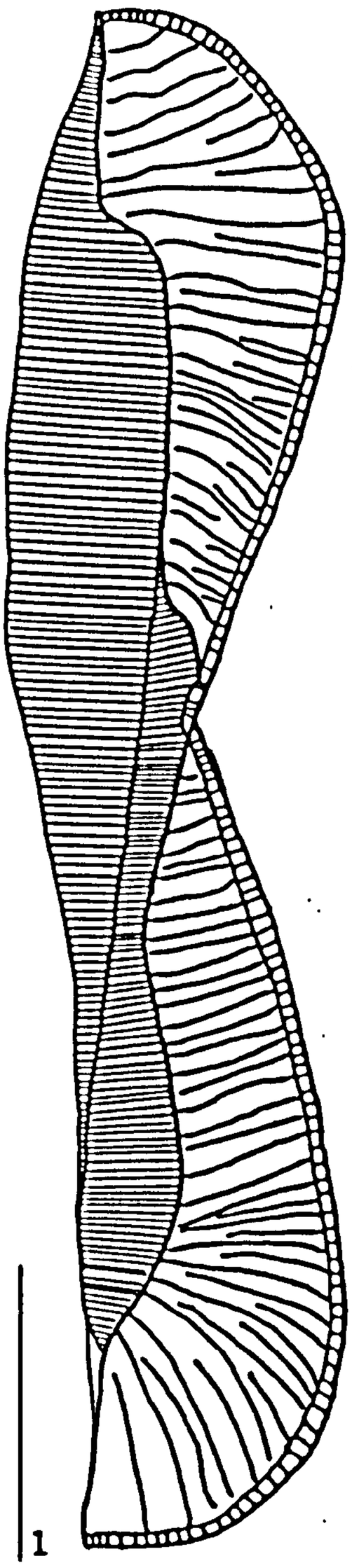
Fig. 1 Amphiprora paludosa Sm

Fig. 2 Amphiprora paludosa var. duplex Donkin

Fig. 2a A. paludosa var. duplex Donkin (frustule)

GENUS: Tropideneis

Figs. 3-4 Tropideneis sp nov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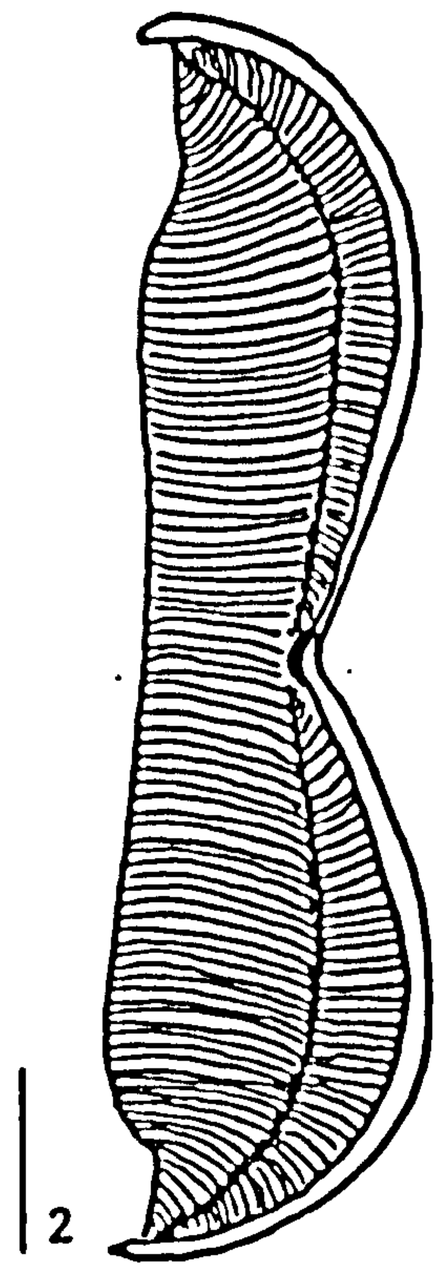
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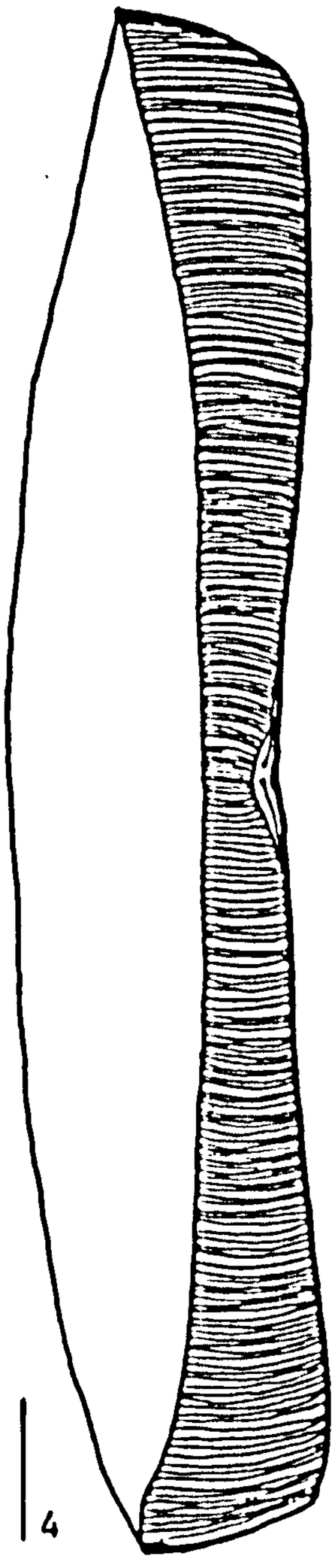

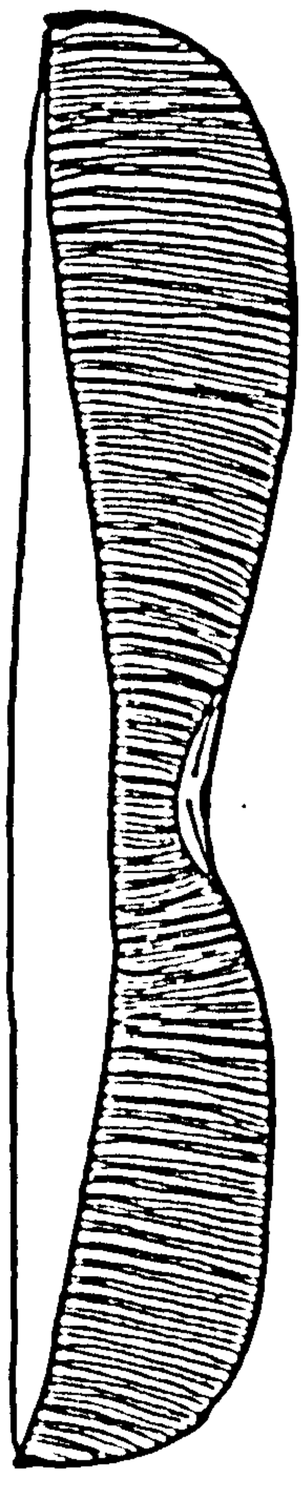
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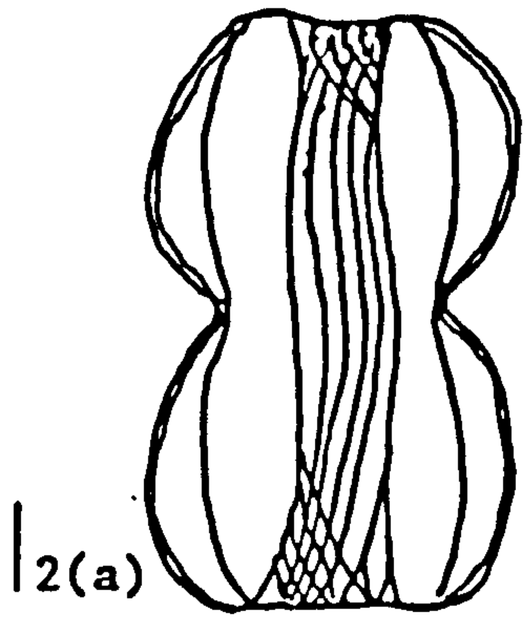
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PLATE 7

GENUS: Diploneis

Fig. 1 Diploneis elliptica Kütz

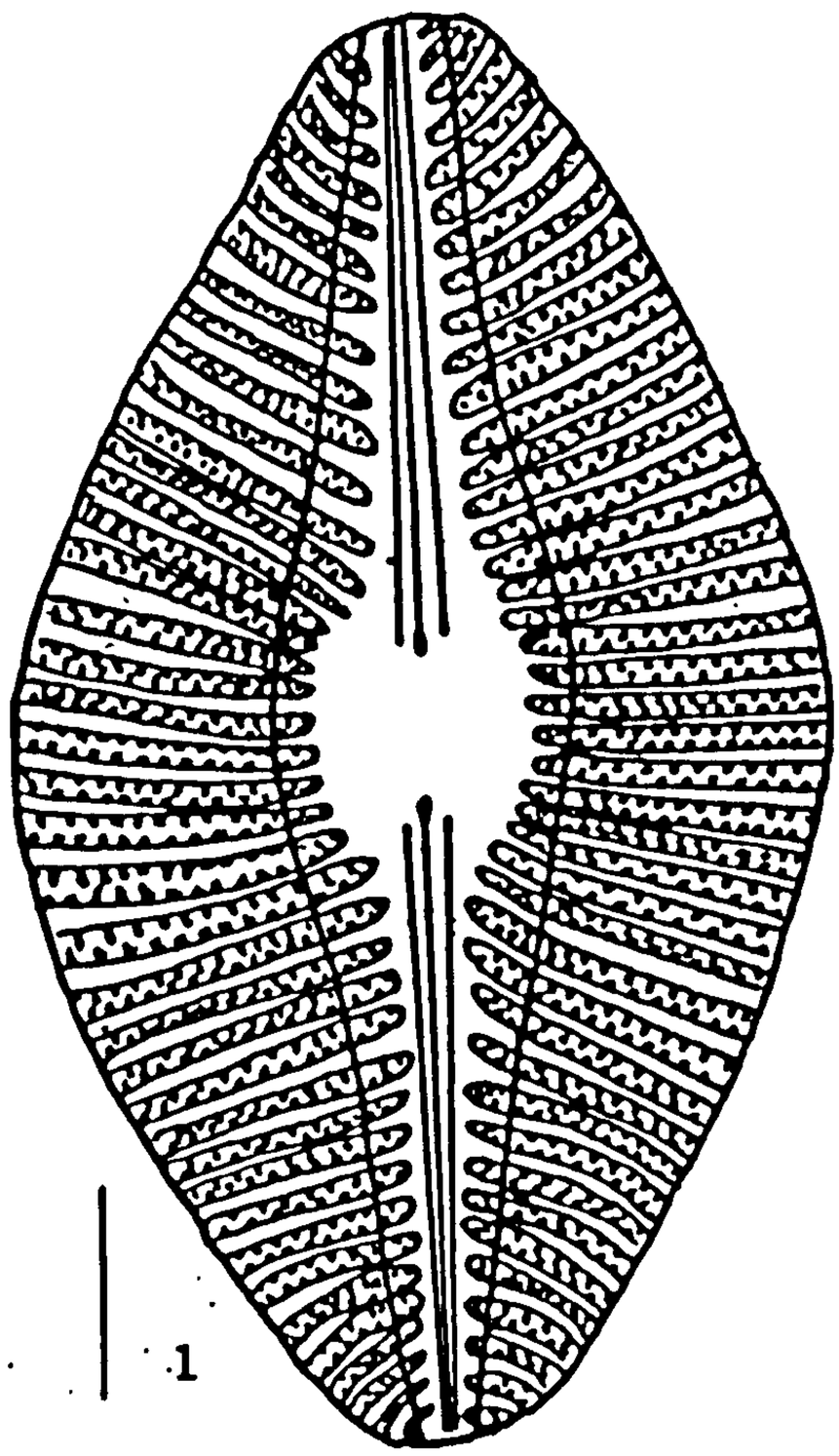
Fig. 2 Diploneis littoralis (Donkin) Cleve

GENUS: Stauroneis

Fig. 3 Stauroneis spicula Hickie

Fig. 4 Stauroneis amphyoxis var obtusa Gregory

Fig. 5 St. amphyoxis var. obtusa Gregory, in girdle view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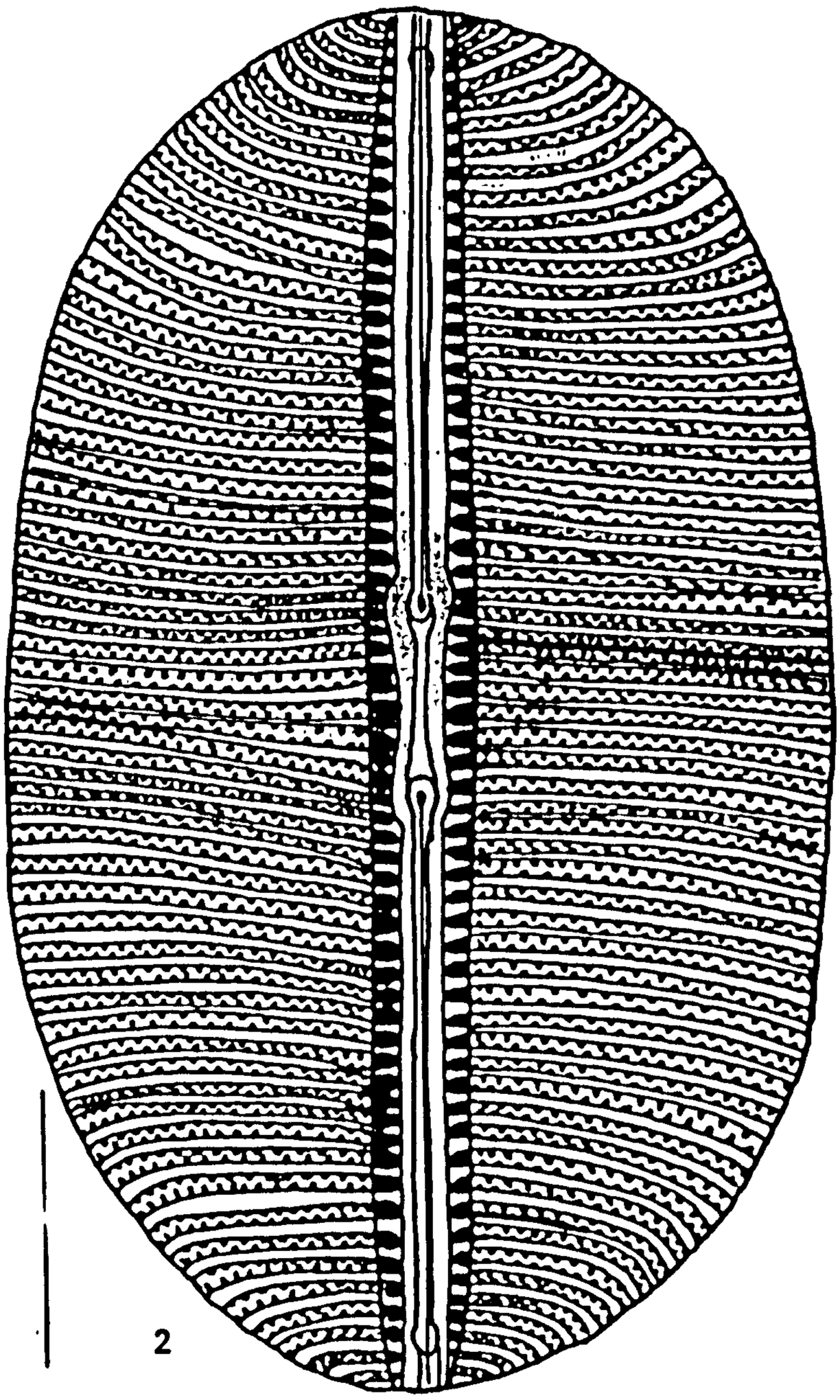
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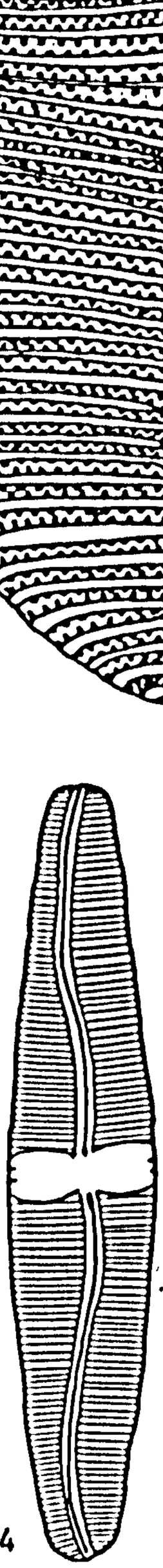
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5

PLATE 8

GENUS: Navicula

GROUP 1: Orthostichae

Figs. 1-4 Navicula cryptocephala Kütz

GROUP 2: Lineolatae

Fig. 5 Navicula cari Ehr.

Fig. 6 N. cari var.

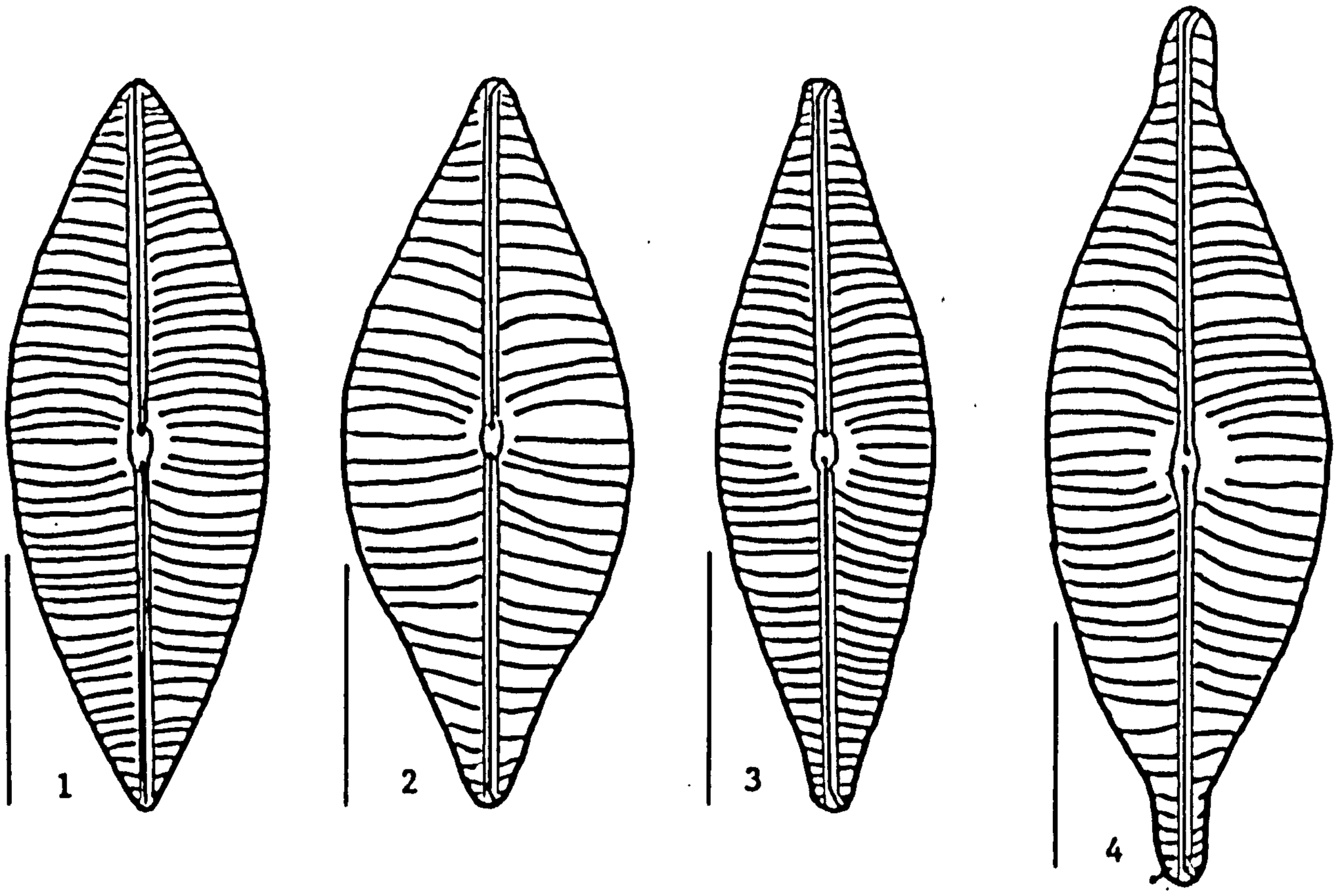
Fig. 7 N. cincta (Ehr.) Kützing

Fig. 8 N. digito-radiata (Greg.) Ralfs. in girdle view

Fig. 9 N. digito-radiata (Greg.) Ralfs.

Fig. 10 N. hungarica f. elliptica Schulz.

Fig. 11 N. hungarica f. elliptica in girdle view (live cell)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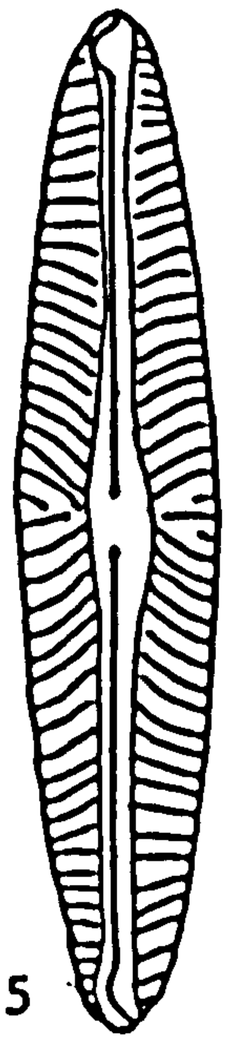
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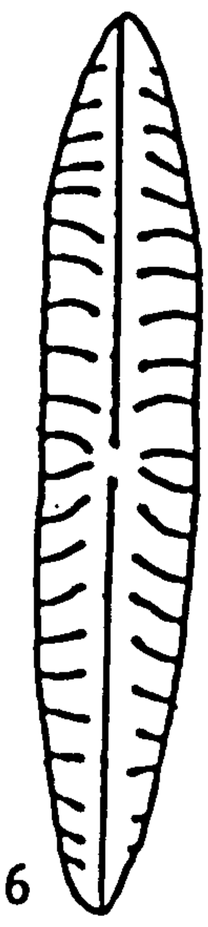
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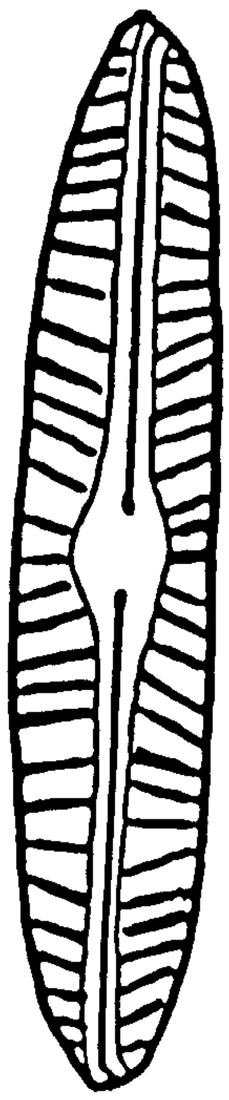
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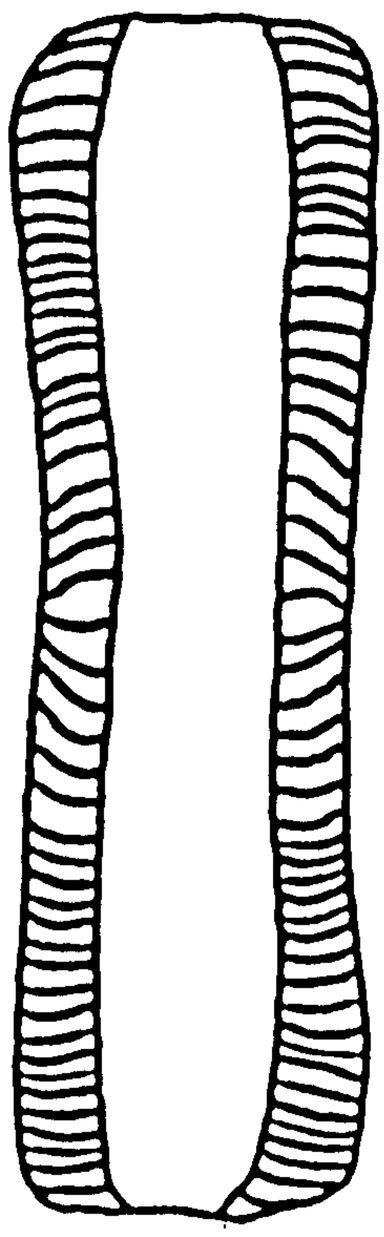
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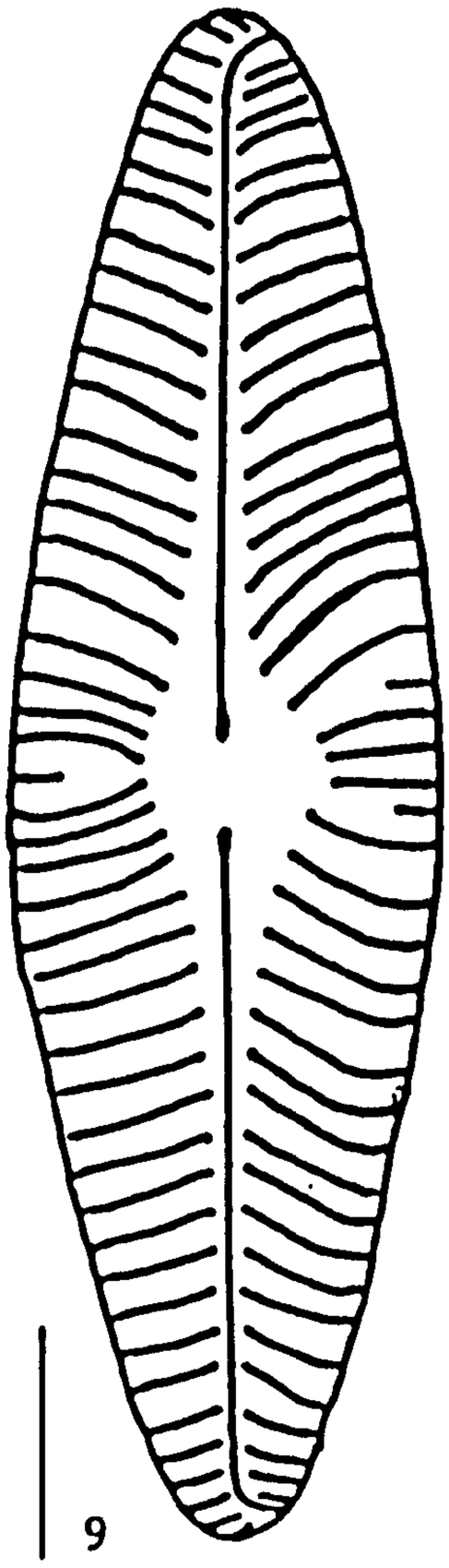
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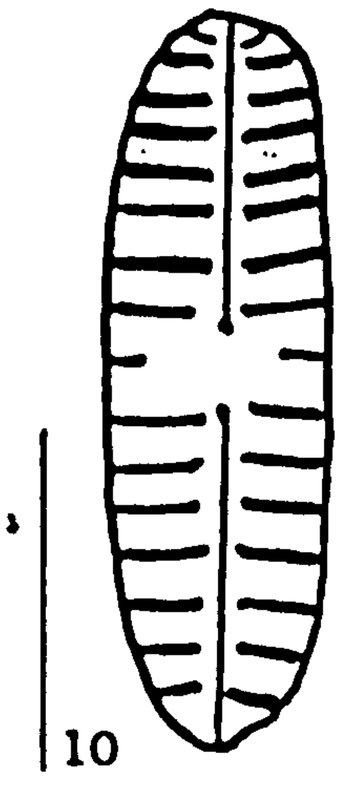
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11

PLATE 9

GENUS: Navicula

GROUP 2: Lineolatae

Figs.1-2 Navicula palpebralis Bréb. ex Smith

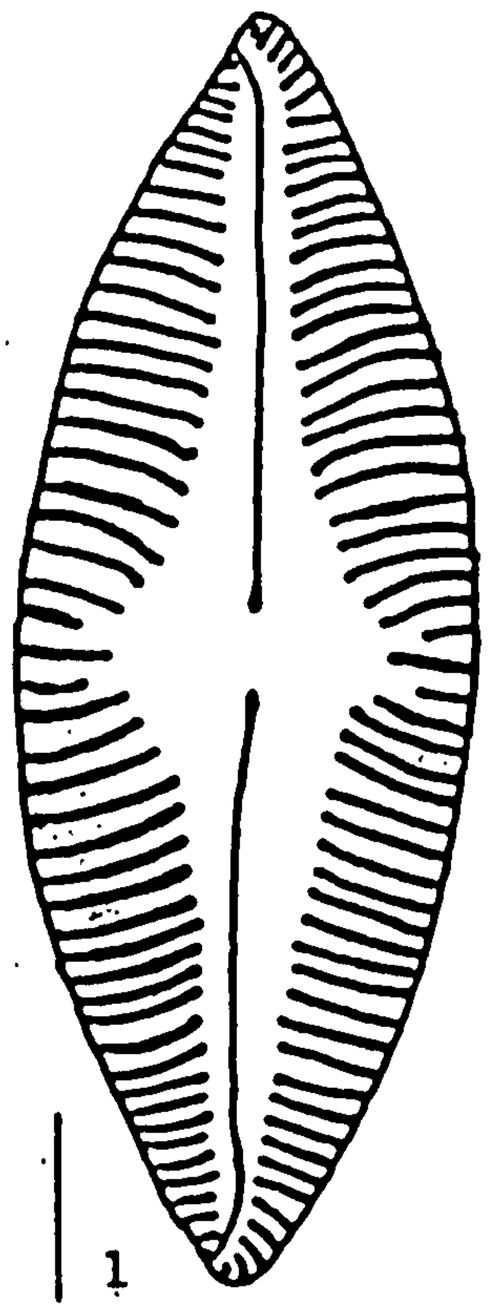
Fig. 3 N. peregrina (Ehr.) Kütz

Fig. 4 N. rostellata Kütz

Fig. 5 N. viridula Kütz focusing on upper surface of valve face

Fig. 6 N. viridula Kütz focusing on lower surface of valve face showing raphe ends

PLATE 9



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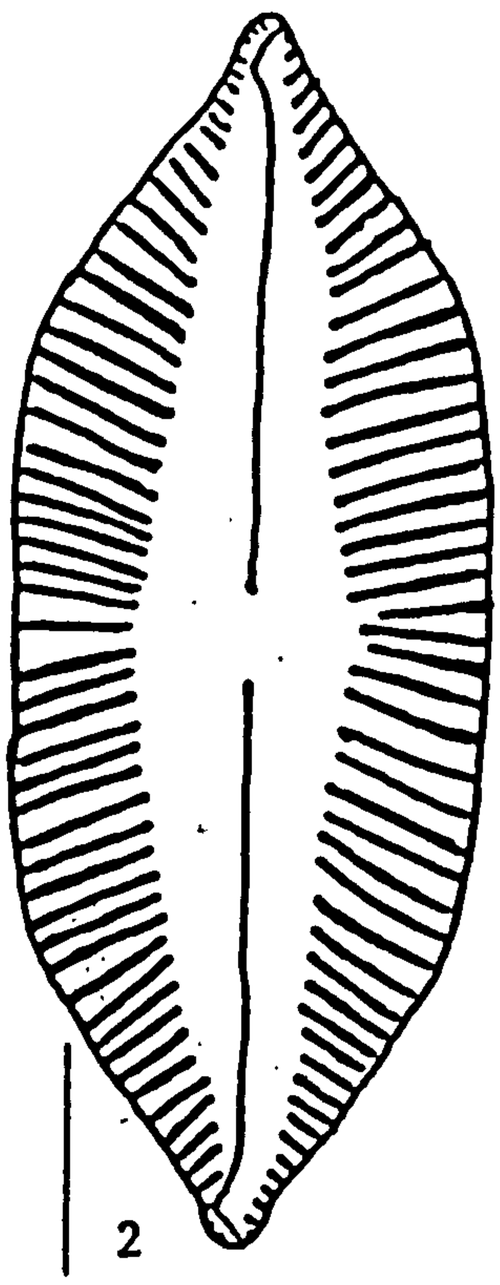

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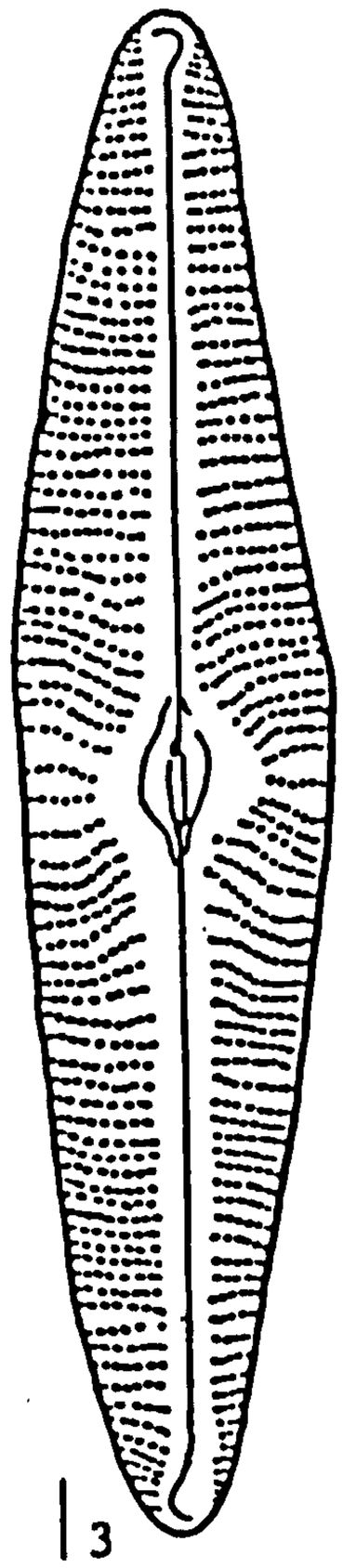

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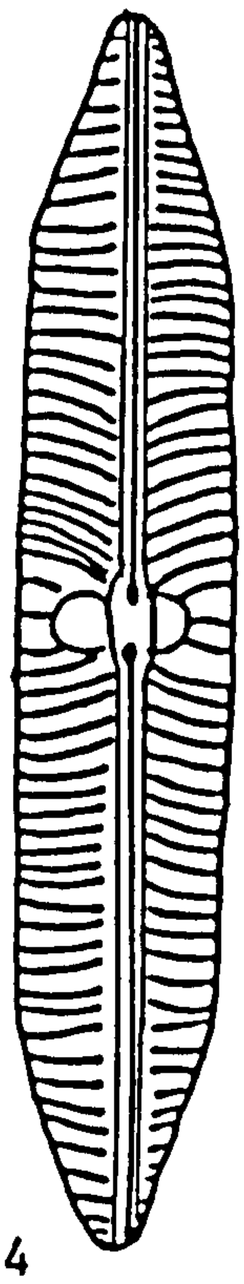

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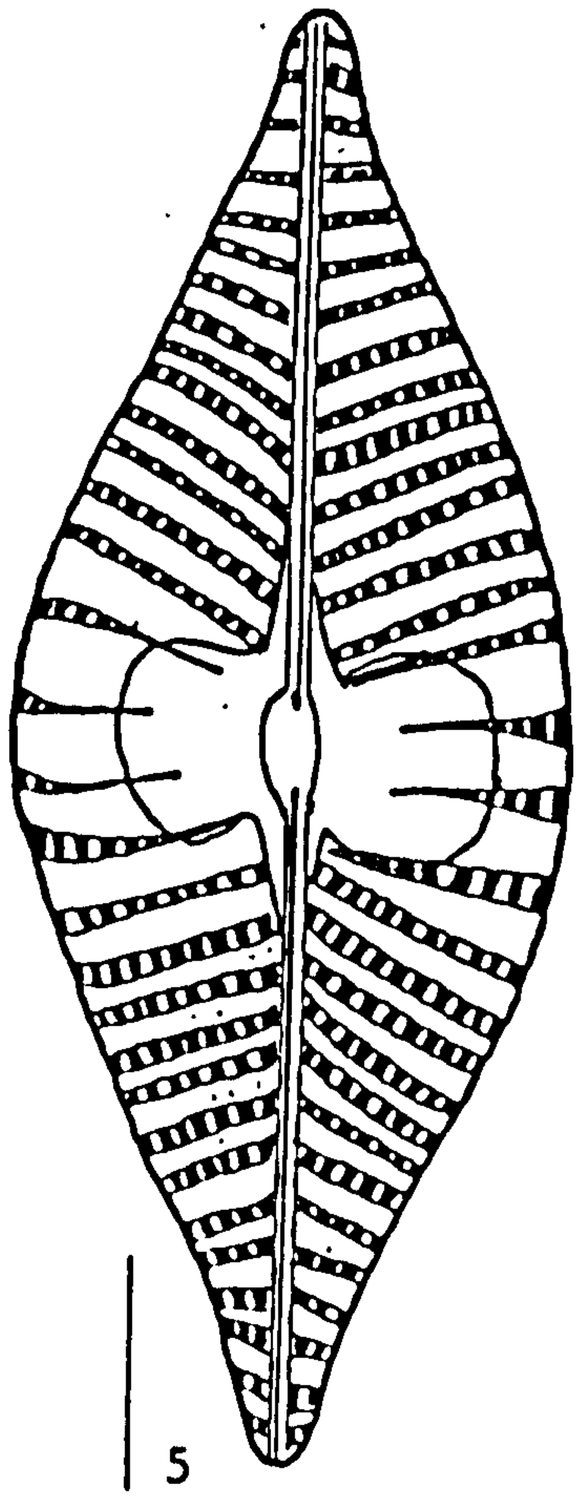

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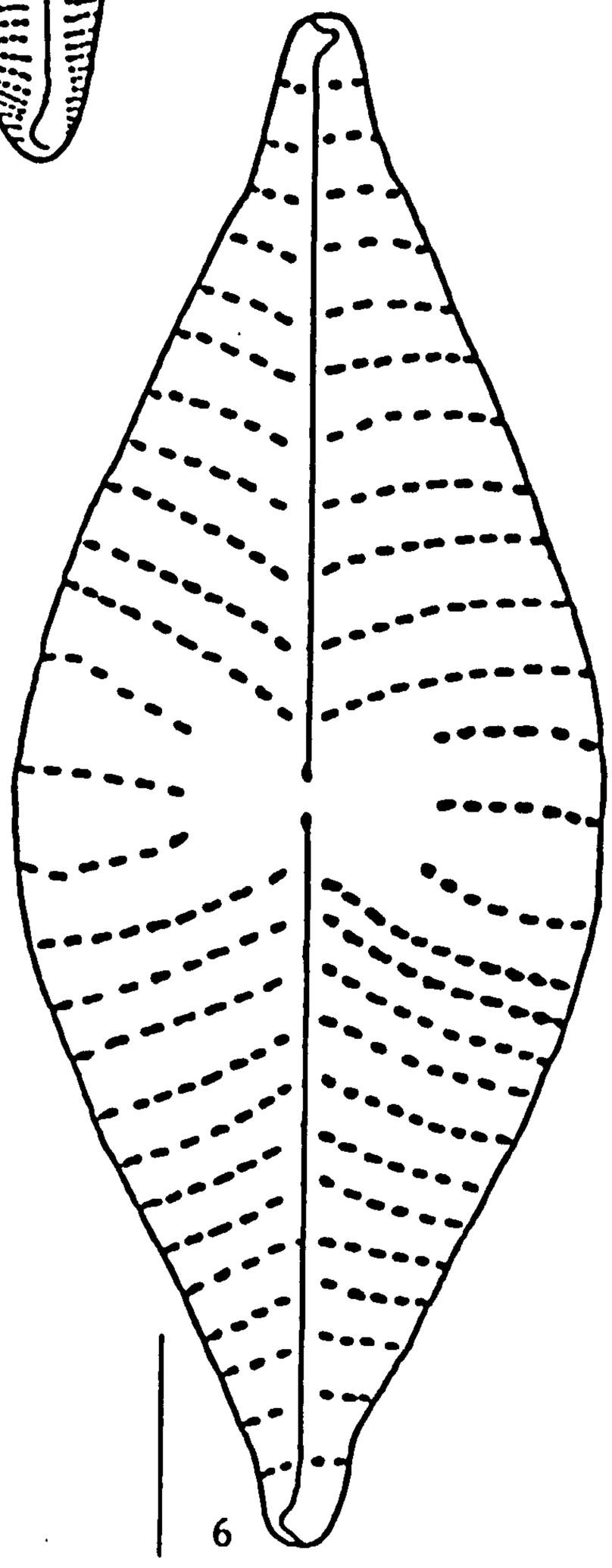


6

PLATE 10

GENUS: Navicula

GROUP 3: Retusae

Fig. 1 Navicula retusa Bréb.

Fig. 2 N. retusa Bréb. in girdle view

GROUP 4: Punctatae

Fig. 3 N. humerosa Bréb.

GROUP 5: Lyratae

Fig. 4 N. forcipata Grev.

Fig. 5 N. pygmaea Kütz

GROUP 6: Microstigmaticae

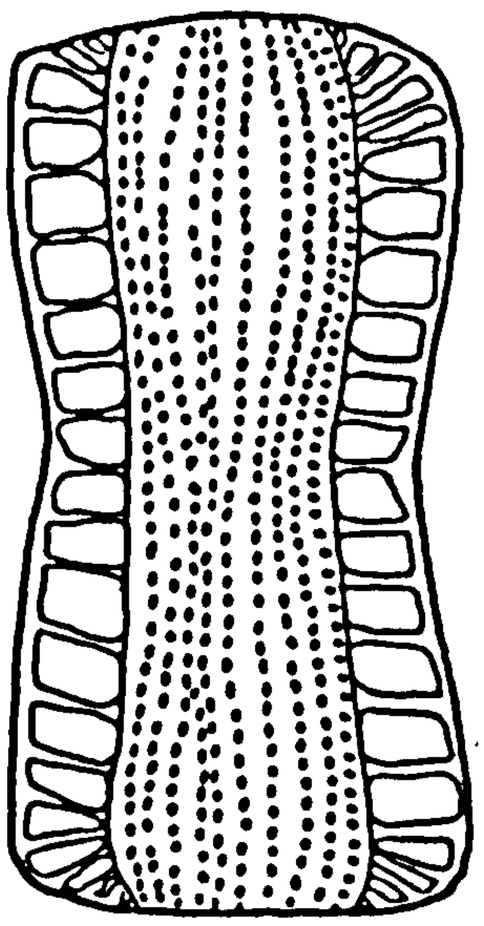
Figs. 6-9 N. protracta f. elliptica Gallik

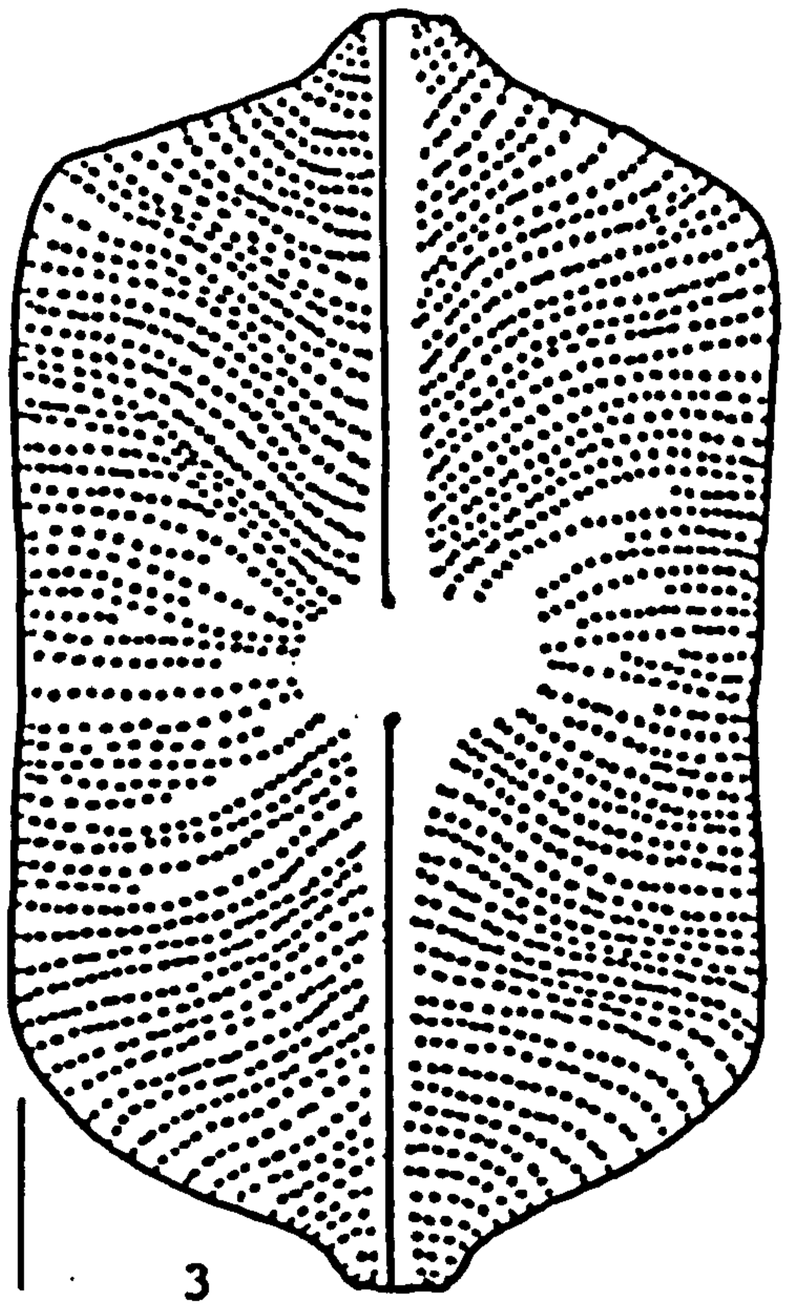
Fig. 10 N. protracta f. elliptica Gallik in girdle view

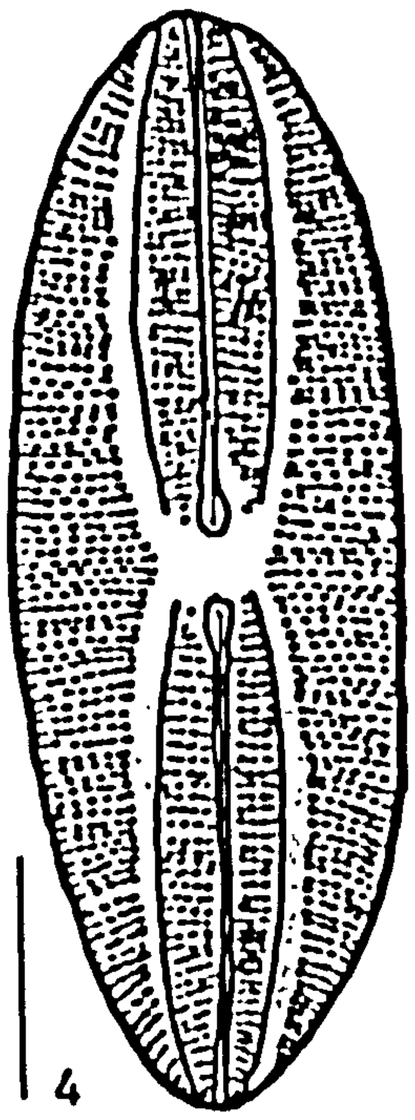
Fig. 11 N. scoliopleura Schmidt

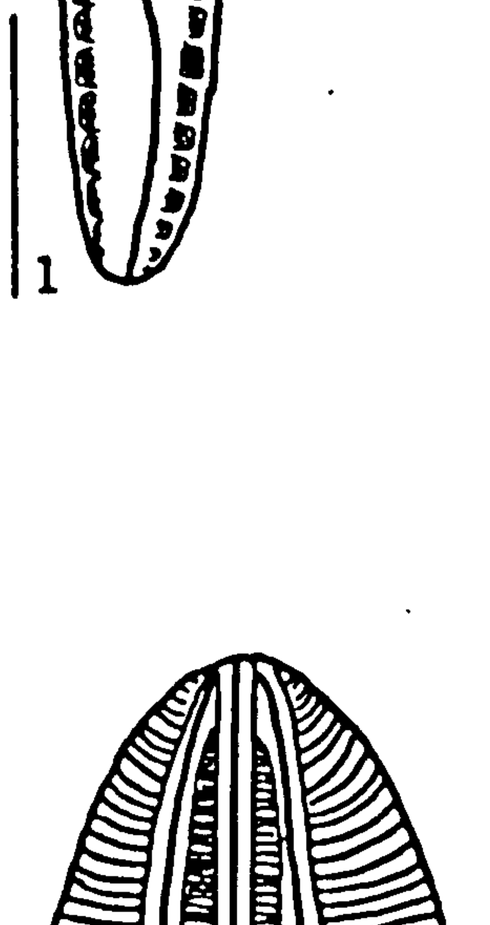
Fig. 12 N. scoliopleura Schmidt in girdle view

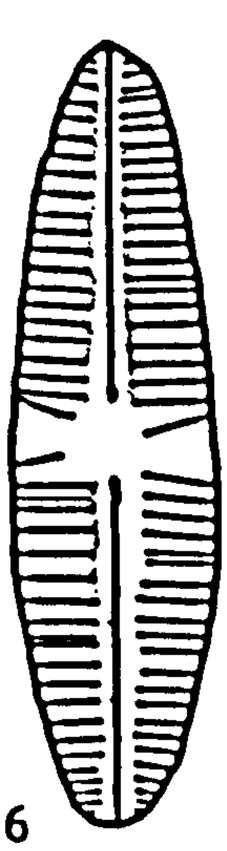
PLATE 10

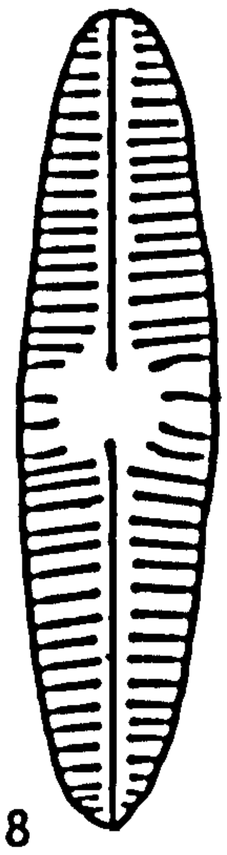


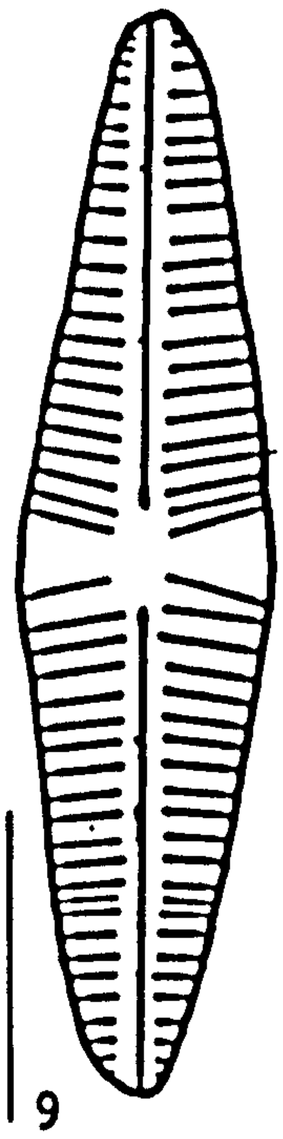


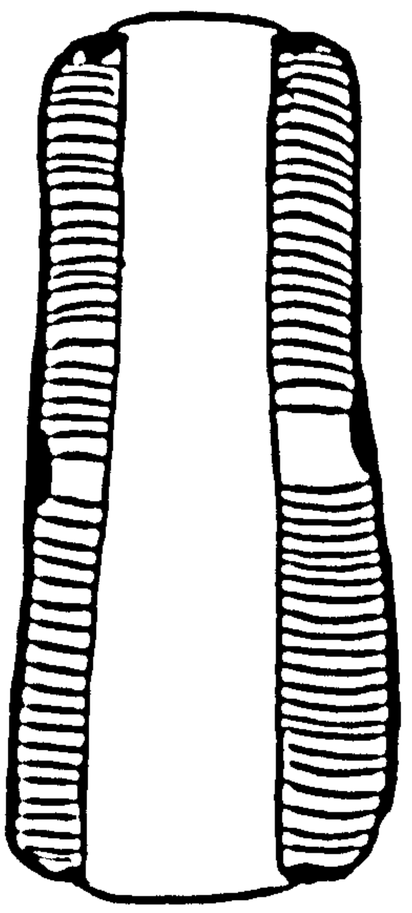


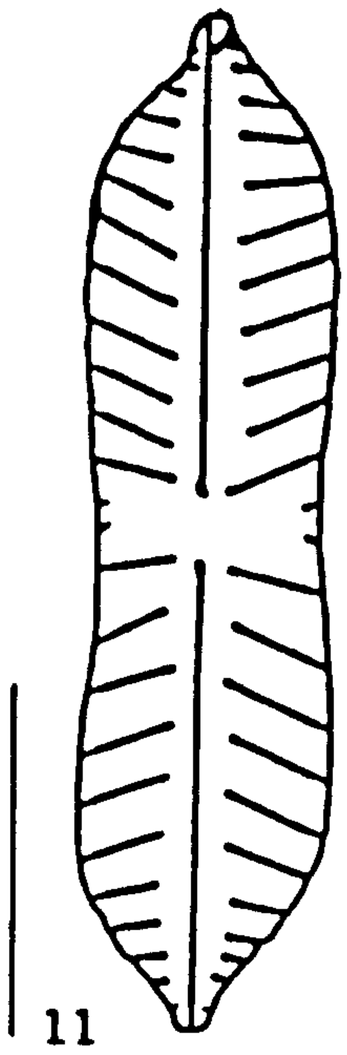












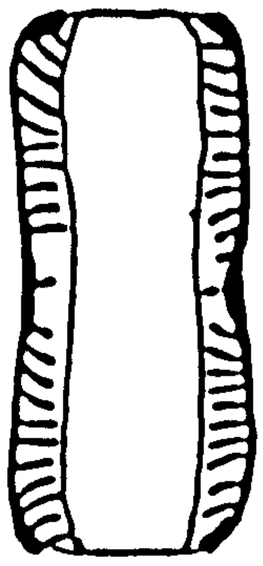


PLATE 11

GENUS: Caloneis

Fig. 1 Caloneis brevis (Greg.) Cleve

Figs. 2-3 C. limosa (Kütz) Patrick

Fig. 4-5 C. subsalina (Donkin) Hendey

Fig. 5(a) C. subsalina (Donkin) Hendey showing raphe end

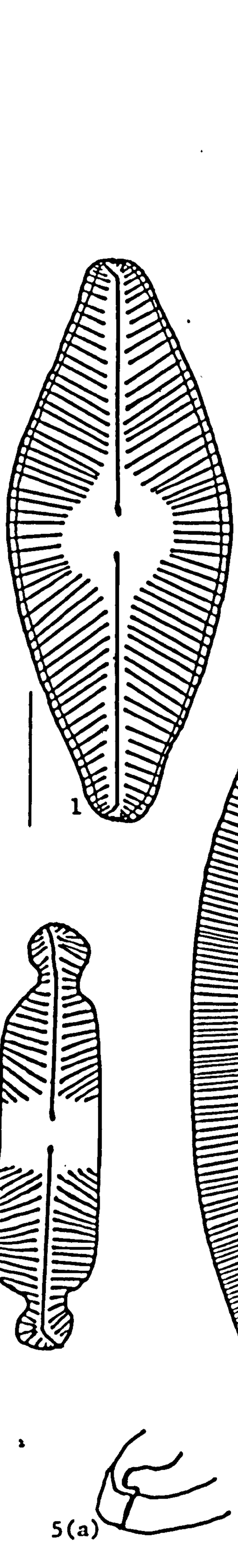
Fig. 6 C. westii (Smith) Hendey

Fig. 6(a) C. westii (Smith) Hendey showing raphe end

GENUS: Pinnularia

Fig. 7 Pinnularia lundii Hust.

PLATE 11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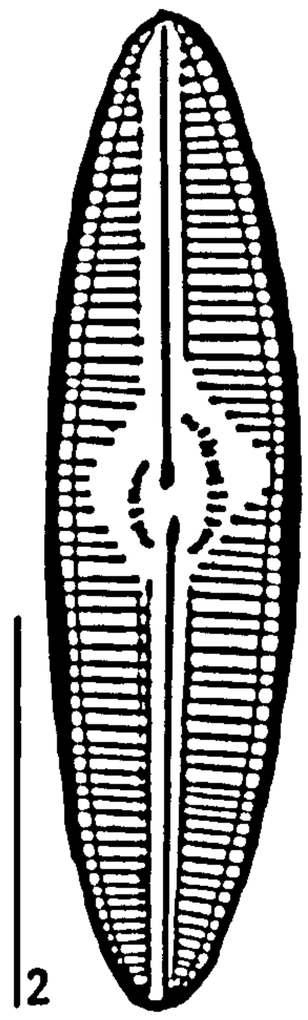
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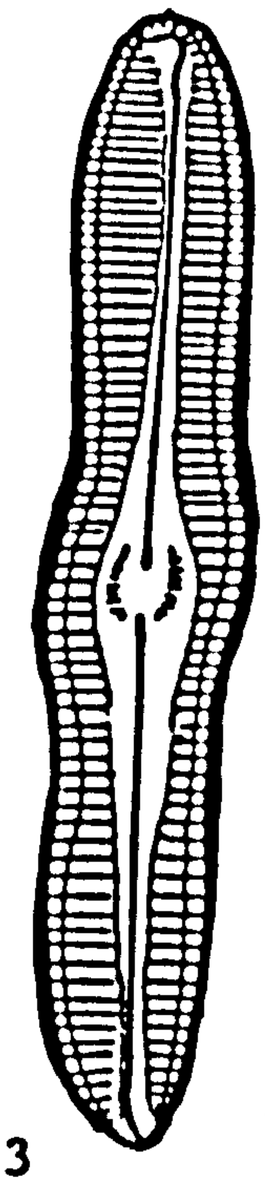
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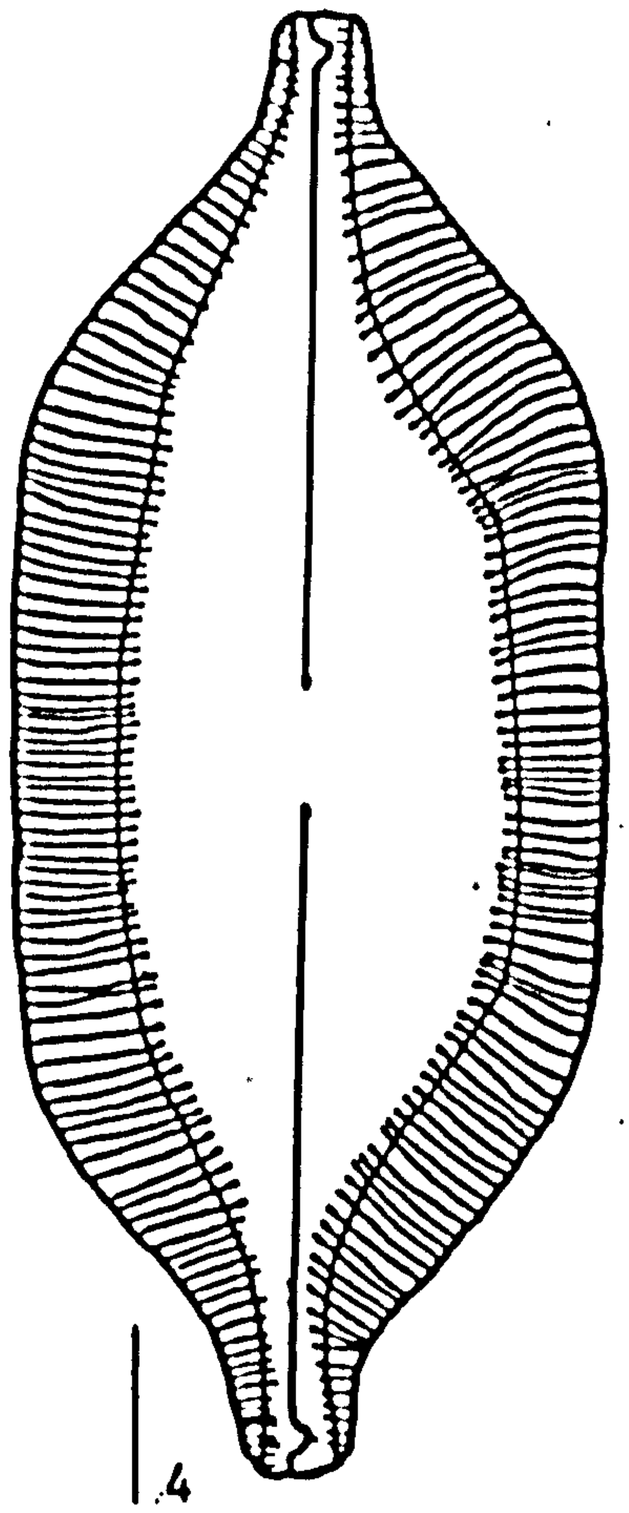
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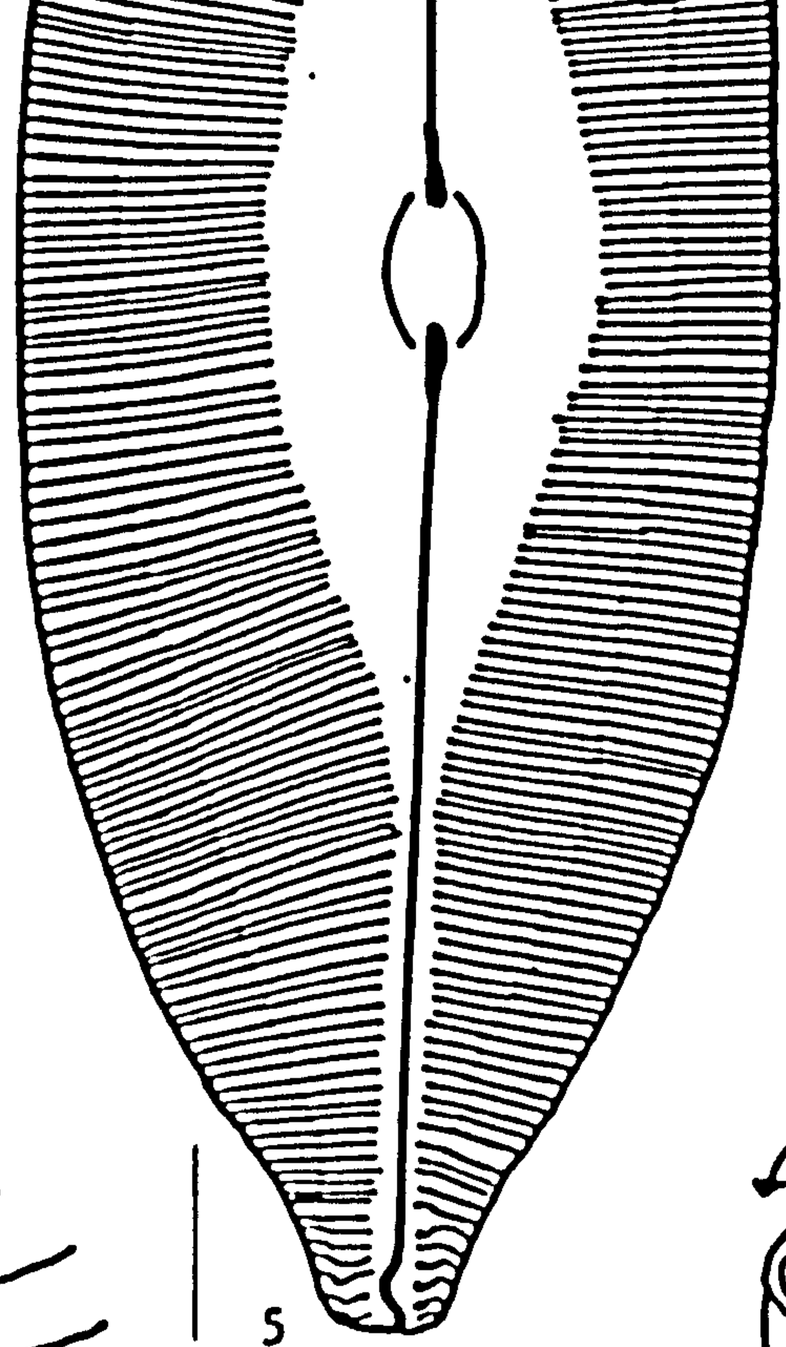
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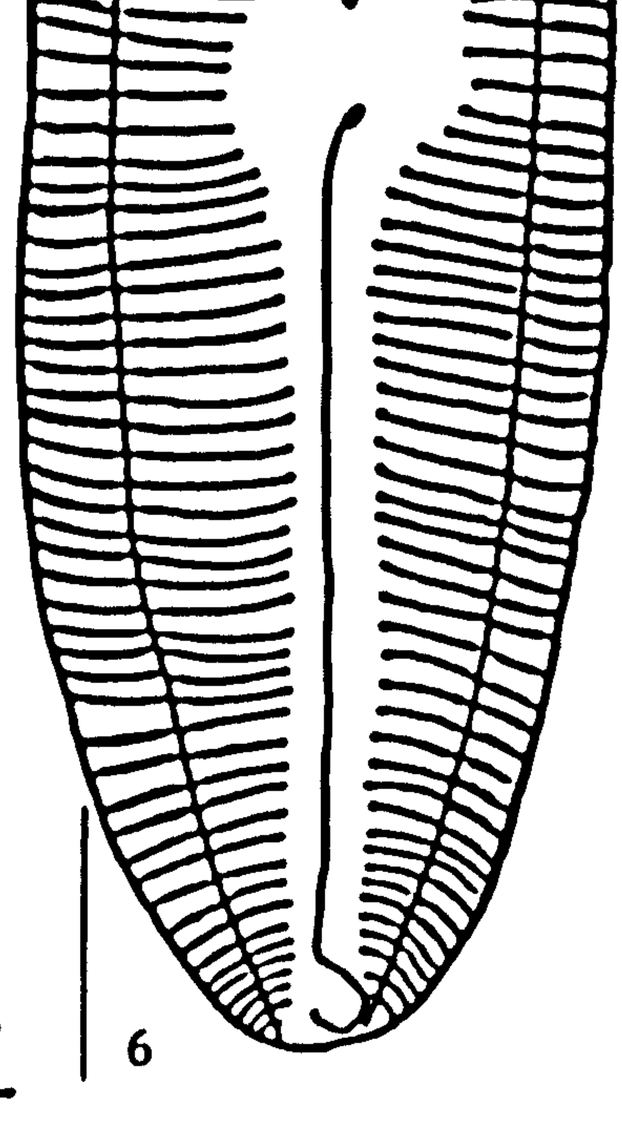
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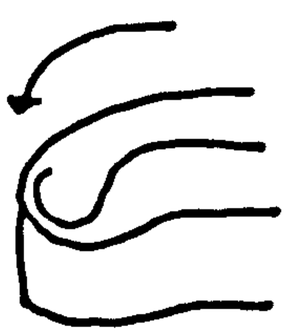

6(a)

PLATE 12

FAMILY: CYMBELLACEAE

GENUS: Amphora

Fig. 1 Amphora bacillaris Greg.

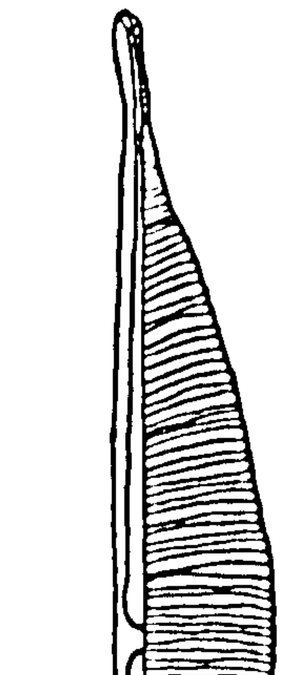
Fig. 2 A. exigua (Gregory) Cleve

Fig. 3 A. lineolata Ehr.

Fig. 4 A. ovalis var. libyca (Ehr.) Cleve

Fig. 5 A. proteus var. Impressa A.Cl. nach Brockmann

Fig. 6 A. pusio Cl.N. nach Cleve



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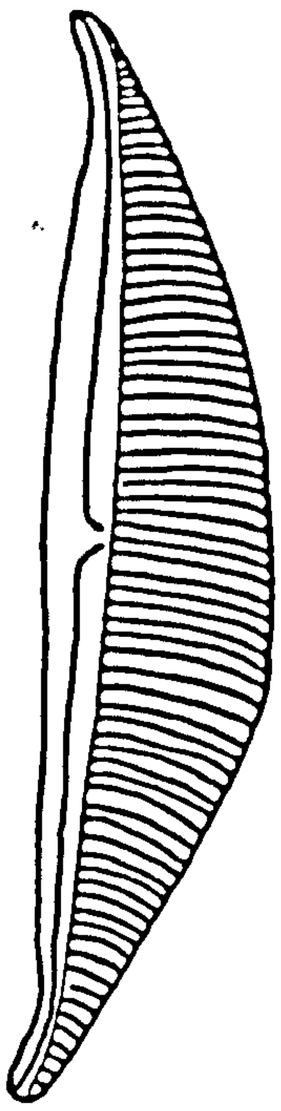

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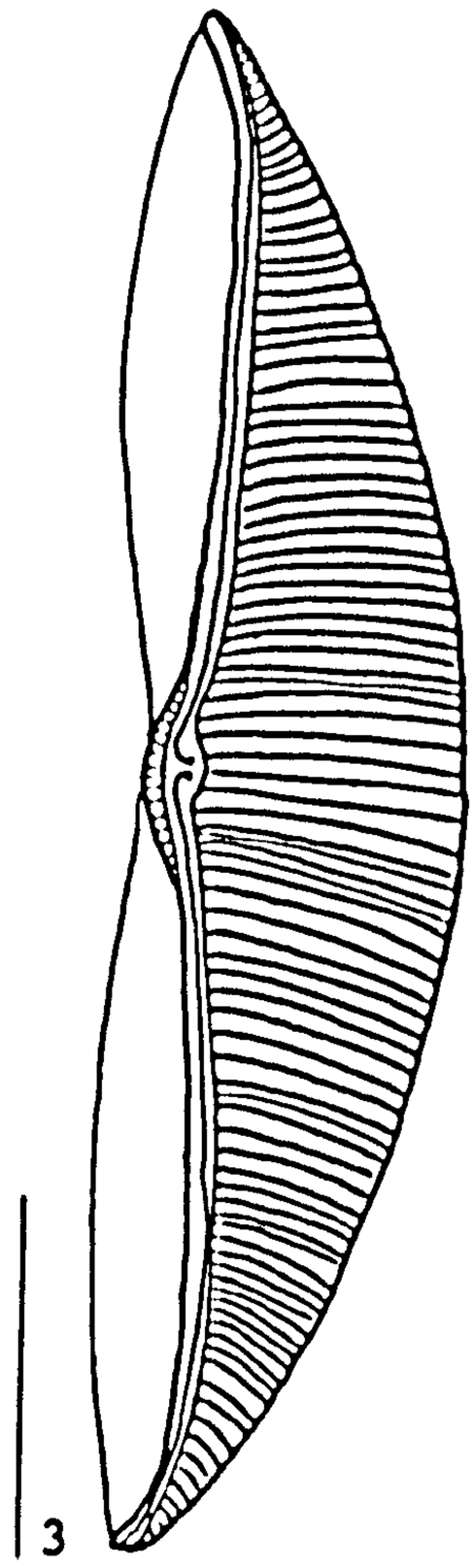

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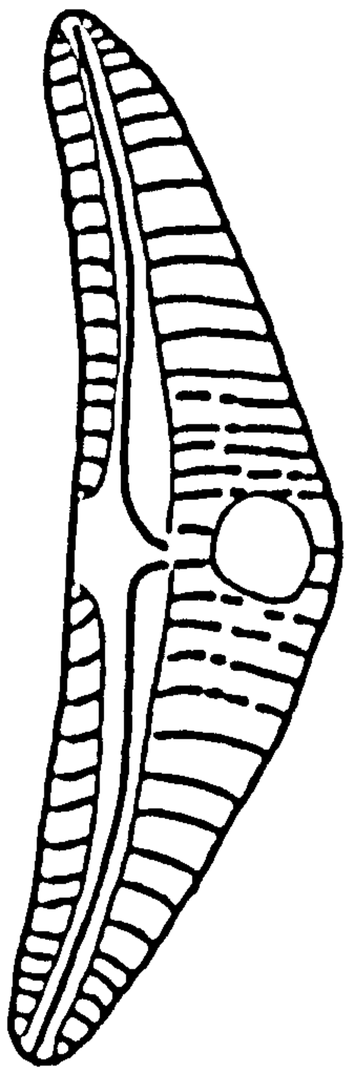

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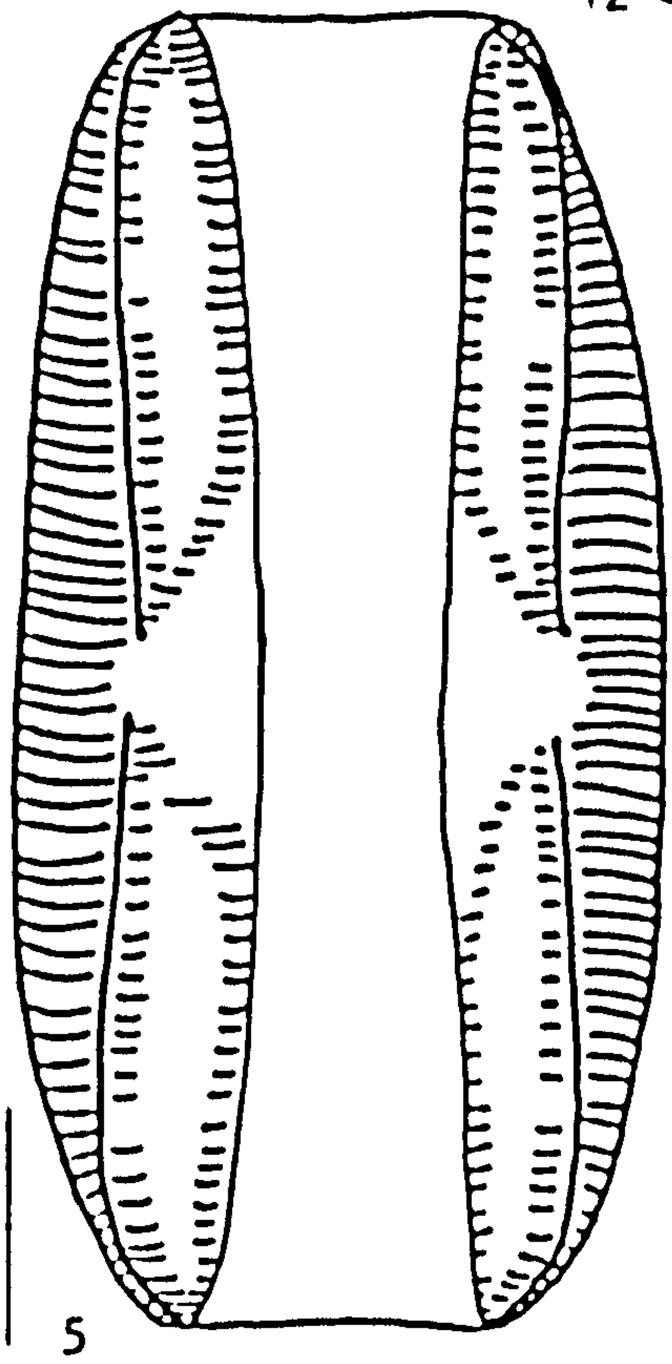

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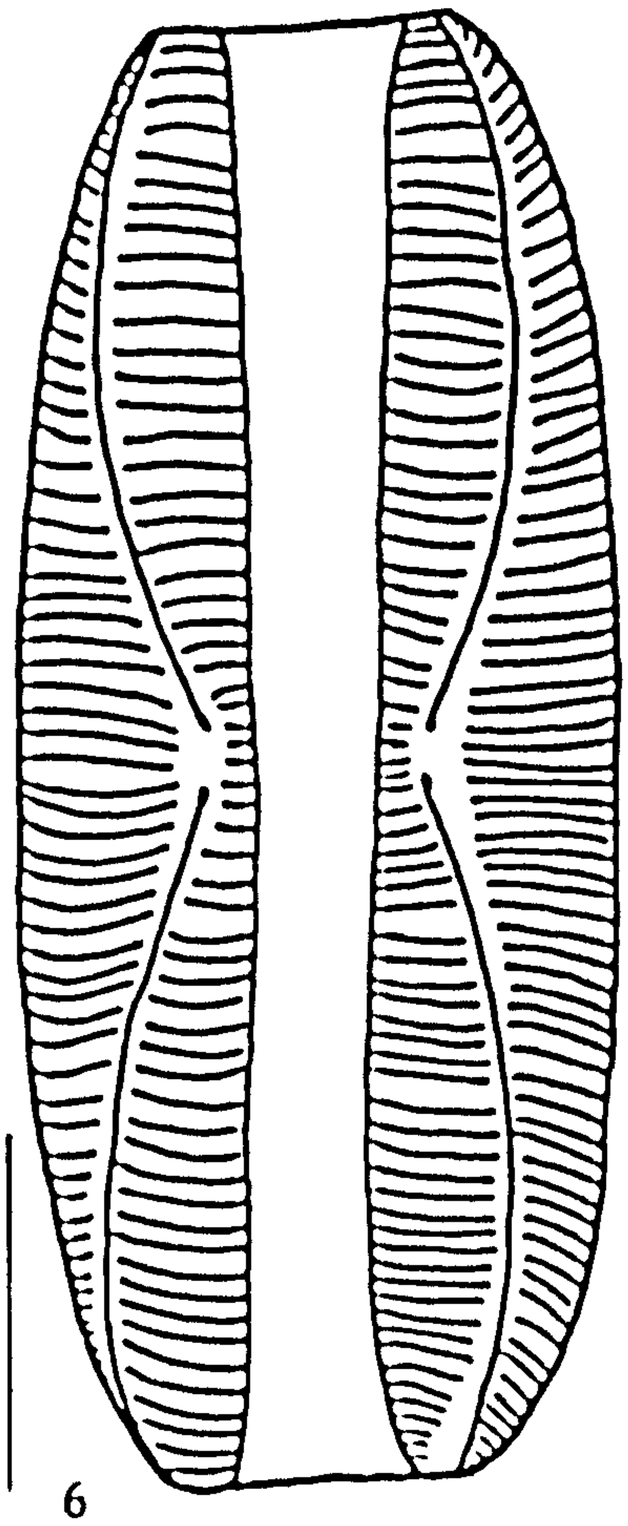

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PLATE 13

FAMILY: EPITHEMIACEAE

GENUS: Rhopalodia

Fig. 1 Rhopalodia operculata (Agardh) H. Skansson

FAMILY: NITZSCHIACEAE

GENUS: Cylindrotheca

Fig. 2 Cylindrotheca gracilis (Breb. ex Kütz) Grun. (frustule)

GENUS: Bacillaria

Fig. 3 Bacillaria paxillifer (O.F. Müller) Hendey

GENUS: Hantzschia

Fig. 4 Hantzschia marina (Donk.) Grun.

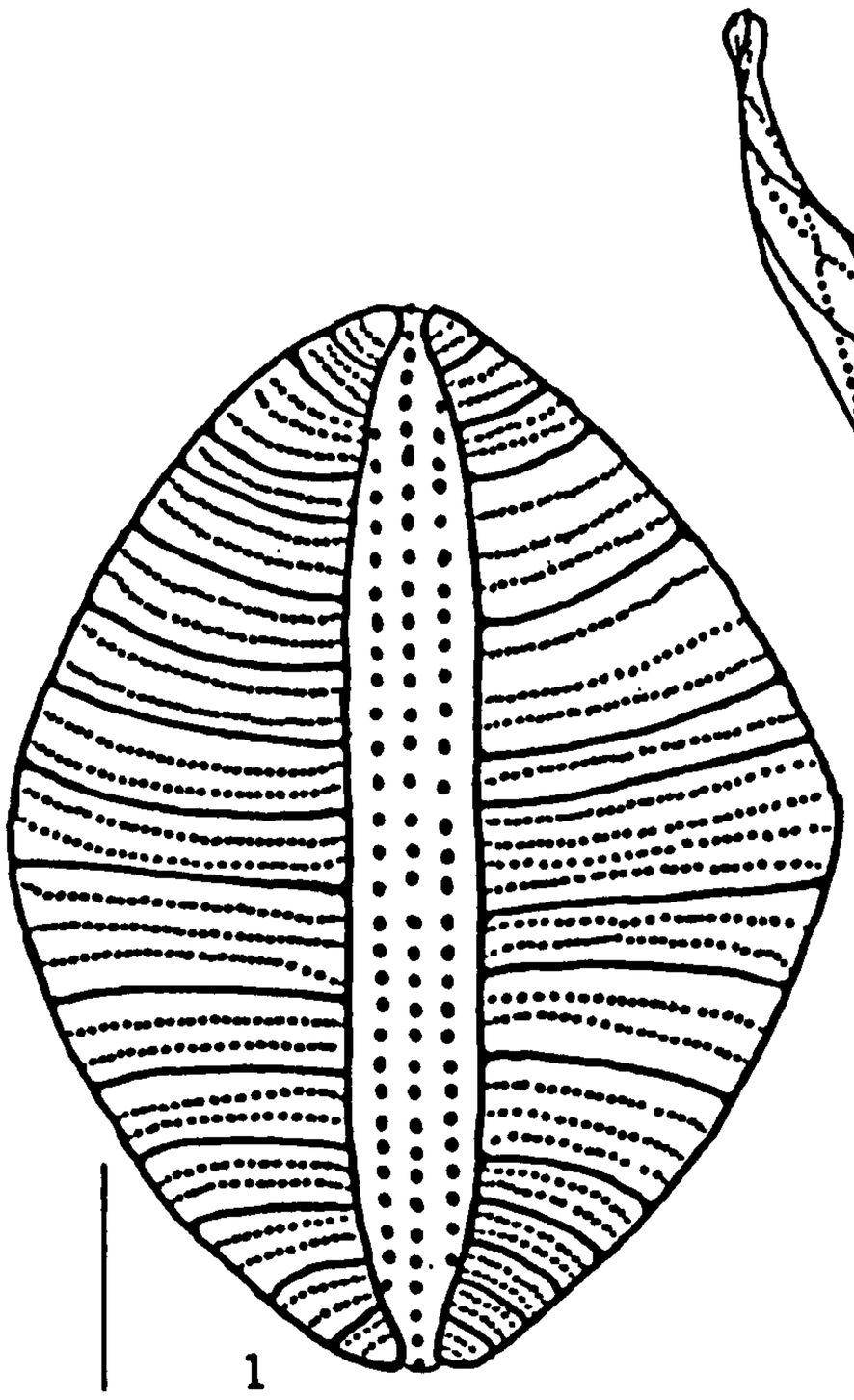
Fig. 5 H. marina (Donk.) Grun. in girdle view

Fig. 6 H. virgata var. gracilis Hust.

Fig. 7 H. virgata var. gracilis Hust. in girdle view

Fig. 8 H. virgata (Roper) Grun. var. virgata

Fig. 9 H. weyprechtii Grun.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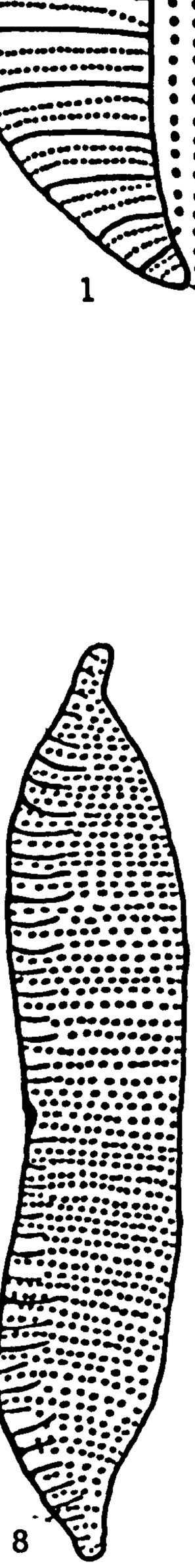
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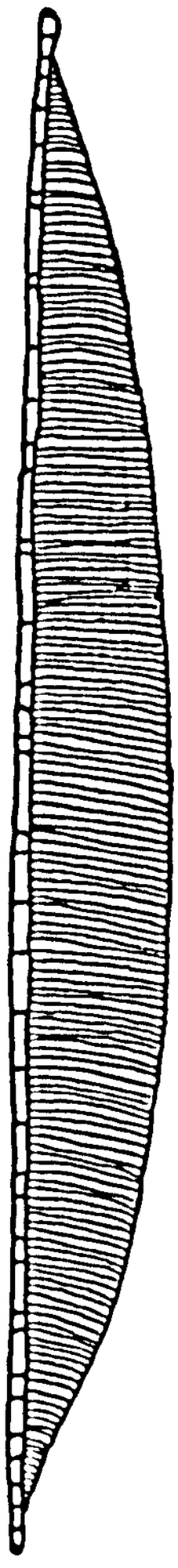
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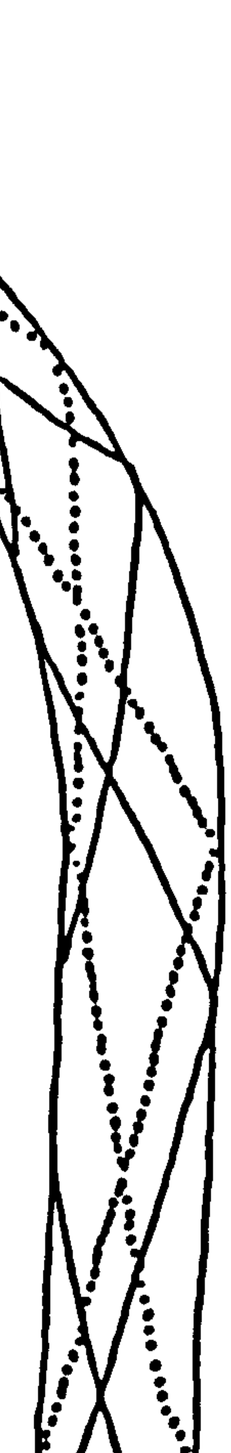
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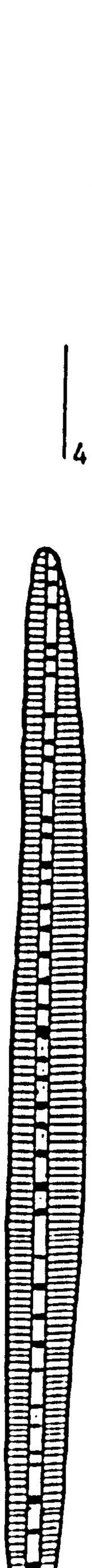
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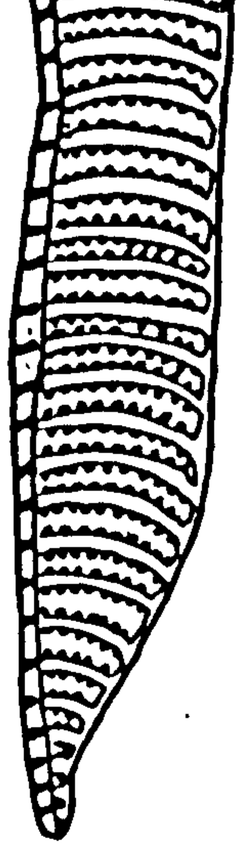
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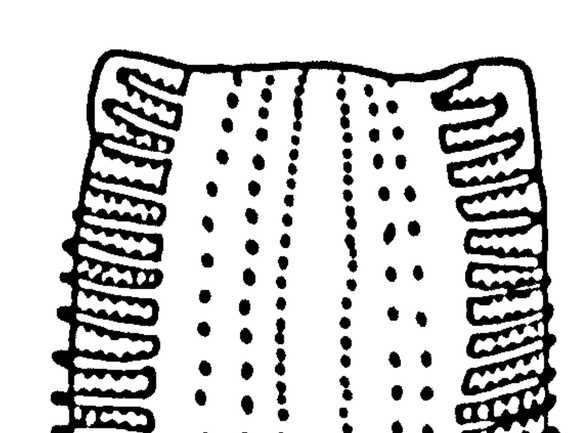
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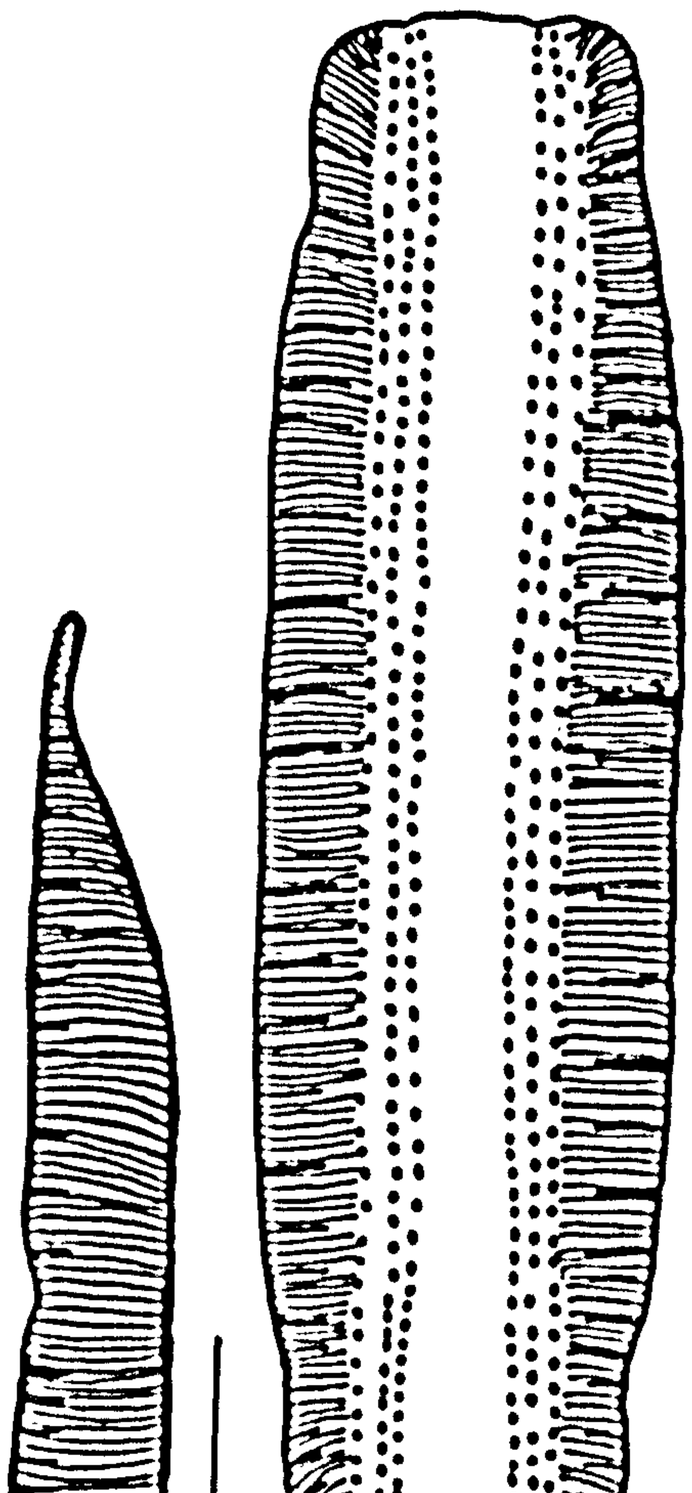
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PLATE 14

GENUS: Nitzschia

GROUP 1: Tryblionellae

Fig. 1 Nitzschia acuminata (Smith) Grun.

Fig. 2 N. debilis (Arnott) Grun.

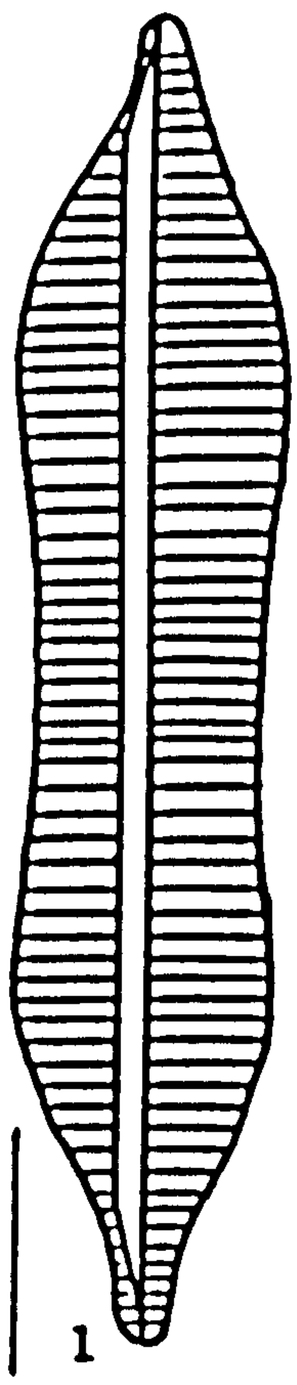
Fig. 3-4 N. hungarica Grun.

Fig. 5 N. navicularis (Bréb. ex Kütz) Grun.

Fig. 6 N. tryblionella Hantzsch. in Rabenhorst

Fig. 7 N. tryblionella var. levidensis (Smith) Grun.

PLATE 14



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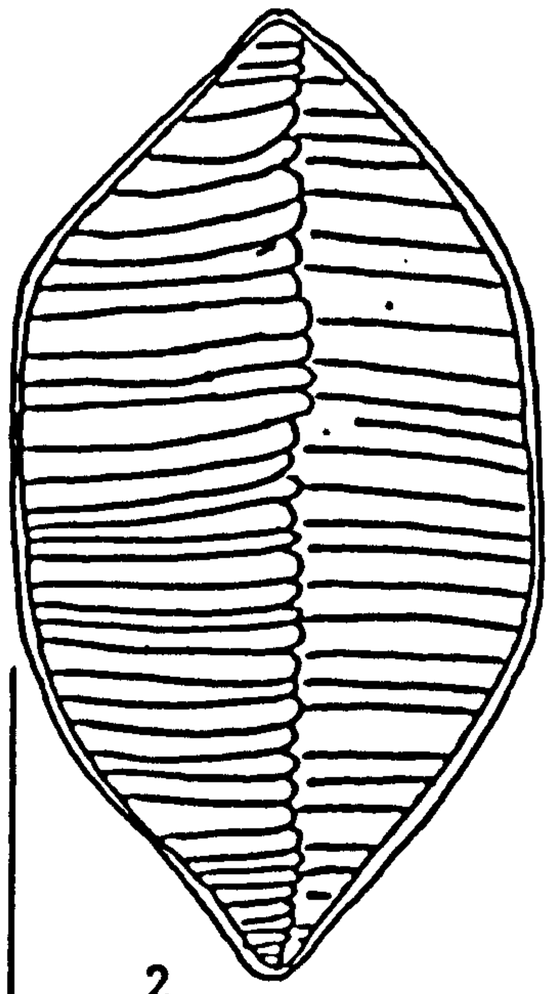

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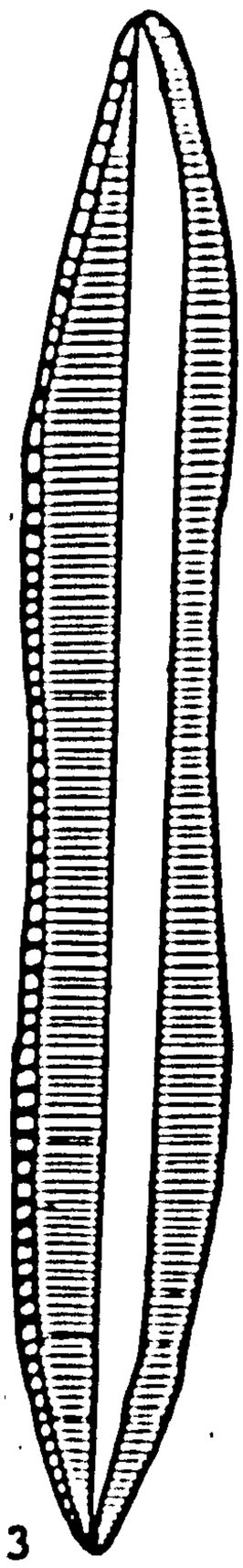

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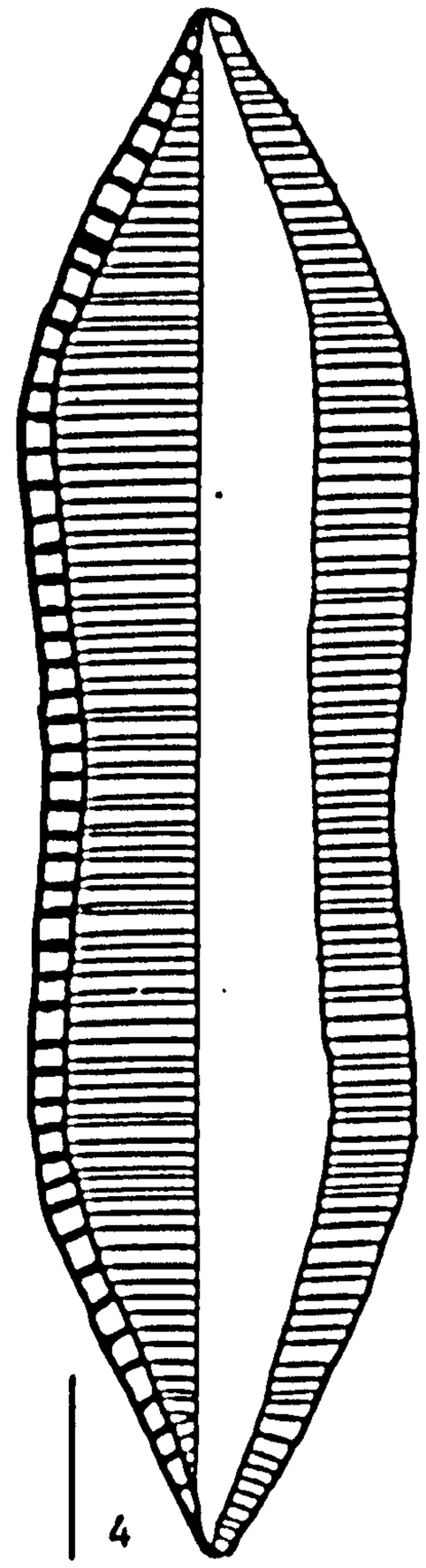

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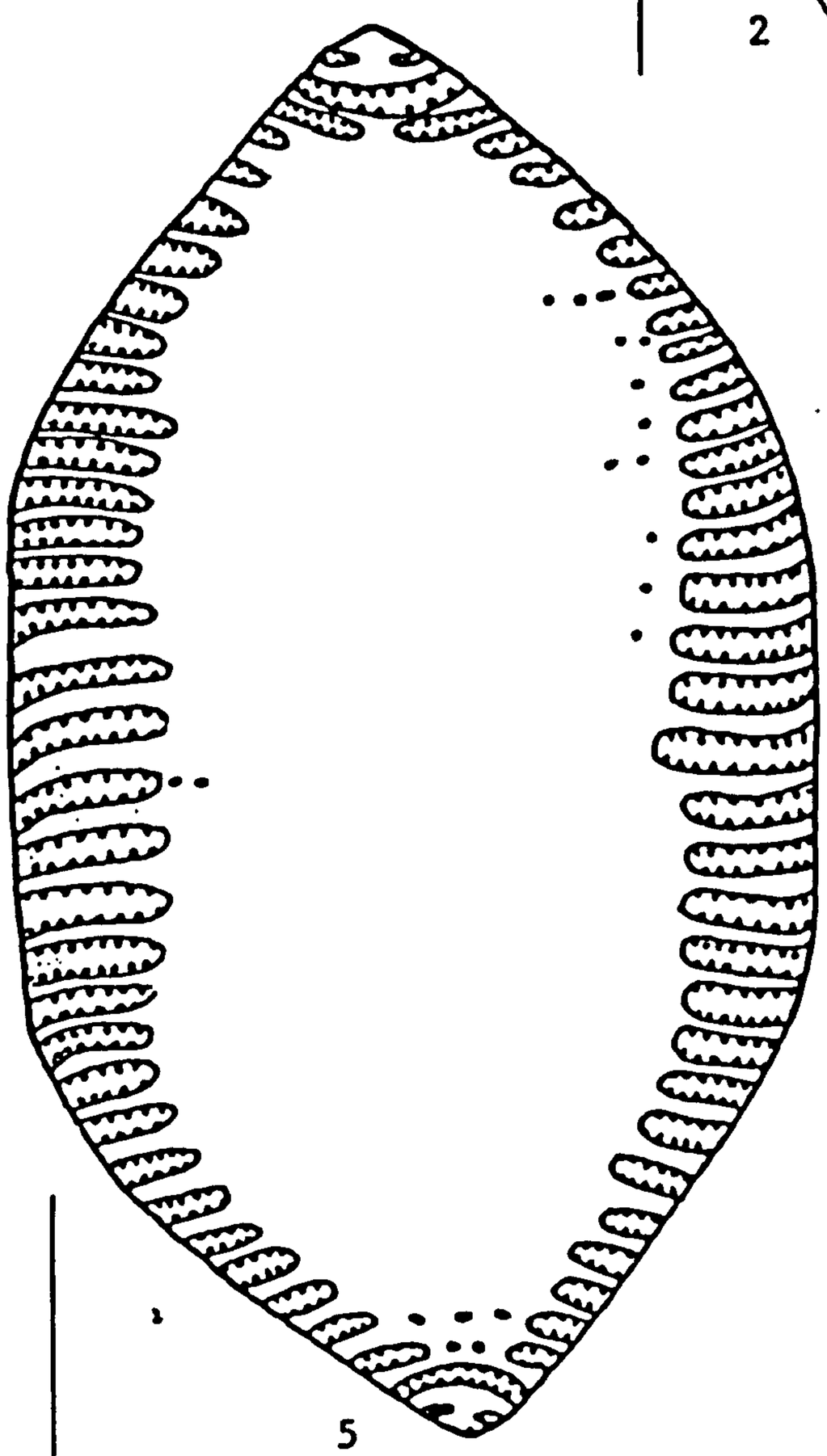

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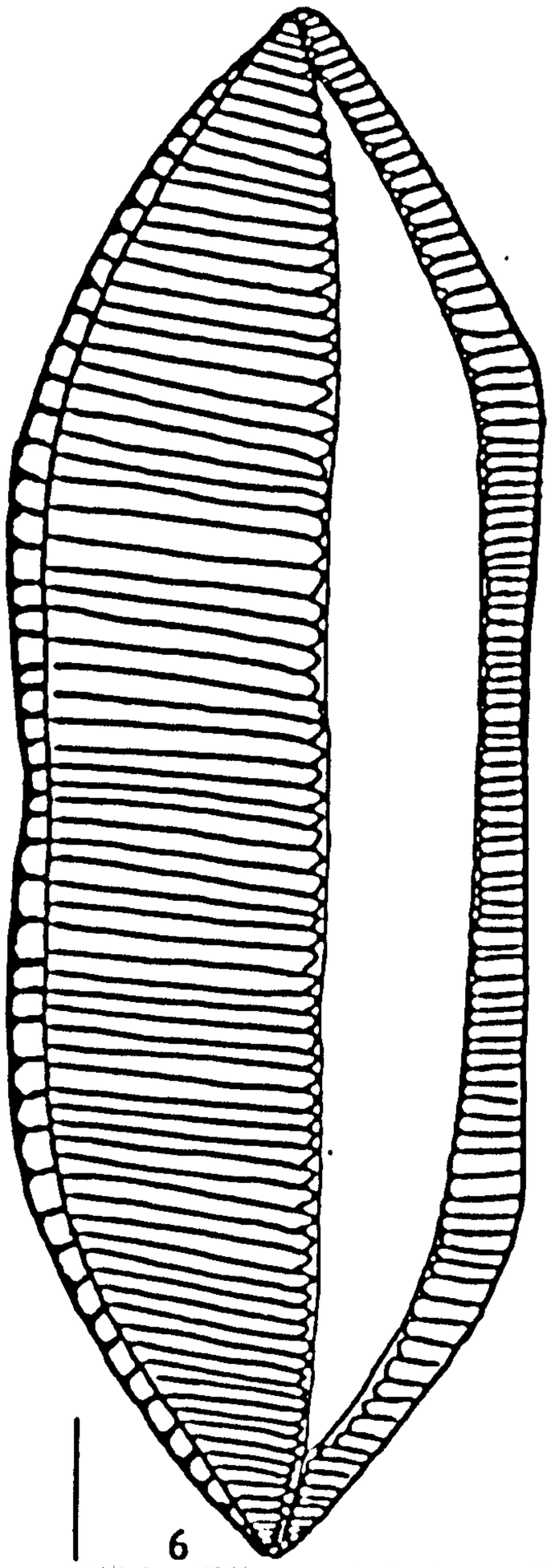

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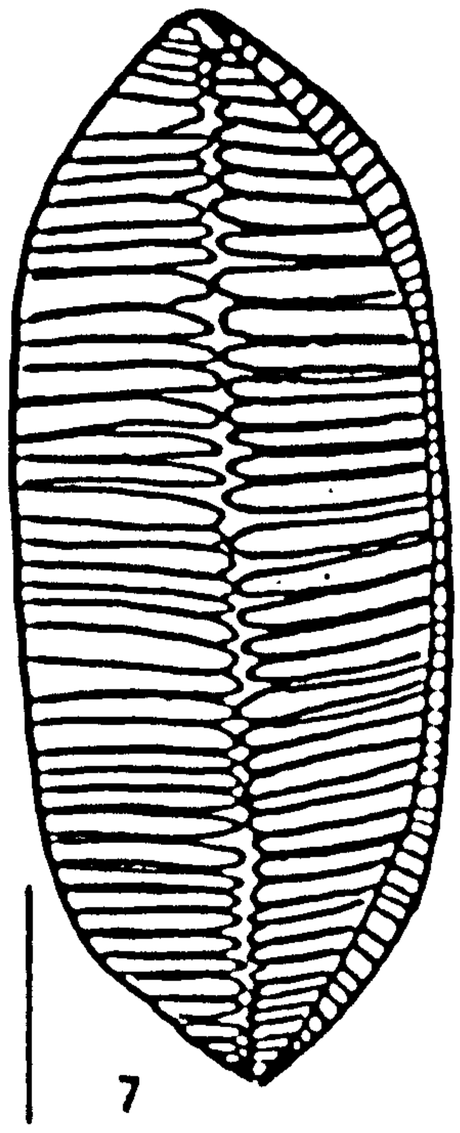

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PLATE 15

GENUS: Nitzschia

GROUP 2: Dubiae

Fig. 1 Nitzschia dubia Smith

GROUP 3: Costatae

Fig. 2 N. epithemioides Grun.

GROUP 4: Spathulatae

Fig. 3 N. linkei Hust.

Fig. 4 N. linkei Hust. in girdle view

Fig. 5 N. spathulata var. hyalina Greg.

GROUP 5: Lanceolatae

Figs. 6-8 N. microcephala Grun.

Fig. 9 N. paleacea Grun.

PLATE 15

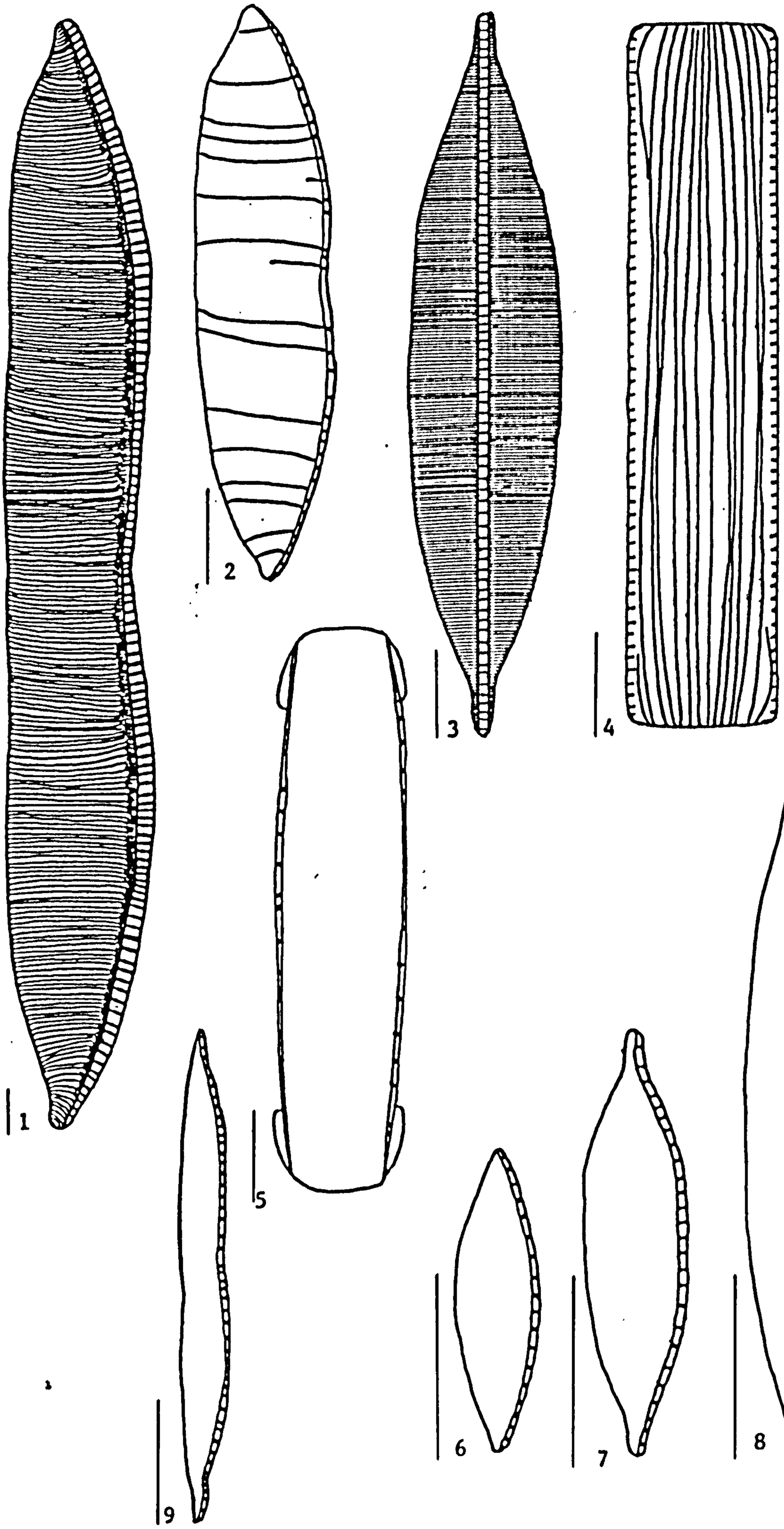


PLATE 16

GENUS: Nitzschia

GROUP 5: Lanceolatae

Figs. 1-4 Nitzschia vacillata Giffen

Fig. 5 Nitzschia sp.

GROUP 6: Sigmoideae

Fig. 6 N. sigma var.

Fig. 7 N. sigma var. rigida (Kütz.) Grun.

Fig. 8 N. vermicularis f. genuina m.h. (x400) in girdle view

Fig. 9 N. vermicularis f. genuina m.h. (xl,000) in valve view

GROUP 7: Nitzschiellae

Fig. lO N. closterium (Ehr.) Smith

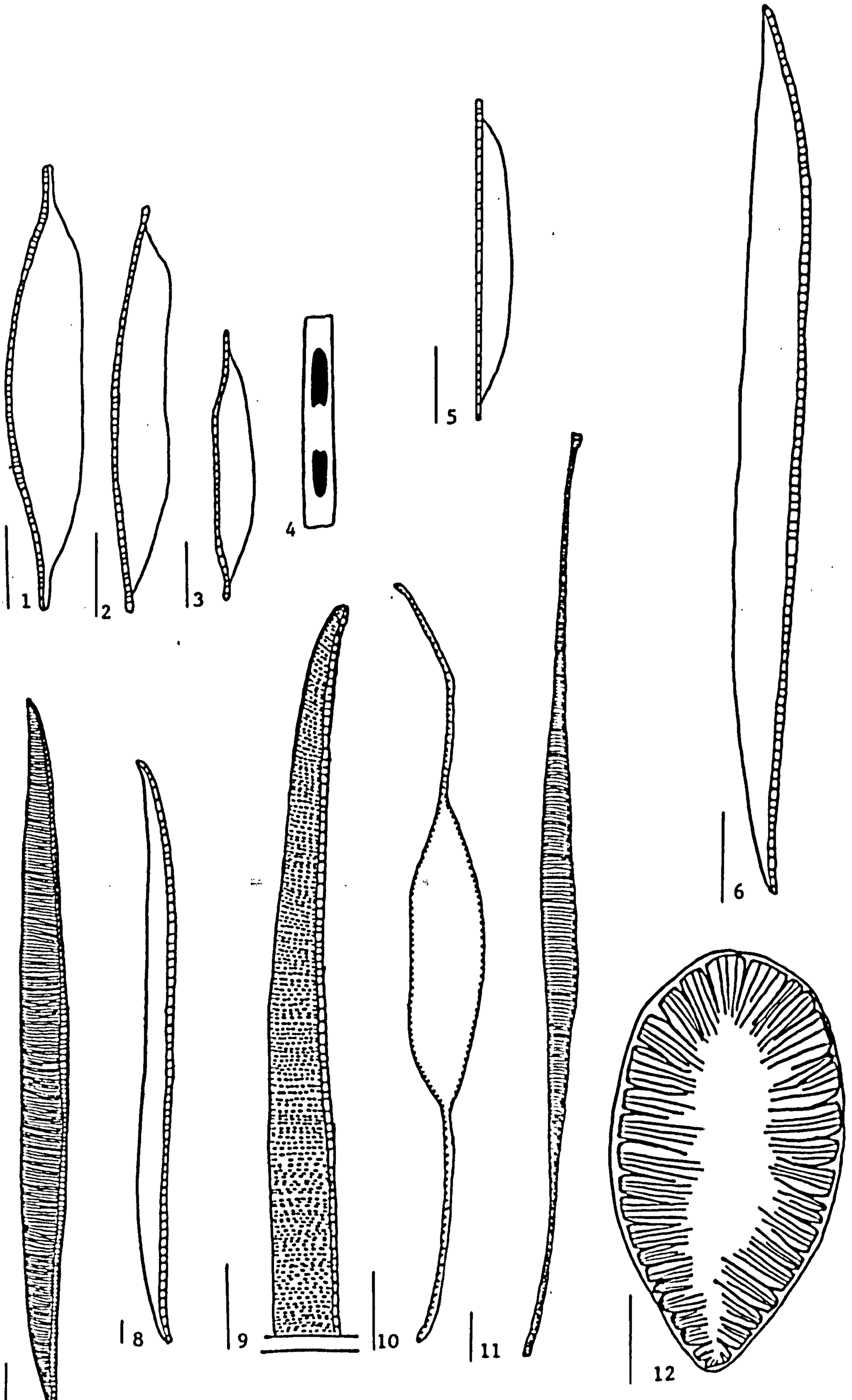
Fig. 11 N. lorenziana Grun.

FAMILY: SURIRELLACEAE

GENUS: Surirella

Fig. 12 Surirella ovata Kütz.

PLATE 16



CHAPTER 5

GENERAL DISCUSSION

The present investigation was designed to elucidate the population dynamics of the epipelon. The species composition of the various assemblages were identified, and a detailed microscopic examination revealed an ecosystem in microcosm of high diversity and complexity. The array of diatom taxa positioned along the physical gradients of the transect displayed considerable temporal, spatial, and morphological variability. The growth reponses of this community can be related to the dynamic physical environment.

Lightis the primary resource for biomass production (Admiraal 1980). Not only were diatoms abundant, but different dominant taxa grew where light intensities were low. Light intensities were also lower at sites which were submerged by the tide for longer periods, viz the lower sandflat and mudflat; here biomass was also low. The latter observations would agree with Dijkemas' (1975) field observations in the Wadden Sea. Perhaps these sites provide a habitat which enable the more low-light tolerant taxa to grow successfully.

If light availability was a cause of stressful conditions, it would be more likely to be from the lack of sufficient irradience, rather than over exposure. Admiraal (1980) has shown that epipelic diatoms do not display photoinhibition in culture or in field incubators. This is attributed to the diatoms' ability to migrate beneath the sediment surface. At Berrow abundant saltmarsh vegetation covers much of the mud surface, and light availability is no longer controlled solely by the diatoms' locomotive ability. Shading by the saltmarsh vegetation, may in some cases, not permit sufficient light to reach the mud surface, thereby causing stress. Lower down the shore on the sandflat, the

sediment surface is covered by tidal waters which are the "murkiest" in Britain (Kirby & Parker 1977); this water undoubtedly filters out the light for considerable periods during daylight hours. Furthermore a large number of taxa co-habiting on the sediment will be competing for the available light. Therefore competition along a light-depth gradient might become severe. Under such conditions taxa with effective migratory behaviour may grow more successfully (Round 1979) However species specific vertical migration rhythms may be one way of reducing this element of competition.

As light intensity increases in Spring and Summer, temperature also increases. While it is difficult to disentangle the influence of light and temperature on growth, some of the more distinguishing features can be noted. While light influences the accumulation of energy, temperature affects the metabolic rate. High division rates of epipelic diatoms in the field have been recorded at what would normally be inhibitory temperatures in culture (Admiraal 1980). Short term exposure to very high temperatures are not believed to cause inhibition. At Berrow the highest surface sediment temperatures were 27^{o}C. Such a high temperature was rarely observed, therefore high temperatures are an unlikely stress factor. Population density increased with an increase in temperature. Therefore it would seem feasable that this factor also has an important impact on the growth rate of the epipelon at Berrow. At low temperatures population density was low, but barren samples were never encountered during these periods. Therefore temperature was probably slowing down division rates, but not depleting the population completely.

It is possible that a temperature-depth gradient exists within the sediment. If so, diatoms could move down to a depth where temperature conditions are the least stressful. A microprobe to measure temperature

insitu would be required to see if such a depth gradient exists.

A microprobe measurement would also be useful for measuring salinity. Since salinity appears to be primarily responsible for spatial changes along the transect. Three observations lead to this conclusion. First the horizontal spatial positions of the diatoms, change along the salinity gradient. Secondly, localized changes in the salinity appear to cause localized changes in the position of certain species along the transect such as in the case of Amphora ovalis var. libyca. No other physical factor can account for changes in localized spatial distribution so well or so consistently. Thirdly, where conditions of extreme salinity occur specific taxa will grow in great abundance e.g. Navicula cincta, or Rhopalodia operculata. A microprobe measuring the veritcal gradient of salinity within the sediment would allow the worker to examine spatial position, in terms of depth, adding further information to the data already collected.

Other physical factors which run in parallel with the salinity gradient may also influence spatial changes in diatom assemblage structure, e.g. levels of organic matter or, pH. Their respective roles are not clear. Levels of organic matter appear to have an important influence on the spatial positions of the diatoms on Berrow saltmarsh. While there was a change in the dominant species in successions from podl sites to mound sites, there was also an increase in levels of organic matter from pool to mound. It is impossible to establish if the growth response was influenced more by the quantity of organic matter, or a change in the chemical make-up of the organic material. Perhaps both are important. A study of the processes of mineralization would help to gain insight into the physico-chemical conditions of the sediment. In addition a study of the hydrodynamics of sediment transport during tidal flow

might explain some features of diatom distribution.

Mean pH readings were slightly higher (alkaline) in spring-summer, when population density is highest, and small sized cells grow in abundance. Similar field observations have been recorded at Nord-Finistère France, where small sized cells are thought to form a distinct sub-group of the epipelic diatom population (Riaux 1983). Higher pH values in the interstitial water have been shown to limit the availability of inorganic carbons (Rasmussen et al. 1982). It is possible that one of the consequences of this stress is the predominance of small sized cells. A small sized cell would have a greater surface area to volume ratio, so a cell with a proportionally larger surface area, would have a better chance of absorbing inorganic carbons as the supply decreases. However a small sized cell would have greater problems counter-acting increased osmotic stress from high interstitial salinity, which is also recorded during the summer. Perhaps the stresses invoked by high pH conditions are greater than high interstitial salinity, so the growth of such small taxa as Navicula spp and Nitzschia microcephala agg will be encouraged.

This does not mean that large sized cells are not responding to these stress factors. A different strategy for coping with high pH and salinity must be employed. In order to assess their response to these stresses, a larger surface area of the sediment must be sampled to record their seasonal growth more precisely.

Another factor which might indicate conditions of stress is water content. When consistently low water content measurements were recorded in the sandflat, the population density crashed. During severe dry periods either the slides counted were barren, or more saline tolerant taxa grew

in larger numbers e.g. Amphora exigua, and Nitzschia epithemioides. The exact mechanism employed to cope with desiccation remains unclear. As described in Section 1. One possible response by the cell, is to produce a mucilage coat covered in silt. This might allow the cell to retain its water moisture. Another moist refuge might be an empty mucilage tube of a blue-green alga. Diatoms were often either intimately attached, or inside the mucilage coats of Lyngbya or Hydrocoleus. However these activities were observed at all months of the year, not just during dry conditions. There may be other reasons to account for this behaviour, e.g. camoflage to avoid predation. A more quantitative and critical study of mucilage production is required to gain a better understanding of its function.

Dry conditions on the sandflat are soon relieved by the innundation of the tide. However tidal disturbance may have a greater influence on biomass production. Where tidal submergence occurs on a daily basis over the sandflat, total cell counts were low. Where tidal innundation is only occasional biomass is much greater. It would be very difficult to quantify the number of cells being swept off the sediment surface. It is possible the tide may keep coherent clusters of diatoms in suspension in a semi-planktonic state. These organisms may have an entirely different ecology, only part of which can be seen when they resettle onto the sediment (as on the mudflat), and are subsequently sampled. Therefore the present study cannot yield any data about productivity on this part of the shore. Other studies have also shown little seasonal growth of the epipelon inhabiting disturbed sandy sediments (McIntire & Moore 1977, Whiting 1983).

The diatoms survive in a web of stressfull conditions, which change according to position on the shore and with time. Such a variable

environment would explain why such great variability and tolerance are observed. The general relationships discussed correspond with those from the Eems-Dollard estuary in Holland. Admiraal (1980) considers 6 main processes to be responsible for the formation and turnover of biomass in the epipelon:

1) Photosynthesis
2) Cell burial and vertical migration
3) Loss through respiration, mortality, and excretion
4) Consumption by fauna
5) Heterotrophic utilization of organic substrates
6) Transport by tidal currents.

All of the above play very important and fundamental roles at Berrow. However the ecosystem described at Berrow is more complex. The presence of saltmarsh vegetation creates a more variable habitat which will cause greater variability in the 6 main processes listed above. In response to this more variable environment, a more diverse diatom flora will be sustained. With greater diversity, even greater variability will be encountered because of greater stress from intraspecific competition. Therefore the interactions of all the factors which influence diatom growth will be much harder to disentangle. Some of these relationships can be summarized by the following diagram:

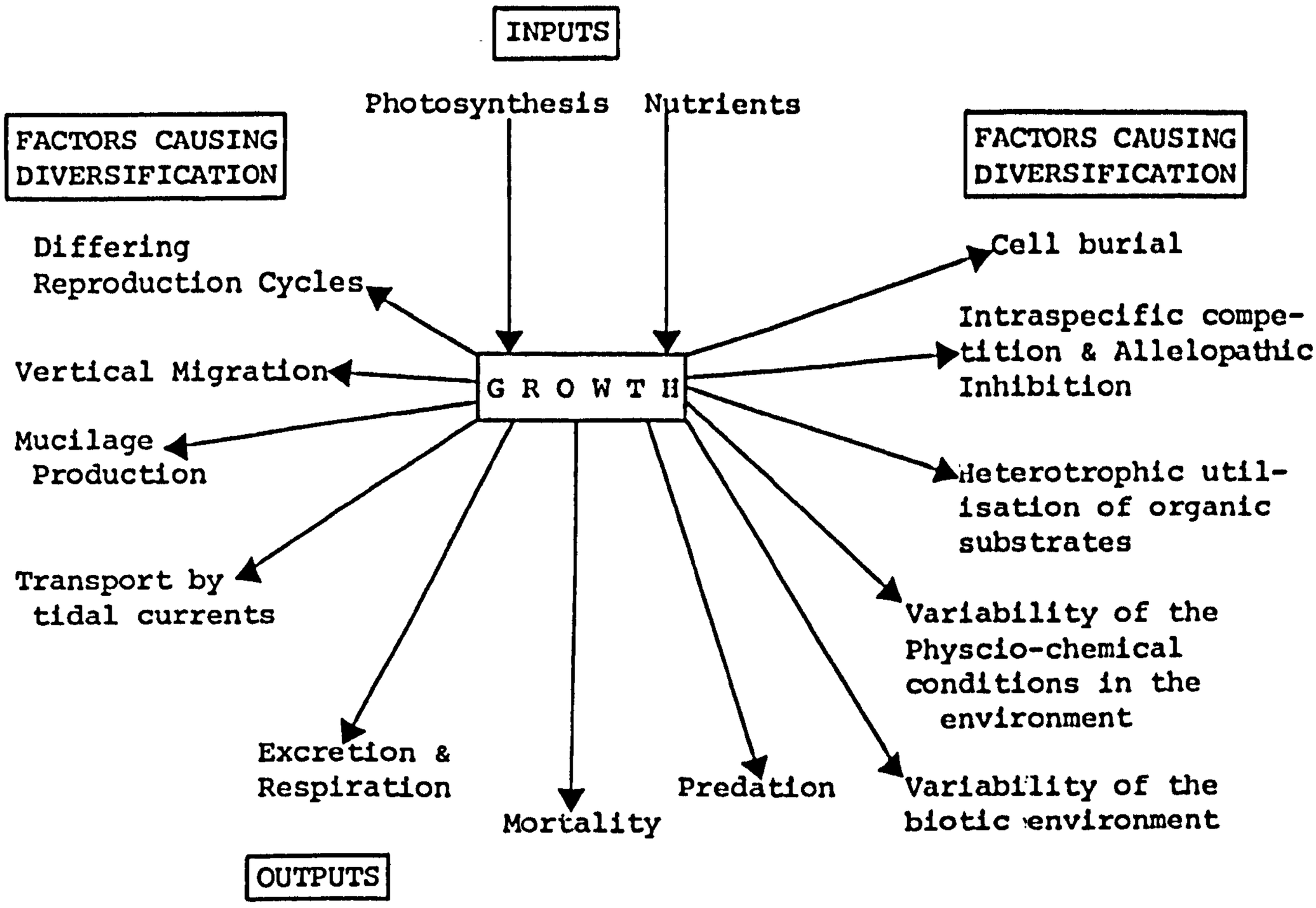


FIG.5 Diversification of the energy flow system

The number of factors which will cause variability far out number the inputs and outputs of what under less complicated circumstances would be a simple energy flow system. It is not surprising that a clear picture of the population dynamics of the epipelon cannot be presented.

This project provides the foundation for a more intensive analysis both in the field and in the laboratory. The next step is to examine diatom distribution in the field in terms of their physiological capabilities. The complexity of this habitat, requires the worker to achieve a greater understanding of the causes of variability. As has already been indicated, physical variation within the sediments can be further analysed by a closer examination of the micro-structure of the substrata insitu, which would lead to an examination of both vertical and horizontal gradients of all physical factors. Further examination of the micro-ecosystem could be achieved by freezing the sectioning undisturbed

surface sediment cores. Then the relationships between the position of the cells within the cores, and the physical nature of the sediment could be determined. Those features could then be related to measurements obtained by microprobe analysis.

In order to analyse morphological variability of the diatoms a much more intensive field sampling strategy is required. Valve and cell morphology should be examined in relation to reproduction cycles and the environment.

A more detailed chemical analysis of the interstitial water including major nutrients, micronutrients, heavy metal concentrations, and ionic composition would give much more information and may lead to a better understanding of the present data.

A diverse diatom population will sustain a wide range of benthic predators from ciliates to large bivalves. Each predator will have a different feeding strategy. The questions which will require further clarification are: How does predation affect diatom morphology? What are the diatoms defense mechanisms? How does the seasonal growth of the predators affect seasonal fluctations in diatom growth or spatial position?

There are many other aspects of community interactions to consider e.g. intraspecific competition, particularly where species diversity is high. Understanding how diatoms alter their growth strategies according to competative stress would help to clarify the roles of the main inputs and outputs of biomass production.

Computer analysis may help to clarify and simplify large amounts of field

data that have been compiled. The cluster and principal coordinate analyses undertaken in the present study have clearly demonstrated that only a limited amount of information can be aquired from data that has been condensed and summarized. This is not surprising since the cluster analysis attempts to describe constant relationships from a dynamic environment. This does not lead to the conclusion that structural relationships hypothsized from numerical analysis are invalid, but that such methods have their limitations. Multivariate statistical analysis can be used as one of many tools to obtain maximum information from field data. A variety of computer techniques are required to analyse the field data in different ways. Further computer analysis of the data from samples taken at Berrow would give much more information on community composition parammeters. It may be advisable to use different sampling strategies so that cells could be identified more accurately, in order to apply species diversity and redundancy measures to the data. The coverglass method was adequate for the aims of the present study, but because of the grouping together of many taxa, a much lower diversity is recorded than is truely present in the field. Another aspect of the field data which could be more quantitatively analysed is the relationship between the physical factors and the dominant taxa, using a discriminant analysis.

Once the population dynamics of the epipelon is more clearly understood, using the variety of techniques discussed, their biomass may be related to other organisms within the environment. Not just in terms of the bio-energetics of the preditor-prey relationship, but also in terms of the entire food web. If benthic diatoms are such important primary producers in estuarine mudflat ecosystems, then their impact on other organisms should ultimately be placed into perspective.

The greater our understanding of the ecology of the epipelon the more effectively these organisms which inhabit this substrata can be used as ecological indicators. This would have great practical applications, particularly in the event of the construction of the barrage in the Severn estuary. Changes in ecological conditions will then be closely monitored. So the present studies offers information which will enable future researchers to address more practical and complex questions which have thus far remained ellusive and confusing.

SUMMARY

1. An array of diatom taxa grow along the physical gradients of a transect of 16 sites crossing a saltmarsh, sandflat, and mudflat.

2. The physical conditions change substantially across two areas: the saltmarsh and sandflat. The presence of vegetation in the saltmarsh leads to lower light intensities at many of the sites. Salinities recorded in this area were freshwater-brackish, while pH was neutral, and levels of organic matter, and watercontent were high. In contrast the sandflat and mudflat have no vascular plant vegetation. Saline-hypersaline salinities, high pH and low levels of organic matter were recorded. The interstitial water-content was low at low tide, but tidal submergence occurs daily over these areas. Tidal scour is believed to have a more important role on the sandflat and mudflat.

3. A variety of methods to study the algal flora were tested prior to regular field sampling. A centrifugation and a coverglass method for obtaining data on algal populations are compared. It was concluded from initial trials, that a centrifugation technique caused more problems than it solved. Considerable time would be required

to refine this method. The coverglass technique proved to be both quick, simple, and it served the aims of this study. Therefore it was selected as the method used for regular sampling, inconjunction with various preparations for valve identification.

4. The percentage of valves derived from empty frustules on the sediment surface was signficantly high at all sites, and in all months of the year. Higher ratios of empty frustules to live cells were counted at sandflat and mudflat sites where sediments are more severely distributed by tidal innundation. These results confirm that it is crucial to count live cells in any long term sampling strategy.

5. Live cells display an extremely patchy pattern over the sediment. Graphing the variance against the seasonal mean cell counts showed that the variance was proportional to the square of the mean. The Neyman Type A equation is suggested as a possible model to explain this relationship.

6. Temporal changes in diatom assemblage structure does not display a repeated annual cyclic pattern at most sites. New dominant taxa appeared each year. Therefore a long term investigation examining temporal changes over many years would be necessary to establish the nature of the cycles. Maximum diatom growth occurs in the summer months, following the blue-green algal bloom in spring, and a smaller diatom growth is observed in autumn.

7. The spatial positions of different benthic taxa studied show a gradual transition along the transect. A high degree of spatial overlap is observed in the positions of taxa on the saltmarsh, but little spatial overlap is observed between taxa inhabiting the

saltmarsh and sandflat. Most taxa could compete equally successfully at a wide range of sites, measured by niche breadth (Bj). Most taxa had a Bj of 5-6.

8. Field observations suggest that increased irradiance and temperature encourages abundant benthic growth. Salinity, pH, and levels of organic matter influence spatial positions of the benthos. Extremes of salinity, low watercontent, and alkaline pH values are believed to encourage growth of more stress tolerant taxa. One possible conequence of alkaline pH conditions may be the growth of small sized cells.

9. A centroid cluster analysis for each years data revealed strong associations between specific pairs and triplets of taxa. The relationships observed, recurred each year. Taxa which were the most strongly associated were those with restricted spatial positions, and brief seasonal occurrence. Other taxa grouping into large clusters at more distant levels within the dendrograms had broad spatial positions and grew over many months in the year. Many factors are considered to influence assemblage structure.

10. Most species and varieties identified showed a remarkable degree of variability in morphology. Seventy different taxa have been described out of the 120 different species and varieties identified.

R E F E R E N C E S

ADMIRAAL, W. 1976 Experiments with Mixed Populations of Benthic Estuarine Diatoms in Laboratory Microecosystems. Botanica Marina Vol.20 pp. 479-485

ADMIRAAL, W. 1977a Influence of Light and Temperature on the Growth rate of Estuarine Benthic Diatoms in Culture. Marine Biology Vol.39 pp. 1-19

ADMIRAAL, W. 1977b Influence of Various Concmetrations of Orthophosphate on the Division Rate of an Estuarine Benthic Diatom Navicula arenaria in Culture. Marine Biology Vol.42 pp.1-8

ADMIRAAL, W. 1977c Tolerance of Estuarine Benthic Diatoms to High Concentrations of Ammonia, Nitrite Ion, Nitrate Ion and Orthophosphate. Marine Biology Vol.43 pp.307-315

ADMIRAAL, W. 1977d Salinity Tolerance of Benthic Estuarine Diatoms as tested with a Rapid Polarographic Measurement of Photosynthesis. Marine Biology Vol.39 pp.11-18

ADMIRAAL, W.; & PELETIER, H. 1979a Sulphide Tolerance of Benthic Diatoms in Relation to their Distribution in an Estuary. British Phycological Journal Vol.14 pp.185-196

ADMIRAAL, W.; & PELETIER, H. 1979b Influence of Organic Compounds and Light Limitation on the Growth rate of Estuarine Benthic Diatoms. British Phycological Journal Vol.14 pp.197-206

ADMIRAAL, W.; & PELETIER, H. 1980a Influence of Seasonal Variations of Temperature and Light on the Growth rate of Cultures and Natural populations of Intertidal Diatoms. Marine Ecology - Progress Series Vol.2 pp.35-43

ADMIRAAL, W.; & PELETIER, H. 1980b Distribution of Diatom Species on an Estuarine Mudflat and Experiemental Analysis of the Selective Effect of Stress. Journal of Experimental Marine Biology and Ecology Vol.46 pp.157-175

ADMIRAAL, W. 1980c Experiments on the Ecology of Benthic Diatoms in The Eems-Dollard Estuary. Published by Biologish Onderzoek Eems-Dollard Estuarium Publicaties en Verslagen Number 5

ADMIRAAL, W.; PELETIER, H.; & ZOMER, H. 1982 Observations and experiments on the population dynamics of epipelic diatoms from an estuarine mudflat. Estuarine & Coastal Shelf Science Vol.14 pp.471-487

ADMIRAAL, W.; BOUWMAN, L.A.; HOEKSTRA, L.; & ROMEYN, K. 1983 Qualitative & Qualitative Interactions between Microphytobenthos, & Herbivorous meiofauna on a Brackish Intertidal mudflat. International Revue der Gesamten Hydrobiologie Vol.68 pp.175-191.

ADMIRAAL, W.; & WERNER, D. 1983 Utilization of limiting concentrations of orthophosphate and production of extracellular organic phosphates in cultures of marine diatoms. Journal of Plankton Research Vol.5 No.4 pp.495-513

ADMIRAAL, W.; PELETIER, H.; & BROUWER, T. 1984a Experimental Analysis of the seasonal succession patterns of Diatom species on an Intertidal Mudflat. Oikos Vol.42 pp.30-40

ADMIRAAL, W. 1984b (manuscript) The Ecology of Estuarine sediment-inhabiting Diatoms from Progress in Phycological Research Vol.3 ed. Round, F.E. & Chapman, D.J. Biopress Ltd. Bristol U.K.

ALEEM, A.A. 1950 The diatom community inhabiting the mudflats at Whitstable. New Phytologist Vol.49 pp.174-188

AMSPOKER, M.C.; MCINTIRE, C.D. 1978 Distribution of Intertidal diatoms associated with sediments in Yaquina estuary, Oregon. Journal of Phycology Vol.14 pp.387-395

AVERY, B.W.; & BASCOMBE, C.L. ed. 1974 Soil Survey Laboratory Methods, Published by Harpenlen, Technical Monograph 6

BARBER, H.G.; & HAWORTH, E.Y. 1981 A guide to the morphology of the Diatom Frustule. Freshwater Biological Association scientific Publication No.44

BASCOMBE, C.L.; & BERNEYE, G. 1961 A Calcimeter for Routine use on soil samples, Chemistry and Industry Vol. pp.1826-1827

BASSINDALE, R. 1943 Studies on the Biology of the Bristol Channel XI. The Physical Environment and Intertidal Fauna of the Southern Shores of the Bristol Channel and Severn Estuary. Map on Plate 1, Journal of Ecology Vol.31-32, 1943-44 pp.1-29

BOLEY, G.M. 1942 The Vegetation of Berrow North Somerset. Proceedings of the Bristol Naturalist Society 1939-1944 Vol.9 pp.427-433

BOWEN, R.A.; STONGE, J.M.; COLTON, J.R.; J.B.; & PRICE,S.B. 1972 Density - gradient centrifugation as an aid to sorting planktonic organisms I Gradient materials. Marine Biology Vol.14 pp.242-247

BRAARUD, T. 1951 Salinity as an Ecological factor in Marine Phytoplankton. Physiologia Plantarum Vol.4 pp.28-34

BROCKMANN, C. 1950 Die Watt-Diatomeen der Schleswig-Holsteinischen Westküste. Abhandlungen Der Senckenbergishchen Naturforschenden Gesellschaft Nr.478 pp.3-26 and plates

BROWN, D.H.; GIBBY, C.E.; & HICKMAN, M. 1972 Photosynthetic rhythms in Epipelic algal populations. British Phycological Journal Vol.7 pp.37-44

BROWN, L.M. 1982 Photosynthetic and Growth Responses to salinity in a Marine Isolate of Nannochloris Bacillaris (Chlorophyceae) Journal of Phycology Vol.18 pp.483-488

CADÉE, G.C.; & HEGEMAN, J. 1974 Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Research Vol.8 pp.260-291

CARPENTER, E.J.; VAN RAALTE, C.D.; & VALIELA, I. 1978 Nitrogen fixation by algae in a Massachusetts saltmarsh. Limnology & Oceanography Vol.23 pp.318-327

CASTENHOLZ, R.W. 1964 The Effect of Daylength & Light Intensity on Growth of Littoral Marine Diatoms in Culture. Physiologia Plantarum Vol.17 pp.951-963

CLEVE, P. T. 1894-1895 Synopsis of the naviculoid diatoms Parts I & II Kongliga Svenska Vetenskaps-Akademiens Handlingar, Bd.26, p.1-194 pl.1-5; Bd.27, p.1-219, pl.1-4

CLEVE, P.T.; & GRUNOW, A. 1879-1880 Beitrage zur Kenntniss der artischen Diatomeen. Kongliga Svenska Vetenskaps. Akademiens Handlingar, Bd.17, Nr.2, 121S, 7 Taf.

CLEVE-EULER, A. 1951-1955 Die Diatomeen von Schweden und Finnland. Kongliga Svenska Vetenskaps-Akademiens Handlingar Serien 1-5, 959pp. Stockholm

COLES, S.M. 1979 Benthic microalgae populations on intertidal sediments and their role as precursors to salt marsh development. Part II of Ecological processes in Coastal Environments ed. Jefferies, R.L. & Davey Blackwell publ., Oxford.

COLIJN, F.; & VAN BUURT, G. 1975 Influence of light and temperature on the photosynthetic rate of marine benthic diatoms. Marine Biology Vol.31 pp.209-214

COLIJN, F.; & NIENHUIS, H. 1978 The Intertidal Microphytobenthos of the "Hole Weg" shallows in the German Wadden Sea. Forschungsstelle Insel und Küstenschutz, Norderney, Jahresbericht Vol.29 pp.149-174

COOK, L.L.; & WHIPPLE, S.A. 1982 The Distribution of edaphic diatoms along environmental gradients of a Louisiana saltmarsh. Journal of Phycology Vol.18 pp.64-71

COWDER, R.C. 1941-1942 The Vegetation and formation of Sand Dunes at Berrow. Student project report lodged in the Botany Department, Bristol University

COX, E.J. 1984 Some Taxonomic and ecological considerations of morphological variation within natural populations of Benthic Diatoms (Abstract) 8th Symposium on Living and fossil diatoms - Paris 1984

DARLEY, W.M.; MONTAGUE, C.L.; PLUMLEY, F.G.; SAGE, W.W.; & PSALIDES,A.T. 1981 Factors limiting edaphic algal Biomass and productivity in a Georgia saltmarsh. Journal phycology Vol.17 pp.122-128

DIJKEMA, K.S. 1975 Verennend onderzoek naar de invloed van abiotische faktoren op benthische diatomeeën in de oostelijke Waddenzee. Publications and Reports of the Eems-Dollard project 1974-5 29pp.

DONAGHAY, P.L.; DE MANCHE, J.M.; & SMALL L.F. 1978 On Predicting Phytoplankton Growth Rates from Carbon nitrogen ratios. Limnology & Oceanography Vol.23, No.2 pp.359-362

DRUM, R.W.; & WEBBER, E. 1966 Diatoms from a Massachusetts Salt March. Botanic Marina Vol.9(½) pp.70-77

EATON, J.W. 1967 Studies on The Ecology of Epipelic Diatoms. Ph.D Thesis Botany Dept. Bristol University

EATON, J.W.; & MOSS, B. 1966 The estimation of numbers and pigment content in epipelic algal populations. Limnology & Oceanography Vol.11 pp.584-595

EDGAR, L.W.; & PICKETT-HEAPS, J.D. 1983a The Mechanism of diatom locomotion. I An ultrastructural study of the motility apparatus. Proceedings of the Royal Society London B218, pp.331-343

EDGAR, L.A.; & ZAVORTINK, M. 1983b The mechanism of diatom locomotion II. Identification of action. Proceedings of the Royal Society London, B218 pp.345-348

EDGAR, L.A.; & PICKETT-HEAPS, J.D. 1984 (manuscript) Diatom Locomotion from Progress in Phycological Research Vol.3. ed. Round, F.E; & Chapman, D.J. pp.Biopress Ltd., Bristol U.K.

EDSBAGGE, H 1965 Vertical Distribution of Diatoms. Svensk Botanisk Tidskrift Vol.52(4) pp.463-465

EHRLICH, A. 1978 The diatoms of the hypersaline solar lake (Ne Sinai) Israel Journal of Botany, Vol.27 pp.1-13

EPPLEY, R.W.; & CYRUS, C.C. 1960 Cation Regulation and Survival of Red Alga Porphyra perforata in Diluted and concentrated sea water. Biological Bulletin Vol.118 pp.55-65

ESTRADA, M.; VALIELA, I.; & TEAL, J.M. 1974 Concentration and Distribution of Chlorophyll in Fertilzed Plots in a Massachusetts Salt Marsh. Journal of Experimental Marine Biology and Ecology Vol.14 pp.47-56

FEDEROV, U.D; MAKSIMOV, N.N.; & KHROMOV, V.M. 1968 Effect of light and temperature on primary production of some unicellular green algae and diatom algae. Fiziologie Rastenii Vol.15(4) pp.640-651

FENCHEL, T.M.; & RIEDL, R.J. 1970 The sulphide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Marine Biology Vol.7 pp.255-268

FENCHEL, T.M.; & STRAARUP, B.J. 1972 Vertical distribution of photo-synthetic pigments and the penetration of light in marine sediments. Oikos Vol.22 pp.172-182

FERNS, P.N.; METTAM, C.J.; GILLHAM, M.E.; & OWEN, M. 1976 The Severn Estuary a Heritage of Wildlife. publ. by Severn Estuary Conservation Group U.K. ed. FERNS, P.N.

FISCHER, H. 1964 Verhalten und Resistenz mariner Diatomeen gegenüber Veränderungen der Salzkonzentration. Helöglander wis-senschaftlich Meerensunterschungen Vol.10 pp.64-72

FREY, B.E.; & SMALL, L.F. 1980 Effects of micronutrients & Major nutrients on natural phytoplankton populations. Journal of Plankton Research Vol.2 pp.1-22

GARGARI, A.S. 1980 Preliminary Investigations Into the Ecology of the Intertidal Diatoms of the Mersey Estuary. Ph.D. thesis Dept. of Biology, University of Salford

GENSTAT REFERENCE MANUAL 1983 A General Statistical Program. Publ. by the Numerical algorithms group Ltd. c Lawes Agricultural Trust. Rothamsted Experimental Station, Oxford

GERMAIN, H. 1981 Flore Des Diatomées eaux douces et saumatres Societe Nouvelle Des Editions Boubée 11, place Saint-Michel, 75006 Paris

GIFFEN, M.H. 1967 Contributions to the Diatom Flora of South Africa III. Diatoms of the Marine Littoral Regions at Kidd's Beach near East London, Cape Province, South Africa. Nova Hedwigia 13(½) pp.245-292

GINZBURG, M.; & GINZBURG, B.Z. 1981 Interrelationships of light, temperature, sodium chloride and carbon source in growth of halotolerant and halophilic strains of Dunaliella. British Phycological Journal Vol.6 pp.313-324

GOW, T.A.K.; & MCLEAN, R.O. 1983 (abstract) Community and Distribution Studies of the Benthic Diatom Flora in the Upper Clyde Estuary. Paper No.3 from the Symposium on Structure and Function of Brackish Water and Inshore Communities, Edinburgh

GOW, T.A.K; CURTIS, D.J.; & MCLEAN, K.O. 1984 (abstract) Studies on the Benthic Epilithic Diatoms of the Clyde Estuary (Scotland) from the Eighth Symposium on Living and Fossil Diatoms, Paris pp.85

HÅKANSSON, H. 1979 Examination of Diatom Type Material of C.A. Agardh. Nova Hedwigia, Beiheft 64 pp.163-168

HARPER, M.A.; & HARPER, J.F. 1968 Measurements of diatom adhesion and their relationship with movement. British Phycological Bulletin Vol.3(2) pp.195-207

HARPER, M.A. 1977 Movements from the Biology of Diatoms. Chapter 8 pp.224-249, 1977 Blackwell Scientific Publications, Oxford. ed. D. Werner

HENDEY, N.I. (1964) An Introductory Account of the Smaller Algae of British Coastal Waters Part V: Bacillariophyceae Diatoms. Ministry of Agriculture, Fisheries and Food. Fishery Investigations Series IV, London.

HOC, S. 1980 Blaualgen unterdrücken das Diatomeen-Wachstum. Mikrokosmos Heft 11, pp.360-362

HOPE-SIMPSON, J.F.; & WILLIS A.J. 1955 Vegetation. Chapter 6 of Bristol and its Adjoining Counties, ed. MacInnes, C.M.; & Whittard, N.F. pp.91-93

HOPKINS, J.T. 1964a A Study of the Diatoms of the Ouse Estuary, Sussex II. The Ecology of the Mud-flat Diatom flora. Journal of the Marine Biological Association U.K. Vol.44 pp.333-341

HOPKINS, J.T. 1964b A Study of the diatoms of the Ouse Estuary, Sussex III. The seasonal variation in the littoral epiphyte flora and the shore plankton. Journal of the Marine Biological Association U.K. Vol.44 pp.613-644

HUSTEDT, F. 1930 Die Süsswasser-Flora Mitteleuropas Heft 10 Bacillariophyta (Diatomeae). Ed. A. Pascher, Jena Verlag von Gustav Fischer

HUSTEDT, F. 1939 Die Diatomeen flora des Küstengebietes der Nordsee vom Dollart bis zur Elbemündung. I. Abhondlungen, natur-wissenschaft-licher verein zu Bremen, Bd.31, Heft 3, S. 571-577, 123 Textfig.

HUSTEDT, F. 1961-1966 Die kieselagen Deutschlands, Österreichs und der Schweitz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In Rabenhorst, L.(ed.).Kryptogamen flora 7. 2581 pp. Leipeig (4 Parts)

HÜTTUNEN, P.; MERILÄINEN, J. 1978 New freezing device providing large unmixed sediment samples from lakes. Annales Botanici Fennici Vol.15(2) pp.128-136

IMBERGER, J.; BERNMAN, T.; CHRISTIAN, R.R.; SHERR, E.B.; WHITNEY, D.E.; POMEROY, L.R.; WIEGERT, R.G.; & WIEBE, W.J. 1983 The Influence of water motion on the distribution and transport of materials in a saltmarsh estuary. Limnology & Oceanography Vol.4 pp.201-214

IWAI, T. 1962 Eological studies on the phytoplankton of brackish water ponds. Journal of the Faculty of Fisheries, Mie University, Mie Prefecture. Vol.5(3) pp.412-506

JOHNS, J. 1984 A species list of common diatoms in hypersaline lakes, Preston Clifton, Martin Tank, and a string of minor lakes located in coastal strip of land, the Yalgorup National Park, Western Australia (32° 30'5, 116° 15'E) Climate-mediterranean. A paper presented at the Eighth International Symposium on Recent and Fossil Diatoms, at the diatom workshop on hyper-saline environments, Paris

JAMES, T.M. 1934 (No title) Student project report Botany Department, Bristol University

JITTS, H.R.; MCALLISTER, C.D.; STEPHENS, K.; & STRICKLAND, J.O.H. 1964 Cell Division Rates of Some Marine Phytoplanktones as a function of Light & Temperature. Journal of the Fisheries Research Board of Canada. Vol.21(1) pp.139-156

JOINT, I.R. 1981 Growth and Survival of Estuarine Microalgae in Feeding & Survival Strategies of Estuarine Organisms. ed. N.V. Jones & W.J. Wolff, Plenum Press, N.Y. & London.

JONGE, de, V.N.;& BOUMAN, L.A. 1977 A Simple Density Separation Technique for quantitative Isolation of Meiobenthos using the colloidal silica LUDOX-TM. Marine Biology Vol.42 pp.143-148

JONGE, de V.N. 1979 Quantitative Separation of Benthic Diatoms from Sediments using Density Gradient Centrifugation in the Colloidal Silica LUDOX-TM. Marine Biology Vol.51 pp.267-278

JONGE, de V.N. 1980 Fluctuations in the Organic Carbon to Chlorophyll & Ratios for Estuarine Benthic Diatom Populations. Marine Ecology Progress Series Vol.2 pp.345-353

JØRGENSEN, E.G. 1960 The Effect of Salinity, Temperature and Light intensity on Growth and chlorophyll formation of Nitzschia ovalis . Washington D.C. Carnegie Institute Year book 59 pp.348-349

KAIN, J.M.; & FOGG G.E. 1958 Studies on growth of marine phyloplankton. I Asterionella Japonica Grun. Journal of the Marine Biological Association U.K. Vol.37 pp.397-413

KENDALL, O.D. 1936 The Coast of Somerset Part I Proceedings of the Bristol Naturalists Society 1935-1938 Vol.8 pp.186-208

KENDALL, O.D. 1938 The Coast of Somerset Part II Proceedings of the Bristol Naturalists Society 1935-1938 Vol.8 pp.497-506

KIRBY, R.;& PARKER,W.R. 1975 Sediment Dynamics in the Severn Estuary. In an Environmental Appraisal of the Severn Barrage. Ed. Shaw, T.L. pp.41-52

KRAMMER, K. 1981 'Zur Deutung einger Schalenstrukturen bie pennaten Diatomeen. Nova Hedwigia Band 35 Braunschweig pp.75-105

LANGE-BERTALOT, H. 1979 Tolerangrenzen u. Populations dynamik benthischer Diatomeen. Archive fuer Hydrobiologie 1. Supplement band Vol.56(2) pp.184-219

LIU, M.S.; & HELLEBUST,J.A. 1976 Effects of Salinity Changes on growth and metabolism of the marine centric diatom Cyclotella cryptica. Canadian Journal of Botany Vol.54 pp.930-937

MAIN, S.P.; & MCINTIRE, C.D. 1974 The Distribution of Epiphytic Diatoms in Yaquina Estuary, Oregon (USA). Botanica Marina Vol.17 pp.88-99

MANN, D.G. 1978 Studies in the family Nitzschiaceae (Bacillariophyta) Vols. I & II Ph.D. thesis Botany Department Bristol University, England.

MANN, D.G. 1981 Studies in the Diatom Genus Hantzschia 3. Infraspecific variation in H. virgata Annals of Botany Vol.47: pp.377-395

MARTIN, J.V. 1970 Salinity as a Factor Controlling the Distribution of Benthic Estuarine Diatoms. Ph.D. thesis Department of Botany, Oregon State University

MCINTIRE, C.D. 1968 Physiological-Ecological Studies of Benthic Algae in Laboratory Streams. Journal Water Pollution Control Part I. Vol.40 pp.1940-1952

MCINTIRE, C.D. 1968 Structural Characteristics of Benthic Algal Communities in Laboratory Streams. Ecology Vol.49 pp.520-537

MCINTIRE, C.D.; & WULFF, B.L. 1969 A Laboratory Method for the Study of Marine Benthic Diatoms. Limnology & Oceanography Vol.14(5) pp.66-678

MCINTIRE, C.D.; & OVERTON, W.S. 1971 Distributional patterns in assemblages of attached diatoms from Yaquina estuary, Oregon. Ecology Vol.52 pp.758-777

MCINTIRE, C.D.; & MOORE, W.M. 1977 Marine Littoral Diatoms-Ecological Condsiderations. In the Biology of Diatoms ed. Werner, D. pp.333-371. Botanical Monographs, Vol.13 Blackwell, Oxford.

MCINTIRE, C.D. 1978 The Distribution of Estuarine Diatoms Along Environmental Gradients, A Canonical Correlation. Coastal Marine Science Vol.6 pp.447-457

MEDLIN, L.K. 1981 Effects of Grazers on Epiphytic Diatom Communities 6th Diatom Symposium of Recent & Fossil diatoms pp.399-411

MEDLIN, L.K. 1983 Community Analysis of Epiphytic Diatom. Ph.D. thesis Department of Botany Texas A & M University

MOORE, W.W. & MCINTIRE, C.D. 1977 Spatial and Seasonal Distribution of Littoral Diatoms in Yaquina Estuary Oregon USA. Botanic Marina Vol.20 pp.99-109

MOUL, E.T.; & MASON, D. 1957 (abstract) Study of Diatom populations on sand and mudflats in the Woods Hole area. Biological Bulletin Vol.113 pp.351

ODUM, E.P. 1971 Fundamentals of Ecology 3rd Edition. Publ. by W.B. Saunder Company, Philadelphia

OPPENHEIM, D.R. (1981) A Quantitative study of vertical migration rhythms in epipelic diatom populations at Berrow estuary. Student project report lodged in Department of Botany, Bristol University, England.

O'QUINN, R.;& SULLIVAN, M.J. 1983 Community Structure Dynamics of Epilithic and Epiphytic Diatoms in a Mississippi Stream. Journal of Phycology Vol.19 pp.123-128

OWEN, M.W. 1973 (abstract) The properties of muds during settling and consolidation. Journal of the Geological Society Vol. 129(4) pp.454-455

PAMATMAT, M.M. 1968 Ecology and Metabolism of Benthic Community on an Intertidal Sandflat. International Revue gesamten Hydrobiologie Vol.53(2) pp.221-298

PARKER, B.C. 1978 Neuston Sampling Chapter 3.5 from Phytoplankton Manual pp.64-67 ed. Sournia, A,UNESCO, Paris

PATRICK, R.; & REIMER, C.W. 1966 The Diatoms of the United States Vol.1 Monograph No.13 of the Academy of Natural Science of Philadelphia,688 pp.64pl

PERAGALLO, H. 1891 Monographie du genre Pleurosigma et des allies Le Diatomiste, t.1, fasc.4 33pp. 10pl.

PERAGALLO, H.; & PERAGALLO,M. 1897-1908 Diatomee Marines De France et Des Districts Maritimes voisins. ed. M.J. Tempère Micrographe - Editeur a Grez-sur-Loing Vol.1 Texte, Vol.2 Atlas 491pp & 87 pl

PIELOU, E.C., 1969 An Introduction to Mathematical Ecology, Publ. by Wiley-Interscience, A Division of John Wiley & Sons, New York, USA

POMEROY, L.R. 1959 Algal productivity in Salt Marshes of Georgia. Limnology & Oceanography Vol.41 pp.386-397

POPE, K.N.S.; & TURNER, M.E. 1938 Map of Marsh North East of Berrow Church, Botany Department Bristol University

POULIN, M.; & CARDINAL, A. 1983 Sea Ice diatoms from Manitounuk Sound Southeastern Hudson Bay (Quebec, Canada).III Cymbellaceae, Entomoneidaceae, Gomphonemataceae and Nitzschiaceae. Canadian Journal of Botany Vol.61,No.1 pp.107-118

PRICE, C.A.; MENDIOLA, L.R.; GOLDSTEIN, M.; BREDEN, E.N.; & MORGENTHALER, M. 1974 Harvest of Planktonic marine algae by centrifugation into gradients of silica in the CF-6 continuous flow zonal rotor. Biological Bulletin Vol.147 pp.136-145

PRICE, C.A., ONGE-BURNS, St, J.M.; COLTON, J.B.; & JOYCE, J.E. 1977 Automatic Sorting of Zooplankton by Isopycnic sedimentation in Gradients of Silica. Performance of a Rho-Spectrometer. Marine Biology Vol.42 pp.225-231

RAALTE van, C.D.; VALIELA, I.; & TEAL, J.M. 1976a The effect of fertilization on the species composition of saltmarsh diatoms. Water Research Vol.10 pp.1-4

RAALTE van, C.D; VALIELA, I.; & TEAL, J.M. 1976b Production of epibenthic saltmarsh algae; Light and nutrient limitation. Limnology & Oceanography Vol.21 pp.862-872

RASMUSSEN, M.B.; HENRIKSEN, K.; & JENSEN, A. 1982 Possible causes of temporal fluctuations in Primary production of the microphytobenthos in the Danish Wadden Sea. Marine Biology Vol.73 pp.109-114

REIMANN, B.E.F.; & LEWIN, J.C. 1964 The Diatom Genus Cylindrotheca Rabenhorst (with a reconsideration of Nitzschia closterium) Journal of the Royal Microscopical Society Vol.83 Pt.3 pp.283-296

REINICKE, F. 1858 Das Einsammeln und Präpariren der Bacillarien. Beitraege zur Neuren.Mikroskopie Vol.1 pp.44-57

RIAUX, C. 1983 Structure d'un Peuplement Estuarien de diatomees epipeliques du Nord-Finistère. Oceanologia Acta Vol.6(2) pp.173-183

RINCE, Y. 1979 Cycle Saisonnier Des Peuplements Phytoplanctonique et Microphytobenthique Des Claires Osteicoles De la Baie De Bourgneuf. Revue algologique Vol.14(4) pp.297-313

ROSS, R.; COX, E.J.; KARAYEVA, N.I.; MANN, D.G.; PADDOCK, T.B.B.; SIMONSEN, R.; & SIMS, P.A. 1979 An Amended Terminology for the Siliceous components of the Diatom Cell. Nova Hedwigia. Beiheft 64 pp 513-533

ROUND, F.E. 1953 An Investigation of 2 Benthic Algal Communities in Malham Tarn, Yorkshire. Journal of Ecology Vol.41 pp.174-197

ROUND, F.E. 1957a A note on some diatom communities in calcareous springs and streams. Journal of the Linnean Society of London Botany Vol.55 pp.662-668

ROUND, F.E. 1957b The Distribution of Bacillariophyceae on some littoral sediments of the English lake district. Oikos Vol.8 pp.16-37

ROUND, F.E. 1957c Studies on Bottom-Living Algae in Some lakes of the English lake District. Part I some chemical features of the sediments related to algal production. Journal of Ecology Vol.45 pp.133-148

ROUND, F.E. 1957d Some Studies on Bottom-Living algae in some lakes of the English Lake District. Journal of Ecology Vol.45 pp.343-360 (Part II).

ROUND, F.E. 1957e Some Studies on Bottom-Living algae in some lakes of the English Lake District Part III The distribution on the sediments of algal groups other than the Bacillariophyceae Journal of Ecology Vol.45 pp.644-664

ROUND, F.E. 1957f Studies on Bottom-Living Algae in some lakes of the English Lake District. Part IV The Seasonal cycles of the Bacillariophyceae. Journal of Ecology Vol.48 pp.529-547

ROUND, F.E. 1960 The Diatom flora of a saltmarsh on the River Dee. The New Phytologist Vol.59 pp.332-348

ROUND, F.E. 1961a Studies on Bottom-Living Algae in some Lakes of the English Lake District Part V The seasonal cycles of the cyanophyceae. Journal of Ecology Vol.49 pp.31-36

ROUND, F.E. 1961b Studies on Bottom-Living Algae in some Lakes of the English Lake District Part VI The effect of depth on the epipelic algal community. Journal of Ecology Vol.49 pp.245-254

ROUND, F.E.R. 1971 Benthic Marine Diatoms. Oceanography and Marine Biology Annual Review Vol.9 pp.83-139

ROUND, F.E. 1979 Occurence and rhythmic Behaviour of Tropideneis lepidoptera in the Epipelon of Barnstable Harbour. Marine Biology Vol.54 pp.215-217

RYTHER, J.H. 1954 The Ecology of Phytoplankton Blooms in Moriches Bay and Great South Bay Long Island, New York. Biological Bulletin Vol.106 pp.198-209

SAUNDERS, R.P.; BIRNHAK, B.I.; DAVIS, J.T.; & WAHLQUIST, C.L. 1967 Seasonal Distribution of Diatoms in Florida In shore Waters from Tampa Bay to Carambas Pass. Florida Board of Conservation Marine Lab Symposium on red tide studies, Pinelles to Collier Counties pp.48-78

SCHRÖDER, H.G.J. 1977 (abstract) Distribution of sulphur-cycle Bacteria in the Eems-Dollard Estuary from Biologisch Onderzoek veenkoloniaal afvalwater ed. Wolf de, P. & Hydrobiological Bulletin Vol.11 pp.7-17

SIMONSEN, R. (editor) 1975 Proposals for a standardization of Diatom Terminology and Diagnosis. Third Symposium on Recent and Fossil Marine Diatoms Kiel September 9-13 1974. Proceedings 1975 VIII, 365 pp, 64pl, 83 Fig. Beiheft 53 zur Nova Hedwigia pp.323-354

SMITH, L. 1979 A Survey of the Salt Marshes in the Severn Estuary (unpublished) Two Vols. submitted to the Nature Concervancy Council CST Report No.265

STEELE, J.H.; & BAIRD, I.E. 1968 Production Ecology of a Sandy Beach. Limnology & Oceanography Vol.13 pp.14-25

SULLIVAN, M.J.; & DIABER F.C. 1975 Light Nitrogen and Phosphorus limitation of edaphic Algae in a Delaware Salt marsh. Journal of Experimental Marine Biology & Ecology Vol.18 pp.79-88

SULLIVAN, M.J. 1976 Long-term Effects of manipulating light intensity and nutrient enrichment on the structure of a saltmarsh diatom community. Journal of Phycology Vol.12 pp.205-210

SULLIVAN, M.J. 1982 Distribution of Edaphic Diatoms in a Mississippi Saltmarsh: A Canonical Correlation Analysis. Journal of Phycology Vol.18 pp.130-133

SUNDBACK, K. 1983 Microphytobenthos on sand in Shallow Brackish Water, Öresund Sweden. Ph.D. thesis Dept. of Marine Botany & Dept. of Systematic Botany, University of Lund, Sweden

TAYLOR, R.W. 1964 Light and Photosynthesis in intertidal benthic diatoms. Helgöländer wissenschaftlicke Meeresuntersuchungen Vol.10 pp.29-37

TEVERSON, R. 1983 Saltmarsh Ecology in the Severn Estuary. MSc.thesis, Department of Zoology Bristol University, Dept. of Energy Contract Agreement No. UKAEA E/SA/CON/1619/51/054

THOMPSON, H.S. 1922 Changes in the Coast Vegetation near Berrow, Somerst. Journal of Ecology Vol.10 pp.53-66

THOMPSON, H.S. 1930 Further Changes in the Coast Vegetation near Berrow Somerset. Journal of Ecology, Vol.18 pp.126-130

THRONDSEN, J. 1978 Centrifugation from Phytoplankton Manual Chapter 5.3 pp.98-103 ed. Sournia, A. publ. UNESCO, Paris

TROTT, P.A. 1970 Some Observations on the changing morphology of Stert Point, Somerset. The Griffin Vol.1 Journal of Geography, N.W. Polytechnic

VYENU, F. 1957 Variation of Diatom Communities and the Schematic Explanation of their Increase in Osaka Bay in Summer Part III Schematic Explanation of Increase of Diatoms in Relation to Distribution of Chlorinity. Journal of the Oceanographic Society of Japan Vol.13(3) pp.107-110

VAN ES, F.B.; & ARKELUAN, M.A. 1980 Influence of Organic pollution on bacterial macrobenthic and meiobenthic populations in intertidal flats of the Dollard. Netherlands Journal of Sea Research Vol.14(¾) pp.288-304

VAN DER WERFF, A; & HULS, H. 1957-1974 Diatomeëenflora van Nederland. Abcoude, Den Haag. (No page numbers, series of plates with explanations).

VAN HEURCK, H. 1896 A Treatise on the Diatomaceae. Translated by W.E. Baxter William Wesley & Son, London pp.558 35pl.

VANLANDINGHAM, S.L. 1967-1978 Catalogue of the Fossil and Recent Genera and species of Diatoms and their Synonyms. Parts I-VII, 3301 Lehre Verlag von J. Crammer

VENRICK, E.L. 1978 Concentrating phytoplankton. The Implications of subsampling. from Phytoplankton Manual Chapter 5.1 pp.75-87 ed. Sournia, A. publ. UNESCO, Paris

VOSJAN, J.H.; & SIEZEN, R.J. 1968 Relation Between Primary Production and Salinity of algal cultures. Netherlands Journal of Sea Research Vol.4(1) pp.11-20

WHEREAT, M. 1934 Ecology of Berrow & Portishead Spartina marsh. Student project lodged in Botany Department Bristol University.

WHITING, M.C. 1983 Distributional patterns and taxonomic structure of diatom assemblages in Netarts Bay, Oregon. Ph.D. thesis, Oregon State University.

WHITLAM, G.C.; LANARASI, T; & COOP, G.A. 1983 Rapid Separation of Microalgae by Density Gradient Centrifugation in Percol . British Phycological Journal Vol.18 pp.23-28

WILDERMAN, C. 1984 (abstract) The Distribution Patterns of Diatom Assemblages along Environmental Gradients in the Severn Estuary, Chesapeake Bay, Maryland. from the Eighth Symposium on Living and Fossil Diatoms, Paris. pp.90.

WILLIAMS, R.B. 1964a The Ecology of Diatom Populations in a Georgia Saltmarsh. Ph.D thesis Harvard University, Cambridge Mass. USA

WILLIAMS, R.B. 1963 Use of netting to collect motile benthic algae. Limnology and Oceanography Vol.8 pp.360-361

WILLIAMS, R.B. 1964 Division Rates of Salt Marsh Diatoms in Relation to salinity and cell size. Ecology 45 pp.887-880

WILSON, C.J.; & HOLMES, R.W. 1981 The Ecological Importance of Distinguishing Between Living and Dead Diatoms in Estuarine Sediments. British Phycological Journal Vol.16 pp.345-349

APPENDIX A SPECIES LIST

Achnanthes brevipes Agardh.
A. delicatula Kütz
A. lanceolata var. rostrata Hust.
A. Linkei Hust.
Actinoptychus senarius (Ehr.) Ehr.
A. undulatus (Bailey) Ralfs.
Amphiprora medulica Peragallo & Peragallo
A. ornata J.W. Bailey
A. paludosa Sm.
A. Paludosa var. duplex Donk.
A. robusta McCall
Amphora affinis (Kütz) V.H. ex de Toni
A. bacillaris Greg.
A. exigua Greg.
A. laevis Greg.
A. lineolata Ehr.
A. ovalis var. libyca (Ehr.) Cleve
A. proteus cf. var. impressa A.Cl.nach Brockman
A. pusio Cl.N. nach Cleve
A. sabyii Salah
A. veneta Kütz
Auricula sp
Bacillaria paxillifer (O.F. Müller) Hendey
Biddulphia alternans (Bailey) V.H.
B. aurita (Lyngbye) Brebisson
Caloneis brevis (Greg.) Cleve
C. limosa (Kütz) Patrick
C. subsalina (Donk.) Hendey
C. westii (Wm. Smith) Hendey
Campylosira cymbelliformis (Schmidt) Grun. in V.H.
Cocconeis scutellum Ehr.
Coscinodiscus sp.
Cyclotella sp.
Cylindrotheca fusiformis Reimann & Levin
C. gracilis (Breb. in Kütz) Grun. in V.H.
Diploneis elliptica Kütz
D. interrupta (Kütz) Cleve
D. littoralis (Donk.) Cleve
D. smithii (Breb. in Wm. Smith)Cleve
Entomoneis paludosa var. hyperborea Grunow
Fragilaria sp
Frustulia vulgaris (Thwaites) De Toni
Gyrosigma fasciola (Ehr.) Griffeth & Henfrey
G. peisonis (Grun.) Hust.
Hantzschia distinctepunctata (Hust.) Hust. in Schmidt
H. marina (Donk.) Grunow
H. virgata var. capitellata Hust. in Schmidt
H. virgata var. gracilis Hust.
H. virgata (Roper) Grunow var. virgata
H. weyprechtii Grun.
Mastogloia smithii var. lacustris Grun.
Melosira granulata (Ehr.) Ralfs.
M. nummuloides (Dillwyn) Agardh.
Melosira sp
Navicula cancellata Donk.

N. cari Ehr.
N. cincta (Ehr.) Kütz
N. cari .. var. carii Grun.
N. cryptocephala Kütz
N. digito-radiata (Greg.) Ralfs
N. forcipata Grenville
N. gregaria Donk.
N. humerosa Brebisson
N. hungarica f. elliptica (Schulz) Patrick
N. maculosa Donk.
N. palpebralis Breb. ex Wm. Smith
N. peregrina (Ehr.) Kütz
N. protracta f. elliptica Gallik.
N. pygmaea Kütz
N. hudsonis Grunow
N. retracta Meister
N. retusa Breb.
N. rhynchocephala Kütz
N. rostellata Kütz
N. scoliopleura A. Schmidt
N. stankovici Hust.
N. subrhynchocephala Hust.
N. viridula Kütz
Nitzschia acuminata (Wm. Smith) Grun.
N. brightwelli Kitton in Pritchard
N. closterium (Ehr.) Wm. Smith
N. debilis var. crassa Pantocsek
N. dubia Wm. Smith
N. epithemioides Grun.
N. hungarica Grun.
N. incomptus Hohn & Hellerman
N. linkei Hust.
N. lorenziana Grun.
Nitzschia microcephala Grun.
N. navicularis (Breb. ex Kütz) Grunow
N. palea (Kütz) Wm. Smith
N. paleacea Grun.
N. sigma var. rigida (Kütz) Grun.
N. sigma var.
N. spathulata var. hyalina Greg.
N. tryblionella Hantzsch. in Rabenhorst
N. tryblionella var. levidensis (Wm. Smith) Grun.
N. thermalis (Ehr.) Averswald
N. vacillata Griffen
N. vermicularis f. genuina mh.
Nitzschia sp
Opephora sp
Paralia sulcata (Ehr.) Cleve
Pinnularia cruciformis (Donk.) Cleve
P. lundii Hust.
Plagiogramma vanheurchkii Grunow
Pleurosigma aestuarii (Breb. ex. Kütz) Wm. Smith
Pl. angulatum Wm. Smith
Pl. attenuatum
Pl. elongatum Smith
Podosira sp

Rhaphoneis surirella (Ehr.) Grunow
Rhizosolenia sp
Rhoicosphenia curvata (Kütz) Grunow
Rhopalodia gibba (Ehr. Kütz) Müller
Rh. operculata (C.A. Agardh.) Hakansson
Stuaroneis amphioxys var. obtusa Gregory
St. spicula
Stauroneis sp.
Surirella gemma Ehr.
S. ovata Kütz
Synedra fasciculata Kütz
S. pulchella (Ralfs. ex. Kütz) Kütz
Thalassiosira sp
Triceratium sp
Tropideneis sp nov.

APPENDIX B

NICHE BREADTH

Calculated from 30 months of counts

Achnanthes delicatula & Achnanthes lanceolata var. rostrata	5.96
Achanthes linkei	6.11
Achnanthes sp	3.51
Amphiprora paludosa	8.81
Amphora bacillaris	8.42
Amphora exigua	13.33
Amphora lineolata	5.34
Amphora ovalis var. libyca	5.39
Amphora proteus var.	5.62
Amphora pusio	1.65
Amphora spl	5.31
Ampora sp2	5.54
Bcillaria paxillifer	6.07
Coloneis limosa	3.06
Caloneis subsalina	11.05
Caloneis westii	6.32
Cylindrotheca gracilis	11.46
Cylindrotheca fusiformis	9.03
Diploneis elliptica	7.88
Diploneis interrupta	2.19
Diploneis littoralis	5.74
Diploneis smithii	4.71
Gyrosigma fasciola var. arcuata	7.85
Hantzschia marina	2.60
Hantzschia virgata var. gracilis	5.53
Navicula cari & Navicula cincta	4.14
Navicula digito-radiata	8.66
Navicula humerosa	5.01
Navicula hungarica f. elliptica	2.11
Navicula spp	14.18
Navicula palpebralis	1.34
Navicula peregrina	7.36
Navicula protracta f. elliptica	4.64
Navicula pygmaea	10.53
Navicula rostellata	2.52
Navicula scoliopleura	6.14
Navicula trivialis	6.33
Navicula viridula	6.15
Nitzschia acuminata	9.70
Nitzschia closterium	11.59
Nitzschia epithemioides	3.43
Nitzschia hungarica	8.46
Nitzschia linkei	1.87
Nitzschia microcephala agg.	12.00
Nitzschia navicularis	4.36
Nitzschia paleacea	6.72
Nitzschia sigma var. & Nitzschia sigma var. rigida	8.14
Nitzschia spathulata	3.42
Nitzschia tryblionella	7.81
Nitzschia tryblionella var. levidensis	5.93
Nitzschia thermalis	9.12
Nitzschia vacillata	9.99
Nitzschia sp.	5.04

Pinnularia lundii	7.43
Pleurosigma aestuarii	5.35
Pleurosigma angulatum	7.78
Pleurosigma attenuattum	5.02
Pleurosigma hippocampus	8.94
Rhopalodia operculata	1.29
Stauroneis amphioxys var. obtusa	5.97
Stauroneis spicula	4.59
Stauroneis sp	6.39
Surirella ovata	3.25
Tropideneis sp (novo sp.)	7.36